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Temporal dynamics of visual working memory

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ABSTRACT

The involvement of the human cerebellum in working memory has been well established in the last decade. However, the cerebro-cerebellar network for visual working memory is not as well defined. Our previous fMRI study showed superior and inferior cerebellar activations during a block design visual working memory task, but specific cerebellar contributions to cognitive processes in encoding, maintenance and retrieval have not yet been established. The current study examined cerebellar contributions to each of the components of visual working memory and presence of cerebellar hemispheric laterality was investigated. 40 young adults performed a Sternberg visual working memory task during fMRI scanning using a parametric paradigm. The contrast between high and low memory load during each phase was examined. We found that the most prominent activation was observed in vermal lobule VIIIb and bilateral lobule VI during encoding. Using a quantitative laterality index, we found that left-lateralized activation of lobule VIIIa was present in the encoding phase. In the maintenance phase, there was bilateral lobule VI and right-lateralized lobule VIIb activity. Changes in activation in right lobule VIIIa were present during the retrieval phase. The current results provide evidence that superior and inferior cerebellum contributes to visual working memory, with a tendency for left-lateralized activations in the inferior cerebellum during encoding and right-lateralized lobule VIIb activations during maintenance. The results of the study are in agreement with Baddeley's multi-component working memory model, but also suggest that stored visual representations are additionally supported by maintenance mechanisms that may employ verbal coding.

1. Introduction

In the last decade, scientific investigations have confirmed that cerebro-cerebellar networks contribute to verbal and visual working memory (Chen and Desmond, 2005; E et al., 2014; Marvel and Desmond, 2010; Stoodley and Schmahmann, 2009; Stoodley et al., 2012). Previous studies have identified two cerebro-cerebellar networks for verbal working memory — the first is between inferior parietal regions and right inferior cerebellum, associated with the phonological store, and the second is between inferior frontal regions and right superior cerebellum, which was found to be linked with articulatory rehearsal processes (Desmond et al., 1997; Chen and Desmond, 2005). Based on these findings, Chen and Desmond (2005) proposed a cross-lateralized cerebro-cerebellar model of verbal working memory, with the right cerebellum being involved in language-related processing. The proposed model has been further verified by transcranial magnetic stimulation (Desmond et al., 2005; Chen et al., 2014; Tomlinson et al., 2014) and functional neuroimaging studies (Macher et al., 2014; Ng et al., 2013). While this pattern of cerebellar activations has been consistently found in a number of studies (E et al., 2014), cerebellar contributions to visual working memory are much less consistently reported. In addition, our meta-analysis of verbal working memory using N-back and Sternberg paradigms showed differential activity in the cerebellum (E et al., 2014), suggesting a possible differing profile for visual working memory as well. For example, Thürling et al. (2012) observed bilateral superior and right inferior cerebellar activations for a N-back visual abstract figures task, but only superior cerebellar activations (more prominent on the right side) were observed when using a Sternberg paradigm for the same visual stimuli. Moreover, in our recent study of visual working memory qualitative inspection of results showed that bilateral superior and left inferior cerebellar regions are activated during a visual Sternberg task using abstract figures (Ng et al., 2013). However, further quantitative examination of the results with laterality index AveLI (Matsuo et al., 2012) revealed that not only superior but also inferior cerebellum is activated bilaterally (unpublished data). Therefore, to further our understanding of cerebellar involvement in visual working memory, investigation into a more precise understanding of cerebellar contributions to each of the key phases of

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visual working memory (i.e. encoding, maintenance and retrieval) is necessary.

One of the most influential working memory models is a cognitive framework proposed by Baddeley and Hitch in 1974. Baddeley conceptualized the working memory model as a system consisting of the central executive that controls cognitive processes, the visuospatial sketchpad that stores and manipulates images and the phonological loop that stores (phonological store) and manipulates (articulatory control rehearsal system) verbal information (Baddeley, 1986). Logie (1995) proposed a further clarification on the nature of visuospatial sketchpad. He introduced a distinction between the visual cache (visual component) and the inner scribe (spatial component). The visual cache performs a function of a temporary store that holds visual images. It stores features of object's physical appearance such as color, shape, visual texture and size. The inner scribe retains spatial information and can be used to rehearse the contents of the visual cache. It has been shown that visuospatial sketchpad can interact with previously stored knowledge when successful identification of the object to be memorized requires association with semantic content about similar-looking objects (Della Sala and Logie, 2002; Repovš and Baddeley, 2006). This suggests that mechanisms involved in active maintenance of objects may rely not only on the visual features of objects, but also on semantic verbal information that are automatically associated with the perceived object (Postle et al., 2005).

In terms of activation lateralization, Baddeley (2000) suggested that visual working memory is represented in the right hemisphere (areas 6, 19, 40 and 47); however the evidence from functional neuroimaging studies is inconclusive. For example, Courtney et al (1997) found that right-lateralized cortical activity changes when memorizing faces whereas Smith et al (1995) reported left-lateralized activations for spatial arrays of abstract shapes. A meta-analysis by Rottschy et al. (2012) of neuroimaging studies that examined visuospatial working memory linked activations in the bilateral middle frontal/precentral cortex, right inferior frontal cortex, left ventral visual cortex and left cerebellum with the visual component (the visual cache) of visuospatial working memory, whereas more posterior regions including bilateral posterior and right inferior parietal regions were associated with the spatial component (the inner scribe) of visuospatial working memory.

