COGNITIVE NEUROSCIENCE

Causal implication by rhythmic transcranial magnetic stimulation of alpha frequency in feature-based local vs. global attention

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Abstract

Although oscillatory activity in the alpha band was traditionally associated with lack of alertness, more recent work has linked it to specific cognitive functions, including visual attention. The emerging method of rhythmic transcranial magnetic stimulation (TMS) allows causal interventional tests for the online impact on performance of TMS administered in short bursts at a particular frequency. TMS bursts at 10 Hz have recently been shown to have an impact on spatial visual attention, but any role in featural attention remains unclear. Here we used rhythmic TMS at 10 Hz to assess the impact on attending to global or local components of a hierarchical Navon-like stimulus (D. Navon (1977) Forest before trees: The precedence of global features in visual perception. *Cognit. Psychol.*, **9**, 353), in a paradigm recently used with TMS at other frequencies (V. Romei, J. Driver, P.G. Schyns & G. Thut. (2011) Rhythmic TMS over parietal cortex links distinct brain frequencies to global versus local visual processing. *Curr. Biol.*, **2**, 334–337). In separate groups, left or right posterior parietal sites were stimulated at 10 Hz just before presentation of the hierarchical stimulus. Participants had to identify either the local or global component in separate blocks. Right parietal 10 Hz stimulation (vs. sham) significantly impaired global processing without affecting local processing, while left parietal 10 Hz stimulation vs. sham impaired local processing with a minor trend to enhance global processing. These 10 Hz outcomes differed significantly from stimulation at other frequencies (i.e. 5 or 20 Hz) over the same site in other recent work with the same paradigm. These dissociations confirm differential roles of the two hemispheres in local vs. global processing, and reveal a frequency-specific role for stimulation in the alpha band for regulating feature-based visual attention.

Introduction

Alpha oscillatory activity (~8–12 Hz) was traditionally associated with lack of alertness, but recent studies link it to functions such as working memory load (Sauseng *et al.*, 2009), visual awareness (Romei *et al.*, 2008a,b; Mathewson *et al.*, 2009; Dugué *et al.*, 2011), spatial attention (Worden *et al.*, 2000; Sauseng *et al.*, 2005; Thut *et al.*, 2006; Capotosto *et al.*, 2009; Romei *et al.*, 2010) and featural attention (Volberg *et al.*, 2009; Snyder & Foxe, 2010). Typically such studies have been essentially correlative in nature, e.g. relating alpha power to condition, or to performance, rather than manipulating alpha activity itself. Brain stimulation at specific frequencies may provide a more causal (i.e. interventional) approach to studying the role of particular frequency bands at particular sites, as with rhythmic transcranial magnetic stimulation (TMS; Klimesch *et al.*, 2003; Thut & Miniussi, 2009; Sauseng *et al.*, 2009; Romei *et al.*, 2010, 2011) or transcranial alternating current stimulation (Pogosyan *et al.*, 2009; Kanai *et al.*, 2010; Feurra *et al.*, 2011a,b). Online combination of such methods

with electroencephalography (EEG; Zaehle *et al.*, 2010; Thut *et al.*, 2011a) provides emerging evidence that rhythmic brain stimulation can be used to target corresponding brain oscillations in a frequency-specific manner (Thut *et al.*, 2011b).

In a recent study illustrating the rhythmic TMS approach, Romei *et al.* (2010) showed that short bursts of rhythmic TMS at 10 Hz alpha (but not at 5 Hz theta or 20 Hz beta frequencies) over left and right occipital or parietal areas, prior to lateralized visual stimuli, selectively impaired visual detection contralateral to the stimulated hemisphere while enhancing detection ipsilaterally. This indicates a causal role for alpha in visual spatial attention, in accord with correlative evidence from EEG (Worden *et al.*, 2000; Sauseng *et al.*, 2005; Thut *et al.*, 2006; Capotosto *et al.*, 2009). Here we tested whether a 10 Hz burst of TMS may also have a causal influence on featural visual attention to global vs. local levels of a hierarchical stimulus (Navon, 1977; Mevorach *et al.*, 2006a; Romei *et al.*, 2011).

