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Facilitation of bottom-up feature detection following rTMS-interference of the right parietal cortex

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ABSTRACT

In visual search tasks the optimal strategy should utilize relevant information ignoring irrelevant one. When the information at the feature and object levels are in conflict, un-necessary processing at higher level of object shape can interfere with detection of lower level orientation feature.

We explored the effects of inhibitory trains of transcranial magnetic stimulation (rTMS) on the right and left parietal cortex in healthy subjects performing two visual search tasks. One task (Task A) was characterised by an object-to-feature interference. The other task (Task B) was without such interference. We found that rTMS of the right parietal cortex significantly reduced reaction times (RTs) in Task A, where object recognition interferes with detection of orientation. This significant RT reduction was present only for the first 10 trials. Interestingly, right parietal rTMS had no effect on Task B. Moreover, rTMS of the left parietal cortex did not modify subjects' RTs in either task. Subjects' accuracy was equally affected by rTMS in both tasks over time.

We suggest that inhibition of the right parietal cortex by means of rTMS facilitates feature-based visual search by inhibiting the interfering feature binding and spatial attentional processes. This allows subjects to accomplish Task A faster.

1. Introduction

There is ample evidence that in a visual task, the decision-making processes take information from various sources or levels of information. At a lower level, the image feature level, information such as the orientation and colour of primitive image edges, are processed by the neural activities in the primary visual cortex (V1). At a higher level, various brain areas, including the parietal area, bind features into objects and extract object identities relying on spatial attention processes (Shafritz, Gore, & Marois, 2002; Treisman, 1998).

According to the type of a visual task, the optimal task strategy should best utilize the relevant information while ignoring the irrelevant information. For instance, as the identity of a letter is irrelevant to its colour, recognizing the letter at the object level is un-necessary for perceiving the colour feature of the letter strokes. When the information at the feature and object levels are in conflict, extra and un-necessary processing at the object level can interfere with a lower level feature detection task to substantially prolong RT.

In a recent visual search study (Zhaoping & Guyader, 2007; see Fig. 1) the authors explored this interference between object and feature levels. This study adopted a task to search for an uniquely oriented bar in an image of many identical "X" shapes. In all X shapes the oblique bars were uniformly oriented except for the target bar, which was oriented in the opposite direction. This unique orientation of the target bar, a feature level information, is detected by the primary visual cortex and its detection is sufficient for performance in the task. However, the identity of "X" is rotationally invariant at the object level. The recognition of its shape in a rotationally invariant manner makes the "X" containing the target bar non-distinct from the background "X"s. Consequently, the viewpoint invariant object level information, if not ignored, can camouflage the target bar. This interferes with the observers' decision based on the initial feature detection, resulting in a few seconds longer RTs than otherwise.

Extracting rotation invariant object identity information requires spatial attentional mechanisms (Stankiewicz, Hummel, & Cooper, 1998). Meanwhile, the utilization of the irrelevant object

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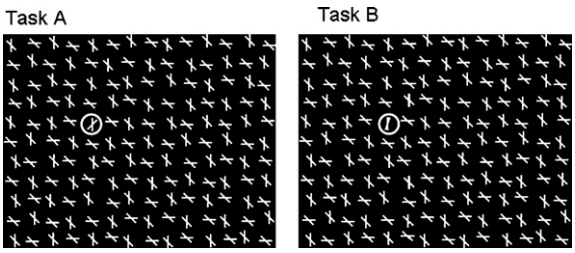

Fig. 1. Tasks A and B experimental stimuli. The search item containing the uniquely tilted target bar is circled.

identity information for a feature search task arises from a sub-optimal task strategy. It has been known that in visual tasks there are two different types of learning. An initial fast learning and a subsequent slower learning stages (Karni & Sagi, 1993). The fast learning stage requires approximately 10 trials, and this is a learning at a strategic level. Indeed, the object-to-feature interference, due to sub-optimal task strategy, is mainly apparent in the initial trials. The slow learning stage takes many more trials and even occurs over several days. This slow learning presumably refines the processes involved in extracting task relevant information.

Based on these observations, one can make the following prediction: if the brain area responsible for spatial attentional control or for binding the vertical bar with the oblique one to become an object (i.e. "X") is temporarily disabled, for example with TMS, then the observers should become faster. By disabling the binding and/or spatial attention, one prevents steps necessary to recognize the object shape in a rotationally invariant manner (Stankiewicz, Hummel, & Cooper 1998), which creates interference under a sub-optimal strategy (see also Thoma, Hummel, & Davidoff, 2004). This facilitation of RTs should be particularly noticeable for the first 10 trials, before the completion of the fast learning stage for a better strategy to ignore the task irrelevant object identity information.

A different prediction can be made if the object containing the target oblique bar is no longer a rotated version of the non-target X shapes. The object level information is no longer in conflict with the task relevant feature level information (Zhaoping and Guyader, 2007). Thus, there should be no object-to-feature interference resulting in longer RTs. We predicted that for this type of task the performance should remain unchanged following rTMS in brain areas involved in object level processing.

