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Somatosensation in social perception

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Preface

The discovery of mirror neurons in motor areas of the brain has led many to assume that understanding other people's behaviour partially relies on vicarious activations of motor cortices. This Review focuses the limelight of social neuroscience on a different set of brain regions: the somatosensory cortices. Somatosensory cortices (SI and SII) have the anatomical connections that enable them to have a role in visual and auditory social perception. Experiments that measured brain activity while participants witnessed the sensations, actions and somatic pain of others consistently show vicarious activation in the somatosensory cortices. Neuroscience is starting to understand how the brain adds a somatosensory dimension to our perception of other people.

Introduction

One of the most exciting developments of the past decade is the discovery that our perception of other individuals involves neurons and brain areas that were thought to be reserved for the control of our own actions and the experience of our own emotions. First, it became clear that seeing or hearing other people's actions recruits neurons¹⁻⁸ (in monkeys) and brain regions (in humans) in the premotor and posterior parietal cortex that are also involved in programming similar actions⁹⁻¹⁸. This has led to the idea that understanding the inner state of other individuals relies on implicit motor simulation, i.e. the activation of motor programs that we would use to perform similar actions¹⁹⁻²³. Our motor cortices seemed no longer 'private' but a part of our social brain, processing the states of others as if they were our own. More recently, it has been suggested that emotional brain areas, including the anterior insula and the rostral cingulate cortex, might perform an emotional simulation of other individuals' experiences, showing activity both when we experience positive and negative emotions and while witnessing those of others²⁴⁻⁴⁵. Electro-stimulation of similar regions of the insula causes measurable changes in the body (e.g. gastric contractions) and induces the perception of changes in the body⁴⁶. This suggests that this emotional simulation involves representations of the body rather than being purely conceptual. Current models of social cognition therefore incorporate the notion that motor and emotional brain regions can contribute to our perception of others by simulating other people's actions and emotions. The somatosensory cortices have so far been ignored by the mainstream of simulation models^{19, 20, 23}. And yet, expressions such as "Her words were really touching!" encapsulate how we intuitively feel that there is a link between the people around us and our sense of touch.

In this Review, we first examine the location and connections of the somatosensory cortices (Fig. 1) to show that, in contrast to the early somatosensory cortices in the central sulcus, all other somatosensory cortices, where the later stages of somatosensory processing take place, receive direct input from areas known to have visual and auditory properties. Second, we show that in agreement with this anatomical evidence, perceiving other people being touched, performing an action or experiencing somatic pain activates the higher stages of somatosensory processing in the primary (SI) and secondary (SII) somatosensory cortices (see Box 1). We will argue that these vicarious activations of somatosensory cortices may have the unique potential to give our perception of other people's experiences a somatic dimension.

Anatomy of the somatosensory system

Somatosensation involves the processing of tactile, proprioceptive and nociceptive information. Here we briefly describe the cortical brain regions involved in the processing of these types of information and examine which of these brain regions receive the visual and auditory information that would be necessary to trigger vicarious responses (Fig. 1).

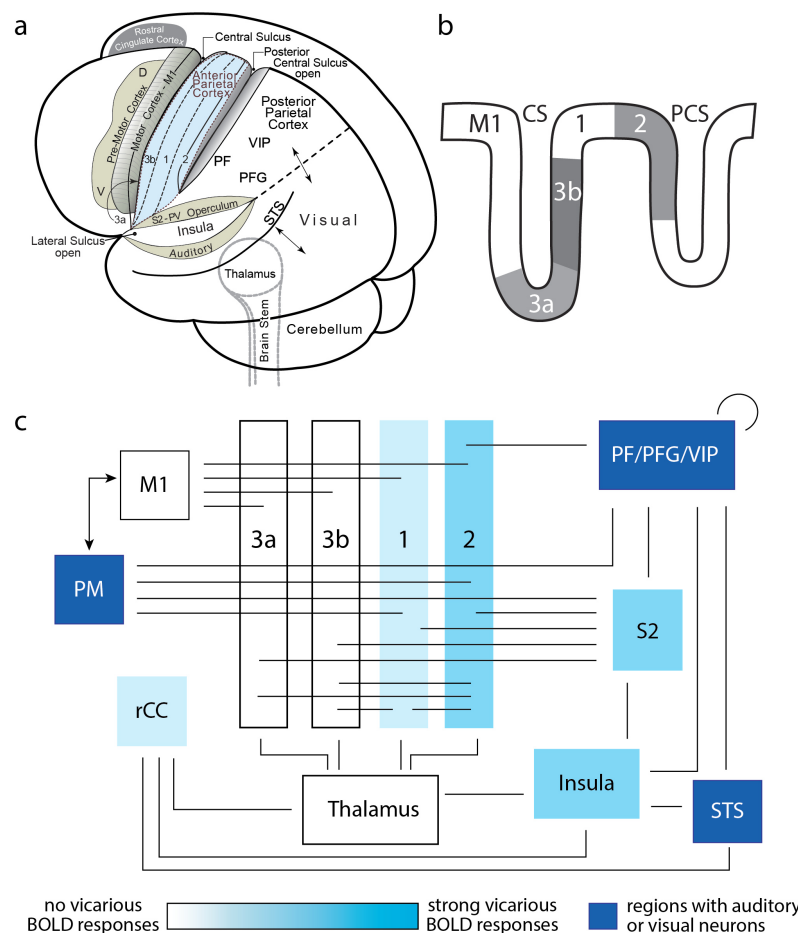


Figure 1: Cortical processing networks for somatosensation

(a) Posteriolateral view of a human brain showing areas and regions involved in somatosensation. The central, postcentral, and lateral sulci have been opened to show the areas within. The superior temporal sulcus (STS) is not opened, but it contains multisensory areas on its banks. Other sulci are not shown. For convenience, the rostral cingulate cortex (rCC) is indicated on the medial wall of the opposite hemisphere. Anterior parietal cortex includes the four strip-like areas of Brodmann, areas 3a, 3b, 1 and 2 in a rostrocaudal sequence. Regions of interest in posterior parietal cortex include the ventral intraparietal area (VIP) and more lateral regions (PF and PFG). The lateral parietal cortex in hidden inside the lateral sulcus. It includes the operculum of the upper bank containing the secondary

somatosensory cortex (SII, composed of the secondary somatosensory cortex proper (S2) and the parietal ventral region (PV), not shown) and the insula with regions for touch and pain. Somatosensory networks ultimately involve primary motor (M1) and dorsal (D) and ventral (V) premotor (PM) areas for action. The thalamus (dashed lines) lies deep in the forebrain. Arrows indicate visual connections with posterior parietal cortex and the multisensory regions of the superior temporal sulcus (STS). **(b)** Schematic representation of the central sulcus (CS), the postcentral sulcus (PCS) the motor cortex (M1) and anterior parietal areas 3a, 3b, 1 and 2. **(c)** Brain regions involved in somatosensation, their main connections and their sources of visual input. Brain regions with neurons that respond to the presentation

of visual stimuli are shown in blue: PM, STS, and areas PF, PFG and VIP. Somatosensory brain regions in which some experiments suggest vicarious responses are shown in blue, with darker blue areas having a stronger BOLD response to observing the touch, actions or pain of others than lighter blue areas.

