



Research report

Hippocampal and posterior parietal contributions to developmental increases in visual short-term memory capacity

David Yoh von Allmen^a, Karoline Wurmitzer^a and Peter Klaver^{a,b,c,d,*}

^a Center for MR Research and Children's Research Center, University Children's Hospital Zurich, Zurich, Switzerland

^b Institute of Psychology, University of Zurich, Division of Psychopathology and Clinical Intervention, Zurich, Switzerland

^c Neuroscience Center Zurich, University of Zurich and ETH Zurich, Zurich, Switzerland

^d Zurich Center for Integrative Human Physiology (ZIHP), University of Zurich, Zurich, Switzerland

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ABSTRACT

Developmental increases in visual short-term memory (VSTM) capacity have been associated with changes in attention processing limitations and changes in neural activity within neural networks including the posterior parietal cortex (PPC). A growing body of evidence suggests that the hippocampus plays a role in VSTM, but it is unknown whether the hippocampus contributes to the capacity increase across development. We investigated the functional development of the hippocampus and PPC in 57 children, adolescents and adults (age 8–27 years) who performed a visuo-spatial change detection task. A negative relationship between age and VSTM related activity was found in the right posterior hippocampus that was paralleled by a positive age-activity relationship in the right PPC. In the posterior hippocampus, VSTM related activity predicted individual capacity in children, whereas neural activity in the right anterior hippocampus predicted individual capacity in adults. The findings provide first evidence that VSTM development is supported by an integrated neural network that involves hippocampal and posterior parietal regions.

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1. Introduction

The amount of information that can be held in visual short-term memory (VSTM) is known to increase substantially from childhood through early adulthood (Gathercole, 1999;

Pickering, Gathercole, Hall, & Lloyd, 2001). The majority of evidence suggests that these improvements depend on changes in attention processing limitations and associated neural networks that include the posterior parietal cortex (PPC) (Klingberg, 2006; Klingberg, Forssberg, & Westerberg, 2002; Olesen, Nagy, Westerberg, & Klingberg, 2003). These

* Corresponding author. University of Zurich, Institute of Psychology, Division of Psychopathology and Clinical Intervention, Binzmuehlestrasse 14, Box 17, CH-8050 Zurich, Switzerland.

E-mail addresses: davidyoh.vonallmen@uzh.ch (D.Y. von Allmen), karoline.wurmitzer@uzh.ch (K. Wurmitzer), p.klaver@psychologie.uzh.ch (P. Klaver).

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changes, however, do not serve as a sufficient explanation for age related capacity increases as suggested by behavioral and psychophysiological studies (Astle et al., 2014; Cowan, Morey, AuBuchon, Zwilling, & Gilchrist, 2010). Instead, other cognitive processes and brain regions might additionally explain developmental improvements in VSTM capacity, which is to date unclear.

In the adult cognitive neuroscience literature, a growing body of research points to a role of the hippocampus in working memory (Finke et al., 2008; Hannula & Ranganath, 2008; Olson, Page, Moore, Chatterjee, & Verfaellie, 2006; Piekema, Kessels, Mars, Petersson, & Fernández, 2006). This idea was supported by recent evidence that neural activity in the hippocampus predicted individual VSTM capacity (von Allmen, Wurmitzer, Martin, & Klaver, 2013). In that study, participants performed a visuo-spatial change detection task during blood oxygenation level dependent (BOLD) fMRI scanning. In high capacity individuals, neural activity in the hippocampus incrementally increased up to set size six, whereas low capacity individuals showed a drop in hippocampal activity when their capacity limit had been exceeded. Within the present study, we aimed to substantiate our previous findings by testing the hippocampus' contribution to VSTM across development. In particular, we asked whether VSTM capacity is predicted by neural activity within the hippocampus across development and whether age related differences in hippocampal activity are linked to developmental increases in VSTM capacity.

