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POSTERIOR PARIETAL CORTEX AND VISUOSPATIAL CONTROL IN NEAR AND FAR SPACE

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Abstract

Neuropsychological studies of patients with visuospatial neglect have shown differences in perceptual deficits for information in near space (i.e. near to the body) and information in far space. It has been suggested that among the many areas of the human brain, a number of areas are associated with a set of spatial maps specialized for visuospatial control related to this spatial distinction. This paper reviews how parietal cortex is thought to be involved in visuospatial neglect in relation to its control of visuospatial attention in the left and right visual fields and at different viewing distances. In particular, the importance of regions of the parietal cortex in the pathogenesis of neglect and in spatial attention and perception is discussed. Parietal cortex may control different distributions of attention across space by allocating specific attentional resources in near and far space while also showing attentional asymmetry across visual fields. Transcranial magnetic stimulation (TMS) as a technique offers the advantage of examining the direct behavioral effect of disruption of many of these areas with excellent temporal and spatial resolution. We discuss the use of TMS and the insights it may offer regarding the roles of these areas in neglect as well as normal visuospatial perception.

Keywords

• Parietal cortex • Precuneus • Visuospatial neglect • Visuospatial attention • Transcranial magnetic stimulation

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Introduction

A patient with visuospatial deficits experiences failure to acknowledge or explore stimuli in space contralesional to their damaged region of cortex, a deficit called visuospatial neglect [1]. For example, a study by Robertson, Mattingley, Rorden and Driver [2], investigated patients with right parietal ischemic lesions with visuospatial neglect symptoms and found a pathological delay in awareness of events in left space. Importantly, when objects were also present on the intact side, these patients also experience a deficit in shifting focal attention into the neglected hemispace [3]. Additionally, they have difficulty distinguishing one object from another on the basis of shape in a visual discrimination task [4]. As well as being a problem for patients, the neuropsychological syndrome of visuospatial neglect has also proven to be a tool assisting in dissection of the functional and anatomical architecture of the systems involved in spatial cognition [5]. The clinical features of visual neglect explain how damage to parietal cortex that appears primarily to code space could eliminate awareness [1].

The neural basis of neglect and spatial cognition involves a number of connected cortical and subcortical brain regions. The parietal component of the dorsal attention network serves as a hub for visuospatial functions across multiple cortical areas within the frontal and temporal lobes [6]. Parietal–frontal white matter damage, involving the *anterior fascicle* or the *superior longitudinal fascicle*, can disconnect large portions of the parietal, parietal–temporal and temporal cortex from frontal areas, and thus can be involved in the pathogenesis of neglect [7]. Moreover, lesions in white matter are particularly associated with chronic neglect [8]. Visual neglect is also associated with lesions that extend anteriorly from the occipital lobe to the parahippocampal region and centered on an area of white matter in the ventromedial temporal lobe, often as a consequence of right-sided posterior cerebral artery stroke [9]. In patients with right inferior parietal lobe *glioma*, intraoperative electrical stimulation (that temporarily inactivates restricted regions during brain surgery) shows that *parietal-frontal* communication is necessary for the symmetrical processing of the visual scene [10]. During the surgical procedure, patients performed a line bisection task with stimulation of the subcortical regions on the floor of the surgical cavity (associated with parietal-frontal white matter pathway) and also the supramarginal gyrus and caudal superior temporal gyrus. Results revealed large rightward deviations, supporting a role for parietal function in spatial awareness.

Multiple coordinate frames in the parietal cortex offer an explanation for why spatial deficits, in humans, appear in multiple coordinate frames after lesions to this area. It has been shown that patients with lesions of intraparietal sulcus (IPS) [11] exhibit reaching inaccuracies which are even more pronounced when they attempt to reach to remembered targets without the benefit of visual guidance [12]. Furthermore, neglect also appears to affect complex spatial representations of visual scenes and patterns and is associated primarily

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with inferior parietal lobule (IPL) damage [13,14]. Loss of awareness following parietal damage arises even though considerable processing still takes place for neglected stimuli [13]. Damage to the IPL may cause neglect by disrupting a system for representing highly-processed figural information, a system therefore in large part dependent on visual inputs from the ventral stream. A study combining spatial and temporal analysis of neural activity evoked by seen and unseen stimuli in neglect patients, using both event-related imaging and electrophysiological measures, revealed that both fMRI (functional magnetic resonance imaging) and ERP (event related potential) results showed contralesional inputs can still activate striate and extrastriate areas in the damaged hemisphere after parietal lesions, even without awareness [15].