EEG data already suggest that pre-stimulus alpha oscillations may play a role in feature-based selection (Snyder & Foxe, 2010), as during global vs. local visual processing (Volberg *et al.*, 2009; Flevaris *et al.*, 2011). Some previous TMS studies have contrasted the impact of left vs. right parietal TMS on local vs. global processing (e.g. Mevorach

et al., 2006a), but no study has applied short rhythmic bursts of 10 Hz TMS, analogous to the Romei *et al.* (2010) spatial attention study, during a local vs. global task. Here we implemented this, using the same local vs. global paradigm recently examined with 5 and 20 Hz bursts of TMS (Romei *et al.*, 2011), so that any frequency specificity of the results could be ascertained.

Materials and methods

Participants

Thirty healthy volunteers (mean age 25.13, range 19–36 years; 15 females) were randomly assigned to either of two stimulation sites (left parietal: mean age 25.87, range 21–37 years, seven females; right parietal: 24.4, range 19–35 years, eight females; 15 volunteers per site). Results from 11 of these participants have already been reported in a previous study (see supplemental information p. 3 and supplemental figure 2b in Romei *et al.*, 2011) while an additional 19 participants were recorded for the present study (*n* = 4 for right hemisphere and *n* = 15 for the left hemisphere). All gave written informed consent in accord with local ethical approval and were right-handed by self-report. The study was conducted in accord with the Declaration of Helsinki.

Visual stimuli and task

The visual stimuli and task represent a modified version of Navon hierarchical letters (Navon, 1977), which have been widely used in previous experiments (see e.g. Mevorach *et al.*, 2006a; Romei *et al.*, 2011); see Fig 1. As in Romei *et al.* (2011), stimuli were presented on a 17-inch monitor with 85 Hz refresh rate on a black background at viewing distance of ∼60 cm. A white central dot indicated fixation for 1.5 s; this was followed by 200 ms of blank screen before visual stimulus presentation.

The stimuli comprised blurred or nonblurred displays to manipulate which level, local or global, was more salient (Mevorach *et al.*, 2006a; Romei *et al.*, 2011). For the nonblurred displays with relatively high local saliency, the Navon stimuli were created from orthogonal combinations of the letters H or S at the global level, and multiple Hs or Ss at the local levels, with the letters in the local dimension alternating between red and white. For the blurred displays with relatively high global saliency, the Navon stimuli were created from orthogonal combinations of H and D, but now all local letters were red and underwent a blurring procedure. For further stimulus details, see Romei *et al.* (2011).

Also as in Romei *et al.* (2011), participants had to detect the presence of a target H, or its absence (S or D instead), at either the local or global level while ignoring the other level (which could be congruent or incongruent in terms of letter identity). The relevant level was fixed for a block of trials, with local and global blocks in random order. Participants responded on a two-choice button box with their right index finger for target presence and right middle finger for target absence.

Experimental procedure

Exactly as in Romei *et al.* (2011), short bursts of rhythmic TMS were applied (see Fig. 1). The key difference was that rhythmic TMS was now administered at 10 Hz on each trial. There were five pulses per trial, with the final pulse coinciding with onset of the global or local
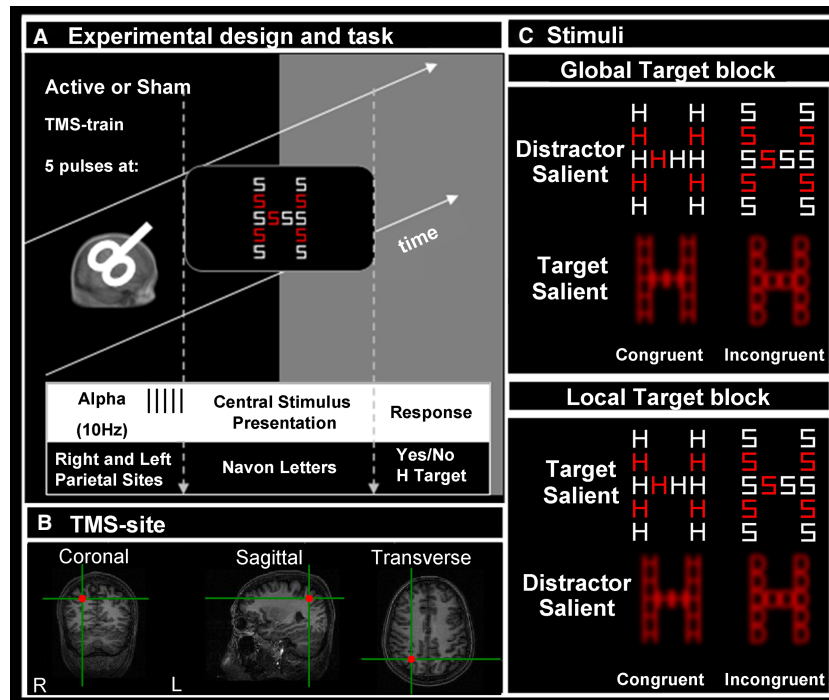

