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Parietal theta burst TMS: Functional fractionation observed during bistable perception not evident in attention tasks

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ABSTRACT

When visual input is ambiguous, perception spontaneously alternates between interpretations: bistable perception. Studies have identified two distinct sites near the right intraparietal sulcus where inhibitory transcranial magnetic stimulation (TMS) affects the frequency of occurrence of these alternations, but strikingly with opposite directions of effect for the two sites. Lesion and TMS studies on spatial and sustained attention have also indicated a parcellation of right parietal cortex, into areas serving distinct attentional functions. We used the exact TMS procedure previously employed to affect bistable perception, yet measured its effect on spatial and sustained attention tasks. Although there was a trend for TMS to affect performance, trends were consistently similar for both parietal sites, with no indication of opposite effects. We interpret this as signifying that the previously observed parietal fractionation of function regarding the perception of ambiguous stimuli is not due to TMS-induced modification of spatial or sustained attention.
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1. Introduction

The functional role of the right parietal cortex in consciousness has long been subject to debate (Brascamp, Blake, & Knapen, 2015; Kleinschmidt, Büchel, Zeki, & Frackowiak, 1998; Knapen, Brascamp, Pearson, van Ee, & Blake, 2011; Lumer, Friston, & Rees, 1998; Rees, Kreiman, & Koch, 2002; Watanabe, Masuda, Megumi, Kanai, & Rees, 2014; Weilnhammer, Ludwig, Hesselmann, & Sterzer, 2013). A recent contribution to this debate has come from several studies that combined transcranial magnetic stimulation (TMS) with bistable perception paradigms (Carmel, Walsh, Lavie, & Rees, 2010; Kanai, Bahrami, & Rees, 2010; Kanai, Carmel, Bahrami, & Rees, 2011; Wood, Schauer, Bak, & Carmel, in preparation; Zaretskaya, Anstis, & Bartels, 2013; Zaretskaya, Thielscher, Logothetis, & Bartels, 2010). In these paradigms, participants view a stimulus that is ambiguous or internally conflicting, leading to periodic fluctuations in the conscious perception of that stimulus over time, even though the stimulus is unchanging. In the present work we focus on one particular set of findings from recent studies that used inhibitory TMS. First, Carmel et al. (2010) and Kanai et al. (2011) used inhibitory TMS to the right anterior

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superior parietal lobule (ant-SPLr) at coordinates previously indicated in a neuroimaging study on bistable perception (Lumer et al., 1998) and found that perception fluctuated more frequently as a result. In other words, inhibitory TMS to this location appeared to destabilise the percept. Interestingly, inhibitory TMS on a more posterior portion of the right superior parietal lobule (post-SPLr), identified based on across-participant correlations between anatomy and perception of ambiguous stimuli, had the opposite effect of reducing the rate of switching between perceptual interpretations (Kanai et al., 2010).

One proposed interpretation of this functional fractionation of the right parietal cortex is that the ant-SPLr is associated with top-down predictions of oncoming sensory stimulation, while post-SPLr processes the error signals that arise from comparing these predictions to actual input (Kanai et al., 2011). In the current paper we test an alternative interpretation. Specifically, the perceptual switch rate during bistable perception is known to be influenced by the allocation of attention to the ambiguous stimulus (Alais, van Boxtel, Parker, & van Ee, 2010; Paffen, Alais, & Verstraten, 2006; Pastukhov & Braun, 2007), and numerous reports show parietal impairment to be associated with altered attention function (e.g. Hilgetag, Théoret, & Pascual-Leone, 2001; Hodsoll, Mevorach, & Humphreys, 2009; Malhotra, Coulthard, & Husain, 2009; Rueckert & Grafman, 1998; Rushworth & Taylor, 2006; Thut et al., 2005). This raises the question of whether TMS-induced alterations in attention allocation could explain the observed effects of parietal TMS on bistable perception. Under this account, the altered switch rate may result from inhibition of brain areas essential for maintaining attention, potentially leading to shorter percept durations, and for producing attentional shifts, potentially leading to longer percept durations. The functional fractionation of the right parietal cortex during bistable perception could hence represent a parcellation into separate attention modules rather than regions that can specifically be associated with prediction and error signal processing.