Previous studies have suggested that the inferior temporal (IT) cortex of the monkeys (Logothetis, Pauls, & Poggio, 1995; Rolls, 2003; Tanaka, 2003), and lateral occipital cortex of humans are involved in processing object shapes (Grill-Spector, Kourtzi, & Kanwisher, 2001; Kourtzi & Kanwisher, 2001). Although the responses in these brain areas to objects are insensitive to sizes and positions of objects, they stay invariant only to small rotations of object images, suggesting that brain areas responsible for the rotational invariance are mainly somewhere else. Behavioral data suggest that spatial attention is involved for mirror reflection invariant object recognition (Stankiewicz et al., 1998), though the brain areas responsible have not been narrowed down. Previous work using fMRI has suggested that the right parietal cortex is involved in feature binding and spatial attention (Shafritz et al., 2002). Therefore, one could predict that interference with the activity of this brain region could paradoxically facilitate performance on a visual search task suffering from object-to-feature interference. Moreover, we were interested to study whether our rTMS procedure has its biggest effect only or mainly in the initial 10 trials, as predicted by the observation that the interference arises from a sub-optimal task strategy assumed to be correctable by a fast learning.

2. Subjects and methods

2.1. Experimental investigation

The experimental investigation comprised two different experiments: experiment 1 and experiment 2. In both experiments we investigated the effect of right rTMS on two visual search tasks as depicted in Fig. 1. In both tasks, the target bar can be detected by its unique orientation in the image. However, in Task A, the target bar is in an 'X' shaped object identical in shape to all background 'X's, making Task A susceptible to object-to-feature interference, whereas Task B is free from the interference since the object containing the target bar has an unique shape in the image. In experiment 1 the target was always present, while in experiment 2 the target was present only in 50% of trials.

Two different subjects groups were used for each experiment. However, both experiments used the same type of stimuli, tasks and procedures.

2.2. Participants

In experiment 1 we used a group of 28 healthy right-handed subjects (mean age: 23 ± 2 years). Subjects were randomly assigned in two groups, according to the hemisphere stimulated: right hemisphere ($N = 14$) and left hemisphere group ($N = 14$).

In experiment 2 we used a group of 14 healthy right-handed subjects (mean age: 21.3 ± 2.8 years). Subjects had normal or corrected to normal vision and were naive to the purpose of the study. For both experiments subjects gave their written informed consent for participation in the experiments.

3. Stimuli

The stimuli used for tasks A and B differ only in the shape of the object containing the target bar which is always uniquely oriented in the image. A task A display consists of 'X'-like shapes, each made of an oblique bar intersecting a vertical or horizontal bar at 45°. The target oblique bar is tilted in the opposite direction to the oblique bars of the distractors. In task B, the target oblique bar intersects the vertical or horizontal bar at only 20°. This makes the 'X' containing the target bar uniquely shaped, so the pop-out of the target bar is free from the object-to-feature interference (see Fig. 1).

The subjects were informed about the uniquely oriented target bar and that this unique orientation could be randomly tilted to the left or right in each trial.

Stimulus displays, viewed at a distance of 40 cm, had 660 object items. Each item had a position randomly displaced, up to ±0.24° visual angle, horizontally and vertically from its corresponding position in a regular grid of 22 rows × 30 columns, spanning correspondingly 34° × 46° in visual angle. Each stimulus bar was 0.12° × 1.1° in visual angle and 48 cd (candela)/m^2 in brightness. The background was black. The target location was randomly one of those closest to the circle of about 15° eccentricity, and beyond 12° of horizontal eccentricity, from the display center. Stimuli stayed on the screen until subjects' response. The fixation stimulus was a bright cross at the display center (Zhaoping & Guyader, 2007).

3.1. Procedures

For both experiments, there were two experimental sessions. One experimental session was without rTMS stimulation, we termed this session baseline. The other session included rTMS stimulation before stimulus presentation, we termed this session rTMS session.

The order of these two sessions was counterbalanced between subjects. There was an appropriate two hours delay to allow for the rTMS effects to wash out when the baseline session was performed after the rTMS session.

Subjects were asked to search among 660 object items for the target item. In experiment 1, they were asked to press a left or right button with right index and middle fingers respectively to indicate whether the target was in the left or right half of the display. In experiment 2, they were asked to press a left or right button with