Parietal cortex and spatial perception of distance (near and far space)

Different words or descriptions are sometimes used in the literature to indicate different regions of space, with near space typically defined as within reaching space (peripersonal space) and far space as extrapersonal space, indicating beyond reaching range. An early study by Zoccolotti and Judica [16] pioneered the use a functional scale of personal space for evaluating neglect in daily life, consisting of separate scales for personal, peripersonal and extrapersonal defects. For instance, patients are required to perform tasks relative to near space (serving tea, dealing cards, describing complex scenes) or for far space (describing a room), while on the personal scale (indicating the subject's body) patients are required to use some objects (comb, razor, powder, eyeglasses) on themselves.

Space is represented in parietal cortex with multiple representations encoding the locations and objects of interest [17]. Parietal cortex may specifically act on information coming from extrastriate cortex to generate a response weighted transformation into the appropriate body co-ordinate system required to act [18]. Conscious stimuli have to reach levels of processing, such as a *feedforward* sweep to parietal cortex and recurrent processing [19,20], beyond initial feature detection. Parietal cortex activity is also strongly modulated by the availability of modality specific attentional resources, and it has been found to be consistently activated in situations where subjects are aware of visual stimuli compared with when they are unaware [21].

In monkey studies, the involvement of parietal cortex in space representation and movement guidance is well established. For instance: single-cell recordings have revealed area 7b has visual receptive fields that respond to movements of stimuli near the face or arm, but not to stimuli in far space [17]. In humans, evidence of posterior parietal cortex (PPC) function in spatial navigation can be observed from neuropsychological studies on parietal patients who, after lesion of their PPC, could no longer orientate and navigate within space. A study by Halligan and Marshall [22] found that a patient with a unilateral right hemisphere stroke showed a severe left neglect for near but not for far space. Furthermore, in patients, dissociations between line bisection performance in near and far space after brain damage suggest that sufficient cortex may remain functional in the PPC to calculate the midpoint of a line, but the responsible regions cannot communicate appropriately with areas that are more generally concerned with near and far spatial perception [23]. Employing a visual search task, a study done by Butler, Lawrence, Eskes and Klein [24] found that within a neglect group the proportion and size of leftward and rightward shifts to consecutive targets was similar. However, this study also showed that the neglect group made a greater proportion of repeated target detections and showed the expected decrease in proportion of target detections as they progressed from right-to-left across the page in both near and far space.

Recent TMS studies and their clinical relevance

Visuospatial neglect is a multifaceted disorder with highly variable symptoms and multiple corresponding areas among patients. Findings from individuals with lesions are supplemented by a variety of studies, including those employing transcranial magnetic stimulation (TMS). Interestingly, many patients with neglect show at least some level of improvement over time following lesions, and it is therefore likely that some of the areas shown to be essential for visuospatial processing are able to compensate to some degree for the damage in other areas. Therefore, to study and observe the selective exploration deficits of distinct portions of space in patients is challenging, considering that lesions in humans are not necessarily comparable to those obtained experimentally in animals, and they may involve more than one cerebral area [25]. In order to investigate specific areas, studies have been done in neurologically healthy subjects [23,26-28]. In an experimental setting, the effect termed as the *neglect-like* effect can be produced by temporary disruption using TMS, which can reverse the typical slight leftward bias seen in healthy subjects into a rightward bias specifically in the analysis of left versus right visual fields. In healthy participants, there can be overestimation of length, magnitude, quantity or luminance of stimuli in the left visual hemispace due to the right hemisphere dominance for visuospatial attention which results in "overattendance" towards the left visual hemispace [27,29-31]. As a neurodisruption technique, TMS offers both temporal and spatial precision and can be employed for the investigation of the relationship between brain and behavior under controlled experimental conditions, allowing comparison of behavioral performance with and without disruption of local neural activity.

