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Individual variation in the location of the parietal eye fields: a TMS study

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Abstract Transcranial magnetic stimulation (TMS) is a popular technique that can be used to investigate the functional role of specific cortical areas with reference to a particular behavioural task. Single-cell recording studies performed in non-human primates have demonstrated that a region of the parietal lobe known as the lateral intraparietal area is specialized in the planning and control of saccadic eye movements. The homologue of this area in humans is termed the parietal eye fields (PEF) and its role in relation to saccades has previously been examined using TMS. In this paper individual variability in the functional effect of parietal TMS on the latency, amplitude and angular direction of visually-guided saccades has been assessed. By examining individual variability in the spatial distribution of scalp-based localization and brain surface anatomy and stereotaxic localizations of the PEF it was shown that the distances between the sites determined by these three methods were not negligible, which raises problems regarding the most reliable anatomical localization technique to use. An assessment of the effect of TMS on saccade metrics (latency, amplitude error and angular error) at a grid of locations over parietal cortex demonstrated a large amount of intra-individual variability in the site where TMS had most affected saccades, leading to the conclusion that there is individual variability in the functional effects of parietal TMS on saccade planning and execution. This study confirms the idea that it may be problematic to use a fixed scalp location for every participant in a study. It may in fact be more appropriate to determine TMS sites functionally on an individual basis if possible. This finding may guide further studies using TMS and saccade planning in order to optimize their capability to investigate this area and to draw meaningful biological conclusions.

Keywords Posterior parietal cortex · Transcranial magnetic stimulation (TMS) · Individual variability · Saccadic eye movements

Introduction

The posterior parietal cortex (PPC) is thought to play an important role in the representation of corporeal and peripersonal space and in the sensorimotor transformations associated with goal-directed movements (Andersen et al. 1997; Rizzolatti et al. 1997; Jackson 2001). Moreover, it has also been implicated in the allocation of visuo-spatial attention; patients with posterior parietal lesions have for example been shown to be disrupted in their ability to shift attention (Posner et al. 1984). Another function performed by the PPC is the integration of information from multiple sensory modalities in order to build up a multimodal representation of the relationship between our body and the world around us. This is necessary for the accurate planning of oculomotor movements, a process also thought to involve this area (Andersen et al. 1997; Colby and Goldberg 1999). This multimodal spatial representation is continually updated to take account of such oculomotor movements, thereby maintaining spatial constancy despite the constant shifts of gaze that we perform (Ross et al. 2001).

Within a specific region of the PPC, termed the ‘parietal eye field’ (PEF) salient stimuli have been shown to be coded in coordinate frames relative to the centre of gaze (Colby and Duhamel 1996). In non-human primates, this area is located in the inferior parietal lobe (IPL), on the lateral bank of the intraparietal sulcus (IPS) and is thought to be specialised for the spatial processing essential to the planning of saccadic eye movements (Andersen and Gnadt 1989; Andersen et al. 1992, 1997). Evidence to support this can be drawn from single-cell recording studies such as that by Duhamel et al. (1992) who showed that an eye movement that brings a previously flashed visual stimulus into the

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receptive field of a lateral intraparietal area (LIP) neuron, will cause this neuron to fire even though the stimulus is no longer present at the end of the eye movement. Inactivation studies in monkeys provide additional support for the importance of LIP in planning saccades in eye-centred coordinates (Snyder et al. 1997). Li et al. (1999), for example used muscimol injections to investigate the effects of a reversible inactivation of this area in macaques. An increased latency to targets in contralesional space was found for both visual and memory-guided saccades. Memory-guided saccades to contralesional space were also found to be hypometric, whereas for the visually guided saccades this metric was not affected.

The identification of a potential homologue of this area in humans has been attempted through the use of neuroimaging techniques, in particular fMRI (e.g. Heide et al. 2001; Sereno et al. 2001; Medendorp et al. 2003; Merriam et al. 2003). Transcranial magnetic stimulation (TMS) has also been used to functionally investigate the existence of a homologue of area LIP in humans. For instance there have now been a number of studies that have evaluated the effects of applying TMS to the PPC during the planning or execution of saccadic eye movements. Furthermore the majority of these studies have made use of analogous tasks to those used previously in monkey electrophysiology research to study the functional properties of area LIP (e.g. Merriam et al. 2003). The following studies have demonstrated an impairment of saccadic latency following parietal TMS (Elkington et al. 1992; Terao et al. 1998; Muri et al. 2000; Kapoula et al. 2001; Yang and Kapoula 2004) similarly studies by Oyachi and Ohtsuka (1995), Muri et al. (1996) and van Donkelaar and Muri (2002) have shown that saccade accuracy can also be affected by parietal TMS using memory-guided saccade tasks, reflexive saccades and anti-saccades.

