Modulating perceptual complexity and load reveals degradation of the visual working memory network in ageing

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ABSTRACT

Previous neuroimaging studies have reported a posterior to anterior shift of activation in ageing (PASA). Here, we explore the nature of this shift by modulating load (1,2 or 3 items) and perceptual complexity in two variants of a visual working memory task (VWM): a 'simple' color and a 'complex' shape change detection task. Functional near-infrared spectroscopy (fNIRS) was used to record changes in activation in younger (N=24) and older adults (N=24). Older adults exhibited PASA by showing lesser activation in the posterior cortex and greater activation in the anterior cortex when compared to younger adults. Further, they showed reduced accuracy at loads 2 and 3 for the simple task and across all loads for the complex task. Activation in the posterior and anterior cortices was modulated differently for younger and older adults. In older adults, increasing load in the simple task was accompanied by decreasing activation in the posterior cortex and lack of modulation in the anterior cortex, suggesting the inability to encode and/or maintain representations without much aid from higher-order centres. In the complex task, older adults recruited verbal working memory areas in the posterior cortex, suggesting that they used adaptive strategies such as labelling the shape stimuli. This was accompanied by reduced activation in the anterior cortex reflecting the inability to exert top-down modulation to typical VWM areas in the posterior cortex to improve behavioral performance.

Introduction

Visual working memory (VWM) is a short term storage system for visual information that is critical for at least two central aspects of cognition - for the comparison of percepts that cannot be simultaneously foveated and for identifying changes in the world when they occur (Luck and Vogel, 1997). As a result, VWM is central to adaptive functions such as navigation, driving, reading, and so on. Healthy VWM processing is critical throughout the human life span, and deficits in VWM processing have serious consequences for performance during early development and late adulthood.

In healthy ageing, there are marked changes in this cognitive system. Decline in VWM is reported to start as early as in the fourth decade of life with a drop of 0.20 items per decade in both verbal and spatial working memory (Salthouse, 1994). Although these data suggest a dramatic decline in working memory function, other factors might also play a role: factors such as deconditioning of physiological processes following inactivity, arthritis, and declining motor abilities can affect behavioral measures such as accuracy and reaction times.

One way to move beyond motoric deficits is to investigate brain function alongside behavior in younger and older adults.

Studies of WM using functional magnetic resonance imaging (fMRI) implicate a distributed cortical network that spans the frontal, parietal, and temporo-occipital cortices (Druzgal and D'Esposito, 2003; Learmonth et al., 2002; Linden et al., 2003; Ma et al., 2014; Pessoa and Ungerleider, 2004; Postle, 2015; Rypma et al., 2002; Todd and Marois, 2005, 2004). In adults, there is generally an increase in blood oxygen level dependent (BOLD) activation as the number of items to be maintained in working memory (i.e., the load) is increased (Todd and Marois, 2004). In the ageing brain, this trend is maintained, but older adults tend to recruit larger areas of the prefrontal/frontal cortex and also show greater activation than younger adults when the demands of a task are low, for instance, with low working memory load (Cappell et al., 2010; Davis et al., 2008; Reuter-Lorenz and Campbell, 2008; Reuter-Lorenz et al., 2000). However, as load increases, older adults tend to show a drop or plateau in activation levels (Mattay et al., 2006). This has been referred to as the compensation-related utilization of neural circuits hypothesis (CRUNCH; Reuter-Lorenz and Campbell, 2008).

Some cognitive studies have also reported a posterior to anterior shift in ageing (PASA) wherein clusters in the ageing posterior cortex show reduced activation while clusters in the frontal cortex show increased activation relative to younger adults (Anderson, 2000; Cabeza et al., 2004; Davis et al., 2008; Dennis et al., 2007; Grossman et al., 2002; Gutchess, 2014; Reuter-Lorenz and Campbell, 2008; Reuter-Lorenz and Lustig, 2005; Reuter-Lorenz et al., 2000; Rypma and D'Esposito, 2000). More recent commentaries have discussed the nature of this shift in activation (see Monge and Madden (2016) for review). It is possible that deficits in perceptual processing in the posterior cortex lead to increased activation in higher-order processing centres in the anterior cortex. Alternatively, impoverished modulation from higher order centres in the anterior cortex might lead to problems in perceptual processing in the posterior cortex.

To further clarify the relationship between the posterior and anterior cortices in the ageing brain, the present study builds on a recent fMRI study that modulated perceptual complexity and load during a visual working memory task in young adults (Ambrose et al., 2016). In particular, this study used a 'simple' color change detection task and a 'complex' shape change detection task with varying loads. Results showed significantly lower WM capacities for the more complex task and a *selective modulation of posterior cortex* in response to this task manipulation. In particular, clusters in occipital cortex, ventral occipital cortex, intraparietal sulcus, superior intraparietal sulcus, and middle fusiform gyrus all showed an activation plateau at high WM loads for the simple task, but a precipitous decline in activation at the highest load for the complex task.

