Visual Selection and Posterior Parietal Cortex: Effects of Repetitive Transcranial Magnetic Stimulation on Partial Report Analyzed by Bundesen's Theory of Visual Attention

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Posterior parietal cortex (PPC) may contribute to visual selection by exerting top-down influences on visual processing. To seek direct evidence for this, we used 10 Hz repetitive transcranial magnetic stimulation (rTMS) over right or left PPC in nine healthy volunteers during a partial (selective) report task that allows quantitative assessment of top-down control and other parameters. Participants reported digits in a relevant color ("targets") but not those in an irrelevant color ("nontargets") from a brief masked display, in which a target could appear alone or together with an accompanying item (nontarget or target) in the same or opposite hemifield. Generally, a given target is identified better when presented with a nontarget than with another target, indicating top-down selection of task-relevant targets; this applied here with no rTMS or left PPC rTMS. However, rTMS over the right PPC changed the performance pattern. A left target no longer impeded report of a right target more strongly than did a left nontarget, whereas the greater impact of a right target than a right nontarget in disrupting report of a left target was increased. Formal analysis in terms of Bundesen's (1990) theory of visual attention indicated that right PPC rTMS diminished top-down control for the left hemifield while enhancing this for the right hemifield, particularly for bilateral two-item displays. These findings indicate a role for right PPC in top-down spatial selection, which applies even when the target is defined by a nonspatial property (here color).

Key words: parietal; transcranial magnetic stimulation; visual selectivity; extinction; spatial; attention

Introduction

Multiple visual stimuli may compete for limited neural resources (Broadbent, 1958; Harter and Aine, 1984; Bundesen, 1990; Desimone and Duncan, 1995; Driver and Frackowiak, 2001). In visual cortex, competition involves mutual suppression of evoked responses by multiple stimuli (Kwong et al., 1992; Kastner et al., 1998; Reynolds et al., 1999; Fink et al., 2000), but task-relevant stimuli may be advantaged in such competition by top-down signals (Desimone and Duncan, 1995; Desimone, 1998; Reynolds et al., 1999). Some top-down influences on visual cortex may originate from posterior parietal cortex (PPC) (Kastner and Ungerleider, 2000, 2001; Driver and Frackowiak, 2001), as suggested by functional neuroimaging (Hopfinger et al., 2000; Yantis et al., 2002) and by effects of brain damage in patients (Heilman and Valenstein, 1979; Mesulam, 1981; Driver and Vuilleumier, 2001).

However, inferences drawn solely from these methods have some limitations (Walsh and Pascual-Leone, 2003). Functional neuroimaging alone cannot establish the causal involvement of activated areas in attentional control. Patient studies can be hampered by the extent of lesions and possible reorganization after permanent damage.

To seek more direct evidence for the role of PPC in controlling visual selection, we used repetitive transcranial magnetic stimulation (rTMS), which can be used to test the causal role of particular cortical areas by assessing the disruptions that rTMS produces (for review, see Walsh and Cowey, 2000; Walsh and Pascual-Leone, 2003). We applied rTMS to right or left PPC (or none) while participants selectively reported digits in a relevant color ("targets") but not those in an irrelevant color ("nontargets") from brief displays without eye movements (i.e., "partial" or selective report, as opposed to nonselective "whole report"). This classic partial-report procedure (cf. Sperling, 1960; von Wright, 1968) allows analysis in terms of Bundesen's (1990) "theory of visual attention" (TVA) to assess top-down control of visual selection formally.

TVA can be considered a mathematical implementation of limited capacity and biased competition. In TVA, processing efficiency for a single item presented alone characterizes its sensory effectiveness. Competition between concurrent stimuli can impair their processing, revealing their attentional weights relative

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Figure 1. **A**, Example stimulus arrays from the partial-report experimental task, with targets assigned as red (digits in white) and nontargets as green (digits in gray) for the purposes of illustration. Each black-background square here illustrates one possible display type. These different types of display can be organized into five conditions of presentation in each hemifield: i, one target alone; ii, iii, one target accompanied with a same-hemifield nontarget (ii) or target (iii); iv, v, one target accompanied with an opposite-hemifield nontarget (iv) or target (v). Note that those arrays presenting one target in each hemifield concurrently (v) can provide separate scores for the left and right target, respectively. The dashed circles surrounding the digit in condition (v) were not present in the experiment but are added here to emphasize the scored target in a given display condition. N, Nontarget; T, target. **B**, Temporal sequence of a single trial. Participants were required first to report a small white letter in the center to encourage central fixation (also monitored by eye tracking), which was followed by the brief stimulus array (the dashed rectangle here indicates one of the possibilities shown above, in **A**) and a mask. During the right or left PPC rTMS blocks, trains of rTMS pulses at 10 Hz for 500 ms (indicated schematically by lightning flashes) started synchronously with the onset of the stimulus array.

to other stimuli. A measure of top-down control is determined by the ratio of attentional weights for targets (here items with the task-relevant color) versus nontargets (with the task-irrelevant color here). Good top-down control corresponds to task-relevant items being given stronger weights.

The target-defining property in our task was nonspatial (color), whereas PPC is often assumed to contribute primarily to spatial selection (Driver and Vuilleumier, 2001). However, Tsai and Lavie (1988, 1993) proposed that visual selection by nonspatial properties such as color may be implemented by selecting the location of the relevant color. PPC might thus fulfill a role in selecting relevant locations even when color defines the targets (Toth and Assad, 2002). Our results showed that rTMS over right (but not left) PPC affected the efficiency of top-down selection by color in a spatially specific manner, with relative suppression of top-down control for the left hemifield but relative enhancement for the right hemifield, particularly for bilateral displays.

Materials and Methods

Participants. Nine healthy volunteers (three female, age 26–34 years) gave informed consent. All were right-handed according to the Edinburgh Inventory (Oldfield, 1971). The experimental protocol was approved by the local ethical committee and conformed to the declaration of Helsinki and safety guidelines for rTMS research (Wassermann, 1998).