Traditionally, in humans and monkeys, the term 'somatosensory cortices' proper refers to the anterior parietal cortex and the upper bank (operculum) of the lateral sulcus that process tactile, proprioceptive and nociceptive information. The term 'somatosensory system', on the other hand, refers to all the brain regions involved in processing somatosensory information, and refers to the somatosensory cortices proper plus the insula and the rostral cingulate cortex that are thought to process the affective value of somatosensory stimuli⁴⁷.

The anterior parietal cortex consists of four parallel, mediolateral strips of cortex: the classical cytoarchitectonic areas 3a, 3b, 1 and 2 of Brodmann and the Vogts. In humans, Brodmann Area (BA) 3a and 3b roughly correspond to the posterior bank of the central sulcus, BA 1 to the crown of the postcentral gyrus and BA 2 to the anterior bank of the postcentral gyrus (Fig. 1a,b). BA 3a and 3b are sometimes grouped as BA3. All four areas were once considered to be parts of a single "homunculus", a systematic representation of the contralateral body surface known as "SI". Currently, each of the four areas is known to constitute a separate representation with different connections and functions (see ref⁴⁷ for a review). Accordingly, the term 'SI' is now used as a shorthand to refer to BA3a+3b+1+2 when it is unclear to which of the subregions a statement applies or when it applies to all four.

BA 3a receives proprioceptive information, largely from muscle spindle receptors through the ventroposterior superior nucleus (VPS) of the thalamus, and has close anatomical connections with the motor cortex. BA 3b is the primary area for tactile processing, and it receives its major activating inputs neurons in the ventroposterior nucleus (VP) of the thalamus. BA 3b also receives input from small neurons in VP and in the ventroposterior inferior nucleus that are activated by wide-dynamic range (touch into the nociceptive range) and from nociceptive neurons in the spinal cord and brain stem⁴⁸. BA 1 receives strong activating inputs from BA 3b, and thus is thought to be involved in a secondary cortical stage of tactile processing. BA 2 receives inputs from BA3a, BA 3b and 1 and therefore constitutes a third level of cortical processing of tactile and proprioceptive information⁴⁹. This tactile information is combined with proprioceptive inputs from the VPS. Thus, neurons in BA 2 are especially responsive when objects are actively explored or manipulated with the hands so that tactile and proprioceptive afferent information is combined in a process we will term haptics⁵⁰. Of note, BA 2 also receives callosal connections from BA 2 of the other hemisphere, which permits some neurons to respond to stimuli on the ipsilateral as well as the contralateral hand during bimanual exploration^{51, 52}. The connections between areas of anterior parietal cortex are reciprocal in that BA 2 projects back to BA 1, 3b, and 3a.

Importantly, BA 2 also has direct, reciprocal connections with regions of the fundus of the intraparietal sulcus (area VIP) and the inferior parietal lobule (areas PF/PFG in particular) which combine visual, auditory and somatosensory information^{49, 53-55}. Some cells in VIP respond both when a monkey is touched and when it sees someone else being touched in a similar way⁵⁶ whereas some neurons in PF/PFG respond both when the monkey performs a goal-directed action and when it sees another individual perform a similar action⁷. Moreover, these regions are thought to constitute the main source of visual and auditory information to mirror neurons in the premotor cortex⁵⁷. The fact that these regions also project to BA2 makes it plausible that BA2 could demonstrate vicarious activations in response to goal-directed actions of others. From SI somatosensory information is sent to SII; these connections are reciprocal, allowing areas involved in early processing stages to be influenced by areas involved in later processing stages.

SII, which lies on the parietal operculum (OP), has now been divided into two sub-regions termed S2 and PV (the parietal ventral area) in both monkeys and humans⁵⁸, which correspond to distinct architectonic fields, OP1 and OP4, respectively⁵⁹. S2 and PV receive inputs from all four areas of SI and are therefore involved in a third or fourth level of processing. S2 and PV have similar afferent and efferent cortical connections.⁶⁰ These include connections with neighboring cortical regions of the operculum and with a number of brain regions with cells that respond to visual and auditory input. These regions include the PF/PFG and VIP^{54, 55} (both of which also provide input to BA2), secondary auditory areas that are also responsive to somatosensory stimuli⁶¹, and the insula⁶².

For nociception, SI and SII are thought to process the sensory discriminative aspects (i.e. the intensity and location) of pain⁶³. This occurs in parallel with the more affective/motivational processing of nociceptive input that is thought to take place in the insula and the rostral cingulate gyrus⁶³. The posterior insula receives thalamic input associated with the spinothalamic pathway⁶⁴, and cortical inputs from adjoining and nearby cortical areas. Different sectors of the posterior insula seem to be involved in the appreciation of pain, temperature, itch, and pleasant touch⁶⁵, but do not receive pronounced auditory or visual input⁶². This information is then relayed to more anterior sectors of the insula, where it is integrated with input from the frontal lobe, all sensory modalities and limbic structures^{62, 66}. The rostral cingulate cortex also receives nociceptive input from more lateral nuclei in the thalamus (VMpo, MDvc, Pf and CL) and integrates this information with highly processed information from various cortical areas⁶³.

This review of the anatomy of the somatosensory system allows us to draw a number of conclusions (Fig. 2). First, tactile and proprioceptive inputs from the thalamus are initially segregated in separate areas of anterior parietal cortex, but combined in BA 2 and again in SII, enabling haptics. Second, nociceptive information from the thalamus is more broadly distributed to the cortex, with parts of the insula and rostral cingulate cortex especially involved in processing the affective value of nociceptive information. Third, BA 2, the SII complex, the insula, and the rostral cingulate cortex receive direct inputs from regions of cortex responsive to visual and auditory stimuli, while BA 3b and 1 have access to such information only indirectly, through BA2 and SII. Fourth, the anatomical connections suggest that visual or auditory information would most likely influence tactile processing in the SII region, haptic processing in BA 2 and SII, and nociceptive processing in BA 2, SII, the insula, and rostral cingulate cortex. BA 3a, 3b and BA 1 should have, at best, only weaker visual or auditory responses owing to feedback connections from SII and BA 2.