FIG. 1. (A) Experimental design and task. Rhythmic TMS was applied in short bursts of five pulses at alpha frequency (10 Hz) on each trial, with 10 s intervening between successive bursts. Onset of a global or local hierarchical visual stimulus, centered at fixation, coincided with the last TMS pulse of each burst. A sham TMS condition was also conducted (coil tilted at 90° over the same parietal site), in separate blocks randomly intermingled with active TMS blocks. (B) Stimulation site for one representative participant. TMS was applied over a right or left intraparietal sulcus site, determined by neuronavigation with Brainsight and individual anatomical MRI scans, at Tailarach coordinates 28, −51, 50 or −28, −51, 50. (C) Example stimuli. In the global target blocks, observers were asked to detect the presence (vs. absence) of the global letter H (vs. S or D). The local distractors were all Hs, or all Ss or Ds, independent of global identity, leading to equiprobable congruent and incongruent conditions. For blurred stimuli, the global letter was more salient than the local letters; the reverse was true for nonblurred stimuli. In other blocks of trials the same stimuli were used, but the local level was judged instead.

hierarchical letter stimulus (see Fig. 1). Trials, and thus TMS bursts, were separated by 10 s. The experiment comprised six blocks per condition, for active or sham TMS, in separate blocks of 32 trials (≈6–7 min per block), with a total of 960 active TMS pulses (plus 960 sham pulses). The comparison of real to sham TMS is essential for subtracting out any nonspecific effects associated with TMS presentation, such as the click sound etc. (see e.g. Pascual-Leone *et al.*, 1996; Kosslyn *et al.*, 1999; Klimesch *et al.*, 2003; Sauseng *et al.*, 2009; Romei *et al.*, 2010, 2011).

Rhythmic TMS stimulation

Rhythmic TMS was applied at a fixed intensity level of 60% of maximum stimulator output (MSO) using a Magstim Rapid2 Transcranial Magnetic Stimulator via a 70-mm figure-of-eight coil (Magstim Company). We decided to use this fixed intensity of stimulation rather than a tailored intensity for the following reasons: our rationale was to adopt the same procedure as in Romei *et al.* (2011) but also Mevorach *et al.* (2006a). This fixed intensity has been chosen in the past because it roughly corresponds to phosphene thresholds (PT) reported in several studies carried out by us [Romei *et al.*, 2007 (PT = 59.8% MSO); Romei *et al.*, 2008b (PT = 60.73% MSO); Romei *et al.*, 2009 (PT = 64.81% MSO)] and other groups [c.f. Gerwig *et al.*, 2003 (PT = 60.1% MSO); Bestmann *et al.*, 2007 (51.6% and 55.6% MSO); Bolognini *et al.*, 2010 (PT = 64% MSO); etc]. It might be argued that differences in visual cortex excitability might be present between hemispheres across participants, and that intensity should be tailored to each hemisphere separately instead of being fixed. However, previous reports as to hemispheric differences in visual cortex excitability are not consistent (e.g. no systematic differences between left and right PT in Bestmann *et al.*, 2007; Cattaneo *et al.*, 2009; Silvanto *et al.*, 2009). Moreover, as we found different effects in the two hemispheres (see below), rather than TMS of one hemisphere being effective and the other not, it seems unlikely that results may have been biased by differences in effective TMS stimulation intensity.

In a between-participants design, the TMS coil was placed at right or left posterior parietal sites over the intraparietal sulcus (IPS; Talairach coordinates: right IPS 28, −51, 50; left IPS: −28, −51, 50). These sites have previously been shown with fMRI to be coactivated across several attention tasks, including feature-based visual attention (Wojciulik & Kanwisher, 1999). Importantly, these are the same sites as used by Romei *et al.* (2011) with 5 or 20 Hz TMS instead in the same paradigm. We neuronavigated the TMS coil to these target sites in each individual via Brainsight (Rogue Research) in combination with individual structural MRI scans. Coil position for active and sham TMS was identical to that used in Romei *et al.* (2011). The TMS design is in line with current safety guidelines (Rossi *et al.*, 2009).

