Differential and co-involvement of areas of the temporal and parietal streams in visual tasks.

Amanda Ellison[1] and Alan Cowey[2]

1. University of Durham, Cognitive Neuroscience Research Unit, Wolfson Research Institute, Queen's Campus, Stockton-on-Tees, TS17 6BH, UK

2. University of Oxford, Department of Experimental Psychology, South Parks Road, Oxford, OX1 3UD, UK

Address for correspondence:

Facsimile: +44-191-3340452

Telephone: +44-191-3340430

e-mail: amanda.ellison@durham.ac.uk

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Abstract

Transcranial magnetic stimulation (TMS) is particularly useful in teasing apart the contrasting contributions of different anatomical and functional systems in particular aspects of behaviour, for example the involvement of the dorsal and ventral visual streams in tasks involving the perception of distance, shape and colour. In order to investigate the dual involvement of two areas, namely right posterior parietal cortex (PPC) and lateral occipital cortex (LO), in a distance discrimination task, neural processing in both areas was concurrently disrupted using dual site TMS. Although there was no change in error rates, reaction time was significantly lengthened over that seen with TMS over either site alone. This additive effect indicates that both PPC and LO are concurrently active and essential for efficient processing of this task. The second experiment investigated the specificity of function within the ventral stream. Performance was assessed for distance and shape discrimination when TMS was applied to our original LO site and an area rostral to V5 but still part of the lateral occipital complex (rostral LOC) that is activated in form and colour discrimination. Performance deficits were restricted to TMS over LO; no significant impairment for either task followed TMS at the rostral LOC site.

Keywords: Ventral Stream, Dorsal Stream, visual discrimination, transcranial magnetic stimulation.

Introduction

The main cortical processing pathways that underlie visual perception and its motor consequences are often characterised as the dorsal and ventral anatomical streams. Functionally however, the two streams have attracted different terms, from Ungerleider and Mishkin's (1982) "What and Where" pathways to Goodale and Milner's (1992) "What and How" pathways. The latter appellation encompasses an occipito-temporal pathway involved in object and colour recognition and an occipito-parietal pathway terminating within the intraparietal sulcus and concerned with visuomotor transformations. Distinct from this pathway, but implicit to Ungerleider and Mishkin's model, is another area specialised for visuospatial computation and centred more inferiorly in the posterior parietal cortex. Patients with visual neglect caused by damage here have deficits in processing line bisection or landmark tasks. However, when such patients are asked to point to the centre of a screen or outlined square they can do so (Barltelomeo *et al.*, 2003) possibly, but still far from clearly, by making a visual discrimination based on shape rather than lateral extent and thereby recruiting their undamaged ventral stream.

We have previously investigated the specialisation of each of these streams by using transcranial magnetic stimulation (TMS) to disrupt cortical processing with respect to three tasks thought to probe functioning in one or other stream: a task requiring relative spatial distance discrimination, a task requiring shape discrimination, and a task requiring colour discrimination (Ellison and Cowey 2006). We probed the involvement of an area of the ventral stream, the lateral occipital cortex (LO), an area known to be important in object recognition (Ferber *et al.*, 2005; Avidan *et al.*, 2003; Learner *et al.*, 2002; Kourzi & Kanwisher, 2001) and compared the behavioural effect

of TMS to that seen when TMS is applied to right inferior posterior parietal cortex (PPC), known to have visuospatial specialisation (Ellison *et al.*, 2003; Bjoertomt *et al.*, 2002, 2008). We would have expected an involvement of PPC in the spatial distance discrimination task and an involvement of LO in the object discrimination and colour task. However, although the results revealed a dissociation between streams, it was not as clear-cut as previously thought. Neither area seemed to have an essential functional specialisation for the colour task, presumably because areas V4 and/or V8 are more ventral, beyond the effect of TMS, and are sufficient to subserve the colour task we used; and/or area LO is not critical to its processing (Cant & Goodale, 2007). Our results also showed that there are regionally separable processes in the brain for shape-based discrimination and a, albeit less clear, dissociation for a spatial discrimination. On the basis of a neuroimaging study, Fink *et al.* (1997) suggested that "object-based and space-based attention share a common neural mechanism in the parietal lobe". If this were the case, we should have seen involvement of the right PPC in both the object and spatial discriminations, which we did not. Instead, our finding suggests that spatial discrimination recruits a mechanism used in object processing but not vice-versa.

