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8 **SOMATOSENSORY PROCESSING AND BODY REPRESENTATION**  
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## ABSTRACT

Recent years have seen increasing numbers of transcranial magnetic stimulation (TMS) studies focusing on somatosensory processing. Most have focused on the primary somatosensory functions of tactile detection, localization and discrimination, and have applied TMS to primary somatosensory areas. These studies confirm the basic functions of primary somatosensory areas, and the behavioural and physiological effects of different TMS protocols. Fewer studies have investigated higher somatosensory function. Here, we review the somatosensory TMS literature both in and beyond primary somatosensory areas. We discuss the plausibility of modulating multisensory representations of one's own body via TMS, and highlight the potential for TMS to probe higher cognitive functions through the modulation of unimodal perceptual systems such as touch, vision or proprioception.

**KEY WORDS:** Transcranial magnetic stimulation; Somatosensory system; Multisensory integration; Body representation; Tactile remapping.

1 Somatosensory processing involves a broad range of cognitive functions from  
2 straightforward perception (e.g., tactile detection or discrimination) to higher order  
3  
4 cognition based on somatosensory input. However, the use of TMS (transcranial  
5 magnetic stimulation) in the study of somatosensation has been mainly concerned  
6  
7 with primary perceptual phenomena and processes (see Table 1). Higher order  
8  
9 aspects of tactile cognition have been relatively neglected. This bias reflects, in part,  
10  
11 the classical methodological problems associated with studying higher cognition, but  
12  
13 also an overall limitation in understanding more cognitive applications of TMS.  
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## 22 **1. USING TMS TO STUDY PRIMARY SOMATOSENSORY PERCEPTION**