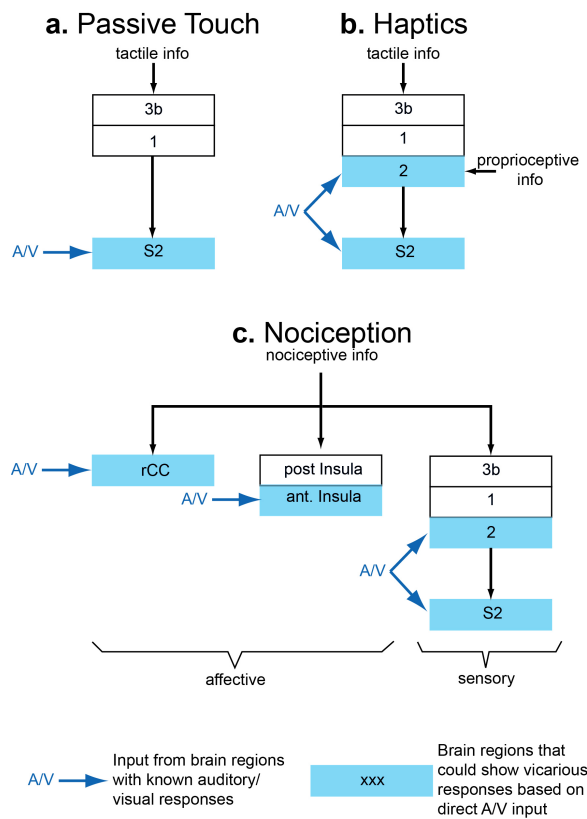


Figure 2: Audio/visual input to tactile, haptic and nociceptive processing

Although somatosensory receptors in the body provide the primary input to the somatosensory system (black arrows), the processing streams for tactile, haptic and nociceptive information all receive input from brain regions where cells respond to auditory/visual (A/V) stimuli (blue arrows). The stage at which such A/V information enters these streams anatomically determines where vicarious somatosensory responses might occur (blue regions). (a) The main pathway for the processing of tactile information resulting from passive touch first receives direct input from brain regions with audio/visual responses at the level of the secondary somatosensory cortex (SII). (b) The pathway that integrates tactile and proprioceptive information (black arrows) when we are actively manipulating an object (haptics) first receives A/V input in both Brodmann area (BA) 2 and SII. (c) Nociceptive information is distributed along multiple parallel streams (important interconnections exist but are omitted for simplicity). Two of these streams are thought to primarily process the affective aspects of pain, and the third stream is thought to process primarily the sensory aspects of being hurt. Each of these streams receive A/V input, at the

level of the rostral cingulate (rCC), anterior Insula, BA2 and SII. 1, 2, 3b, Brodmann areas 1, 2 and 3b; rCC, rostral cingulate cortex.

SII: vicarious tactile processing

Evidence for a role of somatosensory cortices in the perception of other people's somatosensory states originated from an fMRI study. Participants in a scanner were touched on their legs by an experimenter and then watched movie clips of either other people's legs being touched by a rod or, as control stimuli, movies of the same rod moving too far away from the same legs to touch them. Being touched activated the leg representations in both SI and SII. Importantly, viewing other people being touched compared to the control condition also activated SII (but not SI, Figure 3). SII was even activated when participants watched objects (e.g. rolls of paper) being touched compared to movies of the objects not being touched⁶⁷. Other studies also showed SII activity in participants seeing the hands^{68, 69} or the neck and face⁷⁰ of other people being touched in movie clips. One study also replicated the SII activation in response to seeing objects being touched⁶⁸ but another did not⁷⁰. The finding that SII responds to the sight of humans and, sometimes, objects being touched, and the fact the neurons in SII have very large receptive fields⁷¹, suggest that vicarious activation in SII could convey a simulation of the quality of touch one would feel if one were touched in a similar way, rather than the precise body location on which the touch occurred. Interestingly, watching tactile stimulation of more erogenous zones of the body in pornographical movies also activates SII vicariously⁷²⁻⁷⁴.

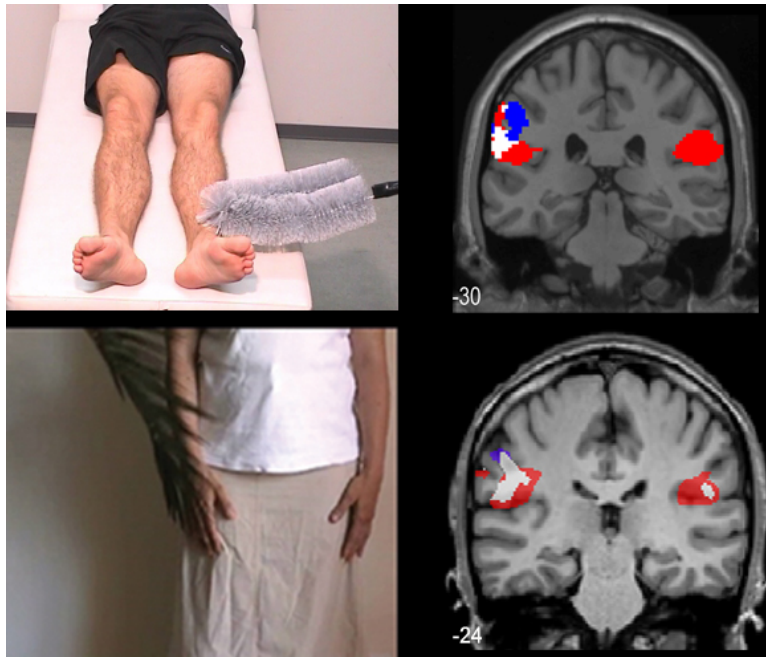


Figure 3: Vicarious tactile activity in SII

Seeing a leg or a hand being touched elicits activity in SII that overlaps with the activity that occurs when the participant him- or herself is being touched on the leg or hand, respectively. The left column shows a still frame from the movie clips used by Keyzers et al.⁶⁷ (top) and Ebisch et al.⁶⁸ (bottom). The right column shows brain regions that are activated exclusively by the experience of touch (red) and by watching the movie clips (blue). The overlap between brain areas (indicating areas that are activated by both the experience of touch and the observation of someone else

being touched) is shown in white. The white numbers refer to the y coordinates in MNI (Montral Neurological Institute) space of the coronal slice.

The above studies showed that, in contrast to SII, SI is only sometimes^(69, 70 but not^{67, 68}) and BA3 never activated during the observation of touch. BA2 and BA1 were only activated if the stimuli showed a human hand delivering the touch⁷⁰ or when the task focused attention on the action of touching⁶⁹. In both cases, the hand representation in SI was activated (z coordinates >40) even when the stimuli showed a face being touched⁷⁰. Importantly, the only study that compared the response to watching movie clips in which the touch resulted from a deliberate human action to the response to movie clips in which touch was accidentally delivered by an object moved by the wind⁶⁸ showed that although activity in SI remained subthreshold in all cases, it was stronger in the deliberate condition. This suggests that BA2 or BA1 activation relates to the toucher rather than to the sensations of the person being touched (see next section).

Bufalari *et al.*⁷⁵ used electroencephalography, which has higher temporal resolution than fMRI, to examine which stages of somatosensory processing are sensitive to visual input. They electro-stimulated the median nerve of their participants to provide a precisely timed somatosensory input, and measured the resulting sensory evoked potentials (SEP) on the scalp. Components of this SEP within 40ms of stimulation reflect subcortical and BA3 activity, whereas later components reflect activity in BA1, 2 or SII⁷⁶. SEPs from participants watching movie clips of a hand being touched by a cotton swab showed that components associated with BA3 were not influenced by this visual stimulus, whereas later components (e.g. the P45) associated with BA1, 2 or possibly SII, were⁷⁵.