Perhaps the dorsal and ventral pathways are processing our "distance" task in different ways, i.e. PPC is basing its analysis on visuospatial properties but LO is using shape information to complete the task. It is also possible that the two pathways interact in order to process the task, with LO providing shape information and PPC spatial information. Both of these hypotheses are consistent with the behavioural effect of increased reaction times with TMS at either site. If the relative timing of involvement of PPC and LO could be determined, the results should help in deciding

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between these two possibilities. If LO and PPC are simultaneously active in parallel they would seem to be processing the task according to their own functional specialisation, be it for shape or space. But if consecutive peaks of TMS interference are seen, it is more likely that LO and PPC work in sequence in order to accomplish the task. Ellison and Cowey (2007) investigated this formulation by using double pulse TMS to provide a brief disruption window of 100ms. Results showed that TMS over LO has an earlier and significantly greater peak of activation than that over PPC, indicating that the ventral stream has a greater earlier involvement in the processing of this visuospatial task and consistent with our previous conclusion that its involvement is based on the shape processing for which the ventral stream is specialised (Kourzi & Kanwisher, 2001; Malach *et al.*, 1995). Accordingly, and in contrast, the later involvement of PPC is presumably based on its established visuo-spatial specialisation (Ellison *et al.*, 2003; Bjoertomt *et al.*, 2002, 2008).

An apparent paradox of our previous studies however is that we were unable to establish any performance deficit (i.e. decreases in accuracy) in these tasks despite robust and replicable reaction time effects. One reason why this may be so in the visuospatial distance discrimination is the joint ability of PPC and LO to process the task in their different ways, thereby making subjects slower to process the task but without abolishing their ability to do it. Therefore, Experiment 1 in the present study was designed to disrupt processing concurrently at both PPC and LO. This should have the effect of increasing reaction times more than that induced by TMS over either site alone, and could even impair the accuracy of response. Alternatively, if reaction times are not significantly greater with dual site TMS this would indicate that LO and PPC do not have an additive effect on processing of this distance task and that

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each area is involved according to its specialisation i.e. information from both regions is not necessary to complete the task.

As several functional imaging experiments point to the activation of a further and more rostral region of lateral occipital cortex of the ventral stream in the discrimination of shape (Doninger *et al.*, 2000; Grill-Spector *et al.*, 1998; Grill-Spector *et al.*, 2001), Experiment 2 examines whether TMS above this region reproduces the effects of TMS over LO. Therefore, Experiment 2 examined this area's involvement in our original distance and shape discrimination.

Methods

Subjects

8 healthy subjects, aged 20-43 (4 females, 4 males) participated in Experiment 1. 10 healthy subjects (6 common to Experiment 1), aged 20-43 (5 females, 5 males) participated in Experiment 2. They were all right handed with normal or corrected to normal vision. Subjects gave their signed informed consent in accordance with the Declaration of Helsinki and with the approval of Durham University Ethics Advisory Committee, and could leave the experiment at any point. Subject selection complied with current guidelines for rTMS research (Wasserman 1998).

Stimuli

All stimuli were presented on a 32 cm x 24 cm VDU driven by a Pentium-4 PC programmed in E-Prime (Psychology Software Tools, Inc). Subjects sat 57.5 cm away from the screen with the centre of the screen at eye level. The subject's head and trunk sagittal midline were aligned with the centre of the screen, with head position controlled by a chinrest.