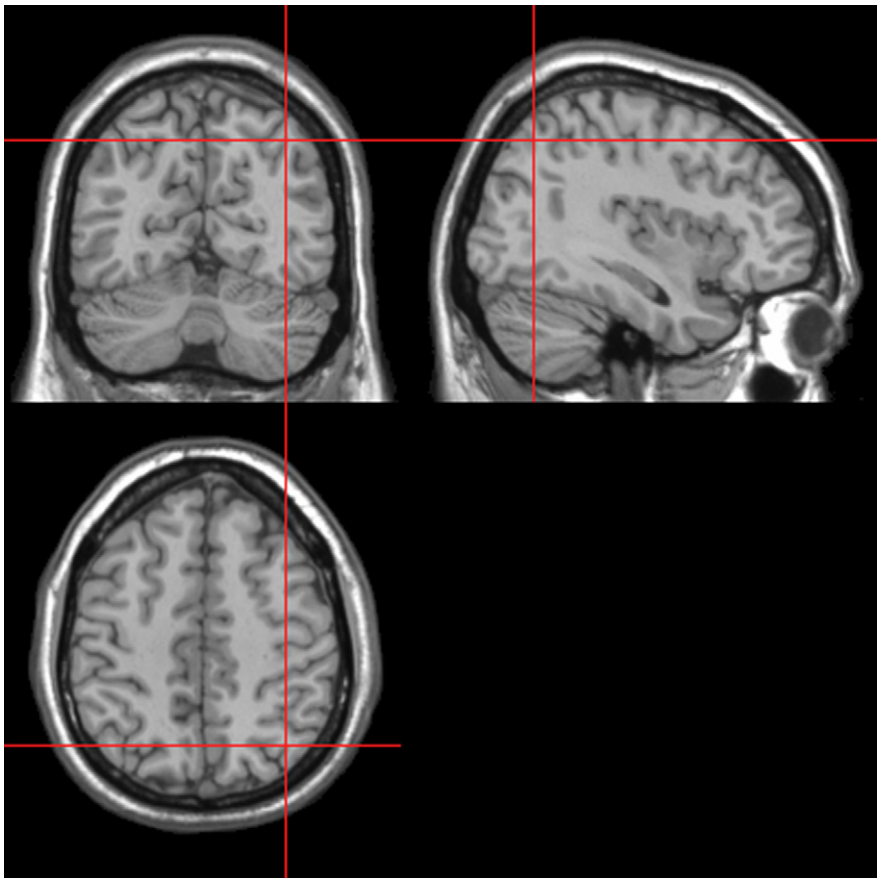

Fig. 2. Coronal (top-left), sagittal (top-right) and axial (bottom) MRI-constructed stereotaxic template of a representative subject indicating the parietal site of stimulation in the right hemisphere (Tailarach coordinates: 38*x* −65*y* 48*z*, corresponding to the right IPS; coordinates of the homologous left parietal site, not shown, were: −39*x* −66*y* 48*z*.

right index and middle fingers respectively to indicate whether the target (target-present trials) was present or absent (catch trials).

There was a training phase before each session in each experiment. In the training phase there were a total of 7 trials comprising both tasks A and B. The training phase was immediately followed by either the baseline or the rTMS sessions.

In experiment 1, subjects viewed 80 stimulus display for each session (baseline and rTMS), with 40 trials for task A and 40 trials for task B. The trials from the two tasks were randomly interleaved in each session. In experiment 2, subjects viewed 40 stimulus display for each session, with 20 trials for task A and 20 trials for task B randomly interleaved. For both tasks A and B there were 10 trials in which the target was present and 10 catch trials in which the target was absent. Target-present and catch trials were randomly interleaved. Response accuracies and reaction times (RTs) were recorded for both experiments.

3.2. rTMS

rTMS trains at 1 Hz frequency and 600 s duration were applied using a MagStim Rapid 2 magnetic stimulator and a figure-of-eight coil (diameter: 70 mm).

In experiment 1, rTMS was applied over two scalp sites, corresponding to P3 and P4 positions of the 10–20 EEG system. In experiment 2, rTMS was applied only to the right parietal site (i.e. P4).

In both experiments, test locations for rTMS were also localized on the scalp by means of a neuronavigation system (Polhemus) using SofTaxic software and co-registering scalp locations to a brain template. The SofTaxic Navigator permits to compute an estimated volume of head MRIs in subjects for whom MRIs are unavailable. The estimated MRIs are calculated with a warping procedure, by acting on a template MRI volume on the basis of a set of points digitized from the subjects scalp. The digitized points are used to compute a subsequent set of reference points which are analogous to a set of points pre-localized on the scalp of the template. The warping procedure is performed using these two corresponding sets of reference points. According to this procedure, the parietal site was situated in the inferior parietal lobule, close to the posterior part of the intraparietal sulcus. This localization corresponds to that reported in previous investigations adopting three-dimensional MRI reconstruction (Herwig, Satrapi, & Schönfeldt-Lecuona, 2003; Koch et al., 2007; Rushworth & Taylor, 2006; see Fig. 2).

The target sites were marked on a tightly fitting Lycra cap worn by the subject, and the coil was maintained in that position for the duration of the experiment. The figure-of-eight coil was applied tangentially on the target scalp site, with the handle pointing posteriorly, so as to induce a current with posterior-to-anterior direction in the underlying brain areas.

The intensity of rTMS was at 90% of motor threshold, defined as the minimal TMS intensity able to elicit a motor twitch in the contralateral hand in 3/6 consecutive stimulations.

The average motor threshold values were $54 \pm 7.2\%$ in the left and $54.3 \pm 4.5\%$ in the right hemisphere ($p > 0.05$).

4. Results

4.1. Experiment 1

In this experiment, a trial was classified as an error if the subject localized the target in the wrong hemispace. An ANOVA was con-

