Neuropsychologia 102 (2017) 197–205

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

The right hemisphere is independent from the left hemisphere in allocating visuospatial attention

Arianna Zuanazzi[a,*], Luigi Cattaneo[b]

[a] Center for Mind/Brain Sciences (CIMeC), Trento, Italy
[b] Department of Neurosciences, Biomedicine and Movement, University of Verona, Verona, Italy

ARTICLE INFO

Keywords:
Hemi-spatial neglect
Inter-hemispheric interaction
Line bisection
Parietal cortex
Transcranial magnetic stimulation
Transcranial direct current stimulation

ABSTRACT

The capacity to allocate visuospatial attention is traditionally considered right-lateralized according to the effects of unilateral cerebral lesions. Contralateral hemi-spatial neglect occurs much more frequently after lesions of the right hemisphere, which has therefore been dubbed as 'dominant'. This pattern of symptoms is supported by functional models that postulate either independence or reciprocal influences between the two hemispheres. Here we specifically explored the dependency of the right hemisphere (RH) from the left hemisphere (LH) in spatial attention. We capitalized on the well-known effect of online transcranial magnetic stimulation (TMS) on the RH in healthy individuals, consisting in transient neglect-like manifestations in the left hemi-space. We assessed whether prior stimulation of the left posterior parietal cortex with a long-lasting neuromodulatory procedure (transcranial direct current stimulation – tDCS) affected the acute effects of TMS on the right posterior parietal cortex. We performed a within-subjects factorial study with two factors: LH tDCS (*sham* or *real*) and RH TMS (*sham* or *real*), resulting in a 2×2 design. The effects on spatial attention were examined separately for the two hemi-spaces by means of a modified line-bisection task. The results indicated that TMS over the RH produced a spatial attention deficit in the left hemi-space alone and the behavioural effects of TMS were not modulated by prior stimulation of the LH. Interestingly, additional analyses showed that tDCS over the LH alone produced a deficit in spatial attention to the right hemi-space. We interpret the current results as evidence for a largely independent contribution of each hemisphere to the allocation of visuospatial attention limited to the contralateral hemi-space.

1. Introduction

The brain is a largely symmetrical structure. However, some cortical functions are unevenly represented in the two hemispheres, and this asymmetry may be systematically biased towards one side. This phenomenon is known as lateralization of brain functions. Lateralized functions are therefore supported by a specialized hemisphere, referred to as the *dominant* hemisphere for that specific function (Hervé et al., 2013). The behavioural capacity to allocate visual attention to portions of space is an active process supported by a brain circuit which is traditionally considered to be lateralized to the right hemisphere (RH). Evidence for right-lateralization or right-dominance of visuospatial attention comes primarily from observations in patients with unilateral cerebral lesions who manifest contra-lesional *hemi-spatial neglect* (hSN). HSN is a neurological symptom characterized by difficulty in directing gaze, reporting or responding to stimuli in the contra-lesional (most commonly left) hemi-space, despite normal visual perception and motor performance (Corbetta et al., 2005). HSN is generally associated with unilateral brain damage (Becker and Karnath, 2007), with over 90% of individuals who develop hSN suffering from RH lesions (especially over the right superior temporal cortex and the right parietal cortex, Karnath et al., 2011; Mort et al., 2003; Verdon et al., 2010), while hSN associated with lesions of the left hemisphere (LH) is extremely rare (Corbetta et al., 2005). Two main hypotheses have been suggested to explain the asymmetry of hSN symptoms. A) It has been postulated that, while the LH controls the shift of attention towards the right side of space, the RH controls the shift of attention towards both sides and can compensate for LH damage (Heilman and Van Den Abell, 1980; Mesulam, 1981). B) Alternatively, Kinsbourne (1977)'s *inter-hemispheric competition hypothesis* suggests that LH orients attention towards the right side of space and the RH towards the left side of space, but the LH exerts a stronger bias. Thus, the attention system would reach a balance through a reciprocal inhibition between the hemispheres. Non-invasive brain stimulation studies with hSN patients using transcranial magnetic stimulation (TMS) or transcranial direct current stimulation (tDCS) have provided a direct evidence in favour of