In our previous (unpublished data) fMRI block design study, we specifically examined the laterality of cerebro-cerebellar networks contributing to visual working memory of abstract patterns. We found that bilateral cerebro-cerebellar networks support visual working memory, including bilateral inferior frontal and inferior temporal regions, and bilateral superior (lobule VI) and inferior (lobule VIIb) cerebellar areas. The results of this study linked visual working memory with bilateral rather than right-left lateralized cerebro-cerebellar networks. However, the design used (block design) did not allow us to determine the precise contribution of each network to the principal components of visual working memory (the inner scribe and the visual store). Consequently, in the current fMRI study we employed an event-related design together with a Sternberg's paradigm (1966) that consisted of abstract visual patterns that were difficult to verbalize. A Sternberg paradigm consists of encoding, maintenance and retrieval phases. Participants are required to perform a specific task in each of the phases and thus separation of the experiment into encoding, maintenance and retrieval can capture the brain changes corresponding to the functions that dominate in each phase. In a typical Sternberg verbal working memory task, the encoding phase is usually not longer than 2 s (e.g. Chen and Desmond, 2005; Marvel and Desmond, 2010; Thürling et al., 2012) as acquisition of verbal information occurs quickly; thus there is not enough time for rehearsal processes to occur in that phase. Instead, rehearsal of verbal information can be measured in the maintenance phase, which has long enough duration to allow the contents of the store to be refreshed. In contrast, pilot studies of our visual working memory task with complex abstract patterns showed that the encoding of visual information requires a longer duration whereas maintenance of the representations (when the external stimuli guidance is removed) needs to have shorter duration in order to achieve sufficiently high accuracy rates of 80%. The cognitive demands involved in different memory modalities appear to lead to a different temporal distribution of rehearsal processes in the Sternberg paradigm. For this study, we propose that there is a higher probability that rehearsal will occur in the encoding phase because the 4 s duration allows and requires that the contents of the store be refreshed. However, it is also possible that the rehearsal will still be present in maintenance if visual representations are refreshed in mental imagery, but given that the maintenance phase duration is only 1 or 2 s, it is likely that storage processes will be emphasized more. Discrimination between the visual contents maintained in the cache and response formation will take place in the retrieval phase. Hence, the Sternberg paradigm is ideal to allow close examination of the temporal dynamics of the network activity across the three phases.

It is noted that previous studies listed in the meta-analysis of Rottschy et al. (2012) did not always consider the importance of the inferior cerebellum as it was not routinely included in data acquisition due to field-of-view limitations. Therefore, it is not possible to rule out the importance of this region to visual working memory on the basis of previous studies. Moreover, studies which focus on cerebellar function have provided evidence that both inferior and superior cerebellum contribute to visual working memory (e.g. Ng et al., 2013; Yeh et al., 2007; Salmi et al., 2010). Further support for cerebellar involvement in visual working memory is provided by neuropsychological and stimulation studies. Patients with cerebellar lesions have deficits in encoding relevant visuospatial information (Baier et al., 2014) and double-pulse TMS over left inferior and left superior cerebellum in healthy subjects diminishes task performance during a visual working memory task but not during a verbal working memory task (Chen et al., 2014). These findings suggest cerebellar lateralization for visual working memory even though results from functional neuroimaging studies usually reveal bilateral cerebellar activations (see E et al., 2014 for review). In the current study we propose that not only superior cerebellum but also the inferior cerebellum contributes to visual working memory.

Thus, the aim of the present study was to clarify the involvement of the cerebellum in visual working memory. We utilized an event-related design in our study to examine cerebro-cerebellar networks in encoding, maintenance and retrieval processes. Based on findings described above on cerebellar contributions to visual working memory and cross-lateralized cerebro-cerebellar networks for verbal working memory (Chen and Desmond, 2005), we hypothesized that during the encoding phase the left-lateralized superior cerebellum (crus I, lobule VI) and right-lateralized frontal regions will show increased activations, during the maintenance phase the left-lateralized inferior cerebellum (lobule VIIb) and right-lateralized parietal regions will be more active and in retrieval we will observe right-lateralized frontal and temporal activations together with superior cerebellar vermis activations.

2. Methods

2.1. Subjects

40 subjects (20 females and 20 males; mean age 23.2 ± 1.9 years) participated in the study. Participants were right-handed (Edinburgh Handedness Inventory score: mean = 88.4; SD = 12.6), had no history of neurological conditions, psychiatric conditions or noticeable brain abnormalities. Informed consent was obtained for all participants and the study was approved by the Institutional Review Board at the Nanyang Technological University and the National Health Group.

2.2. Task design

A modified Sternberg visual working memory task consisting of abstract patterns that were difficult to verbalize (Ng et al., 2013) was