

Somatosensation in social perception

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Abstract | The discovery of mirror neurons in motor areas of the brain has led many to assume that our ability to understand 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. These have anatomical connections that enable them to have a role in visual and auditory social perception. Studies that measure brain activity while participants witness the sensations, actions and somatic pain of others consistently show vicarious activation in the somatosensory cortices. Neuroscientists are starting to understand how the brain adds a somatosensory dimension to our perception of other people.

Vicarious activation

Activation of a brain region that is normally involved in processing the observer's own actions and sensations, but that 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.

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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 neurons^{1–8} (in monkeys) and brain regions (in humans) in the premotor and posterior parietal cortices that are also involved in programming similar actions^{9–18}. This has led to the idea that understanding the inner state of other individuals relies on implicit motor simulation — that is, the activation of motor programs that we would use to perform similar actions^{19–23}. 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 brain areas involved in emotion processing, including the anterior insula and the rostral cingulate cortex (rCC), might perform an 'emotional simulation' of other individuals' experiences, showing activity not only when we experience positive and negative emotions but also when we witness those of others^{24–45}. Electrostimulation of similar regions of the insula causes measurable changes in the body (for example, gastric contractions) and induces the perception of changes in the body⁴⁶. This suggests that emotional simulation is not purely conceptual but involves representations of the body. 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 mainstream simulation models^{19,20,23}. However,

expressions such as "Her words were really touching" encapsulate the intuitive link between the people around us and our sense of touch.

In this Review, we first describe 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, the higher stages of somatosensory processing in the primary somatosensory cortex (SI) and secondary somatosensory cortex (SII) are activated when we perceive other people being touched, performing an action or experiencing somatic pain (BOX 1). We suggest that these vicarious activations of somatosensory cortices may have the unique potential to provide a somatic dimension to our perception of other people's experiences.

Anatomy of the somatosensory system

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

Traditionally, in humans and monkeys the term 'somatosensory cortices' refers to the anterior parietal cortex and the upper bank (operculum) of the lateral sulcus, which process tactile, proprioceptive and nociceptive information. The term 'somatosensory system' refers to all of the brain regions involved in processing somatosensory information, and includes the somatosensory

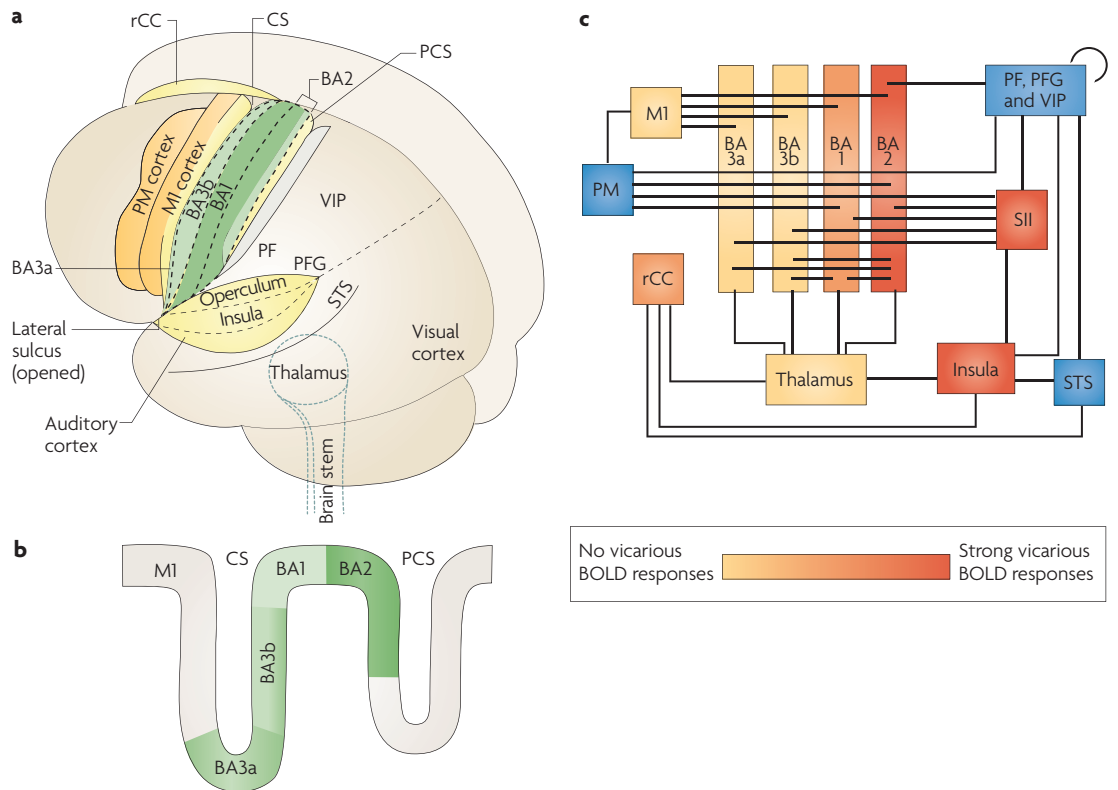


Figure 1 | Cortical processing networks for somatosensation. **a** | Posterolateral view of a human brain showing areas and regions involved in somatosensation. The central sulcus (CS), posterior central sulcus (PCS) and lateral sulcus have been opened to show the areas within. The superior temporal sulcus (STS) is not opened, but it contains multisensory areas on its banks. Other sulci are not shown. For clarity, the rostral cingulate cortex (rCC) is indicated on the medial wall of the opposite hemisphere. The anterior parietal cortex includes the four strip-like areas of Brodmann area 3a (BA3a), BA3b, BA1 and BA2 (shown in green) in a rostrocaudal sequence. Regions of interest in the posterior parietal cortex include the ventral intraparietal area (VIP) and more lateral regions (PF and PFG). The lateral parietal cortex is inside the lateral sulcus. It includes the operculum of the upper bank, which contains the secondary somatosensory cortex (SII), composed of the secondary somatosensory cortex proper (S2) and the parietal ventral region (PV)), and the insula, which has regions for processing touch and pain. Somatosensory networks ultimately involve the primary motor (M1) cortex and the dorsal and ventral premotor (PM) areas for action. The thalamus (dashed grey lines) lies deep in the forebrain. **b** | Schematic representation of the CS, the PCS, the M1 cortex and the anterior parietal areas BA3a, BA3b, BA1 and BA2. **c** | Brain regions involved in somatosensation, their main connections and their source of visual input. Functional MRI experiments suggest that vicarious activation occurs in some somatosensory brain regions; the strength of the blood oxygen level-dependent (BOLD) response in these regions to observing the touch, actions or pain of others is indicated by the colour. In addition, there are brain regions with neurons that respond to the presentation of visual or auditory stimuli that also show vicarious activation; these are the PM, STS and areas PF, PFG and VIP (shown in blue).

cortices proper plus the insula and the rostral cingulate cortex, which 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 3 (BA3a and BA3b) roughly correspond to the posterior bank of the central sulcus, BA1 to the crown of the postcentral gyrus and BA2 to the anterior bank of the postcentral gyrus (FIG. 1a,b). All four areas were once considered to be parts of a single ‘homunculus’, a systematic representation of the contralateral body surface known as ‘SI’. It is now known that each of the four areas constitutes a separate representation with different connections and functions⁴⁷. Accordingly, the term ‘SI’ is now used to refer to BA3a + BA3b + BA1

+ BA2 when it is unclear to which of these subregions a statement applies or when it applies to all four.