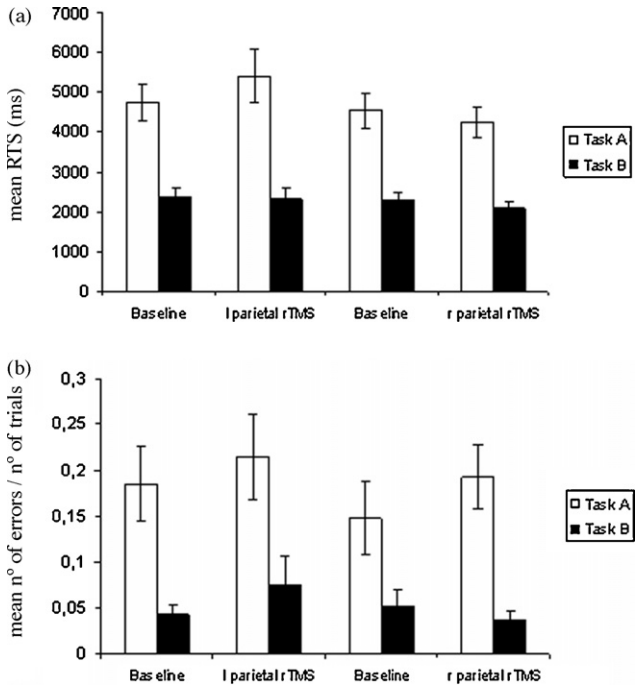

Fig. 3. Experiment 1. Baseline and post-rTMS performance for all trials (40 trials for task A and 40 trials for task B) in each session. (a) RTs; (b) Fraction of errors (mean number of errors/number of trials). In each panel, the left part of the figure represents left (l) parietal TMS and the corresponding baseline condition, and the right part of the figure represents right (r) parietal TMS and the corresponding baseline condition.

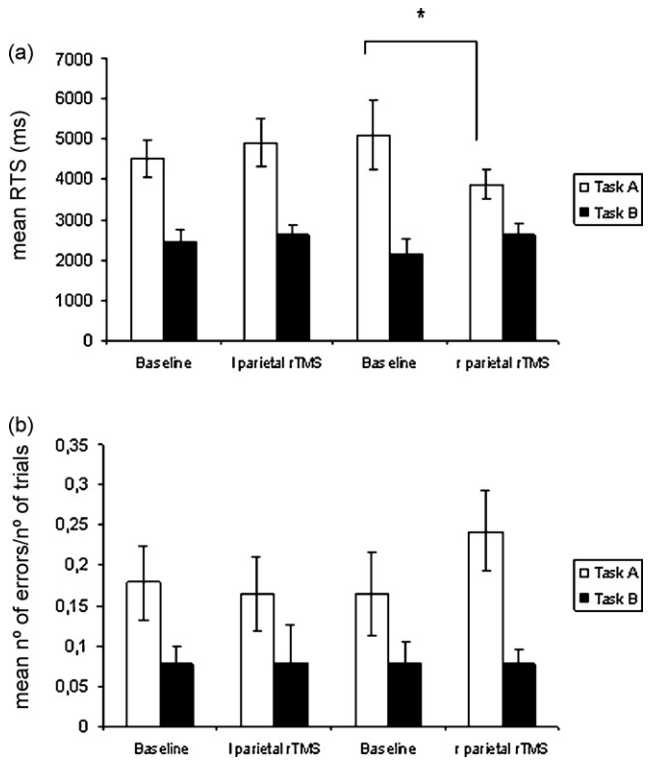

Fig. 4. Experiment 1. Baseline and post-rTMS performance in the first block of 10 trials of task A and 10 trials of task B. (a) Mean RTs; (b) fraction of errors (mean number of errors/number of trials). In each panel, the left part of the figure represents left (l) parietal TMS and the corresponding baseline condition, and the right part of the figure represents right (r) parietal TMS and the corresponding baseline condition.

ducted on RTs and errors on all trials, with task (A vs. B) and Session (Baseline vs. rTMS) as within-subject factors and Hemisphere (right vs. left) as a between-subject factor.

The average duration of the 80 trials was 6.49 ± 2.08 min. This was calculated as the summation of RTs the 40 A trials and the 40 B trials, including the time duration between trials at baseline.

4.2. RTs

The ANOVA showed only a significant main effect of Task ($F = 76.8$; d.f. = 1.26; eta square = 0.74; $p < 0.0001$). The other main effects of Hemisphere and Session as well as the three interactions (Session × Hemisphere; Task × Hemisphere; Session × Task × Hemisphere) were all not significant (Hemisphere: $F = 1.35$; d.f. = 1.26; eta square = 0.05; $p = 0.25$; Session: $F = 0.01$; d.f. = 1.26; eta square = 0.0007; $p = 0.89$; Session × Hemisphere: $F = 1.08$; d.f. = 1.26; eta square = 0.04; $p = 0.30$; Task × Hemisphere: $F = 0.005$; d.f. = 1.26; eta square = 0.0002; $p = 0.36$; Session × Task × Hemisphere: $F = 1.85$; d.f. = 1.26; eta square = 0.06; $p = 0.18$) (see Fig. 3a).

4.3. Errors

The ANOVA on number of errors showed only a significant main effect of Task ($F = 32.03$; d.f. = 1.26; eta square = 0.55; $p < 0.0001$). The other main effects of Hemisphere and Session, as well as the three interactions were all not significant (Hemisphere: $F = 0.39$; d.f. = 1.26; eta square = 0.01; $p = 0.53$; Session: $F = 2.88$; d.f. = 1.26; eta square = 0.10; $p = 0.10$; Session × Hemisphere: $F = 0.32$; d.f. = 1.26; eta square = 0.01; $p = 0.57$; Task × Hemisphere: $F = 0.10$; d.f. = 1.26; eta square = 0.003; $p = 0.75$; Session × Task × Hemisphere: $F = 2.79$; d.f. = 1.26; eta square = 0.09; $p = 0.11$) (see Fig. 3b).