Stimuli and procedure (partial-report experimental task). The general procedure was modified from a previous study (Duncan et al., 1999) (see also Peers et al., 2005) that studied effects of permanent brain damage with Bundesen's (1990) TVA approach.

Stimulus arrays comprised one or two digits ($\sim 0.5^\circ$ in height) at the corners of an imaginary square ($9.4^\circ \times 9.4^\circ$) centered on fixation against a black background (Fig. 1A). Digits were randomly chosen from the set 02345689 in red [Commission Internationale de l'Eclairage (CIE), $x = 0.618, y = 0.346$] and/or green (CIE, $x = 0.279, y = 0.577$) matched for luminance (20 cd/m^2). At the beginning of each session, participants were instructed that either the red digits or the green digits were targets for the upcoming session. Targets were thus flexibly defined by color, in an instruction-dependent or top-down manner. Figure 1A illustrates the possible presentation conditions. A target item may appear alone (four display types, corresponding to each corner of the imaginary square), accompanied by a nontarget (eight display types, because with a target at four possible positions, the nontarget could appear in the same or opposite hemifield), or accompanied by another target (four display types, corresponding to same-hemifield target columns or opposite-hemifield rows). Diagonal arrangements were not possible in the two-item displays (Fig. 1A). Each type of display was presented equally often in a random order.

As illustrated in Figure 1B, each trial began with a central cross (0.3° , white color). To further encourage central fixation, this was replaced for 300 ms by a small central letter (0.5° in height, white color) that participants immediately read aloud. The experimenter then pressed a key, and, 100 ms later, the stimulus array was presented briefly (median duration of 160 ms; mean duration $\pm$ SD across the four testing sessions for individual participants ranging from 125 to 205 ± 14 to 31 ms, see below).

This array was masked by a rectangular pattern with random pixels in red and green. Participants verbally reported the identity of any digits in the specified target color [e.g., reporting all red digit(s) while ignoring any green digit or vice versa] at their own speed. For displays presenting two target digits, participants had to report both in any order and to indicate their order of report. Their verbal responses were keyed in by the experimenter.

During the experiment, participants sat with head fixed by a chinrest and head strap. Stimuli were presented on a 17-inch video graphics array display (Trinitron Multiscan 200 GS; Sony, Tokyo, Japan) at 100 Hz and 1024×768 pixel resolution, with a viewing distance of 57 cm. Presentation of stimuli and response recording were controlled with E-prime 1.0 (Psychology Software Tools, Pittsburgh, PA); fixation was monitored by an infrared limbus tracking technique (IRIS; Skalar Medical, Delft, the Netherlands) and analyzed with DASYLab 5.0 (DATALOG, Mönchengladbach, Germany), which confirmed that participants maintained central fixation and that rTMS did not trigger blinking responses.

Participants performed four sessions of this task over 4 separate days, two with red as the specified target color and two with green as the target color. Each session consisted of an initial practice phase followed by four experimental blocks. During the practice phase, the duration of the stimulus array was set by a staircase procedure (Cornsweet, 1962), adjusting durations by 10 ms every eight trials if needed, to achieve 75% accuracy over 16 consecutive target-alone trials (averaging over the four possible target locations). The obtained duration of the stimulus array was then

applied to all four subsequent experimental blocks, including two blocks of no rTMS, one block of left PPC rTMS, and one block of right PPC rTMS, in pseudorandom order with 10 min breaks between blocks. Given that each single session used the same display duration for all rTMS conditions (no rTMS, right or left PPC rTMS) and that the durations were functionally equivalent (i.e., all set at 75% accuracy for target-alone trials), data collected across sessions were pooled together for each individual participant. Each block consisted of 128 trials, yielding a total of 1024 trials for the no rTMS condition and 512 trials for right or left PPC rTMS conditions per participant.

Stimuli and procedure (color-report control task). To ensure that any rTMS effects on top-down selection by task-relevant color in the above partial-report task were not attributable to any effects on gross color perception, we also conducted a control task of color report (Duncan et al., 1999). The stimulus array was now a single digit in red or green at one of the four possible positions (eight display types); these positions were identical to those used in the partial-report task. Each type of display was equally probable. Participants gave verbal reports for the color of any digit presented (i.e., reporting “red” or “green”) at their own speed. Participants completed this task in one session, which began with practice to determine the duration equivalent to 75% accuracy, followed by four experimental blocks in pseudorandom order. The four blocks consisted of two blocks without and two blocks with PPC rTMS (one for the left and one for the right PPC), with 64 trials in each block.

rTMS. Magnetic stimulation was generated by a Magstim Super Rapid stimulator (Magstim, Whiteland, UK) connected to a 70 mm figure-of-eight coil held by a mechanical arm. The sites of rTMS were specified by frameless stereotaxy, using a Polaris infrared tracking device (Northern Digital, Waterloo, Ontario, Canada) andBrainsight software (Rogue Research Inc, Montreal, Quebec, Canada). With coregistration of the T₁-weighted magnetic resonance brain image to surface landmarks of the head in each participant, PPC stimulation was centered on the dorsal part of the angular gyrus between the intraparietal sulcus and the upper end of the superior temporal sulcus (for an example, see Fig. 2). Each participant's brain image was also spatially normalized to Talairach space (Talairach and Tournoux, 1988) using FSL software (Jenkinson and Smith, 2001; see www.fmrib.ox.ac.uk/fsl), which uses the canonical Montreal Neurological Institute (MNI) template. This gave mean coordinates of the stimulation center at 43, −65, 51 (SD of 5, 6, 4 mm) for the right PPC and −40, −65, 53 (SD of 3, 3, 4 mm) for the left PPC.

