Developmental Cognitive Neuroscience 17 (2016) 19–27

Contents lists available at ScienceDirect

Developmental Cognitive Neuroscience

journal homepage: http://www.elsevier.com/locate/dcn

The neurodevelopmental differences of increasing verbal working memory demand in children and adults

V.M. Vogan[a,b,*], B.R. Morgan[a], T.L. Powell[a], M.L. Smith[a,c], M.J. Taylor[a,b,c]

[a] Diagnostic Imaging, Hospital for Sick Children, Toronto, ON, Canada
[b] Applied Psychology and Human Development, Ontario Institute for Studies in Education, University of Toronto, Toronto, ON, Canada
[c] Department of Psychology, University of Toronto, Toronto, ON, Canada

ARTICLE INFO

Article history:
Received 22 April 2015
Received in revised form 26 August 2015
Accepted 13 October 2015
Available online 5 November 2015

Keywords:
Verbal working memory
Functioning magnetic resonance imaging
Development

ABSTRACT

Working memory (WM) – temporary storage and manipulation of information in the mind – is a key component of cognitive maturation, and structural brain changes throughout development are associated with refinements in WM. Recent functional neuroimaging studies have shown that there is greater activation in prefrontal and parietal brain regions with increasing age, with adults showing more refined, localized patterns of activations. However, few studies have investigated the neural basis of verbal WM development, as the majority of reports examine visuo-spatial WM.

We used fMRI and a 1-back verbal WM task with six levels of difficulty to examine the neurodevelopmental changes in WM function in 40 participants, twenty-four children (ages 9–15 yr) and sixteen young adults (ages 20–25 yr). Children and adults both demonstrated an opposing system of cognitive processes with increasing cognitive demand, where areas related to WM (frontal and parietal regions) increased in activity, and areas associated with the default mode network decreased in activity. Although there were many similarities in the neural activation patterns associated with increasing verbal WM capacity in children and adults, significant changes in the fMRI responses were seen with age. Adults showed greater load-dependent changes than children in WM in the bilateral superior parietal gyri, inferior frontal and left middle frontal gyri and right cerebellum. Compared to children, adults also showed greater decreasing activation across WM load in the bilateral anterior cingulate, anterior medial prefrontal gyrus, right superior lateral temporal gyrus and left posterior cingulate. These results demonstrate that while children and adults activate similar neural networks in response to verbal WM tasks, the extent to which they rely on these areas in response to increasing cognitive load evolves between childhood and adulthood.

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1. Introduction

Working memory (WM) allows for the temporary storage and manipulation of information (Baddeley, 1992). WM capacity, the number of items that can be held in WM at one time, plays an important role in the development of other complex cognitive skills, such as reading ability (Engle, 2002; Cain et al., 2004), math performance (Dumontheil and Klingberg, 2012), social ability (Dennis et al., 2009), as well as in general intelligence (Colom et al., 2007; Engle et al., 1999), overall learning (Gathercole and Alloway, 2004) and academic achievement (Gathercole et al., 2004a; Alloway, 2009). Impaired WM capacity has been linked to a number of neurodevelopmental disorders, such as Attention Deficit Hyperactivity Disorder (ADHD; see Martinussen et al., 2005) and Autism Spectrum Disorder (ASD; Southwick et al., 2011), and various learning (Hwang and Hosokawa, 2007; Wang and Liu, 2007) and language processing difficulties (see Wright and Fergadiotis, 2012).

Behavioral studies have documented improvements in WM ability throughout childhood to adulthood (e.g., Conklin et al., 2007; Gathercole et al., 2004b; Huizinga et al., 2006; Zald and Iacono, 1998). Whereas many other executive function components show development typically only up until mid-adolescence, WM continues to show *protracted* development well into young-adulthood (Huizinga et al., 2006), making it particularly susceptible to developmental disturbances. Structural brain changes throughout development are associated with refinements in various cognitive functions, including WM (Tamnes et al., 2013). Specifically, changes in structure and function of brain regions involved in WM, such as parietal and frontal regions, occur later than many regions, consistent with the protracted maturation of WM functions (Sowell et al., 1999). Given the key role WM plays in cognitive maturation, it is

* Corresponding author at: Diagnostic Imaging, Hospital for Sick Children, 555 University Avenue, Toronto, Canada M5G 1X8. Tel.: +1 416 813 7654x304299.
E-mail address: Vanessa.vogan@sickkids.ca (V.M. Vogan).

http://dx.doi.org/10.1016/j.dcn.2015.10.008
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important to understand and characterize the neural basis of this development.

Recent functional neuroimaging studies that have examined the neural underpinnings of WM across development have shown that with increased age, children and adolescents exhibit greater activation in prefrontal (Klingberg et al., 2002; Scherf et al., 2006) and parietal (Nagel et al., 2013; Spencer-Smith et al., 2013; Klingberg et al., 2002; Scherf et al., 2006) regions on visuo-spatial WM tasks. Adults showed similar neural patterns as children and adolescents on these tasks, but with more refined, localized activation (Scherf et al., 2006), and some increased activity in "performance-enhancing" regions, such as the dorsolateral prefrontal cortex (DLPFC; Jolles et al., 2011; Scherf et al., 2006). For example, Scherf et al. (2006) found that children showed limited recruitment of critical WM substrates (DLPFC and parietal regions) during a visuo-spatial WM task, and instead relied mainly on ventromedial prefrontal regions. However, they observed more specialized networks (i.e., DLPFC, ventrolateral prefrontal cortex [VLPFC] and supramarginal gyrus) as adolescents moved into adulthood. This developmental pattern of brain activity has also been characterized as a shift from posterior to anterior activation, with adults showing increased activity in the DLPFC and VLPFC (Kwon et al., 2002; Scherf et al., 2006). Thus, previous literature suggests that the development of higher-level WM function involves a combination of increasing localization within core WM regions and their integration with performance-enhancing regions.