4.4. Sequential block analysis

The results of the previous analysis clearly indicate that task A is more difficult than task B. It is likely that this increased difficulty is due to object-to-feature interference. It is well known that strategic learning may occur, usually completed after the first 10 trials (Karni & Sagi, 1993), to reduce this interference by ignoring the object information (Zhaoping & Guyader, 2007). We therefore decided to analyze the rTMS effects over time by investigating whether rTMS differentially affect the four different trial periods. We conducted four separate ANOVAs on the four sequential blocks of 10 trials on RTs and errors for both tasks A and B. Task and Session were within-subject and Hemisphere (right vs. left) was between-subject factor.

4.5. Trials 1–10

The average duration of the first 10 trials was 1.60 ± 0.85 min. This was calculated as the summation of RTs the first 10 A trials and the first 10 B trials, including the time duration between trials at baseline.

4.6. RTs

Significant main effects of Task and Session × Task × Hemisphere interaction were found ($F = 42.67$; d.f. = 1.26; eta square = 0.62; $p < 0.0001$; $F = 5.85$; d.f. = 1.26; eta square = 0.18; $p = 0.02$, respectively. See Fig. 4a).

Interestingly, right parietal rTMS selectively decreased RTs in Task A ($p = 0.005$) but not in Task B ($p = 0.23$). In contrast, left parietal rTMS did not modify RTs in either task (A: $p = 0.33$; B: $p = 0.70$).

The other main effects of Hemisphere and Session, as well as the three interactions were all not significant (see Appendix A).

4.7. Errors

A significant main effect only of Task was found ($F = 15.07$; d.f. = 1.26; eta square = 0.36; $p < 0.001$. See Fig. 4b). The main effects of Hemisphere, Session, as well as the four interactions were all not significant (see Appendix A).

4.8. Trials 11–20, 21–30 and 31–40

The average duration for the trials 11–20 was 1.57 ± 0.63 min, for the trials 21–30 was 1.48 ± 0.45 min and for the trials 31–40 was 1.42 ± 0.47 min. Again, this was calculated as the summation of RTs of the first 10 A trials and the first 10 B trials, including the time duration between trials at baseline.

Exactly the same RTs and error analyses adopted for the first 1–10 trials were used to analyze the remaining three sequential blocks of 11–20, 21–30, 31–40 trials.

The ANOVA on RTs showed only a significant main effect of Task for each of the three sequential blocks of trials (Trials 11–20: $F = 70.84$; d.f. = 1.26; eta square = 0.73; $p < 0.0001$; Trials 21–30: $F = 40.43$; d.f. = 1.26; eta square = 0.60; $p < 0.0001$; Trials 31–40: $F = 64.67$; d.f. = 1.26; eta square = 0.71; $p < 0.0001$). The other main effects of Hemisphere and Session as well as the four interactions for each of the three sequential trials were not significant (see Appendix A).

The ANOVA on number of errors showed only significant main effect of Task for each of the three sequential blocks of trials (Trials 11–20: $F = 20.08$; d.f. = 1.26; eta square = 0.43; $p = 0.0001$; Trials 21–30: $F = 25.87$; d.f. = 1.26; eta square: 0.49; $p < 0.0001$; Trials 31–40: Task: $F = 28.06$; d.f. = 1.26; eta square: 0.52; $p < 0.0001$). The other main effects of Hemisphere and, Session as well as the four interactions for each of the three sequential blocks of trials were not significant (see Appendix A).

4.9. Practice effects

The sequential block analysis clearly indicates that our significant enhancing effect on task A is present only in trials 1–10. In this analysis we entered data for the first 10 correct trials of tasks A and B either of baseline or of right parietal rTMS irrespectively as to the order of the two sessions. Thus, it could be argued that the improvement observed in task A may be due to some kind of "practice effect" due to the fact that the critical task A rTMS trials may have occurred after the baseline session.

We further analyzed the subjects' performance in baseline vs. right parietal rTMS for the first 10 trials using only the data of the session which was presented first (either baseline or rTMS). An ANOVA was conducted, with the factors Session (rTMS vs. Baseline) as a between-subjects and Task (A vs. B) as a within-subject factor.

The ANOVAs confirmed that rTMS significantly improved RTs only for Task A ($p = 0.02$). No significant effect was found for Task B.

For errors, the ANOVA showed a significant effect only for Task ($F = 13.9$; d.f. = 1.12; $p = 0.002$).

4.10. Learning analysis

To verify the presence of learning effects in task A in subsequent blocks of trials, we analyzed baseline performance in task A in the right rTMS group across the four sequential blocks of 10 trials. An ANOVA revealed a significant difference of the Block effect ($F = 3.98$; d.f. = 3.18; eta square = 0.40; $p = 0.02$). Mean correct RTs were 7261.5 ± 4475.4 ms in trials 1–10, 5963.9 ± 3180.3 ms in trials 11–20, 4382.7 ± 2308.8 ms in trials 21–30, 5258 ± 3208.5 ms in trials 31–40. RTs in trials 1–10 were significantly longer as compared with those in trials 21–30 ($p = 0.003$) and 31–40 ($p = 0.03$).

4.11. Speed–accuracy analysis

We investigated whether the enhancement in subjects' performance in trials 1–10 of task A following right parietal rTMS could be attributed to a speed–accuracy trade-off. We performed a regression analysis on ΔRTs on task A as dependent variable, and errors on task A in baseline and post right rTMS sessions as regressors. The Δ value was calculated by subtracting the baseline RTs from post-rTMS RTs.