While such studies have proven interesting in terms of furthering our understanding of parietal involvement in saccade planning and control, there are a number of problems associated with the use of TMS to investigate this function. For instance, a number of TMS studies have centred TMS stimulation at the P3 and P4 sites of the international 10–20 electrode system (e.g. Elkington et al. 1992; Muri et al. 1996, 2000; Kapoula et al. 2001; van Donkelaar and Muri 2002; Yang and Kapoula 2004). The locations of P3 and P4 can be determined in relation to landmarks on the scalp such as the vertex (e.g. van Donkelaar and Muri 2002), which is itself found using the nasion–inion line and the line between the preauricular points. Coil placement made on the basis of such bony landmarks may lead to problems in terms of the brain region targeted by TMS (Pascual-Leone et al. 1999) and does not allow for potential intraparticipant variability in either the anatomical location of the IPS in relation to the scalp, or, in the functionally effective site of stimulation. The use of digital co-registration to aid coil-positioning allows for individual differences in brain size and anatomy by employing each participant's magnetic resonance

imaging (MRI) scan to determine scalp location. Nevertheless, this technique still fails to take into account the functional significance of a cortical area in relation to task demands (Pascual-Leone et al. 1999).

An alternative to using a small number of fixed scalp locations, e.g. P3 and P4, is to systematically sample across a number of parietal locations. For example, Oyachi and Ohtsuka (1995) were able to identify, using a grid of stimulation sites and coregistration with 3D MRI, the most effective site of stimulation for a memory-guided saccade task. This site was taken as the one that produced the greatest decrease in saccadic accuracy; however, the existence of individual differences in the location of this site were not reported. Likewise Ashbridge et al. (1997) also used a 'hunting' paradigm for determining coil position on a visual search task. The behavioural effects of TMS to an initial scalp location are assessed, and this is then repeated as necessary at adjacent locations until either a 'hot spot' is determined, or a certain threshold number of trials is reached without a site being found for that participant. However, these authors also fail to discuss the existence or extent of individual variability observed using this technique.

In order to evaluate potential individual variability the current study assesses both the spatial distribution of sites determined using three different TMS localization procedures: EEG scalp locations, brain surface anatomy and stereotaxic coordinates, and also the potential existence of functional variability between participants. This is done through the use of a grid of stimulation sites, covering both left and right parietal cortices, similar to those used by Oyachi and Ohtsuka (1995) and Terao et al. (1998), and the effect of TMS on three saccade metrics: latency, amplitude and angular accuracy, are considered.

Methods

Study 1: Comparing localization techniques

Participants

Nine healthy adults (six females, mean age 25.44 years) underwent a procedure to compare sites determined by different localization techniques.

Procedure

This study compared within participant variability in the spatial distribution of scalp locations on the right hemisphere corresponding to the PEF as determined by three alternative localization procedures. The scalp location of the right hemisphere EEG site (P4 in the 10–20 international electrode system), based on that used in previous studies was defined as the spot 3 cm lateral and 3 cm posterior to the vertex. This corresponds to parietal cortex, and was compared against sites found using

two alternative procedures as follows. First, functional imaging studies (Luna et al. 1998; Heide et al. 2001; Sereno et al. 2001; Konen et al. 2004) suggest that the human homologue of PEF is located within or near to the intraparietal sulcus (IPS), although its precise location is still a matter of discussion. Therefore to examine individual variability in the spatial coordinates of the IPS, T1-weighted MRI scans were obtained, and the location of the IPS was defined visually for each participant based upon a comparison of the scan using MRIcro (<http://www.mricro.com>) with a neuroanatomical atlas showing the outer surface of the cerebral hemisphere (Fig. 517 in Gray 1918). The corresponding scalp location was then found using digital co-registration using MRIreg (<http://www.ple.cas.sc.edu/rorden/MRIreg.html>) and Minibird (Ascension Technology Corporation) (Fig. 1a, blue circle). fMRI studies have been used to locate the likely position of the IPS; such studies provide Talairach coordinates for the location of the right IPS (Fig. 1a, orange circle) based on group data of the most active voxels in tasks believed to involve the PEF. Therefore Talairach coordinates were obtained from a recent article examining the function of the right IPS (Mort et al. 2003): $X=36$, $Y=-58$, $Z=58$. The scalp location associated with these coordinates was then found in individual participants by performing digital co-registration as above. The distances between the scalp locations in each participant based on these three techniques were then measured.