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26 The primary somatosensory cortex (SI; see Fig. 1) has been a major anatomical target  
27  
28 of TMS studies. In some cases, these studies focus primarily on TMS methodology  
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30 and the physiology that underlies it, rather than on somatosensory function per se.  
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32 For example, the well defined somatotopic arrangement of SI makes it a suitable  
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34 model system for exploring brain mechanisms of plasticity under different protocols.  
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36 Studies such as summarised in Table 1, have confirmed that single pulse TMS applied  
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38 over SI can be used to mask tactile sensation at the skin, whereas repetitive TMS  
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40 (rTMS) has been shown to modify excitability of the human SI cortex. These basic  
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42 studies also provide unique information about the general principles that shape  
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44 sensory representation. To illustrate this, two studies assessing neuroplastic changes  
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46 in SI are briefly described in the following paragraph.  
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55 Wolters et al. (2005) used paired associative stimulation (PAS) methods of  
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57 conditioning the cortex. Thus, repeated pairings of nerve stimulation with a TMS  
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1 pulse over sensory cortex induced long lasting (up to 30 min) reversible changes on  
2 somatosensory evoked potentials (SEPs) depending on the timing of stimulation.  
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4 Thus, 30 minutes of PAS, in which TMS delivered up to 5 msec prior or  
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6 simultaneously to the subject's N20 peak, induced long-lasting increases in the P25  
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8 component amplitude in a post-TMS condition, while TMS delivered 20 msec before  
9  
10 induced long-lasting decreases. Similarly, Tegenthoff et al. (2005) showed that  
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12 applying high frequency (5Hz) repetitive TMS over the SI index finger representation  
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14 produced improvements in two-point discrimination performance that outlasted  
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16 stimulation by almost two hours. Moreover, functional MRI revealed an enlargement  
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18 of the activation pattern in the index finger representation in SI that correlated with  
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20 the perceptual improvement.  
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39 Relatively few studies have used similar TMS protocols and measures of primary  
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41 perception to explore higher-order processes within primary somatosensory areas  
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43 such as top-down modulations (Avenanti et al., 2007; Balslev et al., 2004, 2007;  
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45 Balsev and Miall, 2008; Fiorio and Haggard, 2005; Harris et al., 2002; Pourtois et al.,  
46  
47 2004). For example, Balslev et al. (2004) showed that 1 Hz rTMS over the primary  
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49 somatosensory cortex reduced proprioceptive acuity on a finger position matching  
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51 task. Interestingly, it also improved trajectory accuracy during mirror tracing,  
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53 suggesting that TMS induced weakening of proprioceptive representations,  
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55 reinforcing the role of vision in cases of visuo-proprioceptive conflict. On the other  
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1 hand, Fiorio and Haggard (2005) used the well-known phenomenon of visuo-tactile  
2 enhancement to investigate possible top-down modulations in the primary  
3 somatosensory cortices. This enhancement on tactile processing is commonly  
4 observed when participants are able to see a body part. Fiorio and Haggard (2005)  
5 found that the visuo-tactile enhancement was significantly reduced when single-pulse  
6 TMS applied over SI, but not when applied over secondary somatosensory areas.  
7 These results suggest that visual information regarding the body may be involved in  
8 the early stages of tactile stimulus elaboration and perception. More specifically, the  
9 authors suggested that the view of a body part could allow an anticipatory tuning of  
10 the primary somatosensory circuits underlying tactile acuity.  
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27 The existing work surrounding somatosensation outside of the primary somatosensory  
28 cortices has also mainly explored primary functions (Cohen et al., 1997; Merabet et  
29 al., 2004; Nager et al., 2004; Oliveri et al., 1999a, 1999b, 2000a; 2000b, 2000c, 2002;  
30 Porro et al., 2007; Ptito et al., 2008; Seyal et al., 1995; Zangaladze et al., 1999). In  
31 particular, Seyal et al. (1995) attempted to disentangle the neurophysiological  
32 correlates of extinction and, more generally, of perceptual awareness. They tested the  
33 effects of right parietal TMS on tactile perception in a group of healthy subjects  
34 carrying out a tactile detection task. Single-pulse TMS applied 50 msec prior to the  
35 delivery of the electrical stimulus increased sensitivity to ipsilateral cutaneous  
36 stimulation. These findings were interpreted as a disinhibition of the contralateral  
37 parietal cortex as a result of the transient dysfunction of the ipsilateral parietal cortex  
38 induced by TMS. More recently, and in contrast, Oliveri et al. (1999a) reported  
39 interference, instead of an increase in sensitivity, after parietal and frontal TMS. In  
40 this experiment, the authors applied single-pulse TMS over parietal and frontal scalp  
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1 sites of healthy subjects, 20 to 40 msec after receiving uni- or bimanual tactile  
2 stimulations. The results seem to confirm the existence of a hemispheric asymmetry  
3 in the representation of personal space, given that right parietal cortex, as compared  
4 with the left, was more sensitive to TMS interference. This was the case with  
5 stimulus detection for both contra- and ipsilateral stimuli (see Nager et al., 2004 for  
6 partially conflicting results). In consideration of both studies, it would seem that  
7 TMS delivered to the right parietal cortex can either increase or decrease tactile  
8 sensitivity depending on the time at which the somatosensory stimulus is delivered  
9 relative to TMS (see also Zangaladze et al., 1999 and Merabet et al., 2004 for further  
10 conflicting results using different approaches over SI and occipital areas).  
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## 34 2. USING TMS TO INVESTIGATE HIGHER SOMATOSENSORY COGNITION