Regression analysis was not significant [$F(2,11) = 0.01$; $p = 0.98$; $R^2 = 0.003$]. The RTs improvement in Task A following right parietal rTMS was not predicted by either baseline errors ($p = 0.88$) or post right rTMS errors ($p = 0.99$) in the same task.

4.12. Experiment 2

The results of experiment 1 showed a selective enhancing effect of right parietal rTMS on task A. It can be argued that this effect is due to right rTMS inducing an ipsilateral search bias. This may favour the initial processing of the right half of the display, enabling subjects to reach a more rapid decision as to whether the target was present or absent in the right visual field (anonymous reviewer's suggestion). In our experiment 1 a decision can be made merely on the presence or absence of a target in one hemi-field. This search bias may facilitate RTs. Moreover, since task A is more difficult than task B, any effect of right parietal stimulation might be expected to be more prominent for the harder task (as indeed suggested by experiment 1 results). We decided to address more directly this hypothesis with experiment 2. This experiment included target-absent trials, thus altering the pattern of response from left vs. right of experiment 1 to target-present vs. target-absent of this experiment.

We analyzed only RTs and errors obtained following right rTMS. A trial was classed as error if the subject did not localize the target in target-present trials or he/she localized the target in catch trials. An ANOVA was conducted on the first 10 trials with target-present for each Task, excluding target-absent ones. The within-subjects factors were Task (A vs. B) and Session (Baseline vs. rTMS).

4.13. RTs

We found significant effects for Task and Session $\times$ Task interaction (Task: $F = 11.94$; d.f. = 1.13; eta square = 0.48; $p < 0.01$; Session $\times$ Task: $F = 4.78$; d.f. = 1.13; eta square = 0.27; $p = 0.04$). Post hoc analysis replicated and extended the results of experiment 1. Indeed, we found that right parietal rTMS significantly decreased RTs only in Task A ($p = 0.01$). No effect was found in Task B ($p = 0.95$). Fig. 5 depicts mean RTs for Tasks A and B at baseline and following right rTMS.

4.14. Errors

Overall subjects were very accurate in this experiment. The mean number of baseline errors was 0.57/10 (SD = 0.64) for Task A and 0.28/10 (SD = 0.46) for Task B. The mean number of post-rTMS errors was 0.71/10 (SD = 0.91) for Task A and 0.21/10 (SD = 0.42) for Task B. The factors Session, Task and the interaction Session $\times$ Task were not significant (see Appendix A).

5. Discussion

In our study we investigated the effect of right and left parietal rTMS on two different visual search tasks (A and B). Both tasks are unique feature search tasks, with task A but not task B susceptible to the object-to-feature interference. The results of our two experiments together with our learning analysis, demonstrated that right

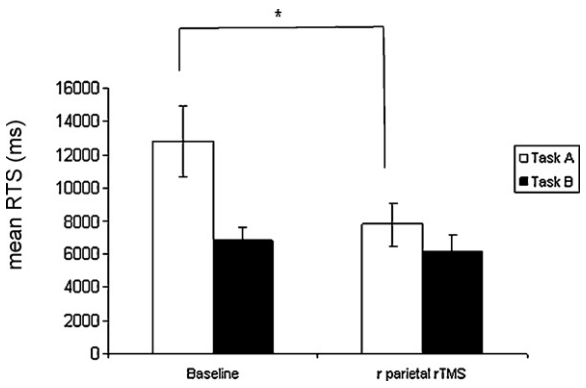

Fig. 5. Experiment 2. Baseline and post-rTMS RTs in the first block of 10 trials of Task A and 10 trials of Task B.

rTMS selectively facilitates performance in task A by significantly reducing RTs. This significant RT reduction was present only for the first 10 trials, as indicated by our sequential block analysis. Interestingly, we found that right parietal rTMS had no effect on RTs on task B. Moreover, left parietal rTMS did not affect RTs in either task. Our analysis of subjects' accuracy revealed that it was unaffected by rTMS in both tasks for the first 10 trials.

Our reported reduction of RTs for the first 10 trials of task A raises the question of whether there may be a speed-accuracy trade-off. However, when we analyzed RTs and errors with multiple regression analysis, we found that the RTs improvement in task A was not predicted by the number of errors in the same task. Therefore it is unlikely that a speed–accuracy trade-off was the basis for the RTs reduction in task A.

It could be argued that task A's RT reduction following right parietal rTMS is due to an ipsilateral search bias favouring initial processing of the right half of the display. This potential spatial bias may have enabled subjects to reach a more rapid decision regarding as to whether a target was present in the right or left visual field in experiment 1. However, we still found a significant RT reduction in experiment 2 following right parietal rTMS. This experiment contained catch trials at difference with experiment 1, altering the subjects' pattern of responses from left vs. right to target-present vs. target-absent. Therefore, RTs facilitation cannot be accounted in terms of a spatial bias.

Our findings that right parietal rTMS selectively facilitates performance in a feature search task susceptible to object-to-feature interference support previous TMS and neuroimaging studies suggesting that right parietal cortex is involved in a wide variety of visual search tasks, some of them involving spatial localization and conjunction-based search (e.g. Ashbridge, Walsh, & Cowey, 1997; Donner et al., 2002; Ellison, Rushworth, & Walsh, 2003; Ellison, Schindler, Pattison, & Milner, 2004; Leonards, Suneart, Van Hecke, & Orban, 2000; Muggleton, Cowey, & Walsh, 2008; Nobre, Coull, Walsh, & Frith, 2003; Rosenthal et al., 1996; Walsh, Ashbridge, & Cowey, 1998).