Results

The mean distance between the visually-defined location of the IPS and the Talairach coordinates was 10.1 mm, between the visually-defined location and P4 it was 22.4 mm and between the Talairach coordinates and P4 this was 24.6 mm.

Study 2: Functional localization of PEF using transcranial magnetic stimulation

Participants

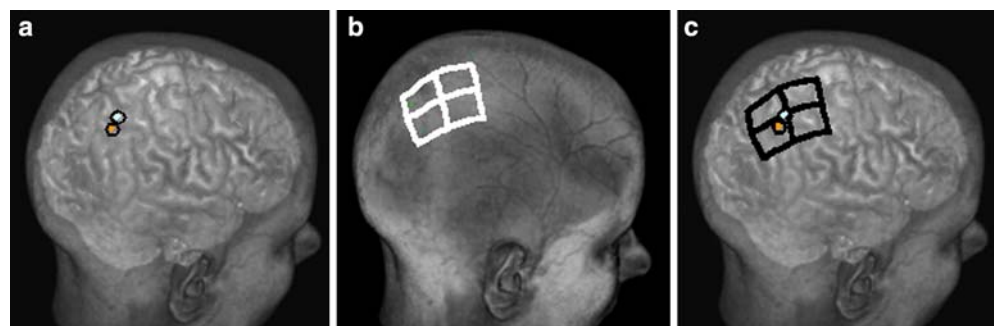
Ten healthy, right-handed adults (six females, mean age 21.2 years) participated in the TMS and eye-tracking task.

Experimental procedure

Two grids of stimulation sites were marked on surgical hoods worn by the participants. The nasion, inion and pre-auricular points were first marked on the hoods, and lines were then drawn through these to locate the vertex. The grids were 4 cm², and made up of 4×2 cm² squares, with a centre at P3 (on the left) and P4 (on the right), i.e. 3 cm lateral and 3 cm posterior to the vertex (Fig 1b). Nine points on each grid were used as stimulation sites, i.e. 3 on each row of the grid, each spaced 2 cm apart.

A Magstim Rapid TMS machine (The Magstim Company Ltd) with a double 70 mm coil was used to deliver TMS. During real stimulation the coil was placed flat and tangential to the scalp surface at each of the grid points; during sham TMS trials the coil was held perpendicular to the scalp with one end of the coil positioned at the centre of the grid on the hemisphere being tested. Thus although a magnetic field was no longer induced in the cortex the participants still heard the clicking sounds accompanying the magnetic pulse, and still felt the coil against their head. This procedure controls for the accessory cues provided by sensory inputs accompanying TMS, such as the click sounds, which may themselves affect saccadic reaction time (Terao et al. 1998); the contraction of muscles in the scalp, however, would not be felt during sham TMS. The wand was always held with the handle at the back of the head, so that the current would flow in a postero-anterior direction, which has been shown to be most effective for a Magstim Rapid coil (Kammer et al. 2001). Stimulation was set to 120% of the motor threshold determined for each participant. The order in which participants received left and right hemisphere stimulation was counterbalanced across individuals. Blocks of sham TMS were completed at the start and end of each session. Experimental trials involving stimulation at each of the nine sites within a hemisphere took place between the sham blocks. The order of stimulation for these sites was pseudo-randomly determined by computer. There were 18 blocks of real TMS, each consisting of 15 trials. Each sham block also contained 15 trials. Participants completed 300 trials in total. In all cases TMS was delivered before eye movement onset (see below).

Fig. 1 **a** Visually-defined ROI around the IPS (blue circle), and Talairach location (orange circle). **b** Diagram of grid location on the scalp for the right hemisphere. **c** Spatial location of grid on the brain in relation to the visually-defined IPS (blue circle) and Talairach coordinates for the IPS (orange circle)



Visual display

The stimuli were displayed using a 20 in Dell Trinitron Monitor with a spatial resolution of 800×600 pixels at a frame rate of 100 Hz and a viewing distance of 55 cm. Stimuli were generated using the MATLAB (The MathWorks) Psychophysics Toolbox (Brainard 1997; Pelli 1997). The stimuli consisted of a black central fixation cross and a single black target (3 mm diameter), that could appear on the screen at a variable orientation between 0° and 360°, pseudo-randomly determined by computer, at an amplitude of around 90 mm (based on a normal distribution with mean = 90 mm and standard deviation = 5 mm).