Note that, in accordance with previous studies also stimulating parietal cortex at around PT (Romei *et al.*, 2010, 2011; Thut *et al.*, 2011a), none of our participants reported seeing phosphenes (PT is determined with TMS over occipital cortex).

Data analysis

As instructions emphasized both speed and accuracy of response, we adopted a widely used score (e.g. Townsend & Ashby, 1983; Kennett *et al.*, 2001; Mevorach *et al.*, 2006a) known as inverse efficiency (IE; reaction time divided by proportion correct) as our main dependent measure (exactly as in Mevorach *et al.*, 2006a; Romei *et al.*, 2011). Sham stimulation served as a reference measure (baseline) subtracted from the corresponding active TMS stimulation condition. We

subjected data to a four-way, mixed, repeated-measures ANOVA, having within-participant factors of Level (global vs. local), Incongruency (incongruent vs. congruent displays), and Distractor Saliency (distractor salient vs. target salient) plus the between-participants factor of Hemisphere of Stimulation (right vs. left parietal). For completeness, the same analysis was carried out separately for error rates and reaction times.

Results

We first ran a four-way mixed ANOVA on the sham IE data alone, this representing our reference measure (baseline). This analysis showed the expected impacts of Level, Incongruency and Saliency (see Mevorach *et al.*, 2006a; Romei *et al.*, 2011), but no significant interactions involving Hemisphere. Performance was better overall in the global than local task (IE of 620 vs. 685, $F_{1,28} = 28.94$; $P < 0.00001$), in the congruent vs. incongruent conditions (608 vs. 696, $F_{1,28} = 50.57$; $P < 0.000001$), and with target rather than distractor salient (627 vs. 677, $F_{1,26} = 22.58$; <0.0001), all as expected. The mean IE scores for the sham conditions appear in gray in Fig. 2 (which also shows the active TMS conditions, in black). There were no significant interactions involving Hemisphere of stimulation for the sham data, but there was a marginal tendency for better performance with global processing vs. local when sham TMS clicks were delivered over the right (591 vs. 691 mean IE respectively) but not left (649 vs. 678) hemisphere; (interaction: Level × Hemisphere of Stimulation $F_{1,28} = 3.20$, $P = 0.08$). Importantly, this performance pattern during 10 Hz sham stimulation was not significantly different from the performance pattern of other groups undergoing 5 or 20 Hz sham stimulation instead, but at the same sites in exactly the same paradigm (data from Romei *et al.*, 2011). An ANOVA over all groups showed a non-significant 3-way interaction term of Level × Hemisphere of Stimulation × Frequency of Stimulation ($F_{2,44} = 2.08$, $P = 0.14$). This indicates that the above-reported tendency for hemisphere effects in the sham data can be assigned to nonspecific TMS effects, probably brought about by the unavoidable lateralized TMS clicks. As already observed in previous reports (e.g. Romei *et al.*, 2007, 2010, 2011), this underlines the importance of sham-controlling the active TMS data (Pascual-Leone *et al.*, 1996; Kosslyn *et al.*, 1999), in order to parcel out any residual nonspecific effects induced by TMS clicks being heard on one side or the other.

Another way to control for the nonspecific effect found in sham (but also active) stimulation might be to compare TMS stimulation in its active and sham conditions with the same behavioural condition while TMS is not administered at all. Unfortunately we did not collect data in the total absence of TMS stimulation; we thus lack a true baseline to which active and sham stimulation can be compared. For future studies, it would be worthwhile evaluating subjects' performances without any TMS intervention to evaluate the absolute effect of both active and sham TMS on visual processing.