Fewer studies have examined the neural basis of *verbal* WM development, as the majority of studies utilized visuo-spatial or other nonverbal tasks. Verbal WM is particularly important, given its vital role in linguistic processes that are necessary for language and other higher-level cognitive functions (Smith et al., 1998). Brahmbhatt et al. (2008) found similar activation patterns between adolescents and adults during an *n*-back visual word task, with both groups showing activation in the bilateral fusiform gyrus, anterior cingulate, left precentral gyrus, left superior anterior temporal gyrus, left DLPFC, premotor cortex and left thalamus. Age-related changes were evident in the left parietal lobe, in which adults showed significantly greater activity than adolescents. In addition to the nature of tasks, the pattern of brain activation also depends on the *amount* of information (i.e., load) that needs to be maintained in WM. Previous literature exploring age-related changes in brain activity associated with verbal WM under conditions of increasing load found that adolescents and adults showed a greater increase in activation across load in left parietal (O'Hare et al., 2008; Thomason et al., 2009), left lateral prefrontal (Thomason et al., 2009) and right cerebellar (O'Hare et al., 2008) regions than children. In contrast, Jolles et al. (2011) did not find age-related load sensitivity in children and adults. Also, previous reports used only up to three levels of difficulty.

The present study examined the effects of increasing load, with six difficulty levels in a verbal WM task, and how load-dependent change in brain function differed in children and adults. Prior developmental visual verbal WM studies that included load as a manipulation used complex tasks that required maintenance and reordering (Jolles et al., 2011) or changed stimuli appearance and size (O'Hare et al., 2008; Thomason et al., 2009) as difficulty level increased. In a typical *n*-back task, participants view a series of stimuli and indicate whether the currently presented stimulus matches one presented '*n*' (e.g., 0, 1, 2 or 3) trials prior. As difficulty level increases, the number of interfering stimuli between the target and relevant stimulus increases, requiring the utilization of different mental strategies at each level (e.g., 0-back: recognition; 1-back: maintenance; 2-back: maintenance and monitoring). These manipulations increase both memory load *and* executive function demands (i.e., strategy needed to complete the task) in a non-linear fashion from each level to the next, making function-specific alterations difficult to quantify and relate with specific brain regions. To avoid these confounds, we used a 1-back letter matching task (LMT) which manipulated memory load while keeping executive function uniform across the difficulty levels, allowing us to investigate directly the impact of cognitive load on verbal WM. The executive demands (i.e., procedural strategies for solving the task) were constant across all levels of the LMT; what varied with each level was the number of items (letters) that had to be remembered. A visuo-spatial analogue of LMT has been used successfully to explore WM in functional neuroimaging studies of adults (Arsalidou et al., 2013) and children with and without ASD (Vogan et al., 2014). Observations from these studies point to a linear pattern of WM function across load. Our task can capture neural correlates associated with this linear pattern of activation with cognitive load, and our objective is to determine whether patterns of activation in WM processing change across development.

Understanding the effect of age on brain regions implicated in WM and WM capacity can provide insight into the developmental trajectory of verbal WM networks, and enhance our ability to determine optimal timing for interventions in paediatric populations with WM difficulties. Given previous literature and findings from our recent work using the visuo-spatial version of LMT, we expected frontal and parietal cortical areas associated with WM would be under-recruited in children compared to adults, and these differences would increase with increasing cognitive load. Further, neural activation in both groups would be left-hemisphere dominant, given the verbal nature of the task (e.g., Brahmbhatt et al., 2008), and this localized pattern would be less evident in children who are more likely to demonstrate diffuse activation (Scherf et al., 2006).

2. Methods

2.1. Participants

Twenty-four typically developing children aged 9–15 ($M = 12.8$, $SD = 1.7$; 7 female) and 16 young adults aged 20–25 ($M = 22.7$, $SD = 1.5$; 8 female) were included in the analyses. Sixteen other children (i.e., 40 were tested in total) were excluded from the analyses due to excessive movement ($n = 1$), inadequate task performance ($n = 13$) or a combination of these factors ($n = 2$). A chi-square analysis confirmed that sex distribution did not differ between age groups, $\chi^2_{(1)} = 1.78$, $p = 0.18$). Cognitive function of child participants was assessed using the Wechsler Abbreviated Scale of Intelligence-II (Wechsler, 2003) to ensure IQ > 80 ($M = 114.6$, $SD = 8.1$). All subjects were screened and not included on the basis of any current significant psychiatric comorbidities (APA, 2013), neurological disorders, medical illnesses, prematurity, uncorrected vision, as well as standard MRI contraindicators (e.g., ferromagnetic implants). A history of developmental disorders, learning disability or ADHD was also used to exclude participants. Participants were recruited through email lists, posters in the hospital and community, private schools and word of mouth. Informed consent and MRI scanning were performed at the Hospital for Sick Children in Toronto. Experimental procedures were approved by the Research Ethics Board at the Hospital for Sick Children, and all participants provided informed consent; for the children; parents gave written consent while children gave verbal assent.

2.2. The letter matching task (LMT)

In the current study, LMT is considered a verbal WM task; although it is not auditory in nature, it uses completely verbal (i.e., linguistic) stimuli. Participants were required to attend to letters

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