* Corresponding author. Present address: Computational Cognitive Neuroimaging Laboratory, University of Birmingham, B15 2TT Birmingham, United Kingdom.
E-mail addresses: axz481@bham.ac.uk (A. Zuanazzi), luigi.cattaneo@univr.it (L. Cattaneo).

http://dx.doi.org/10.1016/j.neuropsychologia.2017.06.005
Received 27 November 2016; Received in revised form 7 June 2017; Accepted 8 June 2017
Available online 09 June 2017
0028-3932/

the inter-hemispheric competition hypothesis (Kinsbourne, 1977). Application of TMS or tDCS to the healthy LH (generally the posterior parietal cortex) may, in fact, improve the symptoms of hSN, by restoring the inter-hemispheric balance (Koch et al., 2009; Sparing et al., 2009; for a review, see Müri et al., 2013).

More recently, Corbetta and Shulman (2011) have argued that right-lateralization observed in hSN is not a consequence of lateralization of spatial attention per se, but rather the consequence of an abnormal functioning of the interaction between two different but connected networks. The ventral frontoparietal network (temporoparietal junction - ventral frontal cortex) is indeed right-lateralized and controls for arousal, reorienting of attention and detection of behaviourally relevant target; the dorsal frontoparietal network (intraparietal sulcus – dorsal frontal cortex) is distributed bilaterally and controls for endogenous orienting of attention. According to this framework, the damage of ventral frontoparietal regions would generate abnormalities in the intact dorsal frontoparietal region, thus affecting the inter-hemispheric balance which underlies hSN (Corbetta et al., 2005; Corbetta and Shulman, 2002, 2011).

In support of this framework, fMRI data on healthy individuals have shown that, when participants perform a spatial attention task, lateralization of visuospatial attention processes can be observed for the ventral but not for the dorsal attentional network, which shows instead bilateral activation, although stronger for contralateral stimuli (Corbetta et al., 2000; Shulman et al., 2010). It has to be noted that, despite being symmetric, the activation of left and right dorsal frontoparietal regions might yet have different functions, e.g. there might be an asymmetric influence upon remote brain areas (such as upon visual cortices which represent peripheral fields), with right frontoparietal regions exerting a stronger influence (Ruff et al., 2009; Shulman et al., 2010; see also Vossel, Geng, and Fink, 2014).

Ideally, investigating inter-hemispheric interplays in attentional mechanisms should include modulation of activity of both hemispheres in the same individual. However, this is impractical in patients. Neurostimulation techniques offer a unique opportunity to modulate focal neural activity of one or both hemispheres to produce behavioural changes in healthy individuals. On one hand, previous neurostimulation studies with healthy individuals have shown that unilateral stimulation of the RH may produce ‘hSN-like’ effects (Babiloni et al., 2007; Bjoertomt et al., 2002; Fierro et al., 2001; Giglia et al., 2011; Hilgetag et al., 2001; Meister et al., 2006; Muggleton et al., 2006; Nyffeler et al., 2008; Oliver et al., 2009; Thut, 2004). Moreover, bilateral stimulation brings evidence in favour of the competition hypothesis, i.e. ‘hSN-like’ effects produced by concurrent left- and right-hemisphere inhibition cancel each other out (Dambeck et al., 2006; Szczepanski and Kastner, 2013). On the other hand, multimodal studies measuring functional activity contralateral to the stimulated hemisphere have shown contrasting results, some of them contradicting the competition hypothesis, i.e. showing a decrease in neural activity for the stimulated RH and also for of the homologous LH (Bagattini et al., 2015; Ricci et al., 2012), others favouring it, i.e. showing a reduction in neural activity for the stimulated RH but an increase in neural activity for the homologous LH (Petitet et al., 2015; Plow et al., 2014).