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39 The preceding discussion has focussed on TMS studies of *primary* somatosensory  
40 functions of detection, localisation and discrimination that both SI and areas beyond  
41 primary cortices subserve. Several additional aspects of somatosensory function  
42 depend on more posterior areas within the parietal lobe. These secondary  
43 somatosensory functions were traditionally described as ‘integrative’ or ‘associative’,  
44 although these terms are not particularly informative. In fact, the common feature of  
45 higher somatosensory function is the multisensory integration of a single somatic  
46 percept, such as touch, pain, or proprioception, within a general representation of  
47 one’s body as a whole. The somatic senses carry information about an external  
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1 stimulus, but also information about or relevant to the body or the self. In contrast,  
2 vision and hearing carry information about external objects, but do not carry  
3 information *about* the eye, the ear, or the self to the same extent. Relatively few TMS  
4 studies have focussed on higher somatosensory function, perhaps because the tasks  
5 and measures required are more complex than for primary somatosensory studies.  
6  
7 Here, we will review three TMS studies that focus on three key integrative aspects of  
8 somatosensory function: cross-modal links between sensory stimuli (Ro et al., 2004),  
9 the internal model of one's own body (Tsakiris et al., 2008), and the capacity to track  
10 one's body positions through space as one moves (Bolognini and Maravita, 2007).  
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24 Ro et al.'s (2004) investigation began from the well-documented dominance of vision  
25 over touch. Participants were repeatedly stroked on the right hand with a soft brush,  
26 under various visual conditions. When participants gazed towards their left hand, but  
27 saw via a mirror their right, brushed hand, appearing at the location of the left hand,  
28 some apparently reported sensations on the left hand, which was never touched. This  
29 provides evidence that vision dominates over touch in this particular multisensory  
30 situation. Ro et al., also found that this conflict increased the detection of faint  
31 electrocutaneous stimuli in the left, for several minutes following brushing. This may  
32 reflect an effect of multisensory conflict on primary somatosensory function, since  
33 tactile detection may be localised to primary somatosensory cortex (Cohen et al.,  
34 1991). However, an alternative explanation could be that visual evidence of stroking,  
35 in the absence of tactile evidence, induced a response bias in the channels processing  
36 somatosensory signals. When single-pulse TMS was delivered over presumed 'area 5  
37 (see Fig. 1) and the intraparietal region' of the right parietal cortex, but not right  
38 frontal cortex, this enhancement of tactile detection was reversed, and tactile  
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1 desensitisation was found. The TMS was timed 50 msec prior to electrocutaneous  
2 stimulation. This timing is known to mask detection of electrocutaneous stimuli over  
3 sensorimotor areas (Seyal et al., 1992). However, simple masking could not explain  
4 Ro et al.'s result, because parietal TMS did not influence baseline detection rates in  
5 the absence of visual-tactile conflict. Although the somatosensory function measured  
6 here is primary (i.e., stimulus detection), the study focuses on *modulation* of this  
7 function by multisensory brain areas. Ro et al. (2004) suggest that the parietal cortex  
8 modulates the gain of primary somatosensory systems responsible for detection.  
9 Conflict situations increase somatosensory gain because of "an attempt to provide  
10 congruency between these two sensory modalities". That is, when vision suggests  
11 touch should be present, tactile gains are boosted. It is unclear, however, why this  
12 perceptual strategy is adaptive. In minor multisensory conflicts, the more reliable  
13 signal is generally given a stronger weighting, typically producing a visual dominance  
14 (Ernst and Banks 2002; but see also Van Beers et al., 2002). In contrast, in the major  
15 conflict of the present situation, total absence of any tactile signal leads both to a  
16 complete visual over-ride, but also an increased tactile gain. The visual over-ride may  
17 explain referred sensations on the untouched left hand. Reweighting to achieve fusion,  
18 and over-ride to produce illusory sensations, appear to be two quite different forms of  
19 multisensory interaction. Future TMS experiments could usefully explore whether  
20 they share a common neural basis or not. Interestingly, the gain modulation measured  
21 by Ro et al. would seem to occur rapidly and continuously, since disruption of parietal  
22 cortex influenced tactile detection at similar timings to disruption of SI. In  
23 conclusion, this study suggests that TMS can reveal the processes of cross-modal  
24 links between the senses, by disrupting intermediate level multisensory  
25 representations that integrate somatic perception.