Aside from the known effect of attention allocation on bistable perception, other evidence also lends credence to this alternative account. Independent of the above mentioned work on bistable perception, a functional parcellation of right parietal cortex is suggested by work that shows superior regions to be associated with attentional shifts and spatial attention (Müller-Plath, Ott, & Pollmann, 2010; Vandenberghe & Gillebert, 2009; Yantis et al., 2002), and work that implicates more inferior regions in sustained attention and non-spatial tasks (Husain & Rorden, 2003; Kelley, Serences, Giesbrecht, & Yantis, 2007; Malhotra et al., 2009; Pardo, Fox, & Raichle, 1991; review in Vandenberghe, Molenberghs, & Gillebert, 2012); a separation that is approximately consistent with the distinction between the more superior ant-SPLr and the more inferior post-SPLr. Support for this model has primarily come from lesion studies on neglect and sustained attention summarised below.

A common attention deficit associated with right parietal lesions is left hemispatial neglect, which is a disorder characterised by a lateralised visual information processing bias, which is not due to abnormal early sensory perception, but rather comes from an inability to attribute saliency to stimuli within the contralesional visual field, or to take notice of information in the affected sensory space (Mesulam, 1981, 1985). While damage to either hemisphere can lead to neglect of contralesional space (Heilman, Watson, Valenstein, & Damasio, 1983), the effect is materially stronger for right-parietal lesions (Critchley, 1953; Heilman & Van Den Abell, 1980), causing more severe and long-lasting deficits (Stone, Halligan, & Greenwood, 1993). For instance, patients have trouble in eating from the left side of their plates or reading a clock when its hands are on its left half as if their attention is permanently shifted away from the left and almost "magnetically attracted" to the right side of their visual field (Gainotti, D'Erme, & Bartolomeo, 1991).

Several studies have transiently elicited spatial attention effects that resemble neglect, by applying TMS to the right parietal cortex of healthy participants (e.g. Bjoertomt, Cowey, & Walsh, 2002; Fierro et al., 2000; Hilgetag et al., 2001). With regard to our current question considering a potential role of attention in mediating the effect of TMS on bistable perception, it is relevant to ask whether the induction of these spatial attention effects is dependent on the exact location of parietal stimulation. In particular, what is the effect of inhibitory TMS on lateralised spatial attention specifically at the parietal loci indicated by stimulation studies on bistable perception (Carmel et al., 2010; Kanai et al., 2010)? The existing literature is agnostic towards whether the precise localisation of the TMS site will yield a different result, in part because the relevant studies on lateralised spatial attention, being somewhat older, selected their stimulation sites based on EEG electrode positions (Fierro et al., 2000; Hilgetag et al., 2001) and functional tests (Bjoertomt et al., 2002), whereas the more recent studies on bistable perception characterised their stimulation sites in terms of standard brain coordinates, using neuronavigation based on participants' individual MRI scans (Carmel et al., 2010; Kanai et al., 2010, 2011). Reliably translating between these various localisation methods is not straightforward (Rushworth, Ellison, & Walsh, 2001; Rushworth & Taylor, 2006; Sack et al., 2009), making it difficult to assert whether the test sites in the previous literature on lateralised spatial attention overlap with the precise test sites in the literature on bistable perception.

A second attentional function in which we were interested because of proven links to right parietal cortex and, moreover, a plausible relation to the bistable perception findings, was sustained attention, or vigilance (e.g. Adler et al., 2001; Malhotra et al., 2009; Rueckert & Grafman, 1998; Sarter, Givens, & Bruno, 2001; Whyte, Polansky, Fleming, Coslett, & Cavallucci, 1995). This refers to the ability to maintain good performance on tasks requiring attention over prolonged periods of time. A relation to the bistable perception findings is conceivable in the sense that the perceptual switch rate is known to depend on the amount of attention paid to the stimulus inducing bistable perception (Alais et al., 2010; Paffen et al., 2006; Pastukhov & Braun, 2007), so that any TMS-induced change in this amount could lead to altered switch rates. Several studies link sustained attention to right parietal cortex, but evidence does not consistently point to any specific subregion (Malhotra et al., 2009; Serences & Yantis, 2007; Thakral & Slotnick, 2009).

In the current study, we asked whether the fractionation of parietal cortex in the conscious perception of bistable stimuli reflects a fractionation in function pertaining to spatial and sustained attention. Existing studies do not allow this assertion,

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