BA3a 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. BA3b is the primary area for tactile processing and receives its major activating inputs from neurons in the ventroposterior nucleus (VP) of the thalamus. BA3b also receives input from small neurons in the VP and in the ventroposterior inferior nucleus (VPI) that are activated by a broad range of stimulation intensities (including touch in the nociceptive range) and from nociceptive neurons in the spinal cord and brain stem⁴⁸. BA1 receives strong activating inputs from BA3b and thus is thought to be involved in a secondary cortical

Nociception

The sense through which we perceive damage caused to our own body — for example, by excessive heat, 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.

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).

First, to identify the 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 regions (the dorsal premotor cortex (dPm) and ventral premotor cortex (vPm)) and, through forward models, somatosensory brain regions. The first table summarizes which brain areas were active during both action execution and action perception and reveals that Brodmann area (BA2) was consistently activated during the execution and observation of other people's actions.

Method*	BA3a	BA3b	BA1	BA2	SII	dPM	vPM	PF/PFG	Refs
<i>Observing an action</i>									
T	?	?	?	++	+	++	++	++	9
V	-	-	-	++	+	++	++	++	16
V	-	-	-	+	-	++	+	++	10
A	+	+	+	++	+	++	++	++	12
A	+	+	+	++	+	++	++	++	11
A	+	+	+	++	+	++	++	++	14
<i>Hearing an action</i>									
A	-	+	+	++	++	++	++	++	17
V	-	-	?	++	++	++	++	++	18

++, regions that were significantly activated by both action observation (or action sounds) and action execution and that include a local maximum; +, regions that had significant activation but were located at the fringe of larger clusters that were centred elsewhere; -, no significant activity found using methods V or A;?, activation tables were not detailed enough to determine activity of the region using method T. *Method used to determine the involvement of a brain area. A, analysis of the [Statistical Parametric Mapping \(SPM\) Anatomy Toolbox](#) or the [Juelich Histological Atlas](#) to determine from statistical parametric maps the regions containing voxels that were active during both action observation and execution; T, coordinates provided by published activation tables entered into the SPM Anatomy Toolbox; V, visual inspection of the published figures (BA2 is 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).

Only a small number of studies have measured brain activity in participants who both experienced pain and perceived another individual's pain. To identify brain regions involved in the perception of other people's pain, we also incorporated studies that included only a 'pain observation' condition. We used the activation tables in the published manuscripts in combination with the SPM Anatomy Toolbox to verify that the primary somatosensory cortex (SI), the secondary somatosensory (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 and reveals that participants observe specific body parts being harmed consistently report activity in SI.

SI	SII	AI	rCC	Refs
<i>Seeing arbitrary cues signalling that someone is in pain</i>				
-	-	+	+	28*
-	+	+	+	32*
<i>Seeing the faces of people in pain</i>				
-	-	+	+	29*
-	-	+	+	45
-	-	+	+	39*
-	-	+	+	38
<i>Seeing hands (or feet) in painful situations[‡]</i>				
-	-	+	+	44*
+	?	+	+	31
+	+	+	+	30
+	+	+	+	12
+	+	+	+	13*
+	+	+	+	37
+	+	+	+	40
+	+	+	+	41

+, 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; -, a peak in this region is not reported in any of the conditions; ?, it is unclear whether this region is activated. *This study measured brain activity in participants who both experienced pain and perceived another individual's pain. [‡]For example, being picked by a needle.

stage of tactile processing. BA2 receives inputs from BA3a, BA3b and BA1 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. Neurons in BA2 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 that we will term *haptics*⁵⁰. Notably, BA2 also receives callosal connections from BA2 of the other hemisphere, and these connections enable some neurons to respond to stimuli on both the ipsilateral and the contralateral hand during bimanual exploration^{51,52}. The connections between areas of anterior parietal cortex are reciprocal in that BA2 projects back to BA1, BA3b and BA3a.

Importantly, BA2 also has direct, reciprocal connections with regions of the fundus of the intraparietal sulcus (such as the ventral intraparietal area (VIP)) and the inferior parietal lobule (areas PF and PFG in particular), which combine visual, auditory and somatosensory information^{49,53–55}. In monkeys, some cells in VIP respond both when the monkey is touched and when it sees another individual being touched in a similar way⁵⁶, whereas some neurons in PF and 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 for mirror neurons in the premotor cortex⁵⁷. The fact that these regions also project to BA2 makes it plausible that BA2 could be activated vicariously when one observes the 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.

In monkeys and humans⁵⁸, SII, which lies on the parietal operculum (OP), can be divided into two subregions termed S2 and PV (the parietal ventral area), 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. They also have similar afferent and efferent cortical connections⁶⁰, including connections with neighbouring cortical regions of the OP and with a number of brain regions containing cells that respond to visual and auditory input. The latter regions include the PF, PFG and VIP^{54,55} (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 (that is, the intensity and location) of pain⁶³. This occurs in parallel with the affective and motivational processing of nociceptive input, which 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 input 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 they do not receive pronounced auditory or visual input⁶². This information

is relayed to more anterior sectors of the insula, where it is integrated with inputs from the frontal lobe, from all sensory modalities and from limbic structures^{62,66}. The rCC receives nociceptive input from more lateral nuclei in the thalamus (posterior part of the ventromedial nucleus (VMpo), ventrocaudal part of the medial dorsal nucleus (MDvc), parafascicular nucleus (Pf) and centrolateral nucleus (CL)) and integrates this information with highly processed information from various cortical areas⁶³.

This summary 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 the anterior parietal cortex but are then combined in BA2 and sent to SII, enabling haptics. Second, nociceptive information from the thalamus is more broadly distributed to the cortex, with parts of the insula and rCC specifically involved in processing the affective value of nociceptive information. Third, BA2, the SII complex, the insula and the rCC receive direct inputs from regions of cortex that are responsive to visual and auditory stimuli, whereas BA3b and BA1 have access to such information only indirectly through BA2 and SII. Finally, the anatomical connections suggest that visual or auditory information would be most likely to influence tactile processing in SII, haptic processing in BA2 and SII, and nociceptive processing in BA2, SII, the insula and rCC. BA3a, BA3b and BA1 should have, at best, only weaker responses to visual or auditory information through feedback connections from SII and BA2.

SII: vicarious tactile processing

Evidence for a role of somatosensory cortices in the perception of other people's somatosensory states originated from a functional MRI (fMRI) study. Participants in a scanner were touched on their legs by an experimenter and then were shown movie clips of 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 be able to touch them. Being touched activated the leg representations in both SI and SII. Importantly, viewing other people being touched (as compared to the control condition) also activated SII (but not SI; FIG. 3). SII was even activated when participants watched objects (for example, rolls of paper) being touched compared to movies in which the objects were not touched⁶⁷. Other studies also showed SII activity in participants who observed the hands^{68,69} or the neck and face⁷⁰ of other people being touched in movie clips. One study replicated the SII activation in response to seeing objects being touched⁶⁸, although another study did not⁷⁰. The discovery that SII responds to the sight of humans and, sometimes, objects being touched and the fact that 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 experience if one were touched in a similar way, rather than the precise body location at which the touch occurred. Interestingly, watching tactile stimulation of more erogenous zones of the body in pornographical movies also activates SII vicariously^{72–74}.

Haptics

The sense through which we perceive the world by actively exploring it with our body — for instance, finding our keys among a pocketful of coins.