Visual Tasks

One visual task, involving a relative distance discrimination, was used in Experiment 1 and three visual tasks (distance, shape and colour) were used in Experiment 2.. However, the reaction times for the colour task had a high variance and although per cent correct performance was matched to that of the two other tasks the mean reaction times for colour were also much faster than for space and shape. For these reasons the results for colour, which was not central to the main point of the investigation have not been presented. The threshold for 80 per cent correct performance in each task had first to be determined, prior to any experimental TMS blocks, so that tasks were matched as closely as possible for difficulty. In all tasks one item was presented in the centre of the screen with two items presented at a lateral eccentricity, one either side of the horizontal midline as detailed below (see Figure 1). Each trial began with 500ms central fixation cross ($0.5°$ x $0.5°$) after which the three stimuli were presented for 500ms, one of them replacing the fixation cross. The background colour was grey (CIE: x = 0.268, y = 0.295) with a luminance of $37cd/m^2$. When the stimuli disappeared the entire screen instantly changed in luminance and a question box, asking the subject "which item was closer (or the same shape) as the central item, was presented in the centre, entirely covering the previous position of the three stimuli.

This box remained until the subject responded. It therefore also served to backward-mask the stimulus display, making it impossible for the subject to use any retinal persistence to solve the task. There was a 4000ms interval between trials. Task difficulty was titrated by making it progressively more or less difficult according to the following rule. Difficulty was modulated after each set of five trials. After five consecutive correct responses difficulty was increased by one step (steps are described in detail below in the description of each task). If two or more incorrect responses out of five were made, the difficulty was decreased by one step. If there was just 1 error in 5 trials there was no change. Performance was stabilised when performance reached 80% correct (4 out of five) in two subsequent sets. In the subsequent testing sessions subjects were asked to respond as quickly and as accurately as they could but without sacrificing accuracy for speed.

Distance Task:

Stimuli were presented as 3 green (11 cd/m^2, 1º x 1º) squares. One square was presented in the centre of the screen, the other two 5º to the left of the vertical midline. One square (either the top or the bottom at random) was always 3º above or below the horizontal midline. The other square was initially presented at a vertical eccentricity of 4 degrees from the horizontal meridian and progressively it approached it in 0.2º steps until the threshold for 80% correct was reached. The experimental value of the distance of the furthest object from the centre was then set at 0.2º more than the threshold value found. The subject was asked to respond by indicating which of the two eccentric squares was closest to the central square by pressing the bottom button on a keypad if the bottom item was closest and the top button if it was the top item. The top square was the closer item in 50% of trials, at random. See Figure 1.

Shape task:

Two shape sets comprised this task. The first set consisted of a central square (1º x 1º) and in the other set the central shape was an oblong of equal area, subtending 1.47º x 0.69º. Stimuli were presented in the same format as the distance task but position was fixed 5 degrees to the left of the vertical midline and 4º either side of the horizontal midline (see Figure 1). One of the eccentric shapes differed from the central shape by 0.5º in the x and y axis (in order to maintain equal area) initially. It approached the shape of the central item in 0.1 degree steps until threshold was reached for 80% correct. On half of the trials, at random, the central shape was the square and on the other half it was the oblong. The experimental value of the shape different from that in the centre was then set to be 0.1º larger than the threshold value found. The subject had respond by indicating which item was the same shape as the item in the centre by pressing the top or bottom button on a keypad as before The top item was the same shape in 50% of trials. See Figure 1.

FIGURE 1 about here please

TMS

Experiment 1:

Two Magstim™ SuperRapid magnetic stimulators (Magstim, Whitland, Carmarthenshire, Wales) were used to apply pulses at 10Hz for 500ms at 65% of the stimulator's maximum power (*i.e.* 1.3 Tesla). This level of stimulation is just greater than the intensity required to induce movement (when applied over motor cortex) or the perception of phosphenes (over primary visual cortex, V1). The TMS train of 5 pulses began at stimulus onset in each case.

TMS was applied simultaneously over two sites of the right hemisphere previously investigated in isolation: an area corresponding to lateral occipital cortex (LO) and posterior parietal cortex (PPC). LO was stimulated using a 50mm figure-of-eight branding iron coil. PPC was stimulated using a 70mm coil placed tangential to the skull, with the handle pointing forwards, parallel to the mid-sagittal plane. Both coils were held in place by the experimenters. These different coil sizes and configurations were used in order that the two coils could be positioned over occipito-parietal cortex of one hemisphere.