Conventionally, parietal cortex can be localized using the P3/P4 electrode positions of EEG 10–20 system that was defined in terms of the standard scalp electrode positioning system [32], with P3/P4 usually over a posterior part of the angular gyrus in the IPL [11]. Another, more accurate, method for localizing parietal cortex, can be performed using a stereotaxic localization system (for instance: using Brainsight^{tm} neuronavigation software, neuroConn GmbH, Ilmenau, Germany) (for example using Talairach coordinates for rPPC of 42/-58/52 [33] which lies in the region of angular gyrus lateral to the IPS). Unsurprisingly, this greatly improves the anatomical localization before a TMS session [34]. Additionally, functional approaches can be used, employing a visual search experiment, using a hunting procedure with a conjunction search task [35]. In their study, Bjoertomt, Cowey and Walsh [26] applied online repetitive TMS over right PPC that was localized using such a procedure.

Using a landmark task, the exclusive near space shifts of behavioral bias following rPPC TMS were first investigated by Bjoertomt, Cowey and Walsh [26]. The landmark task is a visuospatial task which has widely been used in the clinical assessment of spatial neglect [36]. The results of this study were in line with an earlier near and far space investigation in healthy participants using positron emission tomography (PET) by Weiss, Marshall, Wunderlich, Tellmann and Halligan [23], which supports the suggestion of different neural mechanisms for visual attention with respect to viewing distance and respective dorsal and ventral stream processing. In the same vein, Serino, Canzoneri and Avenanti [37] found that low frequency (1 Hz) repetitive TMS over rPPC diminished the speeding effect of responses due to near sounds but not far sounds, indicated that multisensory interaction in near space depends on the function of PPC. In the same line of study, the first PPC-TMS study to assess performance in near and far space using a visual search task was done by Lane, Ball, Smith, Schenk and Ellison [28]. Using the same TMS protocol as Bjoertomt, Cowey and Walsh [26], they employed the typical random search array (without a comparison of performance in different hemifields) and they also found an effect of parietal TMS only in near space.

In our recent study, we assessed the presence of a left–right performance difference (neglect) in normal individuals in near space and far space using a visual search task, with manual responses, as a consequence of TMS stimulation [38]. In contrast to Lane, Ball, Smith, Schenk and Ellison [28], we used an elliptical conjunction search design that contained elements in the peripheral visual field, with a range of horizontal offsets from the center (see Fig. 1). This design was used because neglect patients show a gradual reduction of perception across space in one or more dimensions [39] and prior research on neglect has typically focused only on one dimension of space, either defining deficits horizontally [30,40,41] or radially [23,28,42,43] separately. Our study showed PPC involvement in search in far space by using a conjunction visual search task with an elliptical peripheral array with a pattern of performance consistent with stimulation resulting in neglect. This revealed that there is presumably a different attentional allocation in near and far space since these tasks presented targets mapped accurately across the human spatial field. It seems that PPC is involved in far space neglect because of the higher level of consistency of target locations that might reduce its typical role in conjunction search in general (as reflected by the absence of an effect with the array in near space). Further study will be needed specifically to directly compare the effects of high and low spatial probability peripheral search array in one experiment (in a within-subject design) to observe the effect of attentional load manipulation in egocentric distance manipulated (near vs. far) spatial perception.

PPC is by no means the only parietal region investigated in terms of neglect involvement