TMS effects on sham-normalized IE

The only significant term in this four-way ANOVA was a two-way interaction between Level and Stimulated Hemisphere ($F(1,28) = 11.65$; $P = 0.002$), indicating that global and local processing were differently modulated depending on whether right or left parietal real-minus-sham rhythmic TMS bursts were applied (see Fig. 3). Follow-up *t*-tests of this two-way interaction revealed that right hemisphere active 10 Hz stimulation impaired global processing (38.88 ± 15.20 IE) relative to sham ($t_{14} = 2.65$; $P = 0.019$) but did
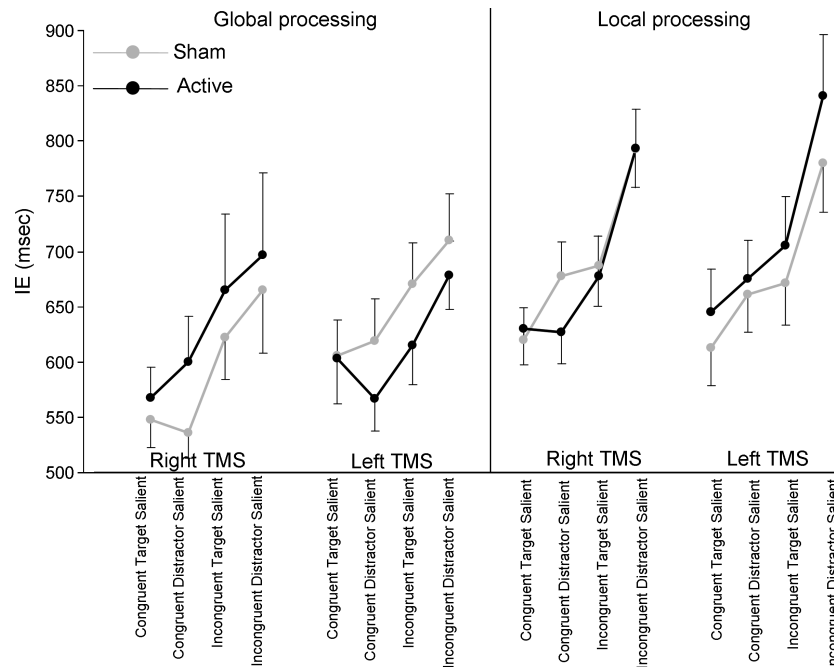
FIG. 2. Baseline performance (sham blocks only; gray lines) vs. TMS-modulated performance (active 10 Hz TMS only; black lines) for global or local target identification as a function of congruency and saliency. Right and left parietal rhythmic TMS stimulation shown separately.

not significantly affect local processing $(-12.02 \pm 15.73$ IE; $t_{14} = -0.79$; $P = 0.44)$. Conversely, left hemisphere active 10 Hz stimulation significantly impaired local processing $(34.86 \pm 16.16$ IE) relative to sham $(t_{14} = 2.23$; $P = 0.04)$, with the trend for global processing being in the opposite direction $(-34.87 \pm 18.30$; $-t_{14} = -1.97$; $P = 0.07$; see Fig. 3A), so clearly different from right-hemisphere 10 Hz TMS. Another way of looking at the same two-way interaction between Level and Stimulated Hemisphere is that global processing was significantly impaired when 10 Hz TMS was applied to the right vs. left hemisphere $(t_{28} = 3.21$; $P < 0.005)$. Conversely, local processing was signifi-cantly impaired when 10 Hz TMS was applied to the left vs. right hemisphere $(t_{28} = 2.15$; $P = 0.04)$. No other terms were significant in the ANOVA (all $F \le 2.60$, $P \ge 0.11$; n.s.).

We also compared performance of the present participants with 10 Hz rhythmic TMS bursts over right or left parietal sites against performance of other groups with 5 or 20 Hz stimulation instead at the same sites in exactly the same paradigm (data from Romei et al., 2011). This confirmed that the present effects of 10 Hz real vs. sham rhythmic TMS are indeed specific to 10 Hz, differing from the 5 and 20 Hz outcomes from the previous study by Romei et al. (2011). Specifically, the impact of real-vs.-sham TMS led to significantly worse performance overall $(P < .05)$ for the global task following right parietal 10 Hz TMS (38.88 IE) than following 5 Hz $(-35.86$ IE) or 20 Hz (13.28 IE). Conversely, following 10 Hz left parietal TMS, the local task was significantly $(P < .05)$ worse (34.86 IE) than following 5 Hz $(-14.46$ IE) or 20 Hz $(-1.87$ IE).

