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Normative shifts of cortical mechanisms of encoding contribute to adult age differences in visual–spatial working memory

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ABSTRACT

The capacity of visual–spatial working memory (WM) declines from early to late adulthood. Recent attempts at identifying neural correlates of WM capacity decline have focused on the maintenance phase of WM. Here, we investigate neural mechanisms during the encoding phase as another potential mechanism contributing to adult age differences in WM capacity. We used electroencephalography to track neural activity during encoding and maintenance on a millisecond timescale in 35 younger and 35 older adults performing a visual–spatial WM task. As predicted, we observed pronounced age differences in ERP indicators of WM encoding: Younger adults showed attentional selection during item encoding (N2pc component), but this selection mechanism was greatly attenuated in older adults. Conversely, older adults showed more pronounced signs of early perceptual stimulus processing (N1 component) than younger adults. The amplitude modulation of the N1 component predicted WM capacity in older adults, whereas the attentional amplitude modulation of the N2pc component predicted WM capacity in younger adults. Our findings suggest that adult age differences in mechanisms of WM encoding contribute to adult age differences in limits of visual–spatial WM capacity.

Introduction

Visual–spatial working memory (WM) refers to the ability to hold small amounts of spatial information "online" for short periods of time. WM capacity is limited, both in younger (Cowan, 2001; Luck and Vogel, 1997), and more so in older adults (Cowan et al., 2006; Sander et al., 2011). Limitations in WM capacity may derive from processing constraints during the initial encoding of the stimuli, their active maintenance, or subsequent retrieval. Individual and age-related differences in WM capacity have mostly been related to processing differences during the maintenance phase. Observers with high WM capacity usually show stronger load-dependent recruitment of task relevant brain regions during WM maintenance, compared to observers with low WM capacity (e.g., Todd and Marois, 2004; Vogel and Machizawa, 2004). The relation between load-dependent modulations of neural activity during maintenance and WM performance pertains for both younger (Todd and Marois, 2004; Vogel and Machizawa, 2004) and older adults (Mattay et al., 2006; Nagel et al., 2009, 2010). In fact, younger and older adults with similar WM capacity also show similar activation patterns during the retention of WM contents (Nagel et al., 2009), suggesting that mechanisms of WM maintenance do not necessarily alter as a function of age, but rather depend on the performance level of an individual, which—one average—is lower in older compared to younger adults.

Prior to WM storage, information needs to be accurately encoded. The encoding process directly influences the precision and accuracy of subsequent WM representations (Awh and Vogel, 2008; Rutman et al., 2010). Thus, any constraints at early encoding stages will necessarily affect later maintenance or retrieval processes. Only recently, studies reported that older adults show deficits in selective attention during WM encoding and suggested that these deficits contribute to age-related declines in WM performance (Gazzaley, 2011; Gazzaley et al., 2008; Zanto et al., 2010). Whereas these findings seem to provide an important clue to understanding reduced WM capacities in old age, they are limited in two main ways. First, thus far, existing studies only investigated age differences of WM encoding for single objects and features, which challenge the generalizability of the findings. Second, none of these studies directly addressed the question whether and to what extent these age group differences during WM encoding can be explained by differences in performance level, or whether they reflect differences in age per se. This seems to be fundamental in order to fully understand how aging alters cognitive and neural mechanisms of WM encoding.

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Here, we studied 35 younger and 35 older adults and asked them to perform a visual–spatial WM task that requires the encoding of multiple independent objects and their locations at once. We manipulated memory load (1 target, 3 targets) and interference by irrelevant items (absent, present). Based on previous research (Babcock and Salthouse, 1990; Borella et al., 2008; Cowan et al., 2006; Li et al., 2008), we expected lower WM capacity in older relative to younger adults, particularly in the high-load condition (3 targets). Furthermore, we expected that the interference manipulation would affect performance negatively, particularly in the high-load condition. To investigate adult age differences in mechanisms of WM encoding and subsequent maintenance, electrophysiological recordings were obtained. We examined event-related potentials (ERPs) elicited by the memory array that index different processes of WM: First, perceptual processing of the stimuli (N1 component; Heinze et al., 1990; Mangun, 1995), second, attentional selection of the stimuli (N2pc component; Eimer, 1996; Luck and Hillyard, 1994a, 1994b), and third, the maintenance of WM contents (contralateral-delay activity, CDA component; Vogel and Machizawa, 2004). Based on a recent study that examined ERP correlates of WM maintenance in different age groups (Sander et al., 2011), we expected older adults to show less load-dependent amplitude modulations of the CDA component (see also, Jost et al., 2011). Of most interest was, however, whether younger and older adults would show differences during WM encoding already, namely in early perceptual processing and/or attentional selection. In contrast to the maintenance stage, thus far these aspects of visual–spatial WM encoding and aging have not been investigated. We expected older adults to show a deficit in their attentional focus, which would be reflected in an attenuation of the N2pc component, relative to younger adults (Li et al., 2012; Lorenzo-Lopez et al., 2008). Furthermore, older adults would possibly engage another encoding mechanism to attenuate the adverse consequences of this deficit on WM performance. Although we did not have specific a priori expectations about the nature of this mechanism, we hypothesized that it would occur during item encoding, possibly during stimulus processing itself (cf., Gazzaley et al., 2008; Störmer et al., 2013). If individual differences during WM encoding contributed to individual differences in WM performance, we would expect that these differences in early ERP components correlate with differences in behavior. To dissociate age effects from effects that might be solely driven by differences in performance level, we separated individuals based on their overall performance within each age group. To be able to compare groups that differ in age but match according to their WM performance, we chose a tertile split and divided observers into sub-groups of 'high'-, 'intermediate'-, and 'low'-performers.