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2 Tsakiris et al. (2008) also used TMS to study integration between vision and touch.  
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5 However, the task, target brain areas and dependent variables focussed more directly  
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7 on representing one's own body than in the case of Ro et al. (2004). They induced the  
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9 well-known 'rubber hand illusion' (RHI) by synchronously stroking a prosthetic hand  
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11 which the participant saw in front of her, and the participant's unseen left hand. This  
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13 produces a strong illusion of incorporation, that the rubber hand is in fact one's own  
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15 hand. A convenient measure of the illusion is the resulting shift in the  
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17 proprioceptively perceived position of one's own hand towards the rubber hand,  
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19 presumably due to standard mechanisms of visual-proprioceptive adaptation.  
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22 Tsakiris and Haggard (2005) showed that the illusion was stronger when viewing a  
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24 prosthetic hand being stroked than a neutral object being stroked. This result suggests  
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26 that a stored visual model of one's own body, i.e., a 'body image', is used to gate or  
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28 modulate how multisensory inputs are interpreted. Tsakiris et al. (2008) used single-  
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30 pulse TMS over the right temporo-parietal junction (rTPJ; see Fig. 1) to investigate  
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32 the process of linking current multisensory inputs to a stored body image. Direct  
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34 cortical stimulation of rTPJ induced out of body experiences (Blanke et al., 2002),  
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36 suggesting a key role of this area in linking the sense of self to the physical body.  
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39 Tsakiris et al. (2008) therefore delivered short period of synchronous visual-tactile  
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41 stroking while viewing either a left rubber hand or a neutral object (wooden spoon).  
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44 Participants reported the position of their left hand after each period of stroking by  
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46 reading a number from a ruler placed in front of them. On some trials, at random, a  
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48 single TMS pulse was delivered to the rTPJ after stroking and before hand position  
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50 judgement. The results in no-TMS trials replicated previous findings: visuo-tactile  
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52 stimulation of the rubber hand produced the proprioceptive shift characteristic of RHI,  
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1 while identical stimulation of the neutral object had no significant effect. However,  
2 TMS over rTPJ reduced the difference between the two visual conditions: weakening  
3 the RHI for the rubber hand, and significantly increasing the RHI for the neutral  
4 object. That is, disruption of the rTPJ weakened the tendency for RHI to be  
5 modulated by the visual fit between the viewed object and one's own body. Tsakiris  
6 et al. concluded that the sense of one's own body depends on two key elements. First,  
7 the brain stores a visual model of one's physical body. This may correspond to the  
8 traditional psychological 'body image', and plays an important role in self-  
9 consciousness. Second, current sensory inputs are tested for fit against the stored  
10 model: if the fit is sufficiently good, the sensations are assimilated to the self,  
11 producing a sense of ownership. Either or both of these elements of higher  
12 somatosensory function are contained in the temporo-parietal junction. The rTPJ  
13 appears to define a boundary between what is part of the body and what is not.

14 Bolognini and Maravita (2007) used repetitive TMS to investigate the dynamic  
15 updating of cross-modal links as the body moves through space. They took advantage  
16 links between visual and tactile perception: irrelevant touch on one hand briefly  
17 facilitates visual perception in the peripersonal space around that hand. In their study,  
18 spatially-localised visual phosphenes (evoked by single-pulse occipital TMS in  
19 blindfold subjects) were facilitated when occipital stimulation was preceded by a brief  
20 vibrotactile stimulus to the hand, but only when the hand was positioned in the region  
21 of space corresponding to the phosphene location. The effect of the tactile stimulus  
22 depended on the location of the stimulated hand in space, not on which hand was  
23 stimulated: crossing the hands, so that the right hand, rather than the left, was now at  
24 the phosphene location lead to right but not left vibrotactile stimuli enhancing visual

1 sensitivity. This shows that the cross-modal link between touch and vision depends  
2 on coincidence in external space, established using proprioceptive signals from the  
3 arm. However, after 20 minutes of repetitive rTMS over the posterior parietal cortex  
4 (PPC; over the presumed homologue of primate ventral intraparietal area; see Fig.1),  
5 this proprioceptive updating was reversed: now touch on the left hand facilitated  
6 detection of left hemifield phosphenes, relative to touch on the right hand, irrespective  
7 of whether the hands were in their normal positions, or crossed the midline.  
8 Crucially, PPC rTMS did not reduce sensitivity to phosphenes, nor tactile-visual  
9 facilitation per se, but only the proprioceptively-mediated spatial modulation of  
10 facilitation. From this pattern of results, Bolognini and Maravita conclude that the  
11 human intraparietal area tracks the proprioceptive position of the hands in space, and  
12 uses these signals to maintain registered multisensory links between touch and vision.  
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31 Taken as a group, these three studies suggest that higher somatosensory functions can  
32 be successfully studied with TMS, in the context of well-designed perceptual  
33 experiments. In all three cases, TMS over posterior parietal regions modulated  
34 presumed multisensory representations of one's own body. In all three cases, these  
35 body representations were studied indirectly, by their modulatory effects on unimodal  
36 perception: touch (Ro et al., 2004), proprioception (Tsakiris et al., 2008) and vision  
37 (Bolognini and Maravita, 2007). TMS is sometimes thought to be more adept for  
38 demonstrating connectivity within primary afferent and efferent pathways, than for  
39 probing higher cognitive functions. These three studies demonstrate that TMS can  
40 also identify the neural structures actively involved in higher-level somatosensory  
41 functions, and perhaps even bodily self-consciousness.  
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### 3. CONCLUSIONS