In the present study, we used the same modulation of task complexity in a VWM task with younger and older adults. The first central question was whether the older adults would show both lower VWM capacity overall, and also lower capacity for the more complex task relative to the simple task. If so, is the modulation of the brain in response to the task manipulation selective to posterior cortex such as with younger adults? This is a critical question with PASA. We know there is some form of posterior decline, but is there still the potential for selective task-specific posterior modulation? And does this modulation resemble the effect with younger adults with a precipitous decline in activation for the complex task? The alternative is that the modulation of the brain in response to task complexity happens primarily in the anterior brain. A central hypothesis in PASA is that the anterior brain might be compensating for posterior decline. If the activation of the anterior cortex is compensatory, we should see differences in this activation pattern as task complexity is manipulated. It is possible, of course, that both the posterior and anterior cortices are affected by the manipulation of task complexity. Here, the pattern of modulation should shed light on interactions between the posterior and anterior brain.

Most previous examinations of VWM at the neural level in adults have used fMRI. In the current study, we used functional near-infrared spectroscopy (fNIRS) because this technology is easier and more convenient to administer with older participants. fNIRS is an optical imaging technique where near-infrared light of two different wavelengths is shone through tissue and is selectively absorbed by oxy-(HbO) and deoxy- (HbR) hemoglobin. fNIRS has been used to explore neural function underlying a wide range of sensory (Bortfeld et al., 2007; Chen et al., 2015; Plichta et al., 2011; Wijeakumar et al., 2012), motor (Gagnon et al., 2012; Huppert et al., 2006) and cognitive functions such as working memory, response inhibition, and task-switching (Cutini et al., 2008; Rodrigo et al., 2014; Wijeakumar et al., 2017). fNIRS is a convenient technique for investigating brain function in response to VWM processing because the regions of interest (ROIs) are near the cortical surface. fNIRS is also cheaper than fMRI, making intensive study of age-related decline more feasible, and older adults do not have to remain completely still in a supine position for lengthy periods of time. Moreover, recent innovations in fNIRS analyses allow

us to obtain voxel-wise measures of functional activation that can be directly compared to fMRI data (Wijeakumar et al., 2017, 2015).

Materials and methods

Participants

Twenty-eight younger and twenty-eight older participants took part in the experiment. All participants reported that they had normal or corrected-to-normal vision. When needed, corrected prescriptions were worn during the tasks. The final analyses consisted of twenty-four younger (age range: 25.4 ± 4.3 years old) and twenty-four older (age range: 70.5 ± 5.2 years old) participants. All participants signed an informed consent form approved by the Ethics Committee at the University of Iowa.

Screening procedures

Both groups of participants were asked to fill in questionnaires to assess if they had any health-related circumstances such as mental health problems, use of medication, or surgeries that would have an impact on task performance. All older participants completed the Montreal Cognitive Assessment to assess the presence of cognitive impairment. Participants who obtained a score of less than 26 (out of 30 points) were excluded. A score of less than 26 implied the presence of mild cognitive impairment. They also completed the Geriatric Depression Scale to identify the presence of depression. Those participants who obtained a score greater than 5 were excluded. A score of 5 or greater might indicate the presence of depression and the need for a more thorough clinical investigation.

Stimuli and design

Details of the experimental paradigms have been described elsewhere (Ambrose et al., 2016). Briefly, colors and shapes were used as stimuli. Colors were equally distributed in CIELAB 1976 color space. We used shapes based on Drucker and Aguirre's RFC-defined stimuli (Drucker and Aguirre, 2009). Four different colors and four different shapes were used. Each color or shape was separated by at least 90° in feature space from the other colors or shapes. The experiments were created and run using E-prime version 2.0 on an HP computer.

Two variants of a Change Detection (CD) task were run (see Fig. 1). In the 'simple' color task, participants were presented with a memory array with colored stimuli of the same shape. After a brief delay, a test array was presented that was either the same as the memory array or one of the colors of the stimuli was changed. The shapes of the stimuli were held constant. In the 'complex' shape task, participants were presented with a memory array with stimuli of different shapes (all stimuli were of the same color). After a brief delay, a test array was presented that was either the same as the memory array or one of the stimuli had a different shape. In both tasks, participants had to indicate
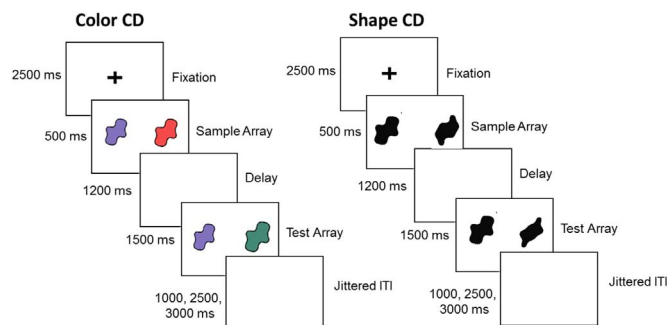
Fig. 1. 'Simple' color and 'complex' shape CD tasks.