Neuropsychologia 69 (2015) 9–21

Contents lists available at ScienceDirect

Neuropsychologia

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

Overlapping neural circuits for visual attention and eye movements in the human cerebellum

Christopher L. Striemer [a,b,*], Philippe A. Chouinard [b,c], Melvyn A. Goodale [b], Sandrine de Ribaupierre [b,d]

[a] Department of Psychology, MacEwan University Edmonton, Alberta, Canada
[b] Department of Psychology and the Brain and Mind Institute, University of Western Ontario, London, Ontario, Canada
[c] School of Psychological Science Public Health, La Trobe University, Bundoora, Victoria, Australia
[d] Department of Clinical Neurological Sciences, Division of Neurosurgery, University of Western Ontario, London, Ontario, Canada

ARTICLE INFO

Article history:
Received 20 June 2014
Received in revised form
13 January 2015
Accepted 16 January 2015
Available online 19 January 2015

Keywords:
Visual attention
Covert attention
Eye movements
Cerebellum
fMRI

ABSTRACT

Previous research in patients with cerebellar damage suggests that the cerebellum plays a role in covert visual attention. One limitation of some of these studies is that they examined patients with heterogeneous cerebellar damage. As a result, the patterns of reported deficits have been inconsistent. In the current study, we used functional neuroimaging (fMRI) in healthy adults ($N=14$) to examine whether or not the cerebellum plays a role in covert visual attention. Participants performed two covert attention tasks in which they were cued exogenously (with peripheral flashes) or endogenously (using directional arrows) to attend to marked locations in the visual periphery without moving their eyes. We compared BOLD activation in these covert attention conditions to a number of control conditions including: the same attention tasks with eye movements, a target detection task with no cueing, and a self-paced button-press task. Subtracting these control conditions from the covert attention conditions allowed us to effectively remove the contribution of the cerebellum to motor output. In addition to the usual fronto-parietal networks commonly engaged by these attention tasks, lobule VI of the vermis in the cerebellum was also activated when participants performed the covert attention tasks with or without eye movements. Interestingly, this effect was larger for exogenous compared to endogenous cueing. These results, in concert with recent patient studies, provide independent yet converging evidence that the same cerebellar structures that are involved in eye movements are also involved in visuospatial attention.

1. Introduction

Traditionally, the cerebellum has been understood to serve two basic yet critical functions: the coordination of motor output (i.e., walking, eye movements, balance, reaching) and motor learning (for a historical review see Glickstein et al., 2009). In recent years, however, several studies investigating patients with cerebellar damage have suggested that the cerebellum may also play a crucial role in higher cognitive functions such as attention, memory, language, and emotion (Schmahmann and Sherman, 1998).

Although the role of the cerebellum in memory, language, and emotion have recently been increasingly reported in the literature (for recent reviews see Marvel and Desmond, 2010; Sacchetti et al., 2009; Stoodley and Schmahmann, 2009; Stoodley and Stein, 2011), the role of the cerebellum in attention has remained more controversial. Specifically, whereas early patient and imaging studies by Courschene and colleagues (Akshoomoff and Courchesne, 1992; Allen et al., 1997; Townsend et al., 1999) seemed to indicate a clear role for the cerebellum in attention, other studies failed to find any attentional impairments in patients with cerebellar damage (Dimitrov et al., 1996; Golla et al., 2005; Haarmeier and Thier, 2007; Yamaguchi et al., 1998).

One influential theory, known as the “premotor theory” of attention (Rizzolatti et al., 1987; Sheliga et al., 1997), suggests that our ability to attend to the periphery (covertly, without moving our eyes) is the result of neural processes related to eye-movement preparation and control, which are carried out by a known network of brain regions including the posterior parietal cortex, frontal eye fields, and superior colliculus. According to this theory, the same neural mechanism that prepares one to move one's eyes also acts as a trigger for shifting attention from one location to the

* Corresponding author at: Department of Psychology, MacEwan University, City Centre Campus, 10700–104 Avenue, Edmonton, Alberta, Canada T5J 4S2. Fax: +1 780 497 5308.
E-mail address: striemerc@macewan.ca (C.L. Striemer).

http://dx.doi.org/10.1016/j.neuropsychologia.2015.01.024
0028-3932/

end-point of an intended eye movement (Colby and Goldberg, 1999; Deubel and Schneider, 1996; Duhamel et al., 1992). Given that eye movements and spatial attention appear to share common neural substrates in the cerebral cortex (Astafiev et al., 2003; Corbetta et al., 1998), one might also expect that regions of the cerebellum that are important for eye-movement control play a role in controlling shifts in spatial attention.

The fact that attention and eye movements are strongly related means it is important to control for eye movements when examining the role of a brain structure in attention. Posner and colleagues (Posner et al., 1980, 1984) developed a paradigm specifically for this purpose. The paradigm measures covert attention: which are changes in location of spatial attention while the eyes remain fixated. During the covert attention task, participants fixate their eyes at one location and attend to peripheral locations presented on the screen to the left and right of fixation. At the beginning of each trial, a cue appears such as a flash of light in the periphery, or an arrow at fixation pointing to the side of space to which the participant is to attend. Following the cue, a target stimulus (e.g., a small circle) appears either in the same location that was cued (termed a “valid trial”) or in the opposite uncued location (termed an “invalid trial”). Participants are reliably faster to respond when the target appears at the cued compared to the uncued location (i.e., the cueing effect) because their attention was previously cued to the location in which the target appeared. In contrast, on invalidly cued trials, the participant must reorient their attention from the cued location to the opposite uncued location to detect the target (Posner et al., 1980, 1984).