It has been suggested that the right parietal cortex also controls spatial attention and feature binding during visual search tasks (e.g. Shafritz et al., 2002; Treisman, 1998). This hypothesis is supported by TMS and neuroimaging studies showing that parietal cortex is involved in different top-down modulations of the visual cortical areas (e.g. Kalla, Muggleton, Juan, Cowey, & Walsh, 2008; Schenkluhn, Ruff, Heinen, & Chambers, 2008; Silvanto, Muggleton, Lavie, & Walsh, 2009; however, for contrasting findings see Hung, Driver, & Walsh, 2005). For example, Ruff et al. (2008) reported that TMS of the right but not left parietal cortex leads to strong changes in fMRI bold activity in V1–V4 regions. Hodsoll, Mevorach, & Humphreys (2009) argued that the right parietal cortex plays a role in modulating top-down and bottom-up attentional effects. Neuroimaging studies have reported right parietal cortex activation in tasks requiring feature binding (Corbetta, Shulman, Miezin, & Petersen, 1995; Petersen et al., 1994).

The spatial attention and feature binding processes supported by the right parietal cortex are often considered a prerequisite for achieving rotational invariant object recognition (Stankiewicz et al., 1998; Treisman & Gelade, 1980). In our view, it is the rotational invariant object recognition that causes interference to a feature detection process carried out by the primary visual cortex (Li, 2002), as in our task A (Zhaoping & Guyader, 2007). Inhibition of the right parietal cortex by means of rTMS facilitates feature-based visual search by inhibiting the interfering processes of feature binding. This allows subjects to accomplish task A faster due to the reduction of interference by a sub-optimal strategy which uses the object identity information requiring feature binding.

It should be noted that our reported facilitatory effect is present only for the first 10 trials of task A. According to the previous literature, 10 trials are comparable with the number of trials needed for fast learning (Karni and Sagi, 1993) of a better task strategy to ignore the irrelevant object identity information. Before the effect of this fast learning is substantial, the contribution of the object information to the task decision should be more devastating. A possible speculation is that any inhibition of the interfering object processes, such as by the rTMS stimulation, should be more effective during the earlier trials before the fast learning is substantially completed.

Our interpretation that rotational invariant object recognition causes interference in task A does not imply that the right parietal cortex is the neural region mediating rotational invariant object recognition. Indeed, there is evidence suggesting that the parietal cortex is involved in viewpoint-dependent object processing. Neuroimaging studies showed that the intraparietal sulcus and surrounding areas show orientation-dependent adaptation effects (James, Humphrey, Gati, Menon, & Goodale, 2002; Valyear, Culham, Sharif, Westwood, & Goodale, 2006). Lesion studies showed that parietal lobe damage impairs the ability to discriminate object orientation, resulting in orientation-invariant object identification and the ability to recognize unusual views of objects (Harris, Harris, & Caine, 2001; Karnath, Ferber, & Bulthoff, 2000; Turnbull, Beschin, & Della Sala, 1997; Warrington & Taylor, 1973). Interestingly, a recent TMS study reported that right parietal TMS applied during performance of object orientation judgment or object identification tasks impaired orientation judgments, but facilitated object identification (Harris, Benito, Ruzzoli, & Miniussi, 2008). This study suggested that the right parietal cortex has a direct role in processing the spatial attributes of objects and an indirect role in object recognition. In our tasks, the effect of right parietal cortex rTMS should be caused by the role of this brain region in feature binding and spatial attention processes which are necessary to achieve viewpoint invariant object recognition (Corbetta et al., 1995; Shafritz et al., 2002; Stankiewitz et al., 1998; Treisman and Gelade, 1980; Treisman, 1998).

The results of the present study highlight the efficacy of transcranial magnetic stimulation not only as a complement to other spatial and temporal imaging techniques but also as a neurorehabilitation strategy. In this field, the inhibitory effect of specific rTMS trains can reveal paradoxical functional facilitations of behavior, due to the inhibition of areas that exert an inhibitory control on that behavior (Kapur, 1996). According to our results, one can predict that patients with focal lesions of the right parietal cortex may not find feature search tasks with confusing object level information, such as our task A, harder than feature search tasks without object-to-feature interference, such as our task B.

Appendix A.

In this appendix we are depicting all the non-significant results obtained for RTs and errors on the sequential block analysis of experiments 1 and 2.

A.1. Experiment 1

A.1.1. Trials 1–10

A.1.1.1. RTs. Hemisphere: $F = 0.15$; d.f. = 1.26; eta square = 0.006; $p = 0.70$; Session: $F = 0.01$; d.f. = 1.26; eta square = 0.0007; $p = 0.88$; Session × Hemisphere: $F = 1.08$; d.f. = 1.26; eta square = 0.04; $p = 0.30$; Task × Hemisphere: $F = 0.005$; d.f. = 1.26; eta square = 0.0002; $p = 0.94$; Session × Task: $F = 3.33$; d.f. = 1.26; eta square = 0.11; $p = 0.08$.