Altogether, these data leave little doubt: as expected from anatomical considerations (Fig. 2a), SII can be vicariously recruited by seeing other people being touched. It seems to be activated when we see humans or objects being touched, possibly conveying a feeling of what it would feel like to be touched in a similar way. However, despite this vicarious SII activation, we are not usually confused about who is being touched. The fact that BA3a and 3b are only recruited when we ourselves are being touched could account for this. The role of the intermediate processing stages that take place in the BA1 and BA2 remain to be further explored but, as we will see below, the intensity of the perceived touch⁷⁵ and the presence of actions in the stimuli^{11, 17, 68} might be important factors in determining their recruitment.

Investigating how virtual (Transcranial Magnetic Stimulation, TMS, induced) or neurological lesions in SII change people's capacity to accurately perceive the sensations of others will be necessary to establish the degree to which SII contributes to social perception. A certain type of synesthesia⁷⁷, however, suggests a link between SII activity and the way we perceive these sensations. About 1% of people experience a vivid sensation of touch on their own body when they see the body of others being touched⁷⁸. This effect is so automatic that these so-called 'mirror touch synaesthetes' often misreport the location on which they are touched if they simultaneously see another person being touched^{77, 78}. In an important experiment, Blakemore *et al.* measured brain activity in one such synaesthete and found that she differed from controls in that she activated her SI (probably including BA3) and SII more strongly than controls when seeing movies of other people being touched⁷⁰. Interestingly, mirror-touch synaesthetes also score higher on empathy questionnaires⁷⁷. Together this suggests that the degree of vicarious activations in somatosensory brain regions, and in particular the involvement of BA3, can indeed determine what it feels like to see other people being touched and, more generally, the vividness with which one might empathically share what other people go through.

BA2: vicarious haptics and proprioception

SI is not only essential for our sense of touch: in humans, lesions to SI lead to devastating impairments in motor control⁷⁹, and in monkeys, deactivation of BA2 impairs the motor control needed for grasping⁸⁰. Does SI also help us perceive the actions of others? Historically, the study of the cortical processing of other individuals' actions has been dominated by the discovery of mirror neurons in monkeys. These neurons, responding both when a monkey performs an action and when it sees or hears another individual perform a similar action¹⁻⁸, have so far been reported in regions involved in motor planning: the ventral premotor cortex^{1, 3-6, 8} and the posterior parietal cortex (area PF/PFG^{2, 7} and the anterior intraparietal sulcus³). Consequently, most theoretical papers regarding the function of mirror neurons focus on the motor (as opposed to the somatosensory) side of action simulation^{19, 20, 23, 81-84}. However, the finding that half the neurons in the ventral premotor cortex also respond to somatosensory stimulation⁸⁵ suggests that the mirror neuron system may have tight functional links with the somatosensory cortices. This begs a question that has so far not been investigated systematically: does SI or SII also contain (mirror) neurons that are active both during the observation and the execution of actions? Intriguing preliminary evidence for this possibility stems from a neuroimaging experiment that indicated that monkeys activate SI and SII both when grasping an object and when seeing another individual performing the same action⁸⁶⁻⁸⁸.

To test if SI and SII might play a role in action perception in humans, we scanned participants while they viewed objects being manipulated and while they manipulated similar objects themselves¹¹. We found that 'shared' voxels (i.e. voxels that were active during observation and execution of goal-directed actions) were not restricted to the ventral premotor cortex and the posterior parietal lobe: the somatosensory cortex, BA2 in particular, contained more shared voxels and did so in more participants than did the ventral premotor cortex (Fig. 4). SII also contained shared voxels (albeit fewer than BA2) and so did the dorsal premotor cortex⁸⁹. Reviewing all six studies examining action observation and execution using fMRI (Box 1) confirmed that BA2 is consistently active during action observation — as consistently as the ventral premotor cortex. In contrast to BA2, more-anterior sectors of SI are rarely and only weakly recruited during the observation of other people's actions. Compared with the observation of passive touch, SII is more weakly recruited during action observation. Hearing the sound of other people's actions also strongly activates BA2 and, to a lesser extent, SII^{17, 18}.

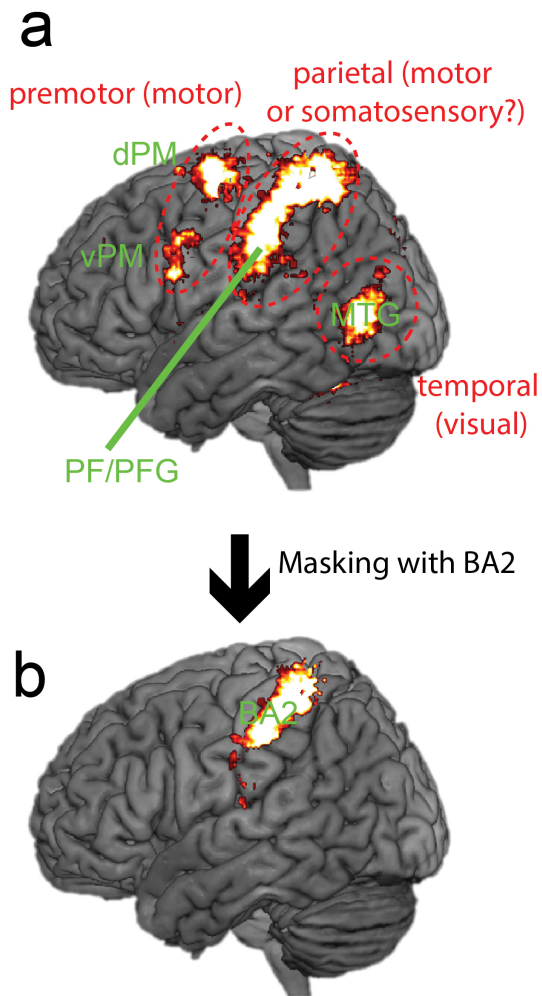


Figure 4: Vicarious activity during the observation of actions

(a) Shared voxels, i.e. voxels that show activity during both action observation and action execution have been reliably identified in four large clusters of brain areas: the dorsal and ventral premotor cortex (dPM, vPM), which are involved in motor control; the posterior mid temporal gyrus (MTG), which is involved in visual perception; and a large cluster encompassing multiple regions of the parietal lobe. This cluster has traditionally been considered to be part of the posterior parietal lobe because it encompasses areas PF/PFG, in which mirror neurons have been recorded in the monkey, thus associating this area with motor control. (b) Showing only those voxels of (a) that fall within BA2 however, shows how much of the parietal shared voxels are actually part of the somatosensory cortex. This indicates that activity in this cluster probably represents vicarious haptic activity instead of vicarious motor activity (adapted from ref. ¹¹).