Previous studies that have examined covert attention in patients with cerebellar injury have produced mixed results. Specifically, Townsend et al. (1999) observed that patients with cerebellar damage or degeneration were slower to orient their attention within the first 100 ms following a cue compared to controls. Attentional orienting in these patients, however, was approximately normal about 800 ms after the presentation of the cue. These results suggest that cerebellar damage may have a greater effect on exogenous (i.e., reflexive) compared to endogenous (i.e., voluntary) attention. Interestingly, structural MRI measures linked the slowed orienting of attention in these patients to decreased volume in cerebellar lobules VI and VII, regions that are known to be part of the “oculomotor vermis” (for a review see Voogd et al., 2012). Other studies, however, have failed to observe the same orienting deficits in patients with cerebellar damage suggesting that the impairments in visuospatial attention were related either to impaired motor output, or to impaired saccadic eye movements, and not to attention per se (Dimitrov et al., 1996; Golla et al., 2005; Yamaguchi et al., 1998).

The inconsistent results reported in the literature may be due to a number of factors such as: (1) differences in the covert attention tasks used, (2) the notion that motor output problems (i.e., motor preparation, response selection) might masquerade as attentional deficits (Haarmeier and Thier, 2007; Ravizza and Ivry, 2001; Yamaguchi et al., 1998), and (3) the fact that many studies of attention in patients with cerebellar injury have used heterogeneous patient groups with diffuse damage (e.g., cerebellar degeneration, focal lesions, tumours) (Dimitrov et al., 1996; Golla et al., 2005). The use of heterogeneous patient groups may be a particularly critical problem because most of these studies examined the effects of cerebellar damage on visuospatial attention only at the group level. Thus, if there are one or two patients with selective lesions who do demonstrate clear attentional deficits, it would not appear in the overall group analysis. More to the point, if patients with lesions or degeneration in different structures within the cerebellum (e.g., vermis vs. lateral cerebellum) are placed in the same group, this implicitly assumes that all areas of the cerebellum should be equally involved in attention (i.e., that any cerebellar lesion should lead to a deficit). This assumption would be clearly false for the cerebral cortex, and there is plenty of evidence to suggest that specific regions of the cerebellum also subserve specific functions (for a review see Glickstein et al., 2009). In summary, the heterogeneity of results in the literature may simply reflect the heterogeneity of the patient populations studied. One notable exception to this is a recent study by Baier and colleagues (Baier et al., 2010). In their study Baier et al., were able to demonstrate that a specific sub-population of patients (8 out of a total of 26) with damage to oculomotor vermal structures were clearly slower at reorienting attention on invalidly cued trials compared to healthy controls, thus confirming the original findings of Townsend et al., (1999) that suggested a link between oculomotor structures in the cerebellum and the control of covert shifts of attention.

In the current study, we sought to provide independent but converging evidence for these findings in healthy individuals using functional neuroimaging. Specifically, in addition to the standard fronto-parietal networks that are commonly engaged in covert attention tasks (for a review see Corbetta and Shulman, 2002), we also wanted to see whether or not any covert attention-related activation could be observed in the cerebellum. For the purposes of the current experiment, there were three primary questions of interest: (1) Does the cerebellum play a role in visuospatial attention in the intact brain? (2) If so, is there any overlap in the regions of the cerebellum that are involved in generating eye movements and shifts of covert visual attention when manual motor outputs (i.e., button presses) are controlled for? And finally, (3) is there any differential involvement in the cerebellum in exogenous compared to endogenous covert attention?

Several previous brain imaging studies have observed cerebellar activation during covert attention tasks (Corbetta et al., 1998, 2000; Lepsien and Pollmann, 2002; Nobre et al., 2000; Rosen et al., 1999). These studies, however, did not adequately control for motor outputs (i.e., button presses or eye movements), so the cerebellar activation in these studies is somewhat difficult to interpret. That is, it is unclear whether the cerebellar activation observed in these previous studies is due to cerebellar involvement in attention, or to the programming or execution of motor responses associated with task performance.

To address these concerns, we performed a block design fMRI study where participants completed separate sets of runs consisting of either an exogenous orienting task in which peripheral cues were used to attract attention, or an endogenous orienting task in which central arrow cues were used to direct attention. For both orienting tasks participants were required to detect the presence of targets via a button press. In addition, participants also completed a number of control tasks during the exogenous and endogenous runs. Specifically, participants completed: (1) an overt attention task, which was identical to the covert attention tasks but required participants to make eye movements, (2) a target detection task that was identical to the covert attention tasks but contained no pre-cues, and (3) a button press task in which participants had to press a button once approximately every two seconds without any spatial pre-cue or target detection required. Using this design we could directly compare regions in the cortex and cerebellum that were involved in attention and eye movements while controlling for button press responses and eye movements.

2. Material and methods

2.1. Participants

A group of fourteen neurologically healthy right-handed