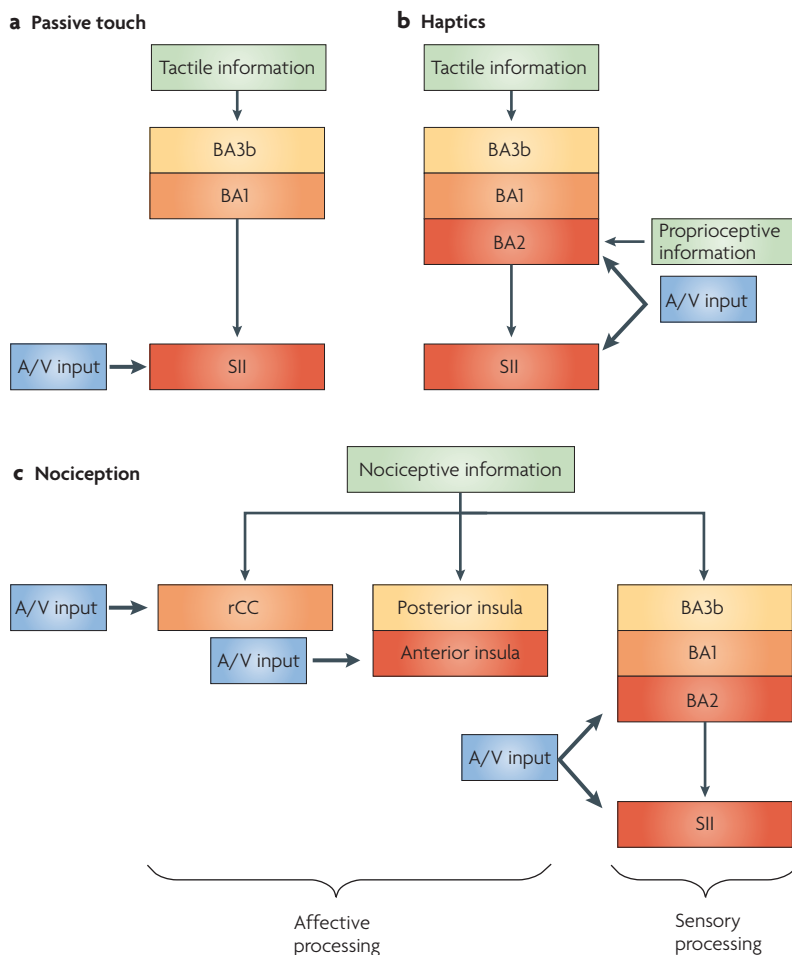


Figure 2 | Audio/visual input to tactile, haptic and nociceptive processing. Although somatosensory receptors in the body provide the primary input to the somatosensory system (shown in green), the processing streams for tactile, haptic and nociceptive information all receive input from brain regions in which cells respond to audio/visual (A/V) stimuli (shown in blue). The anatomical level at which such A/V information enters these streams determines where vicarious somatosensory responses might occur. **a** | The main pathway for the processing of tactile information resulting from passive touch first receives direct input from brain regions with A/V responses at the level of the secondary somatosensory cortex (SII). **b** | The pathway that integrates tactile and proprioceptive information when we are actively manipulating an object (haptics) receives A/V input in Brodmann area 2 (BA2) and SII. **c** | Nociceptive information is distributed along multiple, parallel streams (important interconnections exist but are omitted for clarity). Two of these streams are thought to primarily process the affective aspects of pain, and the third stream is thought to primarily process the sensory aspects of being hurt. Each of these streams receive A/V input at the level of the rostral cingulate cortex (rCC), anterior insula, BA2 and SII.

The above studies showed that, in contrast to SII, SI is activated in some cases^{69,70} but not in others^{67,68} and BA3 is 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. Only one study has compared the brain response to watching movie clips in which the touch

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

resulted from a deliberate human action with the brain response to watching movie clips in which touch was accidentally delivered by an object that was moved by the wind⁶⁸. The study 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 below).

Electroencephalography (EEG), which has higher temporal resolution than fMRI, has also been used to examine which stages of somatosensory processing are sensitive to visual input⁷⁵. The median nerve of participants was electrostimulated to provide a precisely timed somatosensory input, and the resulting sensory evoked potentials (SEPs) were measured on the scalp. Components of these SEPs within 40 ms of stimulation reflect subcortical and BA3 activity, whereas later components reflect activity in BA1, BA2 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 (for example, the P45) associated with BA1, BA2 or possibly SII were influenced⁷⁵.

Together, the above data clearly show that, 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 be 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 BA3b are only recruited when we ourselves are being touched could account for this. The role of the intermediate processing stages that take place in 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} could be important factors in determining their recruitment.

To establish the degree to which SII contributes to social perception, it will be necessary to investigate how virtual (transcranial magnetic stimulation (TMS)-induced) or neurological lesions in SII change people's capacity to accurately perceive the sensations of others. A certain type of synaesthesia⁷⁷, 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 another 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.*⁷⁰ measured brain activity in one such synaesthete and found that she differed from controls in that her SI (probably including BA3) and SII regions were activated more strongly than those of 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 activation in somatosensory brain regions — and in particular the

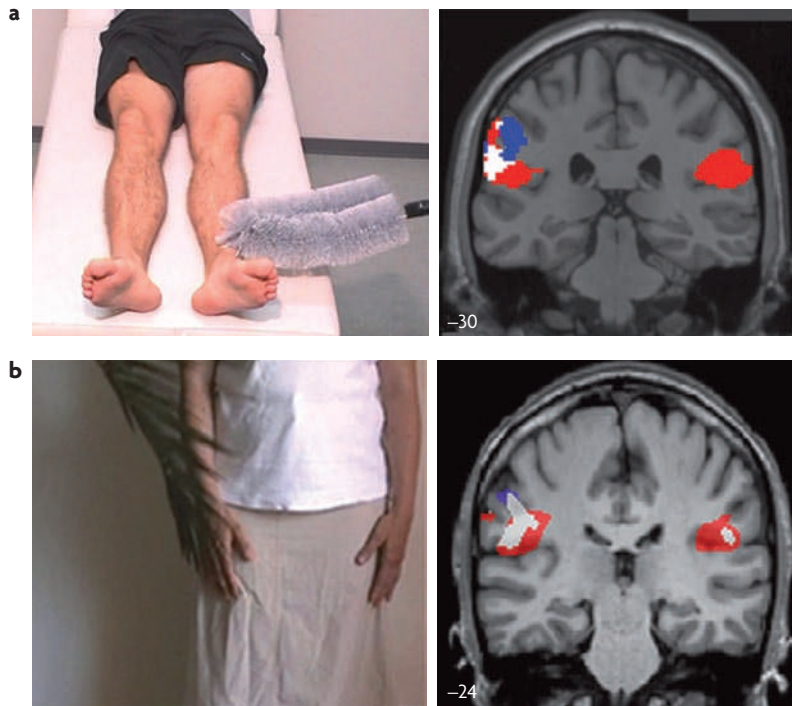


Figure 3 | Vicarious tactile activity in the secondary somatosensory cortex. Seeing a leg or a hand being touched elicits activity in the secondary somatosensory cortex (SII) that overlaps with the activity that occurs when the participant is being touched on the leg or hand, respectively. The left column shows a still frame from the movie clips used by Keyzers *et al.*⁶⁷ (a) and Ebisch *et al.*⁶⁸ (b). The right column shows brain regions that are activated exclusively by the experience of touch (shown in red) and by watching the movie clips (shown in blue). The overlaps between brain areas indicate areas that are activated by both the experience of touch and the observation of someone else being touched (shown in white). The white numbers refer to the y coordinates in the MNI (Montreal Neurological Institute) space of the coronal slice.

involvement of BA3 — can determine what it feels like to see other people being touched and, more generally, the vividness with which one might empathically share other people's physical experiences.