During blocks with rTMS in the partial- and color-report tasks, rTMS was delivered from the onset of each stimulus display, in a train of 10 Hz for 500 ms (Fig. 1B) at 60% of the maximum stimulator output. The intensity/frequency of the rTMS was chosen to be well within the safety guidelines (Wassermann, 1998), whereas the timing and duration of the rTMS ensured that it should overlap with any critical processing in PPC (i.e., during and immediately after presentation of each brief visual display while participants performed the task). Such “on-line” magnetic stimulation, delivered in a small number of pulses (usually one to five) at frequencies of ~10–50 Hz, time locked to discrete trials in a task, have been used to transiently disrupt functions of the brain region targeted with TMS in many previous studies (Day et al., 1989; Pascual-Leone et al., 1994; Oliveri et al., 1999; Rushworth et al., 2001; Bjoertomt et al., 2002; Campana et al., 2002). The effects of on-line TMS, as used here, can be thought of as transiently introducing neural “noise” into the area stimulated (for review, see Walsh and Cowey, 2000; Walsh and Pascual-Leone, 2003). Many TMS studies adopting this interference approach have created a variety of “virtual lesions”; that is, behavioral changes mimicking those produced by lesions involving the same region [suppression of visual detection (Amassian et al., 1989), visual extinction (Pascual-Leone et al., 1994), prolongation of visual search (Ashbridge et al., 1997), akinetopsia (Walsh et al., 1998), aspects of spatial neglect (Fierro et al., 2000), or acalculia (Gobel et al., 2001)], thereby allowing tests of functional localization. Note that TMS differs from other types of neural stimulation [e.g., with implanted electrodes (Moore and Armstrong, 2003)] in many respects but can nevertheless similarly modulate a given region transiently to allow inferences about its function.

Data analysis. Performance was assessed with two types of analysis. First, we considered the raw performance scores, in an assumption-free

Figure 2. The stimulation centers of rTMS over the left PPC (**A**) and the right PPC (**B**) in the T₁-weighted structural image of one participant. The MNI coordinates of the stimulation center (white circle) in this participant were located at −42, −64, 50 for the left PPC and 43, −66, 51 for the right PPC. Dashed lines represent the projected orientation perpendicular to the surface of the coil. For mean coordinates across participants, see Materials and Methods.

approach that nevertheless still demonstrated that the general performance patterns were in accord with Bundesen's (1990) TVA approach. We then proceeded to a second analysis of the parameters as fitted by the TVA model. In both cases, effects of various conditions were assessed by repeated-measures ANOVA (i.e., each participant contributing a score for each condition) with Greenhouse-Geisser correction. Paired comparisons were performed via Newman-Keuls tests. How raw scores are transformed into TVA parameters is briefly outlined below (for additional details, justification, and discussion, see Bundesen, 1990; Duncan et al., 1999).

According to TVA, when a target is presented alone in location i ,

performance P_i is closely approximated by an exponential function (Shibuya and Bundesen, 1988; Bundesen, 1998):

$$P_i = 1 - \frac{1}{e^{A_i}}, \quad (1)$$

where A_i is proportional to the sensory effectiveness for constant exposure duration.

When two objects are presented together, the competition between them is reflected by weight setting. Performance for a target in location i accompanied by a nontarget in location j is given by the following:

$$P_i = 1 - \frac{1}{e^{A_i w_i(T)/(w_i(T) + w_j(N))}}, \quad (2)$$

where $w_i(T)$ is the attentional weight of a target in location i , and $w_j(N)$ is the attentional weight of a nontarget in location j .

Performance for a target in location i accompanied by a second target in location j is given by the following:

$$P_i = 1 - \frac{1}{e^{A_i w_i(T)/(w_i(T) + w_j(T))}}. \quad (3)$$

With $w(N)$ and $w(T)$ derived in each hemisphere, their ratio $w(N)/w(T)$ is designated as α (typically $\alpha < 1$), which indicates the efficiency of top-down control. When α is close to zero, only targets receive significant processing (thus indicating effective exclusion of nontargets, corresponding to effective top-down selection on the Bundesen account). When α approaches 1, adding a target or a nontarget to an array has similar interference effects for the correct report of the accompanying target (thus indicating that targets and nontargets are now treated equivalently, corresponding to a lack of top-down selection).

For each participant during different rTMS conditions, a TVA trial-by-trial fitting program (available at www.psy.ku.dk/cvc/tva) was used to obtain estimates of the above parameters [A_i , $w_i(T)$, and $w_i(N)$ for each of the four possible stimulus locations] that gave a maximum-likelihood fit to 20 raw performance scores (four target positions under five conditions of visual presentation, i.e., presented alone, accompanied with a same-hemifield nontarget/target, or accompanied with an opposite-hemifield nontarget/target) (Fig. 1A).

For both raw performance scores and the various TVA parameters derived from them, initial inspection revealed similar outcomes for the upper and lower positions in the same hemifield. Measurements for each hemifield were therefore obtained by collapsing over upper and lower positions.

Results

All participants completed the task without any adverse effects. rTMS over the PPC did not elicit motor twitches or sensory paresthesias.

Partial-report experimental task

Figure 3 shows the mean performance during left PPC rTMS, no rTMS, and right PPC rTMS conditions, for targets in the left or right hemifield, under various display conditions. Note that Figure 3 suggests a very similar pattern of performance for the left PPC rTMS and no rTMS conditions (top two panels), whereas the right PPC rTMS condition (bottom panel) indicates a different pattern of performance. This was confirmed by the analyses below, which revealed an impact of right PPC but not left PPC rTMS on performance.