Right PPC was identified by using a hunting procedure with the hard conjunction task, as described in Ashbridge *et al.* (1997) in which 10 trials of TMS are given to each site in a 3 x 3 grid (adjacent points 1 cm apart) around a central point 9 cm dorsal to the mastoid-inion and 6cm lateral to the right. The "hotspot" for activation is denoted by a roughly 100ms increase in reaction time over the trials in which no TMS was administered. The position of this area as co-registered with cortical position using BrainSight software (Rogue Research™) is shown in Figure 1. The LO site was chosen in relation to area right V5 (generally corresponding to 3cm above the mastoid-inion and 5cm lateral to the right) which was then precisely identified by localising the area where a train of TMS pulses (10Hz, 500ms) elicited the strongest and most salient moving phosphenes (see Schenk *et al.*, 2005) at the lowest TMS intensity. LO was then calculated to be 1-1.5cm caudal on the skull in a direct line from there towards the inion. This area can be seen to correspond well anatomically with lateral occipital cortex. (see Figure 1).

A control site (vertex) was also stimulated to control for non-specific effects that may result from TMS being administered at two sites. In this, and the two following experiments, TMS was only administered *after* thresholds for 80% correct performance had been determined for each subject. During blocks of TMS the display parameters were never changed, i.e. the method of constant stimuli was used. Trials were administered in ten blocks of 40 trials each block randomised across subjects to minimise either order or practice effects; two blocks with sham TMS with a non-discharging coil held over both LO and PPC sites, two blocks with TMS over LO and PPC in each trial, two blocks with TMS applied over LO alone (and a non-discharging coil held over the PPC site), two blocks with TMS applied over PPC alone (and a non-discharging coil held over the LO site) and finally two blocks with TMS applied over either PPC or LO and vertex. In sham TMS, a coil discharged in close proximity to the subjects' right so that the subjective experience of the noise associated with a TMS pulse was the same as was the tactile experience of a coil placed on the head, however no pulse was administered to the brain. The testing session usually lasted no more than 1.5 hours.

Experiment 2:

One Magstim™ SuperRapid magnetic stimulator was used to apply pulses at 10Hz for 500ms at 65% of the stimulator's maximum power (*i.e*. 1.3 Tesla).TMS was applied over two areas using two 70mm figure-of-eight coils held in place by the experimenter and placed tangential to the skull with the handle pointing backward, parallel to the horizontal and mid-sagittal plane. The two areas of interest were LO (located via the procedure outlined in Experiment 1) and an area 1 – 1.5 cm rostral to V5 (which was located in the same manner as in Experiment 1 above). The same

downward angle of a tangent from V5 to inion for location of LO was employed to locate this site (rostral LOC).

Each of the tasks (distance and shape) were tested in blocks of 40 trials at each site (LO, rostral LOC) and there was also a block of sham TMS. The order of TMS condition and task was randomised within and across subjects to minimise practice effects.

Results

All data were included in accuracy analysis but for the analysis of reaction times outliers beyond ±2 standard deviations of the mean were excluded.

Experiment 1:

Thresholds

The mean threshold achieved across subjects in the distance task was a difference of 0.24º ± 0.17º for 80% correct. This led to a mean fixed distance of 0.40 ± 0.22 for the furthest square in the subsequent experimental sessions with real or sham TMS.

TMS effects

There was no significant difference between the effect of TMS on reaction times when it was applied (a) over LO alone or LO+vertex, or (b) when it was applied over PPC alone or PPC+vertex. Therefore in the subsequent analyses the results within each of (a) and (b) were collapsed.

A one-factor (TMS condition) repeated measures ANOVA revealed a significant difference across all TMS conditions [sham TMS, LO+PPC, LO, PPC] ($F_{(3, 21)} = 5.644$, $p = 0.005$). Subsequent paired t-tests reveal a significant effect of TMS in each condition (LO: $t = -3.794$, df = 7, $p = 0.007$; PPC: $t = 3.440$, df = 7, $p = 0.011$; LO+PPC: $t = -2.828$, df = 7, $p = 0.025$).