BA2: vicarious haptics and proprioception

SI is not just 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 to perceive the actions of others? The study of the cortical processing of other individuals' actions has been dominated by the discovery of mirror neurons in monkeys. These neurons, which respond both when a monkey performs an action and when it sees or hears another individual perform a similar action^{1–8}, have so far been reported in regions involved in motor planning: the ventral premotor cortex^{1,3–6,8} and the posterior parietal cortex (areas PF and 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 of 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: do SI or SII also contain (mirror) neurons that are active during both the observation and the execution of actions? Intriguing preliminary evidence for this possibility stems from a neuroimaging experiment showing that monkeys activate SI and SII when they are grasping an object and when they are watching another individual performing the same action^{86–88}.

To test whether SI and SII might play a part 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 (that is, voxels that were active during both 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 in more participants than the ventral premotor cortex (FIG. 4). SII also contained shared voxels (albeit fewer than BA2), as did the dorsal premotor cortex⁸⁹. A review of six studies that have examined 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}.

However, findings that the same region shows increases in fMRI signals during both the observation and execution of actions (BOX 1) suggest, but do not 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 cases of touch and nociception (see below). 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 represented in these putative visually and auditorially responsive somatosensory neurons. 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 repetition suppression in SI during both the observation and the execution of actions¹⁶. Second, the shallow depth of recording of some of the neurons that 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).

As mentioned above, a limitation of fMRI studies is that activity in a particular brain region during both

Somatosensory evoked potentials

Electroencephalographic (EEG) signals recorded from the scalp that are induced by the repeated application of a somatosensory stimulus to the body or by electrically triggering activity in the somatosensory fibres in peripheral nerves.

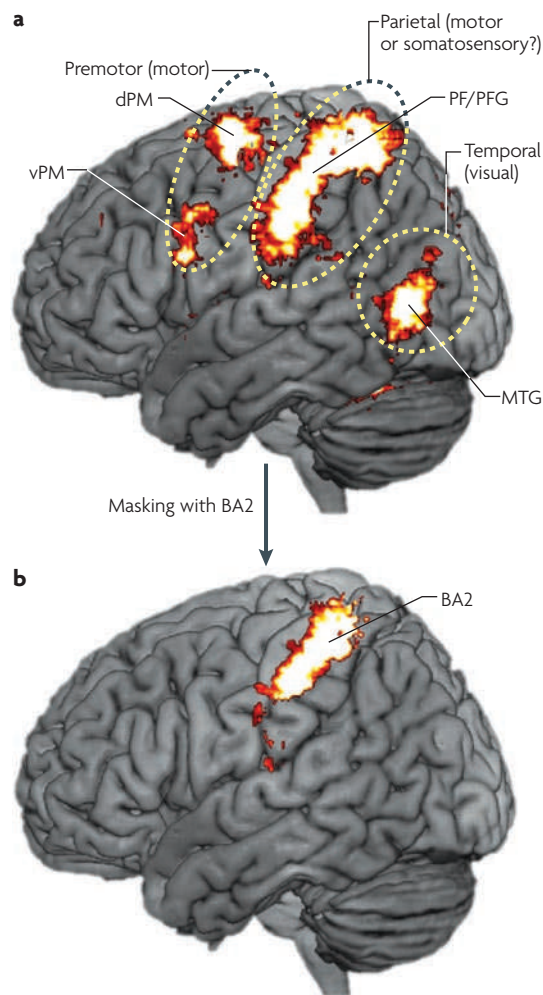


Figure 4 | Vicarious activity during the observation of actions. **a** | Shared voxels, that is, voxels that show activity during both action observation and action execution, have been reliably identified in four large clusters of brain areas: the dorsal premotor cortex (dPM) and ventral premotor cortex (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 and PFG, in which mirror neurons have been recorded in monkeys, thus associating this area with motor control. **b** | However, showing only those voxels of **a** that fall within Brodmann area 2 (BA2) reveals how much of the parietal shared voxels are actually part of the somatosensory cortex. This indicates that activity in this part of the cluster probably represents vicarious haptic activity instead of vicarious motor activity. The figure is based on data from REF. 11.

the execution and perception of an action does not necessarily indicate that both scenarios induce activity in neurons representing the same information (for example, a particular haptic sensation or motor program) — that is, the information being processed might not be the same. 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. Hence, it is possible to be confident that the observation of hand actions specifically triggers the representation of hand actions in BA2 (BOX 1). Additionally, executing hand and mouth actions causes activity in dorsal and ventral SI regions, 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 individual⁹⁰. 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 BA2 (REF. 91). Together, these data suggest that vicarious BA2 activity could provide fine-grained, somatotopically specific representations of other people's actions.

What does vicarious activity in BA2 convey? A number of studies help us to understand what perceptual content vicarious BA2 activity could convey. First, observing hand movements that involve extreme joint stretching (for example, stretching beyond the normal physiological angle) activates BA2 strongly⁹², and deactivating BA2 using TMS reduces motor-evoked potentials in the hand when seeing such extreme joint stretching⁹³. Second, BA2 is more, or sometimes only, active when viewing hands manipulating objects (for example, grasping a cup) compared with actions that do not involve objects (for example, pointing or mimicked grasping)^{94,95}. Additionally, viewing someone move a heavy object activates BA2 more strongly than viewing someone moving a light object⁹⁶.

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 when participants watched a film in which the actors were seen to manipulate objects, vicarious activity in SI was consistently observed⁹⁷. 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 (for example, dancers watching a dance performance^{98–101}). 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.

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 act of touching (for example, following instructions to count the number of touching actions)⁶⁹ activates the hand area of BA2 more than focusing attention on the touched

individual (that is, when the touched individual or object but not the toucher is shown)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 how 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 the performance of those actions. Such a link between the motor and somatosensory system during action observation would be consistent with the link between these two systems during action execution, in which 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 recognized more rapidly¹⁰⁵.

Facial expressions are a special type of action. Experiments that have examined the neural structures involved in both the observation and execution of dynamic facial expressions are in agreement that, akin to observing hand actions, observing the facial expressions of others 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 impair the recognition of facial expressions^{108,109}, which suggests 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 when one observes other people's facial expressions remains to be explored further.

When we perceive the actions of others, we often become aware of their intentions and feelings 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. Further, 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 suggests 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 experiencing what it would feel like to move one's own body in the observed way, respectively. In support of this idea, SI activity is correlated with the accuracy with which a person judges how another person feels¹¹¹.

SI and 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 him or her cut their 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 people¹¹². Neuroimaging research is now starting to shed light on the multifaceted nature of this 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 rCC^{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. This process could trigger a 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 the comparison of fMRI experiments that used different types of stimuli to inform the participant about the pain of others. We describe these studies below.

In a seminal pair of fMRI studies, participants in the scanner were shown a coloured cue on a 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 example, 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 activation in these and various other fMRI experiments (BOX 1) confirms previous findings that perceiving the pain of others vicariously activates the higher levels of affective nociceptive processing — that is, the anterior insula and/or rCC. The somatosensory cortices (SI and SII), however, were only vicariously activated in some conditions, and almost never while people viewed painful facial expressions or abstract cues. This 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 (somatic) 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 involves the somatosensory cortices, but only if one attends to the localized somatic cause of the pain.

Forward model

A system that predicts the consequences of a motor command in sensory (somatosensory in particular) terms.

Qualia

(Plural of quale.) A quality or property as it is perceived or experienced by a person. For instance, although a tomato has the same physical properties regardless of whether it is seen by a typical or a colour-blind viewer, the qualia it will trigger in the two individuals differ substantially, with a 'redness' perception triggered only in the former.