Although participants were free to choose the reporting order for two-target displays, most participants reported in a left-then-right (for bilateral displays) or upper-then-lower (for unilateral displays) order, regardless of rTMS conditions. Left-then-right report order might contribute to (or reflect) the apparent trend for slightly better performance for left than right targets overall (Fig. 3), but, in fact, this did not approach significance ($F_{(1,8)} =$

Figure 3. Mean proportion of correct report of the target for left PPC rTMS (A), no rTMS (B), and right PPC rTMS (C) in the partial-report task. Note that the pattern for right PPC rTMS (see the shaded bars, especially the rightmost circled pair) is different from those for left PPC or no rTMS (compare the shaded bars across panels). Scores are shown separately for targets in the left hemifield (leftmost 5 bars in each panel) or right hemifield. Data are further divided according to five display conditions (see the labels under each panel and the schematic displays under the bottom panel): a target alone; accompanied with a same-hemifield nontarget (N) or with a same-hemifield target (T); and accompanied with an opposite-hemifield nontarget or with an opposite-hemifield target. The schematic displays depict nontargets as N and targets as T, while only showing examples for targets at the upper position (for those at the lower position, see Fig. 1A). The circle surrounding one of the Ts in the T–T bilateral displays was not present in the experiment but is added here to emphasize the scored target in a given condition. Error bars correspond to SE. The asterisked brackets ($p < 0.05$) and one bracket notifying nonsignificance (NS) draw attention to critical pairs of conditions.

0.22, $p = 0.65$ for left vs right targets in two-element displays, when collapsing over other conditions). It did not reach significance even for those conditions in which the trend was most pronounced (i.e., for target–target row displays under no rTMS or left PPC rTMS, $p > 0.1$ in both cases) and hence will not be discussed further. Two participants intermittently reported two targets in the reverse order, but the frequencies of this were similarly low (3–4%) for all rTMS conditions. In summary, rTMS did not affect the order of report, so the rTMS effects described below cannot reflect report order.

For ease of exposition, we first characterize the overall pattern regardless of rTMS and then move on to assessing any impact of rTMS, initially on raw performance scores and subsequently on the parameters calculated by the TVA approach.

Raw performance scores: the overall pattern

The overall performance pattern is consistent with the expectations of the TVA approach. Regardless of rTMS conditions, performance for target-alone displays (single item) was impaired by adding either a nontarget or a target to produce two-item displays ($F_{(1,8)} = 48.71$, $p < 0.0005$ for performance of one- vs two-element displays), indicating some capacity limit. Even adding a nontarget produced some performance cost, but importantly an accompanying target (i.e., another digit in the task-relevant color) was generally more disruptive than a nontarget in the task-irrelevant color ($F_{(1,8)} = 99.11$, $p < 0.0005$ for performance in conditions with an accompanying nontarget vs another target). This indicates some degree of top-down selection (because a greater impact from targets than nontargets indicates higher attentional weights for targets on the Bundesen account). Figure 3 shows such overall patterns, with best performance for conditions with a single target alone, then those with an accompanying nontarget, and then those with a second target. This pattern was consistent, except for one situation under right PPC rTMS, as explained in the next section.

Raw performance scores: the impact of rTMS

We began by comparing performance scores under left PPC rTMS with those under no rTMS and likewise separately for performance under right PPC rTMS relative to no rTMS. We did this as an initial step instead of comparing right and left PPC rTMS first, because starting with the latter comparison might have made it unclear which site of rTMS was producing any effect. As will be seen, left PPC rTMS and no rTMS led to equivalent performance, with only right PPC rTMS producing changes in top-down control (i.e., in the relative impact of adding a target vs a nontarget). Thus, after confirming that left PPC rTMS did not differ from no rTMS, we were then able to use left PPC rTMS as a baseline for direct comparison with right PPC rTMS in subsequent analyses, allowing us to control for any nonspecific effects attributable to rTMS (e.g., possible alerting effects from the sound of the rTMS pulses).

For target-alone (single-item) displays, performance was not affected by rTMS over either hemisphere. The comparison between left PPC rTMS versus no rTMS, in a 2×2 ANOVA with rTMS (none or left PPC) and target side (left or right) as factors, revealed no main effects and no interaction (all F values ≤ 0.02 , NS). A similar analysis comparing right PPC rTMS and no rTMS likewise found no significant differences (again all F values ≤ 0.93 , NS). This indicates that rTMS over left or right PPC did not affect correct identification of a target digit presented alone and thus did not induce any “sensory” impairment for either hemifield.

For the critical two-item conditions, $2 \times 2 \times 2 \times 2$ repeated-measures ANOVAs were conducted with factors of (1) rTMS (present or absent), (2) target side (left or right), (3) display configuration (whether the accompanying item was in the same or opposite hemifield as the scored target), and (4) relevancy of the accompanying item (nontarget or target), to separately examine any effects of left PPC rTMS versus no rTMS or of right PPC rTMS versus no rTMS (for rationale, see above). The comparison of left PPC rTMS versus no rTMS revealed only main effects of relevancy ($F_{(1,8)} = 84.39$, $p < 0.0005$, i.e., worse performance when adding a target rather than a nontarget, as expected), with no main effects or interactions involving the rTMS factor (all F values ≤ 1 , $p \geq 0.35$). Importantly, these results indicate that left PPC rTMS did not impair or change performance relative to that found with no rTMS.

In contrast, the analogous ANOVA comparing right PPC rTMS versus no rTMS for two-element displays now revealed significant influences of the rTMS manipulation. In addition to the usual main effect of relevancy ($F_{(1,8)} = 40.21$, $p < 0.0005$), there was a three-way interaction among rTMS, target side, and relevancy of accompanying item ($F_{(1,8)} = 8.78$, $p = 0.018$), and the four-way interaction also reached significance ($F_{(1,8)} = 32.18$, $p < 0.0005$).