Oculomotor task

Participants were required to make a single visually-guided reflexive eye movement towards the target. A beep was used to signify the start of each trial, at which point a black fixation cross appeared on the screen against a grey background. This remained on until the eye-tracker determined that the participant was correctly focusing on the fixation cross, i.e. the pupil was directed to a region of the screen within 15 mm of its centre. Once this had been established a single black peripheral target was presented. Participants were instructed to execute a saccade to the peripheral target as soon as it was detected. One hundred milliseconds after the appearance of the target a double-pulse of 25 Hz TMS was delivered. The target remained on the screen for a total of 200 ms, after which the screen went blank and the eye tracker continued to record for a further 2 s. The trial then ended and the fixation cross reappeared for the start of the next trial.

Eye-movement recording

A pupil and dual first Purkinje image Video Eyetracker (Cambridge Research Systems) was used with a sampling frequency of 50 Hz and an accuracy of 0.5°–0.25° of visual angle. The calibration involved using a built-in procedure in which 20 small white dots (0.25° arc) appeared on the screen one at a time at positions around a 5×4 grid scaled to 90% of the display size. The dots remained on for 500 ms each and the accuracy of the participant in looking to each region of the screen was then assessed, this procedure was repeated if necessary until the participant had accurately foveated all of the positions on the grid. During the experimental session a video image of the eye could be seen by the experimenter

on a separate computer screen, this made it possible to monitor the participants' position in the eye-tracker throughout the progress of the experiment. Participants viewed the stimuli binocularly, although only the left eye was tracked. An EyeLock headrest (Cambridge Research Systems) attached to the eye tracker was used to keep participants' heads in position, and this was placed on a Vision Science height-adjustable workbench (Cambridge Research Systems).

Data analysis

Plots of eye movement traces using x and y coordinates from eye-position data recorded every 20 ms were analysed. Trials showing artefacts in the eye movement trace, such as blinks were rejected. Three dependent variables were collected from the eye-movement data: latency, amplitude error, and angular error. The latency was defined as the time at which the absolute change in eye position from the start position [calculated as: $\sqrt{(\text{latest}(x)^2 + \text{latest}(y)^2) - (\text{previous}(x)^2 + \text{previous}(y)^2)}$] exceeded a threshold of 25 mm. The end-point of the saccade was determined using a similar algorithm; the participant was taken to be fixating when the change in eye position over two samples remained stable (i.e. < 25 mm). Coordinates for x and y eye position obtained from the eye tracker were converted to obtain the amplitude and orientation of the end point and this was compared to the target position to obtain error data for these measures.

A bootstrapping resampling method with 5,000 iterations was used to statistically assess the probability that the difference between the median for the sham condition and the medians for the TMS conditions at each of the sites were due to chance. This was done separately for the latency, amplitude error and angular error data.

Results

TMS

The frequency of sites on the left and the right hemisphere that showed a significant effect of TMS on each of three saccade metrics is shown in Fig. 2. In total across all 10 participants statistical analyses revealed a significant effect when TMS was applied at 14 sites for latency (2 left hemisphere, 12 right hemisphere) (Fig. 2a), 23 sites for amplitude error (8 left, 15 right) (Fig. 2b) and 14 sites for angular error (6 left, 8 right) (Fig. 2c).

Fig. 2 Frequency of significant TMS sites for **a** latency, **b** amplitude and **c** angular error collapsed across participants



Figure 3 illustrates the differing effects of TMS compared to sham TMS at each of the 18 grid locations for a single participant. These plots are based on P values. For latency (Fig. 3a) the positive P values are represented by the lighter end of the scale, indicating a longer latency than for sham TMS. For amplitude error (Fig. 3b), the scale is the same with positive P values indicating a longer, more hypermetric movement than for sham TMS. The angular errors of the saccades (Fig. 3c) were instead considered in terms of the absolute difference from the angle of the target, as it does not make theoretical sense to predict that TMS would result in errors that are specifically clockwise or anti-clockwise in direction; the difference in angular error for the TMS and sham TMS conditions increases as the scale progresses from dark to light.

Overall, therefore, a large number of the 18 TMS sites showed significant effects for each of the saccade metrics. However, specifically at which site TMS was found to most disrupt eye movements was not uniform across participants. In fact, a large amount of individual variability in the effects of TMS at each site was apparent. Within individual participants no one site on the left or right hemisphere was consistently found to disrupt both latency and error (amplitude or angular).