Some of these studies have identified further 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, such as when a needle is shown penetrating a hand deeply³⁷ as opposed to pricking it⁴⁴. In light of this ‘intensity coding’, it is possible that studies on neutral touch 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.

Although these studies show that, in general, SI and SII are activated when individuals witness the somatic pain of others, substantial inter-individual differences seem to exist. When observing photographs of injuries (for example, an athlete breaking his leg), about one-third of participants report feeling pain on the corresponding part of their own body. The remaining two-thirds report negative feelings without a sense of somatic pain. fMRI showed that vicarious SI and SII activity was triggered by such images only in the participants who experienced localized vicarious pain¹¹². This provides further evidence 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 reasons for the variation of ‘shared pain’ from a generic distress to a specific bodily feeling; only if 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 rCC). Owing to the somatotopic organization of SI, its vicarious activation is likely to add a localized, somatosensory feeling to our empathy for pain in these 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, BA2 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, BA2 and SII activation levels, 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 suggests that vicarious somatosensory activity also participates 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 activation in coordinates that correspond to BA2 or BA1 (REFS 30,31,37,40,42,43), whereas only one explicitly mentions activation in BA3 (REF. 37). Given that the EEG data also point to vicarious activations of BA1, BA2 or SII but not BA3 (REF. 76), it seems that, as for touch and action, vicarious activity for somatic pain is restricted to the higher levels of somatosensory processing (that is, 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 observing the pain of others can be touching in a localized way without causing confusion about who was being hurt (that is, the observer or the observed person). Further evidence for the somatotopic sharing of other people’s pain stems from the study of motor-evoked potentials (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 their distress through vicarious activity in the anterior insula and rCC. If, however, we focus on the somatic causes of that pain, we additionally share its somatic consequences by vicariously recruiting BA1, BA2 and/or SII (FIG. 2c).

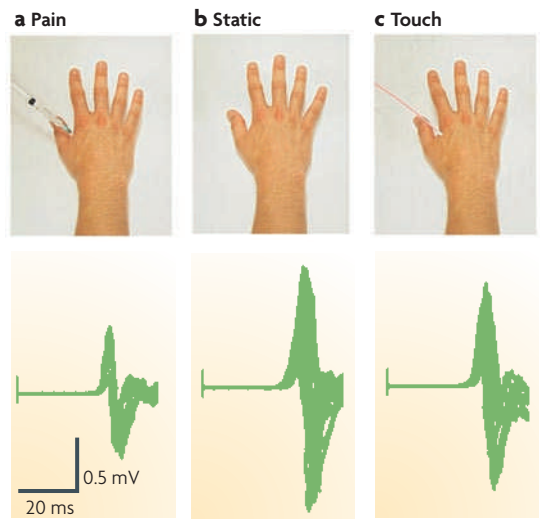
Conclusions and future directions

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 and 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, when we see one person touching another, BA2 seems to primarily represent the action of the toucher, whereas SII seems to represent the tactile sensations of the individual being touched. The notion 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 remains to be investigated to understand the mechanisms and significance of these activations.

There are a number of promising approaches that could be used in the study of these activations. Firstly, single-cell recordings could be used to examine whether the same neurons in somatosensory cortices respond during the experience and observation of somatosensory states. Secondly, multi-voxel pattern classification could be used to analyse data from neuroimaging studies¹¹³ in which the tactile, proprioceptive and nociceptive content of somatosensory and visual stimuli are varied

Box 2 | Vicarious motor-evoked potentials

Stimulating the hand representation in the primary motor cortex using transcranial magnetic stimulation (TMS) leads to activity in muscles of the hand, the so-called motor-evoked potential (MEP). Pinpricking these muscles while TMS is applied reduces the MEP in the pricked muscle but not in neighbouring muscles of the arm¹¹⁸, demonstrating a somatotopically specific effect of nociceptive tactile input. 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 a TMS pulse is applied to the observer also reduces the MEP of the observer's hand muscle^{119–122} (see the figure, part **a**), compared with the MEP during TMS in an observer who watches a video of a static hand (part **b**). This reduction is greatest in the muscle that is seen to be pricked^{119–122}. 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 puncture^{119–122}. Seeing the same hand being touched does not reduce the MEP significantly (part **c**). 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 experiencing 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 to neighbouring muscles of the observed individual showed reduced MEP in neighbouring muscles¹²⁰. The fine-grained somatotopy of these effects suggests that during the observation of pain, vicarious activation may spill over from the SI to the M1 region owing to the strong and reciprocal connections between these two brain regions (FIG. 1).



systematically¹⁰⁰ to examine the cortical areas in which sub-aspects of somatosensation are represented. Thirdly, fMRI studies that analyse effective connectivity could be used to unravel which of the possible anatomical connections reviewed here actually trigger vicarious activity in somatosensory cortices. Finally, to disentangle what qualia each somatosensory cortex may convey, people's reported feelings could be examined during electrostimulation of each of these somatosensory cortices, and this could be combined with analysis of changes in people's perception of others during manipulation of activity in these regions using TMS.

Many open questions remain, but multiple sources of evidence already suggest that vicarious somatosensory activity has a crucial role in empathy and social perception. More-empathic people show stronger activation in BA2 than less-empathic people when they perceive the actions of others¹⁷, 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 us experiencing these states continuously, 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, who have V1 damage, 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 this idea, synaesthetes who experience somatosensory qualia on their own body while witnessing others being touched show vicarious activity in the central sulcus (BA3)⁷⁰. Reducing vicarious BA3 activity in synaesthetes using TMS or other techniques could be used to investigate the role of BA3 in distinguishing our own states from those of others.

Other fields of neuroscience are also starting to recognize that visual input modulates the somatosensory cortices. For example, an elegant series of psychophysical studies has shown 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 likely to be 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 more firmly the idiomatic idea that other people's sensations, pain and actions can be 'touching' and that it will trigger new experiments aimed at further exploring this idea. As a side-product of this research, we will also gain a greater understanding of why people are willing to pay billions of dollars to watch movies, from westerns⁹⁵ to more frivolous genres^{72–74}. It seems that movies can get under our skin as if we were the protagonists themselves.