One likely source for these interactions is suggested by comparing Figure 3, *B* and *C*, which reveals the change in performance pattern for right PPC rTMS. In almost all cases, performance was better for conditions with an accompanying nontarget rather than a target, yet this pattern was not seen for the scores of right-hemifield targets in the opposite-hemifield (row) configuration during right PPC rTMS (Fig. 3*C*, the circled rightmost two bars, as opposed to other pairs of shaded bars; note also the particularly large difference for the fourth and fifth bars in Fig. 3*C*). That is, with right PPC rTMS, an added left target no longer disrupted report of a right target more than an added left nontarget, yet an added right target still disrupted report of a left target more than an added right nontarget (if anything, even more so). These changes in performance pattern thus depended on rTMS $\times$ target side $\times$ display configuration $\times$ relevancy of accompanying item, corresponding to the four-way interaction.

To investigate this further, an analysis was conducted for just the two-item conditions with three factors (target side, display configuration, and relevancy of accompanying item), now separately for right PPC rTMS and no rTMS. This revealed a three-way interaction only for right PPC rTMS ($F_{(1,8)} = 23.41$, $p = 0.001$), but there was no such interaction in the absence of rTMS ($F_{(1,8)} = 3.15$, $p = 0.11$). Additional 2×2 ANOVAs with factors of target side and relevancy of accompanying item were implemented for same- and opposite-hemifield configurations during right PPC rTMS. These demonstrated a significant target side $\times$ relevancy interaction only for opposite-hemifield row displays ($F_{(1,8)} = 28.94$, $p = 0.001$) but not for column displays ($F_{(1,8)} = 0.73$, $p = 0.42$). This reflects the facts that, during right PPC rTMS, report of a left target was much more impeded by adding a right target rather than a right nontarget, indicating relatively good selectivity for an added right stimulus ($F_{(1,8)} = 22.07$, $p = 0.002$) (Fig. 3*C*, fourth and fifth bars, near the asterisk), whereas for a right target, adding a left nontarget or a left target now impeded its report to virtually the same extent, i.e., the greater impact of an added left target was eliminated, indicating relatively poor selectivity for an added left stimulus ($F_{(1,8)} = 0.12$, $p = 0.74$) (Fig. 3*C*, two circled rightmost bars). No such pattern was present in the absence of rTMS (Fig. 3*B*) or with left PPC rTMS (Fig. 3*A*).

Figure 4. The difference in raw performance scores between target–nontarget arrays and target–target arrays (i.e., $P_{TN} - P_{TT}$ for left targets and $P_{NT} - P_{TT}$ for right targets) in the row displays for individual participants. Note how the dashed lines connecting triangle points (representing the data for right PPC rTMS) tend to slope down in each graph, unlike the other rTMS conditions. All participants showed a relatively lower score on the plotted performance difference for right targets (right data points in graphs) during right PPC rTMS, indicating relatively poorer selectivity (less differential impact of added left target than nontarget) for the left hemifield. Also, during right PPC rTMS, six of nine participants (participants 1, 3, 5, 6, 8, and 9) showed a relatively higher score on this measure for left targets (left data points in graph), indicating intact or enhanced selectivity for the right hemifield (i.e., preserved or enhanced differential impact of adding a right target vs nontarget, on report of a left target). The repeated-measures ANOVA statistics in Results formally confirm reliability across the group of participants.

To confirm that the above effects were consistently present in most participants (as already implied by the significant repeated-measures statistics), the differences in raw performance scores between target–nontarget arrays and target–target arrays (i.e., $P_{TN} - P_{TT}$ for left targets and $P_{NT} - P_{TT}$ for right targets) in the opposite-hemifield (row) conditions were plotted for each participant (Fig. 4, noting how the dashed lines connected by triangles all tend to slope down). All participants showed the critical pattern of a relatively lower score on this performance difference for report of right targets (Fig. 4, right points in each graph) during right PPC rTMS than for left PPC rTMS or none. This indicates relatively poor selectivity for the left hemifield under right PPC rTMS (i.e., less differential impact of an added target vs nontarget on the left, for report of a right target). Also, during right PPC rTMS, six of nine participants (participants 1, 3, 5, 6, 8, and 9) showed a relatively higher score on this performance difference for the report of left targets (Fig. 4, left points in each graph), suggesting some tendency for relatively improved (and certainly preserved) selectivity for the right-hemifield stimulus

(i.e., intact differential impact of an added right target vs added right nontarget, because right targets still disrupted report of left targets more than right nontargets under right PPC rTMS; indeed, they tended to do so even more).

An additional approach for investigating the source of the four-way interaction above (i.e., rTMS $\times$ target side $\times$ configuration $\times$ relevancy of accompanying item) is to run three-way analyses (rTMS $\times$ target side $\times$ relevancy) separately for row and column displays. These revealed a three-way (rTMS $\times$ target side $\times$ relevancy) interaction for row displays ($F_{(1,8)} = 60.18$, $p < 0.0005$) but not for column displays ($F_{(1,8)} = 0.69$, $p = 0.43$). Additional comparisons dividing the relevancy factor revealed interactions between rTMS and target side when the accompanying item was a target ($F_{(1,8)} = 34.36$, $p < 0.0005$) but not a nontarget ($F_{(1,8)} = 1.49$, $p = 0.26$). This indicated that, for row displays with one target in each hemifield, right PPC rTMS (vs none) relatively worsened performance for reporting the left target ($p < 0.05$), shifting performance even farther away from that for the corresponding nontarget–target array, whereas right PPC rTMS actually benefited performance for a right target in target–target rows ($p < 0.05$), with right-target performance for these now approaching the level for the corresponding nontarget–target array. The worsened performance for the left target specifically in row target–target displays here, under right PPC rTMS, resembles the contralesional extinction (i.e., failure to report a contralesional target in the presence of an ipsilesional target) in many right parietal patients (Vuilleumier and Rafal, 2000; Driver and Vuilleumier, 2001), whereas the improvement for reporting the right target from row target–target displays may be

reminiscent of improved performance for stimuli ipsilateral to the TMS in some previous work (Seyal et al., 1995; Oliveri et al., 1999; Rushworth et al., 2001), although note that the present effects did not apply for single-target conditions (see above) and may thus be more analogous to extinction.