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5 TMS studies consistently show changes in primary perceptual function following  
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7 stimulation of contralateral primary cortical areas. TMS effects of this kind are  
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9 particularly valuable as an experimental model of cortical plasticity, and as a  
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11 methodological tool for studying the physiological functions of TMS itself. The  
12  
13 majority of studies have focussed on touch, but recent results suggest TMS may also  
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15 be valuable for studying proprioception. TMS studies have also contributed to  
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17 understanding of multisensory integration, both by disruption of multisensory areas  
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19 that modulate primary somatosensory function, and also by allowing controlled  
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21 manipulation of primary perceptual inputs to multisensory perception. More recently,  
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23 some cognitive studies have used TMS to investigate the internal representation of the  
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25 body that outlast specific somatic stimuli. In the future, TMS is likely to prove a  
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27 particularly valuable tool in two research areas which have proved difficult to address  
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29 using other methods. These are: understanding the physiology underlying cortical  
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31 plasticity, and understanding the neural basis of the sense of one's own body.  
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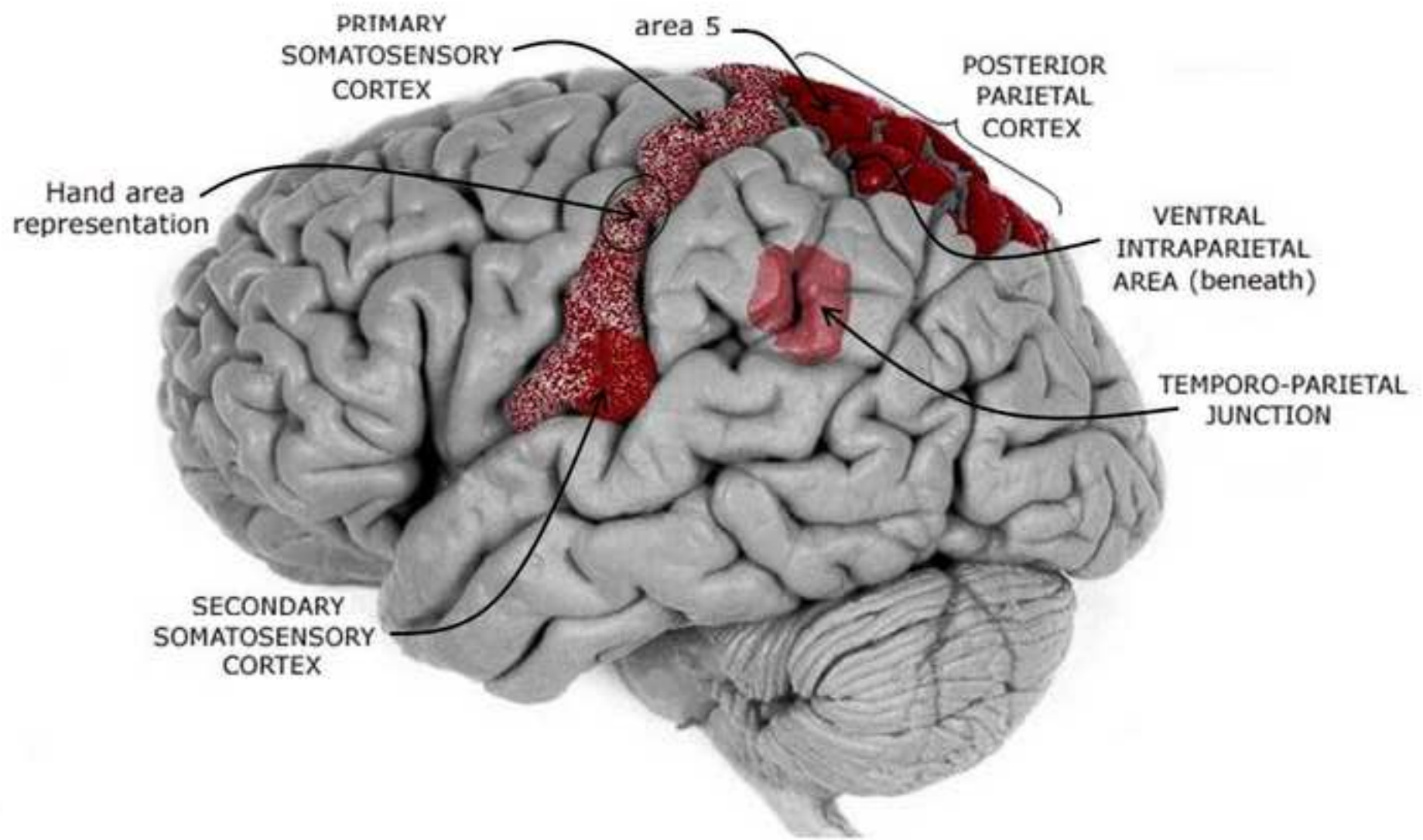
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**FIGURE LEGENDS**