1. Caggiano, V., Fogassi, L., Rizzolatti, G., Thier, P. & Casile, A. Mirror neurons differentially encode the interpersonal and extrapersonal space of monkeys. *Science* **324**, 403–406 (2009).
2. Fogassi, L. *et al.* Parietal lobe: from action organization to intention understanding. *Science* **308**, 662–667 (2005).
3. Fujii, N., Hihara, S. & Iriki, A. Social cognition in premotor and parietal cortex. *Soc. Neurosci.* **3**, 250–260 (2008).
4. Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. Action recognition in the premotor cortex. *Brain* **119**, 593–609 (1996).
5. Keysers, C. *et al.* Audiovisual mirror neurons and action recognition. *Exp. Brain Res.* **153**, 628–636 (2003).
6. Kohler, E. *et al.* Hearing sounds, understanding actions: action representation in mirror neurons. *Science* **297**, 846–848 (2002).
7. Rozzi, S., Ferrari, P. F., Bonini, L., Rizzolatti, G. & Fogassi, L. Functional organization of inferior parietal lobule convexity in the macaque monkey: electrophysiological characterization of motor, sensory and mirror responses and their correlation with cytoarchitectonic areas. *Eur. J. Neurosci.* **28**, 1569–1588 (2008).
8. Umiltà, M. A. *et al.* I know what you are doing: a neurophysiological study. *Neuron* **31**, 155–165 (2001).
9. Grezes, J., Armony, J. L., Rowe, J. & Passingham, R. E. Activations related to 'mirror' and 'canonical' neurons in the human brain: an fMRI study. *Neuroimage* **18**, 928–937 (2003).
10. Filimon, F., Nelson, J. D., Hagler, D. J. & Sereno, M. I. Human cortical representations for reaching: mirror neurons for execution, observation, and imagery. *Neuroimage* **37**, 1315–1328 (2007).
11. Gazzola, V. & Keysers, C. The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cereb. Cortex* **19**, 1239–1255 (2009).
Using unsmoothed data and single-subject analysis, this paper shows that BA2 and SII are involved in action observation and action execution.
12. Gazzola, V., Rizzolatti, G., Wicker, B. & Keysers, C. The anthropomorphic brain: the mirror neuron system responds to human and robotic actions. *Neuroimage* **35**, 1674–1684 (2007).
13. Gazzola, V. *et al.* Aplicas born without hands mirror the goal of hand actions with their feet. *Curr. Biol.* **17**, 1235–1240 (2007).
14. Turella, L., Erb, M., Grodd, W. & Castiello, U. Visual features of an observed agent do not modulate human brain activity during action observation. *Neuroimage* **46**, 844–853 (2009).
15. Buccino, G. *et al.* Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. *Neuron* **42**, 323–334 (2004).
16. Dinstein, I., Hasson, U., Rubin, N. & Heeger, D. J. Brain areas selective for both observed and executed movements. *J. Neurophysiol.* **98**, 1415–1427 (2007).
17. Gazzola, V., Aziz-Zadeh, L. & Keysers, C. Empathy and the somatotopic auditory mirror system in humans. *Curr. Biol.* **16**, 1824–1829 (2006).
18. Ricciardi, E. *et al.* Do we really need vision? How blind people 'see' the actions of others. *J. Neurosci.* **29**, 9719–9724 (2009).
19. Rizzolatti, G. & Craighero, L. The mirror-neuron system. *Annu. Rev. Neurosci.* **27**, 169–192 (2004).
20. Rizzolatti, G. & Fabbri-Destro, M. The mirror system and its role in social cognition. *Curr. Opin. Neurobiol.* **18**, 179–184 (2008).
21. Gallese, V., Keysers, C. & Rizzolatti, G. A unifying view of the basis of social cognition. *Trends Cogn. Sci.* **8**, 396–403 (2004).
22. Keysers, C. & Gazzola, V. Towards a unifying neural theory of social cognition. *Prog. Brain Res.* **156**, 379–401 (2006).
23. Iacoboni, M. & Dapretto, M. The mirror neuron system and the consequences of its dysfunction. *Nature Rev. Neurosci.* **7**, 942–951 (2006).
24. Bastiaansen, J. A., Thioux, M. & Keysers, C. Evidence for mirror systems in emotions. *Phil. Trans. R. Soc. Lond. B* **364**, 2391–2404 (2009).
25. Wicker, B. *et al.* Both of us disgusted in my insula: the common neural basis of seeing and feeling disgust. *Neuron* **40**, 655–664 (2003).
26. Adolphs, R., Tranel, D. & Damasio, A. R. Dissociable neural systems for recognizing emotions. *Brain Cogn.* **52**, 61–69 (2003).
27. Calder, A. J., Keane, J., Manes, F., Antoun, N. & Young, A. W. Impaired recognition and experience of disgust following brain injury. *Nature Neurosci.* **3**, 1077–1078 (2000).
28. Singer, T. *et al.* Empathy for pain involves the affective but not sensory components of pain. *Science* **303**, 1157–1162 (2004).
29. Botvinick, M. *et al.* Viewing facial expressions of pain engages cortical areas involved in the direct experience of pain. *Neuroimage* **25**, 312–319 (2005).
30. Jackson, P. L., Brunet, E., Meltzoff, A. N. & Decety, J. Empathy examined through the neural mechanisms involved in imagining how I feel versus how you feel pain. *Neuropsychologia* **44**, 752–761 (2006).
31. Jackson, P. L., Meltzoff, A. N. & Decety, J. How do we perceive the pain of others? A window into the neural processes involved in empathy. *Neuroimage* **24**, 771–779 (2005).
32. Singer, T. *et al.* Empathic neural responses are modulated by the perceived fairness of others. *Nature* **439**, 466–469 (2006).
33. Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C. & Lenzi, G. L. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc. Natl Acad. Sci. USA* **100**, 5497–5502 (2003).
34. Dapretto, M. *et al.* Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neurosci.* **9**, 28–30 (2006).
35. Jabbi, M., Swart, M. & Keysers, C. Empathy for positive and negative emotions in the gustatory cortex. *Neuroimage* **34**, 1744–1753 (2007).
36. van der Gaag, C., Minderer, R. & Keysers, C. Facial expressions: what the mirror neuron system can and cannot tell us. *Soc. Neurosci.* **2**, 179–222 (2007).
37. Costantini, M., Galati, G., Romani, G. L. & Aglioti, S. M. Empathic neural reactivity to noxious stimuli delivered to body parts and non-corporeal objects. *Eur. J. Neurosci.* **28**, 1222–1230 (2008).
38. Decety, J., Echiois, S. & Correll, J. The blame game: the effect of responsibility and social stigma on empathy for pain. *PLoS ONE* **2**, e1292 (2007).
39. Lamm, C., Batson, C. D. & Decety, J. The neural substrate of human empathy: effects of perspective-taking and cognitive appraisal. *J. Cogn. Neurosci.* **19**, 42–58 (2007).