Our final analysis on the raw performance score, before application of TVA, directly compared right PPC rTMS with left PPC rTMS. (Thus far, we have shown that right PPC rTMS differed in its effects on performance from no rTMS, whereas left PPC rTMS did not. This was an essential first step for knowing which type of rTMS was effective.) The direct comparison of right and left rTMS, which we focus on henceforth, controls for any nonspecific effects of rTMS such as alerting caused by the sound of rTMS. A repeated-measures ANOVA comparing right versus left PPC rTMS for two-item displays showed similar results to the previous comparison of right PPC versus no rTMS, including a main effect of relevancy ($F_{(1,8)} = 148.98$, $p < 0.0005$), a three-way interaction involving rTMS condition, target side, and relevancy

Table 1. TVA parameters in the partial-report experimental task: values of sensory effectiveness A_i , spatial weights for targets $w_i(T)$, and efficiency of control α for each individual participant

Participant	Parameter A_i						Parameter $w_i(T)$						Parameter α					
	Left PPC rTMS		No rTMS		Right PPC rTMS		Left PPC rTMS		No rTMS		Right PPC rTMS		Left PPC rTMS		No rTMS		Right PPC rTMS	
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
1	2.41	1.54	1.88	1.45	1.87	1.41	0.81	0.50	0.98	0.70	0.80	0.75	0.45	0.55	0.63	0.65	0.61	0.14
2	1.54	2.12	1.68	1.74	1.72	2.23	0.72	0.50	0.71	0.65	0.54	0.75	0.32	0.60	0.28	0.62	0.70	0.42
3	1.81	2.25	1.84	2.00	1.98	1.77	0.89	0.54	0.79	0.45	0.61	0.88	0.47	0.70	0.14	0.40	0.56	0.38
4	2.44	2.17	2.52	2.77	2.40	2.41	0.93	0.78	0.96	0.88	0.86	0.81	0.34	0.40	0.49	0.80	0.54	0.23
5	2.31	2.02	2.03	1.89	1.92	1.99	0.87	0.87	0.90	0.87	0.71	0.84	0.44	0.29	0.29	0.35	0.21	0.24
6	2.34	2.26	2.65	2.18	2.74	2.28	0.90	0.83	0.91	0.90	0.78	0.92	0.48	0.42	0.39	0.37	0.57	0.29
7	1.81	2.04	1.78	1.99	2.10	2.38	0.93	0.91	0.90	0.85	0.77	0.89	0.39	0.52	0.61	0.45	0.95	0.45
8	1.98	2.27	1.77	2.57	2.63	1.96	0.91	0.85	0.99	0.78	0.47	0.93	0.24	0.49	0.49	0.84	0.75	0.22
9	2.09	2.62	2.57	2.13	2.22	2.13	0.67	0.81	0.69	0.83	0.59	0.97	0.30	0.73	0.48	0.40	0.60	0.48

of accompanying item ($F_{(1,8)} = 11.45, p = 0.01$), and a four-way interaction ($F_{(1,8)} = 18.33, p = 0.003$) again (Fig. 3).

To summarize, the report of a target was in general more impeded by adding another target than a nontarget, indicating a degree of top-down control that gives preferential processing for targets rather than nontargets. Whereas performance under left PPC rTMS did not differ from no rTMS, right PPC rTMS did affect the raw performance scores and changed the general pattern of performance. For two-target (row) displays with one target in each hemifield, right PPC rTMS relatively decreased performance scores for the left target while increasing those for the right one, relative to no rTMS or left PPC rTMS. Under right PPC rTMS only, adding a target on the left no longer impeded the report of a right target any more than adding a left nontarget (Fig. 3C, two circled rightmost bars). This elimination of the difference between a left nontarget and a left target in their impact on the report of a right target suggests disruption of top-down influences for the left hemifield. Conversely, also under right PPC rTMS, adding a right target now became even more disruptive than a right nontarget in compromising report of a left target (Fig. 3C, fourth and fifth bars), suggesting well preserved top-down control within the right hemifield under right PPC rTMS. These points will now be clarified and confirmed further by analysis of the parameters derived by Bundesen's (1990) TVA approach.

Analysis of TVA parameters

Parameters of the best fits of the TVA were calculated for different rTMS conditions in each participant. Best fits accounted for 58–97% (median, 88%) of the variance in the no rTMS conditions, 64–95% (median, 87%) in the left PPC rTMS conditions, and 53–97% (median, 83%) in the right PPC rTMS conditions. The measure of each parameter for right PPC rTMS will be compared first with that for left PPC rTMS given that this controls for nonspecific effects of rTMS (then with that for no rTMS, for completeness). Parameters from the best fits of the TVA to each participant's individual data are shown in Table 1.

Sensory effectiveness, A_i , was evaluated by the index $A_L/(A_L + A_R)$ to reflect the relative difference across hemifields (an index larger or smaller than 0.5 means a leftward or rightward bias, respectively) (for its distribution, see Fig. 5A). There was neither a significant difference for right versus left PPC rTMS ($F_{(1,8)} = 1.31, p = 0.29$) nor for right PPC versus no rTMS ($F_{(1,8)} = 0.35, p = 0.57$), as expected from their similar raw performance scores for target-alone trials. This indicates that rTMS over the left or

right PPC did not affect the basic sensory processing of a single target in either hemifield.

The spatial bias in overall weighting (regardless of target/nontarget) was evaluated by the index $w_L/(w_L + w_R)$ (for its distribution, see Fig. 5B), where w_L was calculated as the mean of $w_L(N)$ and $w_L(T)$ and analogously for w_R . This index was again similar for right versus left PPC rTMS ($F_{(1,8)} = 3.16, p = 0.11$) and for right PPC versus no rTMS ($F_{(1,8)} = 2.32, p = 0.17$), meaning that rTMS over the left or right PPC did not change the overall spatial weights (that collapse weights for targets and nontargets together).

