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TMS and the functional neuroanatomy of attention

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Abstract

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4 Recent years have witnessed the increasing application of TMS to study the cognitive
5 neuroscience of attention. As a non-invasive method of stimulating discrete cortical regions,
6 this technique has provided new insights into the neural substrates of selection and their
7 temporal dynamics. Key aims and discoveries have included identifying which regions in the
8 frontal and parietal cortex are critical for gating sensory processing, what their timecourse can
9 tell us about the neural networks that support feedforward and feedback processing, and how
10 attentional links are coordinated and maintained between the different senses. Key future
11 challenges will be to understand the relationship between attentional systems and recently
12 documented 'state-dependent' effects of TMS, as well as the integration of TMS and
13 neuroimaging methods to directly illustrate coupling between 'top-down' control regions and
14 their sensory targets.
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1 Coordinated behaviour depends on *selective attention*: the ability to select a limited subset of
2 stimuli for detailed analysis, while suppressing the stream of irrelevant information
3 continuously received by our senses. Over the past three decades, converging evidence from
4 neurophysiology, neuropsychology, and cognitive neuroscience has suggested that selection
5 modulates brain activity at sensory cortical levels (Desimone and Duncan, 1995; Kastner and
6 Ungerleider, 2000; Saalman et al., 2007)}, and that potential sources of control are distributed
7 across a frontoparietal network of brain regions (Corbetta and Shulman, 2002; Corbetta et al.,
8 2008). More recently, TMS studies have provided insights into the functional neuroanatomy
9 of selective processes, revealing not only *which* areas of the healthy human brain are *crucial*
10 for attention, but also *when* they are engaged during the timecourse of information processing.
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20 **1. The Attentional Network: Crucial Regions, Functional Dissociations, and Timing**

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23 What can temporary interruption of brain activity tell us about the neural basis of attention?
24 As might be expected from neuroimaging (Corbetta and Shulman, 2002), neurophysiology
25 (Moore et al., 2003; Saalman et al., 2007) and neuropsychology (Driver and Mattingley,
26 1998), TMS has consistently corroborated the involvement of the posterior parietal cortex
27 (PPC) and frontal eye field (FEF) in visuospatial selection (e.g. Pascual-Leone et al., 1994;
28 Smith et al., 2005; Hilgetag et al., 2001; Grosbras and Paus, 2002). For example, 10 minutes
29 of repetitive slow-rate (1-Hz) TMS over the right PPC has been shown to temporarily mimic
30 the effects of parietal brain damage, inducing a rightward (ipsilesional) bias in spatial
31 attention (Hilgetag et al., 2001).
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41 In addition to confirming evidence from neuroimaging and lesion studies, a complimentary
42 strength of TMS lies in its capacity to reveal previously unseen functional dissociations
43 within and between cortical sub-regions. For instance, TMS evidence suggests that the right
44 angular gyrus (AG) – but not supramarginal gyrus (SMG) – is necessary for reorienting
45 attention covertly between stimuli in opposite visual fields (Chambers et al., 2004a;
46 Rushworth et al., 2001); whereas the right SMG – but not AG – appears to be crucial for
47 deploying attention strategically between the fovea and periphery (Chambers et al., 2004b;
48 Schenkluhn et al., in press). Recent TMS studies of the FEF have also distinguished
49 mechanisms of covert spatial attention from those that mediate saccade planning (Juan et al.,
50 in press; see also (Juan et al., 2004), thus providing a unique test of the ‘premotor’ theory of
51 attention (Rizzolatti et al., 1987; Corbetta et al., 1998).
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1 In a similar vein, we have previously applied parietal TMS to test whether multisensory links
2 in spatial attention are mediated by a supramodal system, or instead by distinct modality-
3 specific mechanisms. Neuroimaging studies have generally described a predominance of
4 common activity in frontal, parietal and temporal regions during spatial selection in different
5 sensory modalities (e.g. Eimer and van Velzen, 2002; Macaluso et al., 2002), suggesting that
6 attention may be mediated by a supramodal system. In contrast, our TMS studies have
7 suggested that some parietal activity can be *critical* for covert spatial orienting in vision but
8 not in touch, thus providing evidence of modality-specific attentional control (Chambers et
9 al., 2004b; Chambers et al., 2007).

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12 In addition to revealing which cortical areas are crucial for attention, the temporal resolution
13 of TMS has provided a novel perspective on how selection unfolds over time. Across the
14 frontoparietal network, the timecourse of critical involvement varies substantially, ranging
15 from very early effects in the FEF (e.g. 40-80ms post-stimulus onset, O'Shea et al., 2004) to
16 later effects in the parietal cortex (e.g. 270-370ms, Müri et al., 2002). Some regions, such as
17 the right AG, appear to be required for visuospatial orienting during multiple time periods
18 (90-120 and 210-240ms), suggesting that distinct feedforward and/or feedback stages may be
19 vital for controlling visual attention (Chambers et al., 2004a). In this regard, it is noteworthy
20 that attentional processing in the FEF can occur prior to initial processing in the primary
21 visual cortex (~60-100ms; e.g. Romei et al., 2007; Kammer, 2007), suggesting that
22 frontoparietal systems may participate in feedback processes that tune neural response
23 properties of the visual cortex in advance of afferent geniculostriate input.