An investigation of the speed/accuracy trade-off across conditions was carried out using an Inverse Efficiency Analysis (median/proportion of correct responses: Townsend and Ashby, 1983). There was no significant difference in this value across

conditions as indicated by a one factor repeated measures ANOVA ($F_{(3, 21)} = 2.379$, p = 0.073).

Reaction times resulting from TMS at each site were normalised with respect to the baseline (sham) reaction time according to the following formula [TMS_x – sham TMS]/sham TMS x 100, where x denotes the TMS condition, in order to calculate the effect of TMS in each condition (see Figure 2) for comparison across conditions. There was a significant difference of TMS effect across conditions ($F_{(2,14)} = 4.853$, p = 0.025, see Figure 2).

FIGURE 2 about here please

The mean error rate ± standard error across all sites was 85.61 ± 0.50 and as can be seen from Figure 3, no significant differences were noted between conditions.

FIGURE 3 about here please

Experiment 2:

Thresholds

The mean threshold achieved across subjects in the distance task was a difference of 0.25º ± 0.14º for 80% correct. This provided a mean fixed distance of 0.39 ± 0.19 for the furthest square in the subsequent experimental task. In the shape task, performance reached threshold at a 0.09º ± 0.05º difference in shape, leading to a mean fixed 0.15º ± 0.08º difference in the experimental session. Across both tasks, the chosen stimulus values corresponded to about 90% correct in each subject to

maximise the effect of TMS on reaction time in each task without encountering the problem of ceiling effects.

TMS effects

There was no significant effect of TMS on error rates at either site in either task. However, a two factor (task [distance, shape] x TMS [LO, rostral LOC, sham]) repeated measures ANOVA revealed a main effect of TMS ($F_{(2, 18)} = 6.095$, p = 0.010) on reaction times. In order to further investigate these differences two paired t-tests were carried out per task. TMS over LO in both the distance task and shape task resulted in significant increases in reaction time (distance: t = -2.607, df = 9, p = 0.028; shape: t = -5.136, df = 9, p = 0.001).

Figure 4 about here please

A two factor (task [distance, shape] x TMS [LO, rostral LOC] repeated measures ANOVA carried out to investigate the effect of TMS over each site revealed a main effect of TMS ($F_{(2, 1)} = 14.067$, p = 0.005). Further post-hoc paired t-tests revealed that this results from a significantly greater effect on reaction times when TMS was applied to LO over that seen at the rostral LOC site in the distance task (t = 2.277, df = 9, p = 0.049) and the shape task (t = 4.151, df = 9, p = 0.002) when normalised reaction times were compared as above.

Discussion

Experiment 1 replicated our previous finding that TMS disrupts processing within right LO and PPC, by significantly lengthening reaction times in a visuospatial distance discrimination. Therefore both areas must be involved in the processing of this task, if only one area was necessary, no additive effect would be seen. What is the nature of their involvement? LO seems to have a functional specialisation for shape in agreement with neuropsychological results (Goodale *et al.*, 1994) and functional imaging (Kourtzi and Kanwisher, 2001; Malach *et al.*, 1995). It seems reasonable to assume that some shape based processing must contribute to how the brain computes the distance discrimination, thus reinforcing the dissociation reported by Bartelomeo and colleagues (2003) that when patients with left neglect are asked to point to the middle of a screen or shape they are unimpaired, presumably as a result of their intact ventral stream.

The current study sought to investigate the effect that simultaneous disruption to both areas LO and PPC would have on performance. Whilst a performance deficit in terms of accuracy was again absent, dual-site TMS does in fact further lengthen reaction times. This is additional evidence that PPC and LO are both necessary for the most efficient processing of this task. The finding cannot be explained by the fact that there were two discharging coils on the head at the same time as no significant difference was found between conditions when vertex plus either LO or PPC was also stimulated as a control site. Although it would seem that each area can process this task according to its functional specialisation, it may be that both areas must ideally be active in order to process this task quickly and efficiently. There is already tentative evidence for such a co-operative account from a timing study that found LO had a

greater and earlier peak of disruption than PPC in this task (Ellison & Cowey, 2007). The question remains however as to whether or not processing at PPC is contingent on this earlier information from LO.