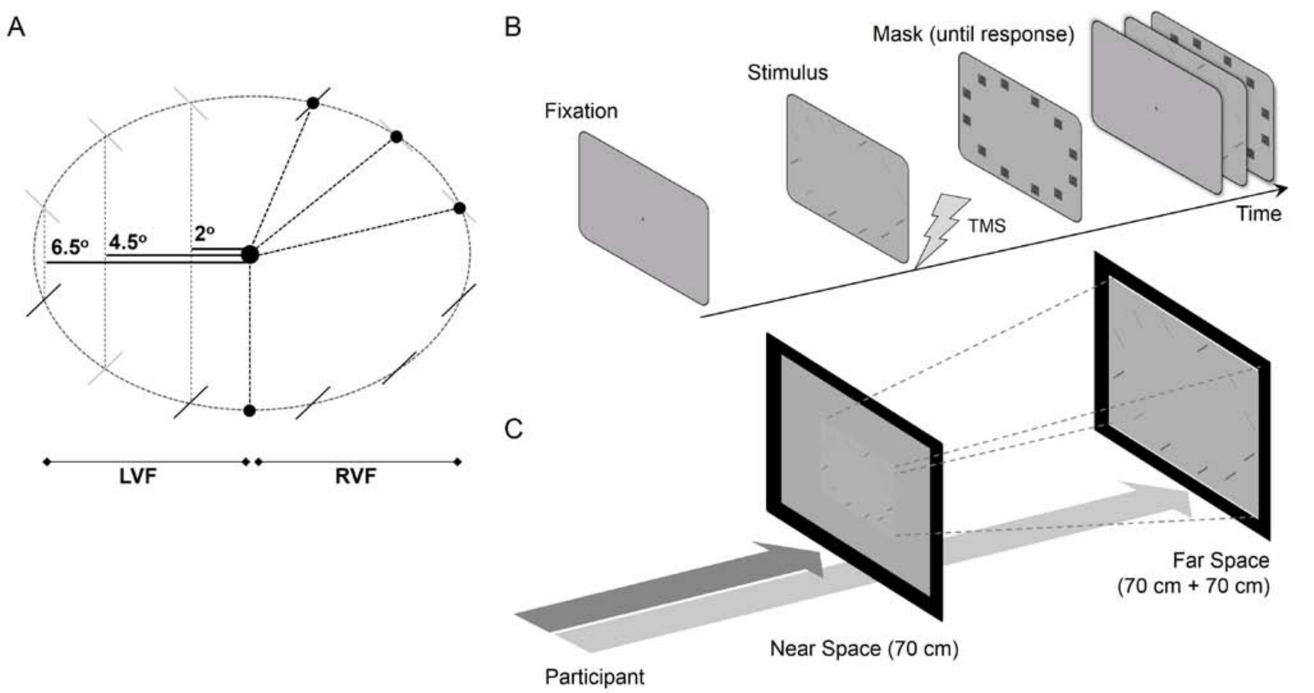

Figure 1. Experiment details of the Mahayana, *et al.* [38] study. A. Target/distractor locations were positioned in an elliptical configuration (LVF: left visual field; RVF: right visual field). B. The stimulation procedure started with a fixation (400 ms) and was followed by the stimulus display (based on individual thresholds, 140-220 ms) and then the mask (until response). Five pulses (10 Hz, 500 ms) 60% intensity TMS were delivered at the onset of the stimuli display. C. Near and far distance parameters (near space condition: 70 cm; far space condition: 140 cm from the monitor).

with TMS. Recently we showed that an area in posterior medial parietal cortex (the precuneus) may also play important role in controlling visuospatial attention in near and far space by showing a rightward shift of the normal bias of perceptual judgments [44] (see Fig. 2 for the details of this study). In our study, a *neglect-like* effect was found on a landmark task as a consequence of TMS delivered over precuneus, specifically for near space stimuli. The shifts of behavioral spatial bias were in line with (lateral) PPC-TMS effects and with earlier PPC TMS work employing the landmark task [26,45,46]. These precuneus and lateral PPC TMS effects may suggest that there is parallel function between precuneus and lateral PPC in the control of spatial attention. The study also investigated the allocation of visuospatial attention in the egocentric framework in the parietal cortex (in particular the precuneus) to look at the attentional asymmetries across visual fields, which is found mainly in neglect patients. The laterality effect in the landmark task used in our study might be explicitly based on spatial categories relevant in neglect (the *left* or *right* judgment responses). The study is possibly the first neurostimulation study (using TMS) that explicitly investigated the role of precuneus in visuospatial attention. Previously the involvement of this area was based on fMRI findings from clinical studies of post-stroke patients [47,48], for instance: the improvements in the neglect tasks, after alertness training [49].

Moreover, this study also explored the different allocation of attentional resources in near and far space by presenting the stimuli in these locations. Neuropsychological studies of patients with visuospatial neglect have previously shown near and far space dissociations for perceptual tasks [16,25,42,50-53]. The evidence of this spatiotopic-dependent neglect (near or far space impairments on perceptual tasks) in patients [22,43,51,52], which could be related to a decrease of awareness and attention in space, shows that parietal cortex (including precuneus) may control different distributions of attention by allocating specific attentional resources in near and far space.

The posterior medial parietal cortex (the precuneus) TMS effect in near space may strengthen the specificity of the role of PPC on visuomotor transformation functions. In the human brain, space coding is a dynamic process and it has been suggested that among the many visual areas of the human brain, there is a set of spatial maps specialized for near and far space. In the future, it is important to investigate the role of precuneus specifically on visuomotor transformation. An example of the investigation of the dynamic process of space coding in humans required subjects to either point or reach, after an intervening eye movement, towards a remembered location of an initially foveally viewed target [54] which showed that the retinocentric reaching representations must be updated during eye movements in order to remain accurate [54,55].