In light of the development of the hippocampus, recent studies demonstrated age related structural and functional changes along its longitudinal axis (DeMaster & Ghetti, 2013; DeMaster, Pathman, Lee, & Ghetti, in press; Ghetti, DeMaster, Yonelinas, & Bunge, 2010; Gogtay et al., 2006). Gogtay et al. (2006) for example reported developmental changes in gray matter volume along the hippocampal anterior–posterior axis, whereas its total volume remained constant. Furthermore, correct episodic retrieval of relational information in adults was associated with neural activity in the anterior hippocampus, whereas children showed the same pattern specifically in the posterior hippocampus (DeMaster & Ghetti, 2013). Together, these findings provide evidence for regional age related changes in the hippocampus that might be as well related to simultaneously occurring progressive and regressive events along its longitudinal axis. Two further questions, therefore, were whether the anterior and posterior hippocampus show different developmental trajectories within the framework of VSTM and whether a possible regressive event in the posterior hippocampus parallels a progressive one in the anterior hippocampus with respect to a posterior-to-anterior shift.

In contrast to the sparse evidence for the role of the hippocampus in VSTM, it is well established that individual and developmental differences in VSTM capacity depend on neural activity in the PPC (Fukuda & Vogel, 2009; Klingberg et al., 2002; Magen, Emmanouil, McMains, Kastner, & Treisman, 2009; Olesen, Macoveanu, Tegnér, & Klingberg, 2007; Vogel, McCollough, & Machizawa, 2005). Another important question can hence be raised whether age related improvements in VSTM capacity may result from an integrated neural network that covers both the hippocampus and the PPC. In this context, we also intended to corroborate previous studies that

reported age differences in working memory activity in the recruitment of the PPC (e.g., Klingberg et al., 2002).

In order to examine these questions, we measured BOLD fMRI in a priori defined subregions in the left/right hippocampus (head, anterior body, posterior body and tail) and PPC in three different age groups (children, adolescents and adults) during the completion of a visuo-spatial change detection task. Similar tasks have been used to probe set size modulated brain activity within VSTM (Todd & Marois, 2004; Vogel & Machizawa, 2004), or to demonstrate that damaged hippocampus affected processing of object-location associations (Finke et al., 2008; Olson et al., 2006).

2. Materials and methods

2.1. Participants

Data were collected from 21 adults (age 19–27 years, mean = 22.2 ± 2.19 years, nine males), 16 adolescents (age 13–17 years, mean = 15.2 ± 1.47 years, six males) and 20 children (age 8–12 years, mean = 10.0 ± 1.34 years, nine males), after giving informed consent according to procedures approved by the Cantonal Ethics Committee Zurich. All participants were German speaking, had normal or corrected-to-normal vision and had no history of neuropsychiatric disorders. Age groups were comparable in terms of their socioeconomic status (educational level of both parents) and did not differ in a common estimate of general nonverbal intelligence (Matrix Reasoning) and an assorted subtest for verbal intelligence (Similarities) that were assessed with the German versions of the Wechsler Intelligence Scale for Children (HAWIK-IV; Petermann & Petermann, 2007) and Wechsler Adult Intelligence Scale (WIE; Wechsler and von Aster, 2009) (data not shown). Additional data from seven children and three adolescents were excluded due to head motion during scanning that exceeded 3 mm, or because of failing to follow the instructions (one child). Within the adult group, we reanalyzed data of the same individuals previously examined (von Allmen et al., 2013).

2.2. Task design

Before beginning the measurement, all participants were trained to perform the task on trials that were not included in the actual task. Fig. 1A shows a sample of a trial used in our change detection task that required encoding, maintenance and retrieval of colored squares, spatially arranged within arrays of different set size conditions. Each trial started with a presentation of a central fixation cross on a light gray background (2000 msec). Then, an array of one, two, four or six objects was presented (800 msec). Subjects were instructed to retain these objects over a short period (900 msec). Finally, a probe array appeared (2000 msec), whereon subjects indicated by button press whether or not the probe matched the study array. A mismatch was introduced by a change of color in one square, while stimulus locations were held constant within a trial. Responses were given with index fingers of the left and right hand. Left-right allocation of response types (match/mismatch) was counterbalanced across subjects. Eighty trials

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