Discussion

Previous research into the role of the parietal lobe in the planning and control of saccades supports the existence of a human homologue of area LIP, the primate 'parietal eye field'. By examining individual variability between the spatial distribution of scalp morphometric locations, brain surface anatomy and stereotaxic coordinates regarding the PEF it was shown that the distance between the sites determined by these three localization techniques had a maximum mean of around 2.5 cm. The grid of sites used in this study covered a large area around P3 and P4 and thus the sites determined by these three procedures would be expected to have been covered by the functionally effective area of the TMS grid. This distance is, however, not negligible and raises

problems regarding the most reliable anatomical localization technique to use.

An assessment of the effect of TMS on saccade metrics (latency, amplitude error and angular error) at a grid of locations over parietal cortex demonstrated a large amount of intra-individual variability in the site where TMS had most affected saccades.

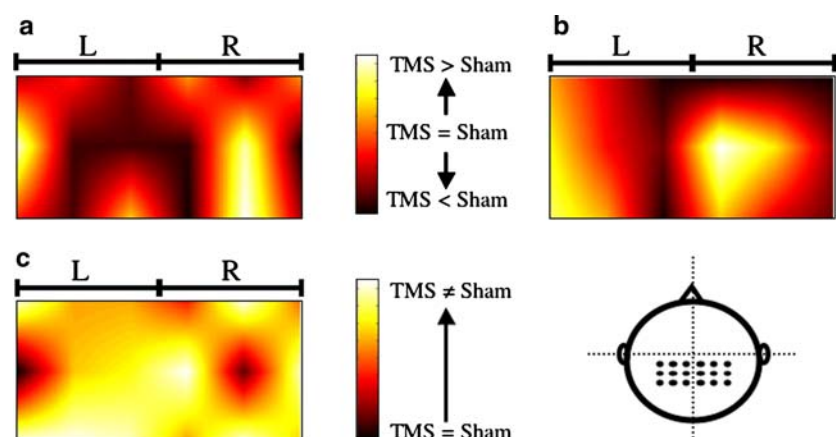
Interestingly, no one parietal site stood out across participants as consistently demonstrating a significant effect of TMS on any of the saccade metrics. Within participants it was also not possible to select a single site that affected all three measures of saccade metrics.

In some participants no significant effects of TMS compared to sham were found at any site for one or more of the saccade metrics; a number of possible reasons could account for this. Firstly within the grid there were 2 cm gaps between the stimulation sites used; although similar sized grids have been used by previous studies (e.g. Terao et al. 1998) there is some evidence to suggest that the spatial resolution of TMS may be more focal than this, possibly as low as 0.5–1 cm (Brasil-Neto et al. 1992). Using a grid with smaller distances between stimulation sites could potentially have revealed a site at which TMS was effective.

This study confirms the idea that it may be problematic to use a fixed scalp location for every participant in a study, e.g. based on bony landmarks as with an EEG site. Given the individual variability demonstrated, using a set site based on bony landmarks for every participant in a study is unlikely to be the most effective method of determining a suitable TMS site. It may in fact be more appropriate to determine TMS sites functionally on an individual basis if possible.

Another important issue to consider when using TMS is the difficulty in knowing the exact area of cortex being targeted; the exact pathway taken by the current following cortical stimulation is not yet fully known. The activation induced by TMS in terms of neuroanatomy may vary across both the area stimulated as well as across participants (Pascual-Leone et al. 1999). The results of the current study demonstrate variability in the effect of TMS across participants when delivered to the parietal lobes. It is possible that TMS to other areas of

Fig. 3 Effect of TMS over the two grids for one participant. **a** Latency, **b** amplitude error and **c** angular error. *Top colour key* shows effect of TMS for latency (**a**) and amplitude error (**b**): positive P values are represented by the lighter end of the scale, indicating a longer latency, or a more hypermetric movement, than for sham TMS. *Bottom colour key* shows effect of TMS for angular error (**c**): lighter areas show largest difference between TMS and sham TMS



association cortex, such as the prefrontal cortex would show a similar pattern of results; this could offer a potential explanation for inconsistent results in terms of the effectiveness of frontal TMS used clinically to treat depression (See e.g. Couturier 2005 for a review of such studies). The combination of neuropsychological tools such as functional imaging and TMS (e.g. Bestmann et al. 2004) may provide further insight into the resultant spread of activation and its associated cortical effects. This may eventually lead to a more clearly defined account of the function–anatomy relationship in this technique and prove useful in terms of optimal coil placement for investigating the functional significance of an area of cortex for a particular task.

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