40. Lamm, C. & Decety, J. Is the extrastriate body area (EBA) sensitive to the perception of pain in others? *Cereb. Cortex* **18**, 2369–2373 (2008).
41. Lamm, C., Meltzoff, A. N. & Decety, J. How do we empathize with someone who is not like us? A functional magnetic resonance imaging study. *J. Cogn. Neurosci.* **22**, 362–376 (2009).
42. Lamm, C., Nusbaum, H. C., Meltzoff, A. N. & Decety, J. What are you feeling? Using functional magnetic resonance imaging to assess the modulation of sensory and affective responses during empathy for pain. *PLoS ONE* **2**, e1292 (2007).
43. Morrison, I. & Downing, P. E. Organization of felt and seen pain responses in anterior cingulate cortex. *Neuroimage* **37**, 642–651 (2007).
44. Morrison, I., Lloyd, D., di Pellegrino, G. & Roberts, N. Vicarious responses to pain in anterior cingulate cortex: is empathy a multisensory issue? *Cogn. Affect. Behav. Neurosci.* **4**, 270–278 (2004).
45. Saarela, M. V. *et al.* The compassionate brain: humans detect intensity of pain from another's face. *Cereb. Cortex* **17**, 230–237 (2007).
46. Penfield, W. & Faulk, M. E. Jr. The insula: further observations on its function. *Brain* **78**, 445–470 (1955).
47. Kaas, J. H. In *The Human Nervous System* 2nd edn (eds Paxinos, G. & Mai, J. K.) 1059–1092 (Elsevier, London, 2004).
48. Craig, A. D. Retrograde analyses of spinothalamic projections in the macaque monkey: input to ventral posterior nuclei. *J. Comp. Neurol.* **499**, 965–978 (2006).
49. Pons, T. P. & Kaas, J. H. Corticocortical connections of area 2 of somatosensory cortex in macaque monkeys: a correlative anatomical and electrophysiological study. *J. Comp. Neurol.* **248**, 313–335 (1986).
50. Lederman, S. J. & Klatzky, R. L. Haptic perception: a tutorial. *Atten. Percept. Psychophys.* **71**, 1439–1459 (2009).
51. Iwamura, Y., Tanaka, M., Iriki, A., Taoka, M. & Toda, T. Processing of tactile and kinesthetic signals from bilateral sides of the body in the postcentral gyrus of awake monkeys. *Behav. Brain Res.* **135**, 185–190 (2002).
52. Killackey, H. P., Gould, H. J., Cusick, C. G., Pons, T. P. & Kaas, J. H. The relation of corpus callosum connections to architectonic fields and body surface maps in sensorimotor cortex of new and old world monkeys. *J. Comp. Neurol.* **219**, 384–419 (1983).
53. Maunsell, J. H. & van Essen, D. C. The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *J. Neurosci.* **3**, 2563–2586 (1983).
54. Lewis, J. W. & Van Essen, D. C. Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. *J. Comp. Neurol.* **428**, 112–137 (2000).
55. Rozzi, S. *et al.* Cortical connections of the inferior parietal cortical convexity of the macaque monkey. *Cereb. Cortex* **16**, 1389–1417 (2006).
56. Ishida, H., Nakajima, K., Inase, M. & Murata, A. Shared mapping of own and others' bodies in visuotactile bimodal area of monkey parietal cortex. *J. Cogn. Neurosci.* **22**, 83–96 (2010).
This single-cell recording study in macaques provides the first systematic evidence of the existence in monkeys of single neurons that respond both when the monkey is being touched and when it sees someone else being touched.
57. Keysers, C. & Perrett, D. I. Demystifying social cognition: a Hebbian perspective. *Trends Cogn. Sci.* **8**, 501–507 (2004).
58. Disbrow, E., Litinas, E., Recanzone, G. H., Slutsky, D. A. & Krubitzer, L. A. Thalamocortical connections of the parietal ventral area (PV) and the second somatosensory area (S2) in macaque monkeys. *Thalamus Relat. Syst.* **1**, 289–302 (2002).
59. Eickhoff, S. B., Grefkes, C., Zilles, K. & Fink, G. R. The somatotopic organization of cytoarchitectonic areas on the human parietal operculum. *Cereb. Cortex* **17**, 1800–1811 (2007).
60. Disbrow, E., Litinas, E., Recanzone, G. H., Padberg, J. & Krubitzer, L. Cortical connections of the second somatosensory area and the parietal ventral area in macaque monkeys. *J. Comp. Neurol.* **462**, 382–399 (2003).
61. Hackett, T. A. In *Evolution of Nervous Systems* (ed. Kaas, J. H.) 109–119 (Elsevier, Oxford, 2007).
62. Mufson, E. J. & Mesulam, M. M. Insula of the old world monkey. II: Afferent cortical input and comments on the claustrum. *J. Comp. Neurol.* **212**, 23–37 (1982).
63. Brooks, J. & Tracey, I. From nociception to pain perception: imaging the spinal and supraspinal pathways. *J. Anat.* **207**, 19–33 (2005).
64. Craig, A. D. & Zhang, E. T. Retrograde analyses of spinothalamic projections in the macaque monkey: input to posterolateral thalamus. *J. Comp. Neurol.* **499**, 953–964 (2006).
65. Björnsson, M., Löken, L., Olausson, H., Vallbo, Å. & Westberg, J. Somatotopic organization of gentle touch processing in the posterior insular cortex. *J. Neurosci.* **29**, 9314–9320 (2009).
66. Augustine, J. R. Circuitry and functional aspects of the insular lobe in primates including humans. *Brain Res. Rev.* **22**, 229–244 (1996).
67. Keysers, C. *et al.* A touching sight: SII/PV activation during the observation and experience of touch. *Neuron* **42**, 335–346 (2004).
This was the first fMRI study to show that SII is active both when people experience touch and when they see other people and objects being touched.
68. Ebisch, S. J. *et al.* The sense of touch: embodied simulation in a visuotactile mirroring mechanism for observed animate or inanimate touch. *J. Cogn. Neurosci.* **20**, 1611–1623 (2008).
69. Schaefer, M., Xu, B., Flor, H. & Cohen, L. G. Effects of different viewing perspectives on somatosensory activations during observation of touch. *Hum. Brain Mapp.* **30**, 2722–2730 (2009).
70. Blakemore, S. J., Bristow, D., Bird, G., Frith, C. & Ward, J. Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. *Brain* **128**, 1571–1583 (2005).
This fMRI case study linked mirror-touch synaesthesia, — that is, the vivid experience of observed touch on one's own body — with hyperactivity during touch observation during touch observation.
71. Krubitzer, L., Clarey, J., Tweedale, R., Elston, G. & Calford, M. A redefinition of somatosensory areas in the lateral sulcus of macaque monkeys. *J. Neurosci.* **15**, 3821–3839 (1995).