A number of studies help us understand what perceptual content vicarious BA2 activity could convey. First, seeing hand movements with more joint stretching (beyond the physiological angle) activates BA2 more strongly⁹⁰, and deactivating BA2 using TMS reduces motor evoked potentials in the hand when seeing such extreme joint stretching⁹¹. Second, BA2 is more, or sometimes only, active when viewing hands manipulate objects (e.g. grasping a cup) compared to

actions that do not involve objects (e.g. pointing or mimicked grasping without an object)^{92, 93}. Additionally, viewing someone move a heavier object activates BA2 more strongly than viewing someone move a lighter object⁹⁴. Together, and in accordance with anatomical considerations (Fig. 2b) these data suggest that BA2 might be particularly involved in vicariously representing the haptic combination of tactile and proprioceptive signals that would arise if the participant manipulated the object in the observed way (Fig. 2b). This conclusion is confirmed by the observation that in participants watching a Western movie, vicarious activity in SI was consistently observed when actors were seen to manipulate objects⁹⁵.

Interestingly, the more motor expertise people have, the more they activate BA2 when observing actions related to their field of expertise - even if they are not directed at objects (e.g. seeing dance for dancers⁹⁶⁻⁹⁹). This suggests that although haptic object manipulation might be the optimal stimulus for BA2, BA2 might underlie our capacity to know what it would feel like to move one's body in an observed way more generally.

A limitation of fMRI studies is that the activity of a particular brain region during both the execution and the perception of an action does not guarantee that both scenarios involve activity in neurons representing the same information (e.g. a particular haptic sensation or motor program). However, the somatotopic organization of SI allows one to link the location of activity (measurable with fMRI) to the representation of a particular body part. One can therefore be confident that the observation of hand actions indeed specifically triggers the representation of hand actions in BA2 (see Box 1). Additionally, executing hand and mouth actions causes activity in dorsal and ventral SI, respectively, and perceiving mouth and hand actions

triggers vicarious activity in the corresponding locations¹⁷. Multi-voxel pattern classification of activity data in SI during action perception can identify the body part that was used for an action performed by another individual¹⁰⁰. Finally, watching movies of right-hand grasping activates the left BA2 more than the right BA2 and watching movies of left-hand grasping activates the right BA2 more than the left BA2¹⁰¹. Together, these data suggests that vicarious BA2 activity could provide fine-grained, somatotopically specific representations of other people's actions.

The consistency with which BA2 is activated during the observation of actions additionally sheds light on the presence of BA2 activity in only some of the touch observation studies mentioned above^{68, 69}. Viewing touch activates BA2 more when touch is delivered by a human hand than by an object⁶⁸. Focusing attention on the action of touching (e.g. following instructions to count the number of touching actions)⁶⁹ activates the hand area of BA2 more than focusing attention on the touched (by showing the touched individual/object without showing the toucher)⁶⁷. Together, these considerations propose a functional complementarity in vicarious somatosensory activity, with BA2 relating to the 'sharing' of the haptic aspects of actions and SII activity to the sharing of passive touch.

In contrast to most reviews on the neural mechanisms underlying action observation^{19, 20, 23, 81-83, 102} we conclude that the observation of other people's actions recruits not only the ventral premotor cortex and posterior parietal cortex involved in programming the observed actions, but also BA2 and, to a lesser extent SII, which are involved in sensing our own body would move and interact with the object in the observed way. The simulation of actions would thus involve both simulating the motor output that would be necessary for performing the observed action and simulating the haptic somatosensory input that would accompany performing those actions. Such a link between the motor and somatosensory system during action observation would be in holding with, and might employ the same neural mechanisms as, that during action execution, where the expectation of touch is a fundamental component of forward models in goal-directed motor control^{103, 104}. Interestingly, one paper also shows that of two similar actions, those that activate BA2 more strongly are those that are recognized more rapidly¹⁰⁵.

Facial expressions are a special type of action. Experiments that have examined the neural structures involved both in the observation and the execution of dynamic facial expressions concur that, akin to observing hand actions, observing the facial expressions of others also vicariously activates ventral sectors of BA2 and/or SII that are involved in sensing self-produced facial expressions^{36, 106, 107}. Real and virtual (TMS) lesions in these somatosensory face representations also impair the recognition of facial expressions^{108, 109}, suggesting that vicarious somatosensory representations of what it feels like to move the face in the observed way contribute to the recognition of other people's facial expressions. In contrast to these findings, studies examining activity during the observation of pained facial expressions have not reported activity in somatosensory cortices^{29, 38, 39, 45}. Under what conditions somatosensory representations of the face are vicariously activated by observing other people's facial expressions thus remains to be further explored.

When we perceive the actions of others, we often become aware of the intentions and the feelings of these others and modify our own actions accordingly. How do the brain areas in this putative extended somato-motor action simulation circuit contribute to these processes? Electrical brain stimulation in awake surgical patients might provide an answer. Stimulating the premotor cortex leads to overt movements but patients firmly deny that they actually moved¹¹⁰. Stimulating the inferior parietal lobule creates a strong intention and desire to move without actual movements taking place¹¹⁰. Finally, stimulation of the somatosensory cortex triggered somatosensory qualia in the hands and body¹¹⁰. This suggest that when we observe the actions of others, premotor, posterior parietal and somatosensory vicarious activity each contribute primarily to a different aspect of the perception of other people's actions:

programming our motor response, sensing the intentions of others and experience what it would feel like to move one's own body in the observed way, respectively. In support of this idea, SI activity indeed correlates with the accuracy with which a person can judge how another person feels¹¹.

Systematic single-cell recordings are needed to investigate whether the same neurons in the somatosensory cortices are involved in both action observation and execution, and what aspect of an action is exactly represented in these putative visually and auditorially responsive somatosensory neurons. This is because finding that the same region shows increases in fMRI signals both during the observation and execution of actions (Box 1) suggests but cannot guarantee that the same neurons in these voxels are involved in both cases: distinct populations of neurons could be involved in observation and execution but be located within the same fMRI voxels¹¹ or changes in fMRI signal could originate from the same neurons, but only reflect subthreshold synaptic input during perception. The same caveat applies to the case of touch and of nociception (see below). Nevertheless, two sources have provided evidence that some of the same somatosensory neurons are active during action observation and execution. First, the only experiment that has examined the presence of mirror neurons in humans using repetition suppression and a whole-brain analysis found that SI shows repetition suppression during both the observation and the execution of actions¹⁶. Second, the shallow depth of recording of some of the neurons which seemed to exhibit mirror properties in the anterior bank of the intraparietal sulcus³ suggests that they may have been located in BA2 (A. Iriki, personal communication).

SI/SII: vicarious nociception

We have all experienced that witnessing the pain of others is aversive. If we see our partner's face expressing intense pain, we feel deeply distressed. If we see her cut her finger with a sharp kitchen knife, we not only feel distress, we often feel compelled to grasp our own finger. About a third of people feel pain on the corresponding part of their own body when they see certain injuries of other people¹². Neuroimaging research is now starting to shed light on this multifaceted nature of empathic pain. In brief, this research shows that if all we know is that another person is in pain, we vicariously recruit brain regions involved in the affective experience of pain: the anterior insula and rostral cingulate cortex^{28, 29, 32, 38, 39, 45}. Here we will show that whenever our attention is directed to the somatic cause of the pain of others, somatosensory cortices also become vicariously activated, and this process could add the more localized, somatic sensation of pain in a particular body part that drives us to grab our finger in the above example. This conclusion stems from comparing fMRI experiments that used different types of stimuli to inform the participant about the pain of others, and which we describe below.