Although IE was the measure of choice here a priori, as also used by Mevorach et al. (2006a) and Romei et al. (2011), for completeness we conducted four-way omnibus mixed ANOVAs separately on RTs and error rates. For RTs, the same pattern was found as for the IE scores, with the only significant term being the two-way interaction between Level (Global/Local) and Hemisphere (Left/Right), $F_{1,28} = 11.49$; $P = 0.002$ (see Table 1). No significant terms were found for errors (all $P > 0.11$; see Table 1).

Finally, as participants responded with their right hand, we tested whether hemispheric differences found might be merely explained by a general slowing in reaction time when active stimulation was applied to the left vs. right hemisphere (by collapsing the reaction times to both local and global tasks). However, this analysis returned no significant slowing in RTs as a function of hemisphere stimulation (Right Hemisphere stimulation 599 ± 24 ms vs. Left Hemisphere stimulation 632 ± 29 ms; $F_{1,14} = 0.80$; $P = 0.39$). Again, as we got different effects from the two hemispheres, rather than one being effective and the other not, it seems unlikely that it merely reflects the fact that subjects responded with their right hand only.

Discussion

Our main finding is that rhythmic bursts of TMS at 10 Hz, over a parietal site known to be activated for featural visual attention (Wojciulik & Kanwisher, 1999), modulates featural attention in a global vs. local task. We found different impacts of 10 Hz TMS over left vs. right parietal sites. Right parietal stimulation disrupted global processing without affecting local processing. Left parietal stimulation disrupted local processing, with any trend for global processing being a benefit instead (thus clearly different from the impact of right parietal stimulation).

Evidence from brain-damaged patients has also indicated differen-tial roles for right and left parietal cortex in global and local processing, with right parietal cortex (and/or temporoparietal junc-tion) apparently involved in global processing, and left parietal in local processing (Robertson et al., 1988; Lamb et al., 1990; Fink et al., 1996; Martinez et al., 1997; Proverbio et al., 1998). The present results accord with this, while going beyond such work in implicating a specific role for the alpha rhythm at these sites. This fits with some previous EEG findings (Volberg et al., 2009), and recent proposals (Snyder & Foxe, 2010; Foxe & Snyder, 2011). Volberg et al. (2009) found that pre-stimulus oscillatory brain activity in the alpha band
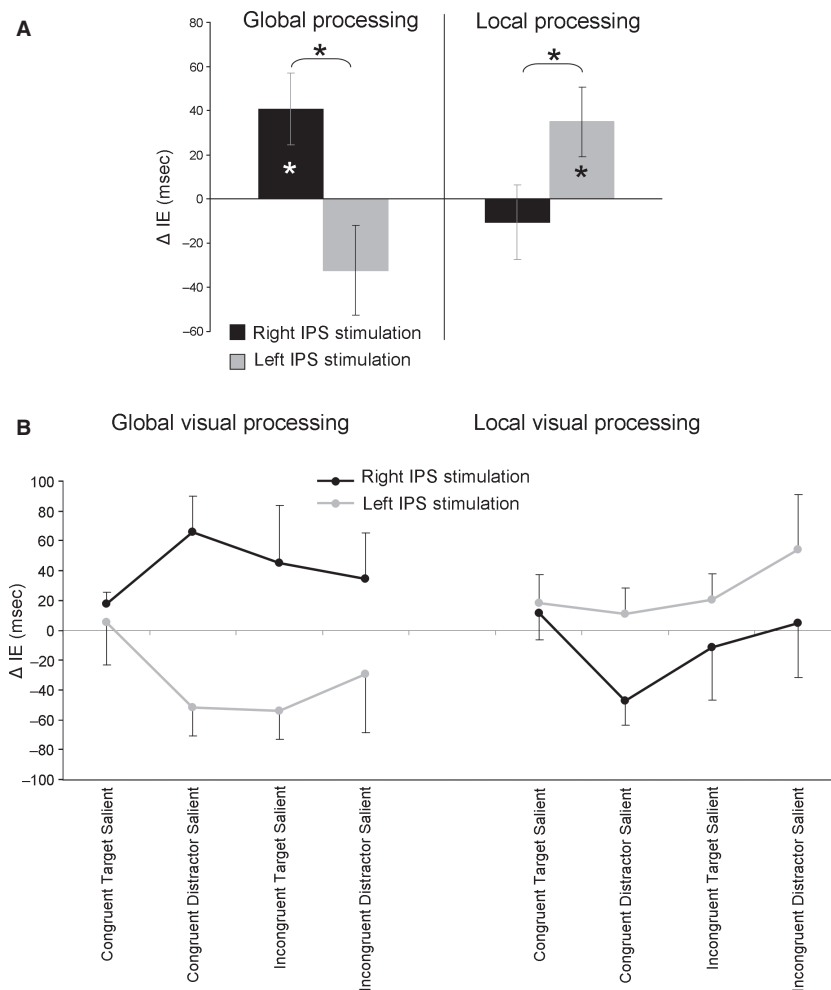
FIG. 3. Effect of rhythmic TMS on performance for global and local target identification as a function of the stimulated hemisphere. (A) Collapsed over Congruency and Saliency, to show the two-way interaction of hemisphere and level. Sham-normalized (active minus sham) effects of rhythmic TMS bursts over right (black bars) or left (gray bars) parietal sites at 10 Hz in the global or local task. Data are collapsed for Congruency and Saliency. The *y*-axis plots mean differences (for active minus sham) in IE (±SEM), so that negative values correspond to improved performance with active TMS while positive values correspond to impaired performance with active TMS. Asterisks indicate significant differences on *t*-tests, either from the null hypothesis of no difference between active and sham TMS, or between pairs of conditions as bracketed. *$P < 0.05$. (B) Data per Congruency and Saliency levels.