72. Arnow, B. A. *et al.* Women with hypoactive sexual desire disorder compared to normal females: a functional magnetic resonance imaging study. *Neuroscience* **158**, 484–502 (2009).
73. Ferretti, A. *et al.* Dynamics of male sexual arousal: distinct components of brain activation revealed by fMRI. *Neuroimage* **26**, 1086–1096 (2005).
74. Hamann, S., Herman, R. A., Nolan, C. L. & Wallen, K. Men and women differ in amygdala response to visual sexual stimuli. *Nature Neurosci.* **7**, 411–416 (2004).
75. Bufalari, I., Aprile, T., Avenanti, A., Di Russo, F. & Aglioti, S. M. Empathy for pain and touch in the human somatosensory cortex. *Cereb. Cortex* **17**, 2553–2561 (2007).
This EEG study used the timing of somatosensory evoked potentials to show that higher stages of the somatosensory cortex are modulated by the observation of touch and pain, but BA3 is not.
76. Allison, T., McCarthy, G. & Wood, C. C. The relationship between human long-latency somatosensory evoked potentials recorded from the cortical surface and from the scalp. *Electroencephalogr. Clin. Neurophysiol.* **84**, 301–314 (1992).
77. Banissy, M. J. & Ward, J. Mirror-touch synesthesia is linked with empathy. *Nature Neurosci.* **10**, 815–816 (2007).
78. Banissy, M. J., Kadosh, R. C., Maus, G. W., Walsh, V. & Ward, J. Prevalence, characteristics and a neurocognitive model of mirror-touch synaesthesia. *Exp. Brain Res.* **198**, 261–272 (2009).
79. Freund, H. J. Somatosensory and motor disturbances in patients with parietal lobe lesions. *Adv. Neurol.* **93**, 179–193 (2003).
80. Hikosaka, O., Takanaka, M., Sakamoto, M. & Iwamura, Y. Deficits in manipulative behaviors induced by local injections of muscimol in the first somatosensory cortex of the conscious monkey. *Brain Res.* **325**, 375–380 (1985).
81. Fabbri-Destro, M. & Rizzolatti, G. Mirror neurons and mirror systems in monkeys and humans. *Physiology (Bethesda)* **23**, 171–179 (2008).
82. Rizzolatti, G., Ferrari, P. F., Rozzi, S. & Fogassi, L. The inferior parietal lobule: where action becomes perception. *Novartis Found. Symp.* **270**, 129–140 (2006).
83. Rizzolatti, G. & Sinigaglia, C. Mirror neurons and motor intentionality. *Funct. Neurol.* **22**, 205–210 (2007).
84. Rizzolatti, G. & Sinigaglia, C. The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Rev. Neurosci.* **11**, 264–274 (2010).
85. Rizzolatti, G. *et al.* Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp. Brain Res.* **71**, 491–507 (1988).
86. Evangelidou, M. N., Raos, V., Galletti, C. & Savaki, H. E. Functional imaging of the parietal cortex during action execution and observation. *Cereb. Cortex* **19**, 624–639 (2009).
87. Raos, V., Evangelidou, M. N. & Savaki, H. E. Observation of action: grasping with the mind's hand. *Neuroimage* **23**, 193–201 (2004).
88. Raos, V., Evangelidou, M. N. & Savaki, H. E. Mental simulation of action in the service of action perception. *J. Neurosci.* **27**, 12675–12683 (2007).
89. Keysers, C. & Gazzola, V. Expanding the mirror: vicarious activity for actions, emotions, and sensations. *Curr. Opin. Neurobiol.* **19**, 666–671 (2009).
90. Etzel, J. A., Gazzola, V. & Keysers, C. Testing simulation theory with cross-modal multivariate classification of fMRI data. *PLoS ONE* **3**, e3690 (2008).
Study showing how multi-voxel pattern classification can be used to examine whether the same representations are recruited during the execution of an action and the perception of other people's actions.
91. Shmuelof, L. & Zohary, E. Dissociation between ventral and dorsal fMRI activation during object and action recognition. *Neuron* **47**, 457–470 (2005).
92. Costantini, M. *et al.* Neural systems underlying observation of humanly impossible movements: an fMRI study. *Cereb. Cortex* **15**, 1761–1767 (2005).
93. Avenanti, A., Bolognini, N., Maravita, A. & Aglioti, S. M. Somatic and motor components of action simulation. *Curr. Biol.* **17**, 2129–2135 (2007).
A TMS study showing that the somatosensory and motor systems interact during the observation of extreme joint stretching.
94. Buccino, G. *et al.* Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur. J. Neurosci.* **13**, 400–404 (2001).
95. Pierno, A. C. *et al.* Neurofunctional modulation of brain regions by the observation of pointing and grasping actions. *Cereb. Cortex* **19**, 367–374 (2009).
96. Molnar-Szakacs, I., Kaplan, J., Greenfield, P. M. & Iacoboni, M. Observing complex action sequences: the role of the fronto-parietal mirror neuron system. *Neuroimage* **33**, 923–935 (2006).
97. Hasson, U., Nir, Y., Levy, I., Fuhrmann, G. & Malach, R. Intersubject synchronization of cortical activity during natural vision. *Science* **303**, 1634–1640 (2004).
By analysing the degree of synchrony among the brain activity of many viewers of the same western movie, this methodologically pioneering study shows that BA2 is active while the hand-object interactions of other people are being observed.
98. Cross, E. S., Hamilton, A. F. & Grafton, S. T. Building a motor simulation *de novo*: observation of dance by dancers. *Neuroimage* **31**, 1257–1267 (2006).
99. Haslinger, B. *et al.* Transmodal sensorimotor networks during action observation in professional pianists. *J. Cogn. Neurosci.* **17**, 282–293 (2005).
100. Calvo-Merino, B., Grezes, J., Glaser, D. E., Passingham, R. E. & Haggard, P. Seeing or doing? Influence of visual and motor familiarity in action observation. *Curr. Biol.* **16**, 1905–1910 (2006).
101. Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E. & Haggard, P. Action observation and acquired motor skills: an fMRI study with expert dancers. *Cereb. Cortex* **15**, 1243–1249 (2005).
102. Rizzolatti, G., Fabbri-Destro, M. & Cattaneo, L. Mirror neurons and their clinical relevance. *Nature Clin. Pract. Neurol.* **5**, 24–34 (2009).
103. Flanagan, J. R., Vetter, P., Johansson, R. S. & Wolpert, D. M. Prediction precedes control in motor learning. *Curr. Biol.* **13**, 146–150 (2003).
104. Miall, R. C. & Wolpert, D. M. Forward models for physiological motor control. *Neural Netw.* **9**, 1265–1279 (1996).
105. de Lussanet, M. H. *et al.* Interaction of visual hemifield and body view in biological motion perception. *Eur. J. Neurosci.* **27**, 514–522 (2008).
106. Hennenlotter, A. *et al.* A common neural basis for receptive and expressive communication of pleasant facial affect. *Neuroimage* **26**, 581–591 (2005).
107. Leslie, K. R., Johnson-Frey, S. H. & Grafton, S. T. Functional imaging of face and hand imitation: towards a motor theory of empathy. *Neuroimage* **21**, 601–607 (2004).
108. Adolphs, R., Damasio, H., Tranel, D., Cooper, G. & Damasio, A. R. A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *J. Neurosci.* **20**, 2683–2690 (2000).
109. Pitcher, D., Garrido, L., Walsh, V. & Duchaine, B. C. Transcranial magnetic stimulation disrupts the perception and embodiment of facial expressions. *J. Neurosci.* **28**, 8929–8933 (2008).
A TMS study showing that the somatosensory cortex contributes to recognizing the facial expressions of other people.
110. Desmurget, M. *et al.* Movement intention after parietal cortex stimulation in humans. *Science* **324**, 811–813 (2009).
111. Zaki, J., Weber, J., Bolger, N. & Ochsner, K. The neural bases of empathic accuracy. *Proc. Natl Acad. Sci. USA* **106**, 11382–11387 (2009).
112. Osborn, J. & Derbyshire, S. W. Pain sensation evoked by observing injury in others. *Pain* **148**, 268–274 (2010).
This combination of psychological testing and fMRI shows that a third of people literally share the pain of other people's injuries on their own bodies and links this feeling to vicarious activity in SI and/or SII.
113. Etzel, J. A., Gazzola, V. & Keysers, C. An introduction to anatomical ROI-based fMRI classification analysis. *Brain Res.* **1282**, 114–125 (2009).
114. Stoerig, P. & Cowey, A. Blindsight in man and monkey. *Brain* **120**, 535–559 (1997).
115. Haggard, P., Christakou, A. & Serino, A. Viewing the body modulates tactile receptive fields. *Exp. Brain Res.* **180**, 187–193 (2007).
116. Botvinick, M. & Cohen, J. Rubber hands 'feel' touch that eyes see. *Nature* **391**, 756 (1998).
117. Lenggenhager, B., Tadi, T., Metzinger, T. & Blanke, O. Video ergo sum: manipulating bodily self-consciousness. *Science* **317**, 1096–1099 (2007).
118. Urban, P. P. *et al.* Different short-term modulation of cortical motor output to distal and proximal upper-limb muscles during painful sensory nerve stimulation. *Muscle Nerve* **29**, 663–669 (2004).
119. Avenanti, A., Minio-Paluello, I., Bufalari, I. & Aglioti, S. M. The pain of a model in the personality of an onlooker: influence of state-reactivity and personality traits on embodied empathy for pain. *Neuroimage* **44**, 275–283 (2009).
120. Minio-Paluello, I., Avenanti, A. & Aglioti, S. M. Left hemisphere dominance in reading the sensory qualities of others' pain? *Soc. Neurosci.* **1**, 320–333 (2006).
121. Avenanti, A., Minio-Paluello, I., Bufalari, I. & Aglioti, S. M. Stimulus-driven modulation of motor-evoked potentials during observation of others' pain. *Neuroimage* **32**, 316–324 (2006).
122. Avenanti, A., Buetti, D., Galati, G. & Aglioti, S. M. Transcranial magnetic stimulation highlights the sensorimotor side of empathy for pain. *Nature Neurosci.* **8**, 955–960 (2005).

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Competing interests statement

The authors declare no competing financial interests.

FURTHER INFORMATION

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