Methods

Participants

A total of 83 participants took part in the study. Data from four younger and nine older participants were excluded from the analysis because more than 30% of their trials were rejected due to artifacts in the EEG recordings. Of the remaining 35 younger adults (18 females, 20 to 31 years, mean age: 26 (+/−2.5) years) and 35 older adults (16 females, 64–76 years, mean age: 71 (+/−3.8) years), all were right-handed, reported normal hearing and had normal or corrected-to-normal vision. Vision was assessed prior to the experiment using standard tables with Landolt rings (Geigy, 1977), and standard color panels. In a separate behavioral session that took place before the experimental session, participants were assessed on marker tests of crystallized intelligence (Lehrl, 1977) and perceptual speed (Wechsler, 1958). As expected, older adults attained lower scores in perceptual speed and higher scores in verbal knowledge relative to younger adults (see Table 1), which is comparable to other studies based on representative lifespan samples (Li et al., 2004). Participants gave informed consent according to the procedures approved by the Ethics Committee of the Max Planck Institute of Human Development.

Stimuli and procedure

Participants performed the experiment in an electrically shielded chamber that was dark throughout the experiment. Stimulus arrays were presented on a 19-in. computer display with a gray background (20.5 cd/m^2) within 8.5°×13° rectangular regions that were centered to the left and right of the vertical midline. Relevant target items were colored squares subtending 0.9°×0.9° visual angle, and irrelevant items were colored rectangles subtending 0.62°×1.3° visual angle. Stimulus positions were created at random for each trial before the experiment and were uploaded for each participant in the same order. Stimulus items had a minimum distance of 1° (border to border). The color of each item was selected at random from a set of six colors (red, blue, green, yellow, cyan, magenta) and a given color could only appear once in an array. The bilateral memory array consisted of one or three target items (i.e., colored squares) in each hemifield. The bilateral presentation provides balanced sensory stimulation to both hemispheres, and thereby allows to isolate activity that is specific to the hemisphere that is contralateral with respect to the to-be-remembered memory array (McCollough et al., 2007). On half of the trials two irrelevant items (i.e., colored rectangles) were presented together with the targets. Each trial began with a 500-ms arrow cue (0.8°×0.8°) presented in the center of the screen, followed by the bilateral memory array that appeared for 300 ms, a blank period of 900 ms, and a test display of 2000 ms (see Fig. 1A for an example task sequence). On half of the trials the test display consisted of one square that was identical to one of the targets; on the other half of the trials the color of the test square differed from the color of the target square in the memory display. When a color change between the memory item and the test item occurred, the new color was randomly selected from any of the nontarget colors (i.e., not used in the memory display before) on 3/4 of the trials (between-switch trials), and was selected from one of the target colors on 1/4 of the trials (within-switch trials). Participants responded by pressing one of two buttons with the left and right index finger to indicate whether the test item was identical to one of the memory items or not. Importantly, the test item needed to match both in color and spatial location to the memory item to be considered identical. The mapping of responses onto response buttons was counterbalanced between participants. The arrow cue pointed to either the left or right side and remained in the center of the screen throughout the trial. The inter-trial-interval was variable between 500 and 1000 ms (rectangular distribution). During this period, the arrow was substituted by a central fixation cross. Participants were instructed to keep their eyes fixated in the center of the screen throughout the task. Number of target items (1, 3), presence of irrelevant items (present, absent), and test item (change, no-change) were randomized within each block. To reduce switching costs, which are affected by aging (e.g., Kray and Lindenberger, 2000), we pseudo-randomized the presentation order of the arrow, with at

Table 1
Demographic and basic cognitive characteristics of the sample.

	Younger adults	Older adults
	M (*SD*)	*M* (*SD*)
Age	26 (2.5)	71 (3.8)
Years of education	13.3 (2.4)	12.2 (4.2)
Identical pictures (processing speed)	34.5 (5.2)	23.0 (3.3)
Spot-A-Word (pragmatics)	18.7 (5.0)	22.3 (5.9)