Figure 1. Principal somatosensory areas stimulated in the studies described in this review.

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Figure 1  
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**Table 1.** Summary of perceptual effects observed when TMS targets the *primary somatosensory cortex* (SI).

| PROTOCOL  | EFFECTS   |
|---|---|
| <b>Single or double pulse TMS</b>                   | <ul style="list-style-type: none"> <li>▪ Attenuated tactile detection when TMS applied 20 msec after tactile stimulation (<i>Cohen et al., 1991</i>)**</li> <li>▪ Attenuated tactile detection when TMS applied 20 to 100 msec after touch - greater inhibition after 20 msec - (<i>Hannula et al., 2005</i>)</li> <li>▪ Attenuated tactile detection and localization when TMS applied 50 msec after tactile stimulation (<i>Seyal et al., 1997</i>)**</li> <li>▪ Attenuated detection of tactile trains when TMS applied 100 msec before or 20 msec after tactile stimulation (<i>McKay et al., 2003</i>)</li> <li>▪ Enhanced the attenuation of tactile detection by adding a low-frequency TMS pulse prior the suprathreshold pulse (<i>Koch et al., 2006</i>)*</li> <li>▪ Disrupted tactile intensity discrimination when TMS applied within 20 and 150 ms after touch (<i>Andre-Obadia et al., 1999</i>).</li> <li>▪ Disrupted tactile frequency discrimination when TMS applied 30 msec prior and 5 msec after the 2<sup>nd</sup> stimulus (<i>Morley et al., 2007</i>)*</li> <li>▪ Disrupted tactile frequency discrimination when TMS applied simultaneous to the first tactile stimulus (<i>Hannula et al., 2008</i>)</li> <li>▪ Disrupted tactile space discrimination and orientation when TMS applied 30 ms after touch (<i>Zangaladze et al., 1999</i>)</li> <li>▪ No apparent effect on SEP amplitude when TMS delivered 10 msec before tactile stimulation (<i>Kujirai et al., 1993</i>)**</li> <li>▪ No apparent effect on SEPs or HFOs following PAS when the ISI was 10 or 25 msec (PAS protocol; <i>Murakami et al., 2008</i>)</li> <li>▪ Modified SEP scalp map following PAS when TMS delivered 2.5 msec prior to N20 peak (PAS protocol; <i>Litvak et al., 2007</i>)</li> <li>▪ Enhanced amplitude of P25 SEP component with concurrent TMS and tactile stimulation (<i>Schürmann et al., 2001</i>)</li> <li>▪ Modified the amplitude of P25 SEP following PAS depending on the ISI. See text for details (PAS protocol; <i>Wolters et al., 2005</i>)</li> <li>▪ Slightly speeded reaction times for tactile detection when TMS pulse delivered 15–23 msec after touch (<i>Raij et al., 2008</i>)</li> </ul> |
| <b>Low Frequency rTMS (<math>\leq 1</math> Hz)</b>  | <ul style="list-style-type: none"> <li>▪ Disrupted tactile frequency discrimination with duration of impairment correlated with TMS duration (<i>Knecht et al., 2003</i>)</li> <li>▪ Disrupted roughness without affecting tactile space discrimination in sighted and blind subjects (<i>Merabet et al., 2004</i>)</li> <li>▪ No apparent effect on sensory thresholds, two-point discrimination thresholds or SEPs (<i>Satow et al., 2003</i>)</li> <li>▪ Enhanced N20p-P25 and P25-N33 SEP amplitudes for up to 15 min. TMS over MI reduced them (<i>Enomoto et al., 2001</i>)</li> <li>▪ Enhanced HFO amplitudes, but not SEPs. Lasted up to 30 min post-TMS (<i>Ogawa et al., 2004</i>)</li> <li>▪ Enhanced early HFO amplitudes and decrease later HFOs. No effect on SEPs (<i>Restuccia et al., 2007</i>)</li> </ul>   |