The critical parameter representing the efficiency of top-down control, α , is indexed as $w(N)/w(T)$ for each hemifield (in effect, the extent of impairment in reporting a target by adding another target instead of a nontarget). Although this parameter is quite variable between individuals (Duncan et al., 1999), right PPC rTMS systemically shifted α_L toward higher values (i.e., lower efficiency of top-down control for the left hemifield) while shifting α_R toward lower values (i.e., higher efficiency of top-down control for the right hemifield) (Fig. 5C). A 2×2 repeated-measures ANOVA with rTMS (left or right PPC) and hemifield (left or right) as factors revealed a significant interaction ($F_{(1,8)} = 20.93, p = 0.002$) (Fig. 6). This interaction reflected right PPC rTMS increasing α_L and decreasing α_R compared with the same parameters during left PPC rTMS (all p values < 0.05). Moreover, α_R was significantly lower than α_L during right PPC rTMS ($p < 0.05$) but not during left PPC rTMS (NS). The same pattern was observed when comparing right PPC with no rTMS instead ($F_{(1,8)} = 19.56, p = 0.002$ for the two-way interaction). Thus, the efficiency of top-down control, while being similar across space with no rTMS and also with left PPC rTMS, was differentially impaired for the left hemifield but enhanced for the right hemifield by right PPC rTMS.

Summary of partial-report results

Performance on the partial (i.e., selective) report task generally showed a greater disruptive effect of an added target than a nontarget, suggesting the presence of some top-down control. Right PPC rTMS modulated this performance pattern, such that adding a left target no longer impeded report of a right target any more than adding a left nontarget, although adding a right target still impaired report of a left target more strongly than adding a right nontarget (indeed even more so). Formal TVA analysis confirmed that the efficiency of top-down control was altered by

Figure 5. Distribution histograms of TVA parameters, as proportions of participants for the following: **A**, the sensory effectiveness parameter, namely $A_L/(A_L + A_R)$; **B**, the spatial bias regardless of target/nontarget, namely $w_L/(w_L + w_R)$; and **C**, the efficiency of top-down control for each hemifield, α_L and α_R . The distribution for each parameter is shown separately for conditions of left PPC rTMS (top panel in each case), no rTMS (middle panel in each case), and right PPC rTMS (bottom panel in each case). During right PPC rTMS, the distribution of α_L was shifted toward relatively higher values (decreased efficiency of top-down control), whereas the distribution of α_R was shifted toward relatively lower values (increased efficiency of top-down control) compared with left PPC rTMS or no rTMS.

Figure 6. Mean estimates of α in each hemifield. Right PPC rTMS relatively increased the α value for the left hemifield while decreasing the α value for the right hemifield.

right PPC rTMS, being reduced for the left hemifield and (perhaps because of this) relatively enhanced for the right hemifield.

Color-report control task

A repeated-measures ANOVA with rTMS (left or right PPC) and target side as factors on the color-report data showed neither main effects nor interactions (all p values ≥ 0.28). Analogous

comparison of right PPC versus no rTMS also found no difference (all p values ≥ 0.32). For TVA analysis, performance was transformed into the estimate of $A_i(\text{color})$ using Equation 1:

$$P_i(\text{color}) = 1 - \frac{1}{e^{A_i(\text{color})}} \quad (4)$$

For the index $A_L(\text{color})/[A_L(\text{color}) + A_R(\text{color})]$, reflecting spatial bias in color discriminability, there was not a significant difference for right versus left PPC rTMS ($F_{(1,8)} = 3.54$, NS) or for right PPC versus no rTMS ($F_{(1,8)} = 1.01$, NS). This confirms that rTMS over either left or right PPC did not affect discrimination ability for colors, and hence the influences shown on the partial-report task above are not attributable to indirect effects on gross color perception.

Discussion

We applied rTMS to right or left posterior parietal cortex, or gave none, during a partial-report (i.e., selective-report) task in which participants reported digits in a specified target color while trying to ignore nontarget digits in another color from a brief masked display. We found that 10 Hz

rTMS over right PPC (but not left PPC), in a time period overlapping with the stimulus and extending into its subsequent processing, altered top-down visual selection (as assessed by the differential impact of added targets vs nontargets on performance) across space. rTMS to right PPC produced a relative loss of top-down selection in the left hemifield but relative enhancement of this in the right hemifield. These effects were particularly pronounced for row displays, which had competing stimuli in both hemifields concurrently.

These effects of right PPC rTMS were not merely attributable to the presence/absence of rTMS, because they were specific to right but not left PPC rTMS. Moreover, instead of causing global, nonspecific effects on performance, right PPC rTMS had a highly condition-specific impact depending on the target side, the row/column format, and the relevancy of an additional item in two-item displays. Specifically, during right PPC rTMS, adding a left target no longer disrupted report of a right target any more than adding a left nontarget (Fig. 3), indicating impaired selectivity on the left side, whereas an added right target now became even more disruptive than a right nontarget in compromising report of a concurrent left target (Fig. 3), indicating improved visual selectivity on the right, perhaps as a consequence of this being impaired on the left. These effects on raw performance were echoed in TVA analyses, which indicated that right PPC rTMS influenced just the efficiency of top-down control in a spatially specific manner (Figs. 5, 6) while producing no effect on sensory effectiveness for the processing of single items, overall spatial biases, or gross color perception.