lateralized differentially, depending on whether participants prepared for either upcoming global or local targets. Snyder & Foxe (2010) reported that alpha oscillatory activity for feature-selective (non-spatial) attention, such as attending specific colours or motions, show a pattern of results that is in line with the inhibitory theory of alpha (Klimesch *et al.*, 2007). Sources located in putative dorsal stream regions showed increased alpha power when motion was irrelevant, whereas sources located in ventral regions increased alpha power when colour was irrelevant, in line with previous associations of the dorsal pathway with motion and the ventral pathway with colour (Mishkin & Ungerleider, 1982). Higher alpha in a specific region was thus associated with less attention to a specific feature, or suppression of task-irrelevant features. Our findings appear in keeping with the inhibitory account of alpha, as we found 10 Hz parietal TMS to causally impair local or global processing, while stimulation at 5 and 20 Hz causally facilitated global and local processing respectively, as previously shown by Romei *et al.* (2011).

The existing literature on hemispheric laterality for global vs. local processing is not without controversy (e.g. see. Boles & Karner, 1996; Fink *et al.*, 1997; 1; : Kéïta & Bedoin, 2011). A large number of

neuroimaging, EEG or patient studies have implicated left and right parietal sites with local or global visual processing (e.g. Robertson *et al.*, 1988; Lamb *et al.*, 1990; Fink *et al.*, 1996; Martinez *et al.*, 1997; Proverbio *et al.*, 1998; Volberg *et al.*, 2009), as also indicated here. Other reports suggest that such hemispheric tendencies can be abolished or even reversed (Bultitude *et al.*, 2009; Bultitude & Woods, 2010), depending on manipulations of relative saliency (Mevorach *et al.*, 2006a), stimulus category (Fink *et al.*, 1997), spatial frequency (Flevaris *et al.*, 2011) and stimulation frequency (Romei *et al.*, 2011).

In an important line of TMS studies (see Mevorach *et al.*, 2006a, 2009, 2010) and patient studies (e.g. Mevorach *et al.*, 2006b), Mevorach and colleagues have argued that relative saliency of global vs. local levels, rather than the actual level *per se*, can be key in determining hemispheric preferences. However, this was not the case in the present dataset, where the key factors proved empirically to be Hemisphere × Level for the 10 Hz rhythmic TMS effects, despite our use here of the same saliency manipulation introduced by Mevorach *et al.* (2006a); see also Romei *et al.* (2011). We note that the online effects of the present TMS protocol (short rhythmic bursts at 10 Hz)