Singer *et al.* performed a seminal pair of fMRI studies. Participants in the scanner saw a colored cue on the screen indicating when another individual, present in the scanner room, received a painful electrical shock^{28, 32}. In a second set of fMRI experiments, participants were informed about the pain of others by viewing facial expressions on a screen^{29, 38, 39, 45}. In the last group, participants viewed images of specific body parts being hurt, for instance a hand being pinpricked or deeply penetrated by a hypodermic needle^{37, 40-44} or a foot being hit by a door^{30, 31}. Comparing the loci of brain activations of these various fMRI experiments (Box 1) confirms that perceiving the pain of others vicariously activates the higher levels of affective nociceptive processing, i.e. the anterior insula and/or rostral cingulate cortex. The somatosensory cortices (SI, SII) however were only vicariously activated in some conditions, and almost never while people viewed painful facial expressions or abstract cues. This has led the authors of one paper to state: "Empathy for pain involves the

affective but not sensory components of pain"²⁸. However, in the eight studies in which the noxious event itself was shown to the subjects^{30, 31, 37, 40-44}, SI and SII were vicariously activated in all but one experiment (Box 1). Empathy for pain therefore does involve the somatosensory cortices, but only if one attends to the localized somatic cause of the pain. Some of these studies have further identified the factors that determine whether somatosensory cortices are activated while subjects view the tactile pain of others: activations in SI are stronger when participants imagine that they are in this painful situation themselves than when they imagine someone else being in that situation³⁰; when they explicitly judge how painful being in that situation would be⁴¹ and when the visual stimulus suggests more intense pain, for instance when a needle is shown penetrating a hand deeply³⁷ as opposed to pricking it⁴⁴. In the light of this 'intensity coding', studies on neutral touch may have failed to find consistent SI activity because the touch stimulus they used was less intense than the painful tactile stimuli used in pain studies that consistently find SI activity.

While these studies show that on average people activate SI/SII while attending to the somatic pain of others, significant inter-individual differences seem to exist. When observing photographs of injuries (e.g. an athlete braking his leg), about one third of the population reports feeling pain on the corresponding part of their own body. The remainder reports negative feelings without a sense of somatic pain. fMRI showed that SI/SII vicarious activity was significantly triggered by such images only in those participant experiencing localized vicarious pain¹¹². This provides further support that vicarious SI and SII activity adds a somatic dimension to social perception and urges us to start exploring the neural basis for such inter-individual phenomenological differences in vicarious experiences.

Together, these studies suggest why 'shared pain' can vary in shape from a generic distress to a specific bodily feeling: only if the participants directly witness an intense, localized, harmful somatic event as the cause for other people's pain do they vicariously activate their somatosensory cortices in addition to the anterior insula and rostral cingulate cortex. Due to the somatotopic organization of SI in particular, its vicarious activation is likely to add a localized, somatosensory feeling to our empathy for pain in these specific conditions. This idea finds further support from an EEG study⁷⁵ in which the P45 component of the SEP, which is thought to originate in BA1, 2 and, possibly, SII⁷⁶, is increased when an individual sees someone else's hand being deeply penetrated by a needle. Interestingly, in this study the BA1, 2 and SII activation level, as measured by the P45 modulation, correlated with the intensity of the pain that participants attributed to the actors in the movie clips⁷⁵. In accordance with the intensity-coding role of the somatosensory cortex during first-hand nociception⁶³, this suggest that vicarious somatosensory activity seems also to participate in conveying a quantitative sense of pain during social perception. Importantly, people do not always perceive the most intense pain as the most unpleasant or aversive⁷⁵, and the P45 modulation did not correlate with how unpleasant or aversive they rated the pain to have been in the visual stimuli⁷⁵. This suggests that our perception of how unpleasant or aversive an experience might have been for someone else depends primarily on structures other than the somatosensory cortices. The insula and cingulate cortex, which are active in all empathic pain experiments^{28-32, 37-45} are the most likely candidates because they are associated with these aspects of pain perception during first-hand pain experiences⁶³.

Although it is difficult to determine from the limited details available from published activation tables which parts of SI are recruited by the observation of other people's body-parts being harmed, of the eight fMRI studies that examined the observation of hands or feet in painful situations, six explicitly report vicarious activations in coordinates that correspond to BA2 or BA1^{30, 31, 37, 40, 42, 43}, whereas only one explicitly mentions activation in BA3³⁷. Given that the EEG data also point to vicarious activations of BA1, 2 or SII but not BA3⁷⁶, it seems that, as for touch and action, vicarious activity for somatic pain is restricted to the higher levels of

somatosensory processing (i.e. regions that receive direct auditory or visual input, Fig. 2c), whereas BA3 remains 'private', only being activated by the first-hand experience of pain. This difference could again account for why seeing the pain of others can be touching in a localized way without causing confusion about who was being hurt (i.e. the observer or the observed person). Further evidence for the somatotopical sharing of other people's pain stems from the study of motor-evoked potentials (see Box 2).

Taken together these data indicate that we can share the pain of others in two ways. If all we know is that the observed person is in pain, we share the affective aspects of his/her distress through vicarious activity in the anterior insula and rostral cingulate cortex. If, on the other hand, we focus on the somatic causes of that pain, we additionally share its somatic consequences by vicariously recruiting BA1/2 and/or SII (Fig. 2c).

Conclusions and future directions

In summary, we have seen that although the truly primary somatosensory cortex, BA3, is only systematically involved in processing signals that originate in our own body, the second (BA1) and third (BA2, SII) cortical somatosensory processing stages can be vicariously recruited by the sight of other people being touched, performing actions or experiencing somatic pain (Fig. 2). In particular, while we see a person touching another, BA2 seems to primarily represent the action of the toucher while SII, the tactile sensations of the touched individual. The realization that our premotor cortex is not the private fort of our own actions but a shared arena in which our actions and those of others can coexist, should now be extended to the somatosensory cortices. Much still needs to be investigated to understand the mechanisms and significance of these activations. Some promising approaches might be single-cell recordings to examine whether the same neurons in somatosensory cortices respond during the experience and observation of somatosensory states; using multivoxel pattern classification to analyse data from neuroimaging studies¹¹³ in which the tactile, proprioceptive and nociceptive content of somatosensory and visual stimuli are varied systematically¹⁰⁰ to examine the cortical areas in which subspects of somatosensation are represented, functional imaging studies that analyze effective connectivity to unravel which of the possible anatomical connections reviewed here actually trigger vicarious activity in somatosensory cortices; a combination of electrostimulating each of these somatosensory cortices and examining what people report feeling and interfering with activity in each of these regions using transcranial magnetic stimulation and analyzing how people's perception of others changes to disentangle what qualia each somatosensory cortex may convey.

