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Somatosensory processing and body representation

Elena Azañón[a,b,*] *and Patrick Haggard*[c]

[a]*Departament de Psicologia Bàsica, Universitat de Barcelona, Barcelona, Spain*
[b]*Parc Científic de Barcelona, GRNC, Universitat de Barcelona, Barcelona, Spain*
[c]*Institute of Cognitive Neuroscience, University College London, UK*

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ABSTRACT

Recent years have seen increasing numbers of transcranial magnetic stimulation (TMS) studies focusing on somatosensory processing. Most have centered 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, however, 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.

Somatosensory processing involves a broad range of cognitive functions from straightforward perception (e.g., tactile detection or discrimination) to higher-order cognition based on somatosensory input. However, the use of transcranial magnetic stimulation (TMS) in the study of somatosensation has been mainly concerned with primary perceptual phenomena and processes (see Table 1). Higher-order aspects of tactile cognition have been relatively neglected. This bias reflects, in part, the classical methodological problems associated with studying higher cognition, but also an overall limitation in understanding more cognitive applications of TMS.

1. TMS and the study of primary somatosensory perception

The primary somatosensory cortex (SI; see Fig. 1) has been a major anatomical target of TMS studies. In most cases, these studies focus primarily on TMS methodology and the physiology that underlies it, rather than on somatosensory function per se. In fact, the well defined somatotopic arrangement of SI makes it a suitable model system for exploring brain mechanisms of plasticity under different protocols. Studies such as summarised in Table 1, have confirmed that single-pulse TMS applied over SI can be used to mask tactile sensation at the skin, whereas repetitive TMS (rTMS) has been shown to modify excitability of the human SI. These basic studies also provide unique information about the general principles that

* *Corresponding author*. Parc Científic de Barcelona, Hospital de Sant Joan de Déu, Edifici Docent, C/ Santa Rosa, 39-57, planta 4a, 08950 Esplugues, Barcelona, Spain.
E-mail address: eazanyon@gmail.com (E. Azañón).
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Table 1 – Summary of perceptual effects observed when TMS targets the SI.

Protocol	Effects
Single or double pulse TMS	Attenuated tactile detection when TMS applied 20 msec after tactile stimulation (Cohen et al., 1991).** Attenuated tactile detection when TMS applied 20–100 msec after touch - greater inhibition after 20 msec - (Hannula et al., 2005). Attenuated tactile detection and localization when TMS applied 50 msec after tactile stimulation (Seyal et al., 1997).** Attenuated detection of tactile trains when TMS applied 100 msec before or 20 msec after tactile stimulation (McKay et al., 2003). Enhanced the attenuation of tactile detection by adding a low-frequency TMS pulse prior the suprathreshold pulse (Koch et al., 2006).* Disrupted tactile intensity discrimination when TMS applied within 20 and 150 msec after touch (Andre-Obadia et al., 1999). Disrupted tactile frequency discrimination when TMS applied 30 msec prior and 5 msec after the 2nd stimulus (Morley et al., 2007).* Disrupted tactile frequency discrimination when TMS applied simultaneous to the first tactile stimulus (Hannula et al., 2008). Disrupted tactile space discrimination and orientation when TMS applied 30 msec after touch (Zangaladze et al., 1999). No apparent effect on SEP amplitude when TMS delivered 10 msec before tactile stimulation (Kujirai et al., 1993).** No apparent effect on SEPs or HFOs following PAS when the ISI was 10 or 25 msec (PAS protocol; Murakami et al., 2008). Modified SEP scalp map following PAS when TMS delivered 2.5 msec prior to N20 peak (PAS protocol; Litvak et al., 2007). Enhanced amplitude of P25 SEP component with concurrent TMS and tactile stimulation (Schurmann et al., 2001). Modified the amplitude of P25 SEP following PAS depending on the ISI. See text for details (PAS protocol; Wolters et al., 2005). Slightly speeded reaction times for tactile detection when TMS pulse delivered 15–23 msec after touch (Raij et al., 2008).
Low-frequency rTMS ($\leq$1 Hz)	Disrupted tactile frequency discrimination with duration of impairment correlated with TMS duration (Knecht et al., 2003). Disrupted roughness without affecting tactile space discrimination in sighted and blind subjects (Merabet et al., 2004). No apparent effect on sensory thresholds, two-point discrimination thresholds or SEPs (Satow et al., 2003). Enhanced N20p–P25 and P25–N33 SEP amplitudes for up to 15 min. TMS over MI reduced them (Enomoto et al., 2001). Enhanced HFO amplitudes, but not SEPs. Lasted up to 30 min post-TMS (Ogawa et al., 2004). Enhanced early HFO amplitudes and decrease later HFOs. No effect on SEPs (Restuccia et al., 2007).
High frequency rTMS ($\geq$5 Hz)	Improved low-frequency discrimination associated with changes in hemodynamic signals in SI for up to 2 h (Pleger et al., 2006). In combination with training improved spatial but not tactile frequency discrimination (Karim et al., 2006). Improved two-point discrimination performance when combined with tactile co-activation (Ragert et al., 2003). Improved two-point discrimination performance correlated with changes in hemodynamic signals in SI (Tegenthoff et al., 2005). Increased cerebral blood flow in visual cortical areas in early-blind subjects (Wittenberg et al., 2004). Reduced the inhibition between electrical pulses - on the N20 SEP component - for up to 1 h (Ragert et al., 2004). Induced a delayed increase - starting 20 min post-TMS - of late HFO amplitudes. No effect on SEPs (Restuccia et al., 2007).
Theta burst stimulation (TBS)	Improved two-point discrimination performance and reduced the inhibition between electrical pulses (Intermittent; Ragert et al., 2008). Reduced contralateral MEPs, and decreased oxy-hemoglobin in contralateral SI and MI areas (Intermittent; Mochizuki et al., 2007). Attenuated P25/N33 SEP amplitudes for up to 13 min after TBS with no effect on MEPs (Continuous; Ishikawa et al., 2007). Enhanced initial SEP amplitudes with maximal effect 15 min post-TBS (Intermittent; Katayama and Rothwell, 2007). Attenuated amplitude of N2 (but not N1 and P2) component of laser-evoked potentials without related analgesic effects (Intermittent, continuous and intermediate; Poreisz et al., 2008).

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 protocol, an off-line condition of pairs of single electrical stimuli followed by TMS, applied over 30 min. In the last 3 sections, rTMS applied offline, minutes before the experimental session. TBS 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 1–2 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 indicate high frequency oscillations; ISI, interstimulus interval; MEPs, motor evoked potentials; MI, primary motor cortex.