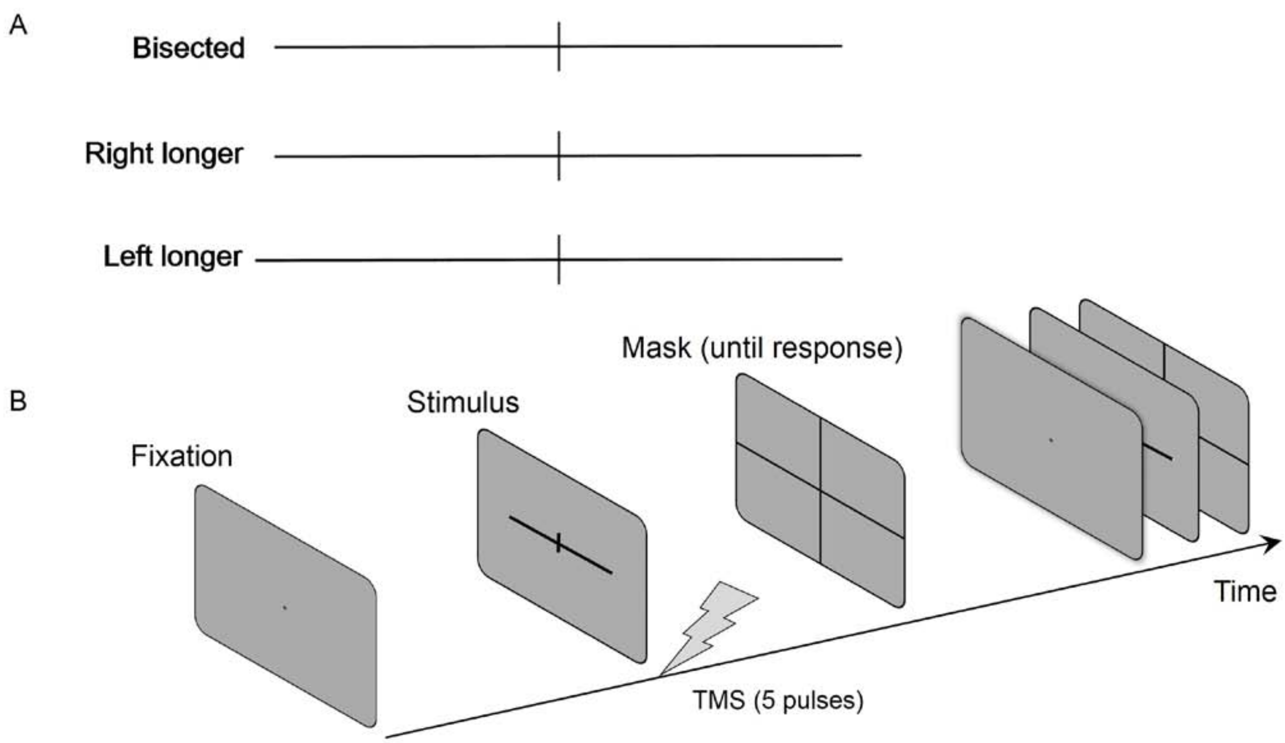

Figure 2. Experiment details of the Mahayana *et al.* study [44]. A. The prebisected line types and characteristics (bisected: 18 and 20º; right longer: 18.5, 19 and 19. 5º; and left longer: 18.5, 19 and 19. 5º). B. Experimental procedure. A fixation was followed by presentation of a prebisected line stimulus and was masked after 200ms, TMS pulses protocol was similar as Mahayana *et al.* study [38] (distance parameters: near space condition: 70 cm; far space condition: 180 cm from the monitor).

Conclusion

Parietal cortex shows differential neural mechanisms based on target spatial mapping. TMS studies allow further testing and refinement of already existing theories that is beneficial for both understanding the neural processes underlying perception and the implications for the interpretation of experiments on the neural basis of visual perception and cognition. Additionally, and importantly, such findings may be of use for conducting patient assessments and neurorehabilitation of spatial deficits patients. Furthermore, they may provide insights to answer the inconsistences found in patients studies related to whether left neglect is manifested in near [22, 43] or far space [51, 52], which remains an issue of interest.

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