Despite all these open questions, multiple pieces of evidence already suggest that vicarious somatosensory activity might play a crucial role in empathy and social perception: more empathic people show stronger activation in BA2 when they perceive the actions of others than less-empathic people¹⁷, synaesthetes who feel the sensations of others activate their somatosensory cortices more strongly than non-synaesthetes⁷⁰, and lesions in the somatosensory cortices impair our capacity to feel the emotions of others^{108, 109}.

Our review raises a further question: how can the somatosensory cortices process the somatic states of others without continuously making us experience these states as qualia on our own body? The fact that BA3 (unlike higher levels of somatosensory processing) is only active during our own somatosensory experiences may be the crucial factor. Blindsight patients¹¹⁴, whose V1 is damaged, process visual information in higher visual areas without experiencing visual qualia. Analogously, people could process the somatosensory states of others in higher level somatosensory regions without experiencing these states as qualia on their own body because BA3 is normally excluded from vicarious processing. In support of that idea,

synaesthetes who experience somatosensory qualia on their own body while witnessing others being touched indeed show high vicarious activity in the central sulcus (BA3)⁷⁰. Reducing vicarious BA3 activity in synaesthetes using TMS or other techniques might help to investigate the role of BA3 in distinguishing our own states from those of others.

In addition, other fields of neuroscience are also starting to realize that visual input modulates the somatosensory cortices. For example, in an elegant series of psychophysical studies, Haggard and colleagues showed that simply seeing a part of one's own body increases the accuracy with which one can localize an invisible tactile stimulus on that body part, and that this effect is most likely due to top-down visual modulation of SI neurons¹¹⁵. In addition, the 'rubber hand illusion' has shown that seeing an object being brushed in synchrony with somatosensory stimulation of our body leads to the illusion that this object has become part of our body^{116, 117}. These phenomena show how intimately visual and somatosensory information integrate in the brain.

We hope that this review will establish the idiomatic idea that other people's sensations, pain and actions can be 'touching' more firmly in the neurosciences and trigger a wave of experiments to further explore this idea. As a side product of this research, we will also gain a better understanding for why people are willing to pay billions of dollars to watch movies – from Westerns⁹⁵ to more frivolous genres,⁷²⁻⁷⁴ movies can get under our skin as if we were the protagonists themselves.

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Glossary

Vicarious activation: a brain region is vicariously activated in an observer if this region is normally involved in processing the observer's own actions and sensations, but is now activated by seeing similar actions or sensations in another person.

Proprioception: the sense through which we perceive the position and movements of our own body

Haptics: The sense through which we perceive the world by actively exploring them with our body. For instance, finding our car keys in our pocket among coins⁵⁰.

Nociception: the sense through which we perceive damage to our own body caused for instance by excessive heat or cold or physical injury.

Muscle spindle receptors: receptors in the muscles that measure changes in muscle-length and hence, changes in the location of the relevant body part.

Median nerve: a nerve, running through the carpal tunnel, that innervates one half of the hand and forearm.

Somatosensory evoked potentials: Electroencephalographic (EEG) signal recorded from the scalp by repeatedly applying a somatosensory stimulus to the body, or

electrically triggering activity in the somatosensory fibres in peripheral nerves, and averaging the resulting stimulus aligned EEG traces.

Qualia: Plural of quale, which is a quality or property as it is perceived or experienced by a person. For instance, although a tomato has the same physical properties when seen by a typical and a color-blind viewer, the qualia it will trigger in the two individuals differ significantly, with a 'redness' perception triggered only in the former.

Forward Model: a system that predict the consequences of a motor command in sensory (somatosensory in particular) terms¹⁰⁴.

Local maximum (in fMRI): 'peak' voxel with higher activation values than any of its neighbors; likely to identify the location of the core of the neural processing occurring in a particular region. It differs from the *global* maximum in that the latter also has a higher activation value than any other voxel in the brain. Applied to altitude maps, the tip of the Eifel tower would be a local maximum, the summit of Mount Everest, the global maximum.

BOX 1: Which studies find activity in somatosensory cortices?

To identify the brain regions that are involved in observing the actions and pain of other individuals we performed a review of the most relevant studies (see tables).

To identify brain regions involved in perceiving actions, we only included functional MRI studies that assessed both the perception and the execution of goal-directed hand actions in the same participants and that performed whole-brain analyses. Studies in which actions were observed for the purpose of imitation were excluded: if action imitation is a goal, observation may include motor planning, which would artificially increase the involvement of premotor and, through forward models, somatosensory brain regions. The first table summarizes which brain areas were active both during action execution and action perception. The “Method” column indicates how the involvement of a brain area was determined: A= we used the anatomy toolbox in SPM (statistical parametric mapping, http://www.fz-juelich.de/inm/inm-1/spm_anatomy_toolbox) or the Juelich Maps in FSL (the FMRIB Software Library, <http://www.fmrib.ox.ac.uk/fsl/data/atlas-descriptions.html#jul>) to determine from statistical parametric maps the regions containing voxels that were active during both action observation and execution. V=we visually inspected the published figures (BA2 was considered to be the anterior bank of the postcentral sulcus, BA1 the postcentral gyrus’s crown, and BA3 the posterior bank of the central sulcus); T=coordinates provided by published activation tables were entered into the SPM anatomy toolbox. The code in the remaining columns is as follows: “++” marks regions that were significantly activated by both action observation and execution and that include a local maximum, “+” marks regions that had significant activation but lie at the fringe of larger clusters that were centered elsewhere. “-” indicates that no significant activity was found using methods V or A, and “?” indicates that the activation tables were not detailed enough to determine activity of the region using method T. Examining the table reveals that BA2 was consistently activated during the execution and observation of other people’s actions.

Study	Method	3a	3b	1	2	SII	dP M	vP M	PF/ PF G
Vision of Action									
Grezes et al., 2003 ⁹	T	?	?	?	++	+	++	++	++
Dinstein et al., 2007 ¹⁶	V	-	-	-	++	+	++	++	++
Filimon et al., 2007 ¹⁰	V	-	-	-	+	-	++	+	++
Gazzola et al., 2007 ¹²	A	+	+	+	++	+	++	++	++
Gazzola et al., 2009 ¹¹	A	+	+	+	++	+	++	++	++
Turella et al., 2009 ¹⁴	A	+	+	+	++	+	++	++	++
Sound of Action									
Gazzola et al., 2006 ¹⁷	A	-	+	+	++	++	++	++	++
Ricciardi et al., 2009 ¹⁸	V	-	-	?	++	++	++	++	++

Only a small number of studies have measured brain activity in participants who both experienced pain and perceived another individual’s pain (marked “*” in the second table). To identify brain regions involved in the perception of other people’s pain we therefore also included studies that only included a pain observation condition. We used the activation tables in the published manuscripts in combination with the SPM anatomy toolbox to verify that SI, SII, the anterior insula (AI) and the rostral cingulate cortex (rCC) are involved in perceiving other people’s pain. The second table summarizes the results of this analysis, with “+” indicating that the paper reports a

peak of activation in this region in at least one of the conditions in which participants perceived the pain of others; “-“ indicates that a peak in that region is not reported in any of the conditions; “?” indicates that it is unclear whether or not that region is activated. This table indicates that experiments in which participants observe specific body parts being harmed consistently report activity in SI.