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26 Evidence of multiple attentional phases in the frontoparietal cortex accords with TMS studies
27 demonstrating at least two periods of processing in the visual cortex (Corthout et al., 1999;
28 Heinen et al., 2005; Laycock et al., 2007), with later stages representing recurrent processing
29 that is likely to be necessary for attention and awareness (Ro et al., 2003; and see Ro, this
30 issue, for review). Indeed, recent work has confirmed that attention directly modulates the
31 excitability of the human visual cortex, as measured through the induction of phosphenes
32 (Bestmann et al., 2007). Furthermore, through the simultaneous combination of TMS-EEG
33 (Taylor et al., 2007; Fuggetta et al., 2006), TMS-fMRI (Blankenburg et al., in press; Ruff et
34 al., 2006; Ruff et al., 2007), and double-coil TMS (Silvanto et al., 2006; Silvanto et al., in
35 press), key sources of modulation have been identified in the PPC and FEF, providing the first

1 direct evidence in humans of a link between top-down control regions and sensory target
2 areas.
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5 **2. Future Directions and Challenges**

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9 Most TMS studies of attention assume that TMS causes a ‘virtual lesion’, interrupting time-
10 critical processing and impairing behaviour (e.g. Chambers et al., 2004a; Rushworth et al.,
11 2001). Recent emphasis in the literature, however, has challenged the utility of this approach.
12 In a series of studies, Silvanto and colleagues have shown that the behavioural effect of TMS
13 depends on the initial activation state of the stimulated cortex (Silvanto and Muggleton,
14 2008a, b; Silvanto et al., 2008; Cattaneo and Silvanto, in press). Whereas TMS interferes with
15 behaviour when a stimulated area is in an activated state, the same stimulation protocol can
16 *enhance* behaviour when activity in the stimulated region is suppressed (Silvanto et al., 2008).
17 This relationship has similarly been observed in measures of cortical excitability: using
18 concurrent TMS-EEG, Romei et al. (2008a, 2008b) have established that lower baseline
19 activity in the α -band, and reduced α -power, increases the likelihood of phosphene induction
20 during occipital TMS. These observations occur in the context of a substantial literature
21 demonstrating that visual cortical excitability can be influenced by a variety of pre-conditions,
22 including sub-threshold sensory stimulation (Ramos-Estebanez et al., 2007), stimulus contrast
23 (Rauschecker et al., 2004), mental imagery (Sparing et al., 2002), and a prior train of
24 repetitive TMS (Borojerdj et al., 2000).
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40 The state-dependence of TMS-induced effects is likely to be a key factor in future studies
41 because attentional conditions also modulate brain activity and may therefore interact
42 differently with TMS (e.g. Bestmann et al., 2007). Activity in the parietal cortex can depend
43 on the directionality of spatial attention shifts (Kelley et al., 2008), and can also be depressed
44 when actively filtering irrelevant information (Shulman et al., 2007; and see also Singh and
45 Fawcett, 2008). These observations highlight the importance of considering how TMS might
46 interact with baseline excitability during attentional states and affect subsequent processing.
47 For instance, might the pre-existing activation state explain why TMS sometimes has
48 facilitatory, rather than disruptive, effects on attention? (Chambers et al., 2006; Seyal et al.,
49 1995; Hilgetag et al., 2001; Thut et al., 2005) One approach to answering this question is
50 through the combination of TMS with methods that are able to monitor ongoing activity, such
51 as fMRI (Bestmann et al., 2004; Ruff et al., 2006; Sack et al., 2007) and EEG (Fuggetta et al.,
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2006; Taylor et al., 2007). In fact, understanding the interaction of TMS and neural states under specific attentional conditions should open a promising future avenue for manipulating latent cortical activity and the subsequent consequences of TMS, either behaviourally (e.g. Cattaneo and Silvanto, in press; Silvanto and Muggleton, 2008b) or through offline repetitive TMS (Silvanto et al., 2008).

More generally, the simultaneous combination of TMS and neuroimaging has the potential to test for definitive links between sources of control in frontoparietal cortex and targets of selection in the sensory cortex. One key question is whether top-down connections are in fact crucial for attentional control, or whether attentional competition can be exclusively resolved higher within the system, for instance within frontoparietal salience maps (Colby and Goldberg, 1999). Furthermore, integrating TMS and neuroimaging will be essential to establish remote effects of TMS stimulation that are not immediately anticipated, and which remain unseen when applying TMS alone.

Overall, TMS studies are providing a fresh perspective on the cognitive neuroscience of attentional control, complementing evidence obtained from neuroimaging, neurophysiology and neuropsychology. Key future challenges will include the combination of TMS with imaging modalities, as well as further development of double-coil protocols (e.g. Silvanto et al., in press; Pascual-Leone and Walsh, 2001). These developments have the potential to uncover differential effects of TMS according to pre-existing activity states, and to test hypotheses concerning functional connectivity and feedback mechanisms in frontoparietal and sensory networks.

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