TABLE 1. Reaction times (RT) and error rates

Task	Local H target				Global H target			
Congruency	Congruent		Incongruent		Congruent		Incongruent	
Stimulation	Left	Right	Left	Right	Left	Right	Left	Right
RT (ms)								
Salient stimuli								
Distractor	10.32 ± 14.31	−36.24 ± 17.95	0.54 ± 26.50	−21.43 ± 17.08	−55.44 ± 18.09	45.95 ± 17.95	−56.66 ± 24.60	−9.71 ± 14.77
Target	30.57 ± 21.51	15.43 ± 16.61	15.40 ± 17.64	4.98 ± 21.14	−17.32 ± 21.65	13.64 ± 9.71	−46.77 ± 16.92	13.56 ± 17.48
Error rate (%)								
Salient stimuli								
Distractor	−0.56 ± 1.02	1.11 ± 2.77	−6.67 ± 2.41	−2.22 ± 2.73	0.00 ± 0.84	−2.22 ± 1.97	−4.44 ± 2.21	−3.33 ± 2.50
Target	−0.56 ± 1.02	1.11 ± 1.65	−2.22 ± 2.30	1.67 ± 2.41	−1.67 ± 1.51	−1.11 ± 0.78	2.22 ± 1.32	0.00 ± 3.03

Values are mean ± SEM. RTs and error rates are of normalized (active minus sham) 10 Hz TMS stimulation.

probably differs from the offline effects of prolonged repetitive TMS protocols (see Thut & Pascual-Leone, 2010) typically used by Mevorach and colleagues (e.g. Mevorach *et al.*, 2006a, 2010; but see also Mevorach *et al.*, 2009); and that Mevorach and colleagues did not stimulate at alpha frequency over parietal sites. Moreover, the sites stimulated also differed. We stimulated posterior parietal cortex over the intraparietal sulcus (at Talairach coordinates 28, −51, 50; or −28, −51, 50) whereas Mevorach *et al.* (2006a) stimulated the right angular gyrus (44, −64, 54) and the left superior parietal lobule (−36, 66, 55), or brain sites underneath P3 and P4 (Mevorach *et al.*, 2009). Schenkluhn *et al.* (2008) reported that TMS over the supramarginal gyrus impaired spatial attention only, while TMS over the anterior intraparietal sulcus disrupted both spatial and featural attention. Future studies should systematically test how different sub-regions of parietal cortex control different levels of attentional selection, such as global and local processing, relative saliency or spatial attention. But importantly the site chosen here allowed a direct comparison to the previous rhythmic TMS work at 5 and 20 Hz of Romei *et al.* (2011) for the same site, thereby allowing us to confirm that the present effects were indeed specific to the alpha frequency range.

Finally, at the request of one reviewer, we discuss whether ocular dominance can alternatively account for the present results. While we cannot test this hypothesis due to the lack of information about ocular dominance in our participants, we do note that visual areas stop being monocular a long way before parietal cortex, thus making it unlikely that eye dominance does matter in explaining our results.

In conclusion, the present rhythmic TMS results causally implicate right parietal alpha frequency in suppression of global attention, and left parietal alpha frequency in suppression of local attention, regardless of relative saliency or distractor congruency. Together with other recent studies, our data add to growing evidence that short bursts of rhythmic TMS can result in online interactions with brain oscillations, differing from offline effects (Thut & Pascual-Leone, 2010). Rhythmic TMS can be used for targeting specific brain functions through stimulation at specific frequencies (Klimesch *et al.*, 2003; Sauseng *et al.*, 2009; Romei *et al.*, 2010, 2011), as shown by frequency-specific rhythmic TMS effects on perception at frequencies where brain oscillations have been linked to spatial attention (e.g. Worden *et al.*, 2000; Thut *et al.*, 2006; Romei *et al.*, 2010), to processing of low or high spatial frequencies (Smith *et al.*, 2006; Romei *et al.*, 2011) and to local vs. global featural attention (Volberg *et al.*, 2009), as for the present new rhythmic TMS results specific to 10 Hz here. A recent TMS-EEG study by Thut *et al.* (2011a,b) indicates that entrainment of oscillations for

local neuronal populations may best explain the impact of the short rhythmic bursts TMS approach, but this study was implemented at rest. Future studies should explore the factors contributing to optimal entrainment. For example they could directly test the impact of rhythmic TMS bursts tailored to individual frequencies (vs. another participant's frequency) on this same oscillatory activity during task execution and its behavioural consequences.

Acknowledgements

Conflict of interest

None.

Abbreviations

EEG, electroencephalography; IE, inverse efficiency; MSO, maximum stimulator output; PT, phosphene threshold; TMS, transcranial magnetic stimulation.

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