Study	SI	SII	AI	rCC
Seeing arbitrary cues signaling that someone is in pain				
*Singer et al., 2004 ²⁸	-	-	+	+
*Singer et al., 2006 ³²	-	+	+	+
Seeing faces of people in pain				
*Botvinick et al., 2005 ²⁹	-	-	+	+
Saarela et al., 2007 ⁴⁵	-	-	+	+
*Lamm et al., 2007 ³⁹	-	-	+	+
Decety et al., 2009 ³⁸	-	-	+	+
Seeing hands (or feet) in painful situations, e.g. pricked by a needle				
*Morrison et al., 2004 ⁴⁴	-	-	+	+
Jackson et al., 2005 ³¹	+	?	+	+
Jackson et al., 2006 ³⁰	+	+	+	+
Lamm et al., 2007 ⁴²	+	+	+	+
*Morrison & Downing, 2007 ⁴³	+	+	+	+
Costantini et al., 2008 ³⁷	+	+	+	+
Lamm & Decety, 2008 ⁴⁰	+	+	+	+
Lamm et al., 2009 ⁴¹	+	+	+	+

Box 2: Vicarious motor-evoked potentials.

Stimulating the hand representation in primary motor cortex using transcranial magnetic stimulation (TMS) leads to activity in muscles of the hand, the so-called motor-evoked potential (MEP) (see the figure, left part). Pinpricking these muscles while TMS is applied reduces the MEP in the pricked muscle but not in neighboring muscles of the arm¹¹⁸, demonstrating a somatotopically specific effect of nociceptive tactile input (see the figure, middle part). Why people show reduced activity in a pinpricked muscle remains poorly understood but interestingly, seeing a video clip of another individual’s hand being deeply penetrated by a needle while the TMS pulse is applied to the observer also reduces the MEP of the observer’s hand muscle, most strongly so in the muscle that is seen to be pricked¹¹⁹⁻¹²² (see the figure). The amplitude of this MEP reduction correlates with the participant’s ratings of the intensity of the pain in the other person caused by the needle puncture¹¹⁹⁻¹²². Seeing the same hand being touched (see the figure, right part) does not reduce the MEP significantly. Participants were additionally asked to mention whether they thought the pain of the observed individual was restricted to the punctured muscle or spread to a neighbouring muscle while MEPs were measured from both of these muscles in the observers. Participants who reported ascribing localized pain only showed MEP reductions in the muscle that was punctured in the video clip, whereas those who thought the pain would have spread in neighboring muscles of the observed individual showed reduced MEP also in neighboring muscles¹²⁰. The fine-grained somatotopy of these effects suggest that they may represent a spill-over from vicarious activations in SI during the observation of pain onto M1 through the strong and reciprocal connections between these two brain regions (see figure 1).

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At-a-glance

- The primary somatosensory cortex is composed of 4 subregions: Brodmann areas (BA) 3a that is primarily proprioceptive, 3b and 1 that are primarily tactile and 2 that combines tactile and proprioceptive information
- Of the somatosensory cortices, only BA2 and the secondary somatosensory cortex (SII) have direct connections with brain regions that are known to have visually and auditorily responsive neurons. This could provide an anatomical pathway for these regions to respond to the sight of other people's somatosensory experiences.
- SII shows elevated activity when people are touched and when they see other people, and in some studies objects, being touched.
- BA2 shows elevated activity both when people manipulate objects and when they see the actions of other individuals, especially when they are directed at objects.

- SI and SII are activated when people experience somatic pain and when they attend to other people's somatic pain.
- Interfering with activity in BA2 and SII impairs the perception of other people's facial expressions.
- Mirror-touch synaesthetes experience observed touch on their own body and one third of the population experiences pain on their own body when they see the injuries of other people. Both groups activate their SI and SII more strongly than other people when viewing the touch and injuries of others, respectively, linking SI/SII activity with the vivid sharing of other people's somatosensory states.
- Unlike BA2 and SII, BA3 seems normally exclusively involved in processing our own somatosensory states. This may help distinguish our own states from those we perceive in others.
- Anatomical and functional data therefore converge to show that the somatosensory cortices, BA2 and SII in particular, can contribute to our perception of other people's inner states by activating representations 'as if' we were experiencing similar tactile, proprioceptive and nociceptive stimuli on our own body.

Biographies

Christian Keysers is a Full Professor for the Social Brain at the Department of Neuroscience and the Scientific Director of the NeuroImaging Center, both at the University Medical Center of the University of Groningen. After a PhD with David Perrett linking activity in the temporal lobe to conscious perception, he worked on mirror neurons in Parma before establishing his own laboratory in the Netherlands. His research extended the notion of 'mirroring' to emotions and sensations by showing that affective and somatosensory brain regions respond to the sight of the emotions and sensations of others. He obtained the Marie Curie Excellence Award of the European Commission and the Researcher of the Year Award of the University Medical Center Groningen as well as distinguished personal grants including a Marie Curie Excellence and a VIDI grant. He has authored over 50 publications that have been cited over 2000 times. He has recently been appointed as Group Leader of the Social Brain Lab at the Netherlands Institute for Neuroscience, a research institute of the Royal Netherlands Academy of Arts and Sciences in Amsterdam.

Jon H. Kaas is a Distinguished, Centennial Professor of Psychology at Vanderbilt University since 1973. He has a longstanding interest in the organization and evolution of the forebrain of mammals, especially primates, including humans, with a focus on sensory and motor systems, and plasticity of sensory and motor systems in developing and mature primates. Research has led to over 280 research publications, and numerous reviews. Kaas has received the Earl Sutherland Prize for Research from Vanderbilt University, the Javitz Neuroscience Investigator Award, the Cajal Club Cortical Discoverer Award, the American Psychological Association Distinguished Scientific Contribution Award, and the American Philosophical Society Karl Lashley

Award. He is an elected member of the National Academy of Sciences, and the American Academy of Arts and Sciences.

Valeria Gazzola is a Tenure Track Research Scientist at the Department of Neuroscience of the University Medical Center and University of Groningen and a Senior Scientist at the Netherlands Institute for Neuroscience of the Royal Netherlands Academy of Arts and Sciences. Her work focuses on the interactions between the motor and somatosensory cortex while we perceive the actions and sensations of others. She obtained the Top Science Publication award of the Dutch NeuroFederation, the BCN prize for the best dissertation and the Van Swindelen Prize for her outreach activities. She further obtained the VENI grant of the Dutch Science Foundation (N.W.O.) to investigate the causal contributions of the primary somatosensory cortex to social perception.