A.1.1.2. Errors. Hemisphere: $F = 0.15$; d.f. = 1.26; eta square = 0.006; $p = 0.69$; Session: $F = 0.72$; d.f. = 1.26; eta square = 0.02; $p = 0.40$; Session × Hemisphere: $F = 1.50$; d.f. = 1.26; eta square = 0.05; $p = 0.23$; Task × Hemisphere: $F = 0.72$; d.f. = 1.26; eta square = 0.01; $p = 0.57$; Session × Task: $F = 0.72$; d.f. = 1.26; eta square = 0.02; $p = 0.44$; Session × Task × Hemisphere: $F = 1.26$; d.f. = 1.26; eta square = 0.04; $p = 0.27$ (see Fig. 4b).

A.1.2. Trials 11–20

A.1.2.1. RTs. Hemisphere: $F = 0.01$; d.f. = 1.26; eta square = 0.001; $p = 0.89$; Session: $F = 0.0001$; d.f. = 1.26; eta square = 0.0001; $p = 0.98$; Session × Hemisphere: $F = 2.22$; d.f. = 1.26; eta square = 0.079; $p = 0.15$; Task × Hemisphere: $F = 0.006$; d.f. = 1.26; eta square = 0.0001; $p = 0.94$; Session × Task: $F = 0.11$; d.f. = 1.26; eta square = 0.004; $p = 0.74$; Session × Task × Hemisphere: $F = 1.38$; d.f. = 1.26; eta square = 0.05; $p = 0.25$.

A.1.2.2. Errors. Hemisphere: $F = 0.74$; d.f. = 1.26; eta square = 0.02; $p = 0.39$; Session: $F = 3.55$; d.f. = 1.26; eta square = 0.12; $p = 0.07$; Session × Hemisphere: $F = 0.48$; d.f. = 1.26; eta square = 0.01; $p = 0.49$; Task × Hemisphere: $F = 0.004$; d.f. = 1.26; eta square = 0.0001; $p = 0.95$; Session × Task: $F = 0.32$; d.f. = 1.26; eta square = 0.01; $p = 0.57$; Session × Task × Hemisphere: $F = 1.56$; d.f. = 1.26; eta square = 0.05; $p = 0.22$.

A.1.3. Trials 21–30

A.1.3.1. RTs. Hemisphere: $F = 3.76$; d.f. = 1.26; eta square = 0.12; $p = 0.06$; Session: $F = 0.37$; d.f. = 1.26; eta square = 0.01; $p = 0.54$; Session × Hemisphere: $F = 0.17$; d.f. = 1.26; eta square = 0.007; $p = 0.68$; Task × Hemisphere: $F = 2.35$; d.f. = 1.26; eta square = 0.08; $p = 0.13$; Session × Task: $F = 3.68$; d.f. = 1.26; eta square = 0.12; $p = 0.06$; Session × Task × Hemisphere: $F = 0.26$; d.f. = 1.26; eta square = 0.01; $p = 0.60$.

A.1.3.2. Errors. Hemisphere: $F = 0.64$; d.f. = 1.26; eta square = 0.02; $p = 0.43$; Session: $F = 3.28$; d.f. = 1.26; eta square = 0.11; $p = 0.08$; Session × Hemisphere: $F = 2.04$; d.f. = 1.26; eta square = 0.07; $p = 0.16$; Task × Hemisphere: $F = 0.18$; d.f. = 1.26; eta square = 0.007; $p = 0.67$; Session × Task: $F = 0.67$; d.f. = 1.26; eta square = 0.02; $p = 0.42$; Session × Task × Hemisphere: $F = 1.005$; d.f. = 1.26; eta square = 0.03; $p = 0.32$.

A.1.4. Trials 31–40

A.1.4.1. RTs. Hemisphere: $F = 3.41$; d.f. = 1.26; eta square = 0.11; $p = 0.08$; Session: $F = 0.008$; d.f. = 1.26; eta square = 0.0001; $p = 0.93$; Session × Hemisphere: $F = 0.24$; d.f. = 1.26; eta square = 0.009; $p = 0.63$; Task × Hemisphere: $F = 3.44$; d.f. = 1.26; eta square = 0.11; $p = 0.08$; Session × Task: $F = 0.79$; d.f. = 1.26; eta square = 0.03; $p = 0.38$; Session × Task × Hemisphere: $F = 0.15$; d.f. = 1.26; eta square = 0.006; $p = 0.70$.

A.1.4.2. Errors. Hemisphere: $F = 0.009$; d.f. = 1.26; eta square = 0.0001; $p = 0.93$; Session: $F = 0.04$; d.f. = 1.26; eta square = 0.002; $p = 0.83$; Session × Hemisphere: $F = 1.148$; d.f. = 1.26; eta square = 0.04; $p = 0.29$; Task × Hemisphere: $F = 0.07$; d.f. = 1.26; eta square = 0.003; $p = 0.78$; Session × Task: $F = 1.22$; d.f. = 1.26; eta square = 0.04; $p = 0.28$; Session × Task × Hemisphere: $F = 0.0001$; d.f. = 1.26; eta square = 0.0001; $p = 1$.

A.2. Experiment 2

A.2.1. Trials 1–10

A.2.1.1. Errors. Session: $F = 0.13$; d.f. = 1.13; eta square = 0.01; $p = 0.72$; Task: $F = 3.70$; d.f. = 1.13; eta square = 0.22; $p = 0.07$; Session × Task: $F = 0.80$; eta square = 0.06; $p = 0.38$.

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