Effects of rTMS versus those of large brain lesions

TVA analyses of partial (i.e., selective) report have previously proved useful to study normal performance (Shibuya and Bundesen, 1988; Shibuya, 1993) and to investigate deficits in pa-

tients with extensive brain damage (Duncan et al., 1999; Peers et al., 2005). Duncan et al. (1999) found some lowering of sensory effectiveness (A_i) and of overall weighting (w_i) regardless of target/nontarget status for the left hemifield in patients with extensive damage over the right parietal/perisylvian regions. However, such a pattern was not apparent for focal right PPC rTMS applied to normals in our study. This different outcome may reflect the broader extent of lesions in those patients (or some long-term changes that might have occurred) as opposed to the transient rTMS-induced disruption targeting at a specific region in normals here. Duncan et al. (1999) observed no specific lesion correlate of top-down control (α) in their patients, but this top-down parameter was highly variable even among their healthy controls (Bundesen et al., 1985; Shibuya, 1993), which could have made any distinction hard to detect. Peers et al. (2005) recently observed some deficits in top-down control in frontal and parietal patients, again using a partial-report task, but the only clear anatomical correlation for this was with lesion size. Given that top-down parameters can vary substantially between individuals (Shibuya, 1993; Duncan et al., 1999; Peers et al., 2005) (Table 1), the within-subject design that was permitted by the transient rTMS intervention here may provide a more sensitive measure for any effects on this parameter than the between-group comparisons that are typically necessary in patient studies.

Spatial specificity of the right PPC rTMS effect

The effect of right PPC rTMS on raw performance scores, and on TVA top-down parameters, was spatially specific in two respects. First, it differentially affected the left and right hemifields, with top-down selectivity being impaired on the left but improved on the right. Second, the effect was more pronounced for row displays (i.e., one competing item in each hemifield concurrently) than for column displays. This latter aspect is reminiscent of extinction commonly associated with right parietal damage (for review, see Driver and Vuilleumier, 2001; Driver et al., 2004). Typically, extinction manifests as a relative disadvantage for the contralesional (left) side and a concurrent advantage for the ipsilesional (right) side during double simultaneous stimulation from both sides. A somewhat analogous pattern (i.e., relative impairment on the left and relative enhancement on the right) was found here with bilateral (row) displays during right PPC rTMS but now specifically for top-down control parameters.

Previous TMS studies have found that disruptions in one hemisphere can lead to benefits in the other (Seyal et al., 1995; Oliveri et al., 1999; Rushworth et al., 2001), a pattern typically attributed to inter-hemispheric competition or disinhibition. The present results accord generally with those findings, showing that rTMS to right parietal cortex can have disruptive influences for the left hemifield, which may then lead to (otherwise paradoxical) relative enhancements for the right hemifield. However, they now show this pattern specifically for top-down parameters, which the TVA approach allowed us to assess for the first time here.

Spatially specific role for right PPC even during color-based selection

Targets and nontargets were distinguished only by color in the present partial-report paradigm, yet spatially specific effects (see above) of right PPC rTMS during top-down selection by color were nevertheless obtained. This provides a new line of evidence in support of previous proposals that selection of targets defined in a top-down manner by a nonspatial property (e.g., color) may be implemented by selecting the location of any item with the target-defining property (Tsal and Lavie, 1988, 1993). Interac-

tions between spatial and nonspatial aspects of visual selection have now been observed in several neurophysiological studies (Treue and Martinez Trujillo, 1999; McAdams and Maunsell, 2000; Saenz et al., 2002). Event-related potentials and magnetic field recordings in humans further show that targets defined by nonspatial feature-based selection can subsequently lead to selection of the location of a likely target (Hopf et al., 2004). Moreover, in a recent study on monkeys, Toth and Assad (2002) recorded single-unit activities from the lateral intraparietal sulcus (area LIP), one possible homolog of the human PPC, while the monkeys selected an eye-movement based on the color or location of a visual cue. A number of LIP neurons were found to show color-selective responses when color became the task-relevant property for defining spatial selection, as here. Thus, there are several precedents for top-down selection by nonspatial properties leading to spatially specific selection (Quintana and Fuster, 1992, 1999). The present study directly establishes a role of the right human PPC in this.

Hemispheric asymmetry and questions for future research

The present results establish a key role for the right (but not left) human PPC in top-down visual selection. Such apparent hemispheric asymmetry is commonly found in human studies of attentional control (unlike more symmetric patterns in nonhuman primates), with lesion evidence (Sterzi et al., 1993; Vallar, 2001) and neuroimaging evidence (Vallar et al., 1999; Fink et al., 2001) from humans both suggesting some form of right-hemisphere specialization for spatial selection. The exact reasons for such asymmetry in the human brain remain an enduring issue, with suggestions including left-hemisphere specialization for language, as well as possible right-hemisphere specialization for representing both sides of space rather than just contralateral space (Heilman and Van Den Abell, 1980; Mesulam, 1999; Driver et al., 2004). On the latter point, it may be noteworthy that here right PPC rTMS did affect both sides of space, albeit in opposite ways (disrupting top-down selectivity on the left but enhancing it on the right, in bilateral row displays). In any case, the present evidence goes beyond previous clinical and neuroimaging observations by showing directly that transient disruption of right PPC can affect the efficiency of just top-down control (but not other TVA parameters) in a spatially specific manner. In contrast, left PPC rTMS had no such effect. Indeed, here we did not find a site in which rTMS disrupted top-down control for right hemifield (left PPC rTMS had no effect on this, whereas right PPC rTMS enhanced it).

Future work could apply the present combination of techniques (i.e., TVA analysis of partial report with on-line rTMS applied to specific sites) to determine the roles of other brain regions in each of the TVA parameters. Whereas rTMS to right PPC did not provide a complete “knock-out” of top-down control (but rather a spatial modulation of this, with disruption for the left hemifield and enhancement for the right hemifield), stimulation of more frontal regions [e.g., frontal eye fields (Grosbras and Paus, 2002; Muggleton et al., 2003; O’Shea et al., 2004; Schall, 2004)] might conceivably do so.

Conclusion

The present study combined rTMS with TVA analysis in a partial-report paradigm. The results directly confirm a role for right PPC in spatially specific aspects of top-down visual selection, as assessed by the TVA approach, even when the targets to be selected are defined by a nonspatial property such as color.

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