In the present study we adopted a novel approach to investigate inter-hemispheric interplays. Rather than using simultaneous bilateral stimulation, we induced a long-lasting neuromodulatory effect on the left posterior parietal cortex by means of tDCS. The well-known online effects of TMS over the right posterior parietal cortex were then tested, superimposed on the after-effect of tDCS over the left posterior parietal cortex. Our study design is asymmetrical between the two hemispheres, i.e. we assessed the effects of prior LH modulation on the way RH TMS affects spatial attention, given that our ad-hoc interest was that of assessing the effects of stimulation of the LH on the predicted ‘hSN-like’ effects of TMS over the RH. This design, in our view, allows us to collect information in favour of one of the possible hypotheses of inter-hemispheric dynamics in the allocation of spatial attention. We hypothesized two possible alternative outcomes on behaviour: 1) *Dependent pattern*: the behavioural effects of TMS over the RH depend on the concurrent cortical state of the LH (i.e. whether tDCS has been previously applied or not to the LH). 2) *Independent pattern*: the cortical state of the LH induced by tDCS does not influence the behavioural effects of TMS over the RH. In our study, we used a *tachistoscopic forced-choice landmark task* to assess the allocation of spatial attention. This task resembles the *line bisection task* (Bisiach et al., 1983) used to test hSN, but in the present case the transector mark is always central and the length of the left and right line segments vary. This task allows relatively independent analysis of the left and right hemi-spaces and has been previously validated as a sensitive tool to neurostimulation (Bjoertomt et al., 2002; Fierro et al., 2001; Giglia et al., 2011).

2. Methods

2.1. Participants

Sixteen healthy participants took part in Experiment 1 (5 M; mean age: 26.06; range: 19–39). Handedness was assessed with the Edinburgh Handedness Inventory questionnaire (Oldfield, 1971): 14 participants were right-handed and two were ambidextrous (mean laterality index: 0.89 ± 0.33; range: −0.26 to 1). Data from two participants were not included in the analysis because they did not fulfil the inclusion criteria (see 2.3). A different group of 16 healthy participants took part in Experiment 2 (5 M; mean age: 25.16; range: 19–35); 15 participants were right-handed and one was ambidextrous (mean laterality index: 0.90 ± 0.21; range: 0.15 to 1). Data of all 16 participants were included in the analysis as they all fulfilled the inclusion criteria (see 2.3). All participants had normal hearing and normal or corrected-to-normal vision. They were not informed of the purpose of the experiment until the end of the experiment. Participants were screened for any relative or absolute contraindications to TMS or tDCS. None had a history of neurological or psychiatric disorders or any contraindications to TMS (Rossi et al., 2009). Informed written consent was obtained from each participant. The study was conducted in the Neurostimulation Laboratory of the University of Trento (Italy) and was approved by the local ethical committee (protocol n. 2013-030).

2.2. Stimuli and behavioural task

Visual stimuli consisted of nine black 1 mm thick horizontal lines, transected by a 1 mm thick and 3 mm high vertical transector always coincident with the centre of the screen, so that the lines' start-points and end-points changed depending on the length of the lines. This manipulation was meant to minimize the use of the start- and end-points as a reference for the relative lengths of the two sides. Lines were pre-transected at one of nine locations, with intervals of ± 2 mm (see Fig. 1). In order to minimize potential bias, increase sensitivity and make the task more demanding, participants were not told about the presentation of an exactly bisected line.

Each trial was presented an equal number of times for each stimulation condition: 10 times in Experiment 1 (only line 5 was presented 20 times) and 20 times in Experiment 2, for an overall total of 200 trials

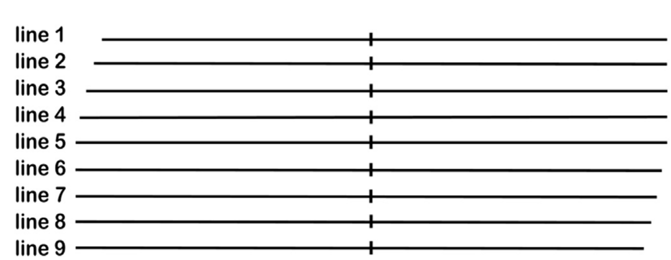

Fig. 1. The nine lines used as visual stimuli. Lines 1, 2, 3 and 4 are right-elongated; line 5 is exactly bisected (72 mm left and 72 mm right); lines 6, 7, 8 and 9 are left-elongated.