Given that two areas specialised for the processing of this task were simultaneously disrupted, it might seem unusual that although response times were lengthened, accuracy in terms of per cent correct performance was unchanged, especially in view of performance decrements in earlier studies. Two notable examples of the latter are those of Corthout *et al*. (1999), in which a single pulse of TMS between 20-60ms or between 100 and 140ms post visual stimulus onset substantially impaired letter recognition, and Cowey *et al.* (2006) in which 10Hz repetitive pulse TMS over V5/MT impaired the discrimination of the direction of global motion in random dot kinematograms. The reason why effects on accuracy occurred in these two studies may stem from the nature of their design. Corthout *et al.* (1999) used very brief, single frame, display times, enabling one pulse to impair processing of a letter that was present for as little as 2-3 msec. Although Cowey *et al.* (2006) used six pulses of rTMS at 10 Hz for half a second, the moving elements in the half-second visual display were present for only one frame (45 msec) before 'jumping' to a new position on the next frame. This means that on half of the 12 frames the change of position would be disrupted by a pulse of TMS. In contrast, our displays were unchanging throughout the 500 ms display period. It is therefore reasonable to conclude that although TMS is disrupting processing for a brief period within each 100 ms inter-pulse-interval, it never completely interferes with the relevant information on which discrimination is based. Instead, it merely delays processing by the summed brief periods of disruption. This is also the reason why a 500ms period of 10 Hz TMS does

not result in an increase of 500 ms in reaction time (see Walsh and Cowey, 2000). In our tasks, it is also the reason why there is no impairment of accuracy in performance; the disruption merely introduces a time delay in the processing that leads to accurate performance.

A further possible explanation for TMS lengthening reaction times without impairing accuracy is that TMS does reduce the visibility of the stimuli and that retinal persistence after both the display and the TMS have ended allows the subject to continue gathering and analysing information for several ms. This was not possible in the present experiment because the stimuli were masked immediately after they disappeared by the question box in the centre of the screen. It is also possible that TMS simply slows the cortical processing being carried out in the area beneath the coil such that subjects reach their decision slightly later but still before the end of the display. However, neither of these possibilities affects the task dependent regional specificity that was revealed, nor the additive affect of dual-site stimulation.

Experiment 2 tested the specificity of area LO in the processing of tasks involving discrimination of distance and shape. Several recent studies (such as Grill-Spector *et al.*, 1998; Doninger *et al.*, 2000; but see Grill-Spector *et al.*, 2001 for review) provided evidence that the entire lateral occipital complex (LOC), from LO caudally to regions extending anteriorly and ventrally into posterior temporal cortex, respond more strongly to intact objects with clear shape interpretations than to control stimuli that do not depict clear shapes. The effects seen in our previous study (Ellison & Cowey, 2006) were replicated in the present study with TMS above area LO but not above rostral LOC. Indeed as Grill-Spector *et al.* (2001) point out, while LOC is

activated strongly in fMRI experiments when subjects view pictures of objects, this does not by itself prove that it is the locus in the brain that performs object recognition. We have now shown, via neuro-disruption, a dissociation of function between two distinct regions of the lateral occipital complex, namely area LO and rostral LOC.

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Figure Legends:

Figure 1: Tasks used (distance & shape) and anatomical localisation of magnetic stimulation sites (right LO, right PPC and rostral LOC).

Figure 2: Ecperiment 1: Reaction times in both sham and TMS conditions for the distance task and normalised TMS effects at each site ± SEM. * denotes significant difference to $p < 0.05$.

Figure 3: Experiment 1: Accuracy across all TMS conditions ±SEM.

Figure 4: Experiment 2: Reaction times ± SEM compared at each site of stimulation for both tasks and normalised TMS effects for both tasks at each site. * denotes $p < 0.05$; *** denotes $p < 0.001$).