| <b>High Frequency rTMS (<math>\geq 5</math> Hz)</b> | <ul style="list-style-type: none"> <li>▪ Improved low-frequency discrimination associated with changes in hemodynamic signals in SI for up to 2 h (<i>Pleger et al., 2006</i>)</li> <li>▪ In combination with training improved spatial but not tactile frequency discrimination (<i>Karim et al., 2006</i>)</li> <li>▪ Improved two-point discrimination performance when combined with tactile co-activation (<i>Ragert et al., 2003</i>)</li> <li>▪ Improved two-point discrimination performance correlated with changes in hemodynamic signals in SI (<i>Tegenthoff et al., 2005</i>)</li> <li>▪ Increased cerebral blood flow in visual cortical areas in early-blind subjects (<i>Wittenberg et al., 2004</i>)</li> <li>▪ Reduced the inhibition between electrical pulses - on the N20 SEP component - for up to 1 h (<i>Ragert et al., 2004</i>)</li> <li>▪ Induced a delayed increase - starting 20 min post-TMS - of late HFO amplitudes. No effect on SEPs (<i>Restuccia et al., 2007</i>)</li> </ul>   |
| <b>Theta Burst stimulation</b>                      | <ul style="list-style-type: none"> <li>▪ Improved two-point discrimination performance and reduced the inhibition between electrical pulses (Intermittent; <i>Ragert et al., 2008</i>)</li> <li>▪ Reduced contralateral MEPs, and decreased oxy-hemoglobin in contralateral SI and MI areas (Intermittent; <i>Mochizuki et al., 2007</i>)</li> <li>▪ Attenuated P25/N33 SEP amplitudes for up to 13 min after TBS with no effect on MEPs (Continuous; <i>Ishikawa et al., 2007</i>)</li> <li>▪ Enhanced initial SEP amplitudes with maximal effect 15 min post-TBS (Intermittent; <i>Katayama et al., 2007</i>)</li> <li>▪ Attenuated amplitude of N2 (but not N1 and P2) component of laser-evoked potentials without related analgesic effects (Intermittent, continuous and intermediate; <i>Poreisz et al., 2008</i>)</li> </ul>  |

**Note:** In the first section, a single or double (\*) pulse TMS applied before or after the presentation of the test tactile stimulus. Also included in this section is the PAS (paired associative stimulation) protocol, an off-line condition of pairs of single electrical stimuli followed by TMS, applied over 30 min. In the last 3 sections, repetitive TMS applied offline, minutes before the experimental session. Theta burst stimulation is also a repetitive paradigm, but bursts of low-intensity stimuli applied in theta frequency. In the 74% of the studies the coil was placed 1 to 2 cm posterior (sometimes also laterally) to the motor hot spot. The rest moved the coil 3 or 4 cm backwards or placed it over PZ of the international 10–20 electroencephalography system (i.e. Andre-Obadia et al., 1999). The articles focusing on the sensorimotor cortex when the target was specifically the motor area (i.e. Seyal et al., 1992, 1993) are not cited, unless specific assessment of posterior brain sites was reported (as a control experiment; 3–4 subjects; Cohen et al., 1991; Kujirai et al., 1993; Seyal et al., 1997; \*\*). In the last case, only these last results are detailed. HFOs indicates high frequency oscillations; ISI, interstimulus interval; MEPs, motor evoked potentials; MI, primary motor cortex; SEPs somatosensory evoked potentials; TBS, theta burst stimulation.