



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.

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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 $8.5^\circ \times 13^\circ$ rectangular regions that were centered to the left and right of the vertical midline. Relevant target items were colored squares subtending $0.9^\circ \times 0.9^\circ$ visual angle, and irrelevant items were colored rectangles subtending $0.62^\circ \times 1.3^\circ$ 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 ($0.8^\circ \times 0.8^\circ$) 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
	<i>M</i> (<i>SD</i>)	<i>M</i> (<i>SD</i>)
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)

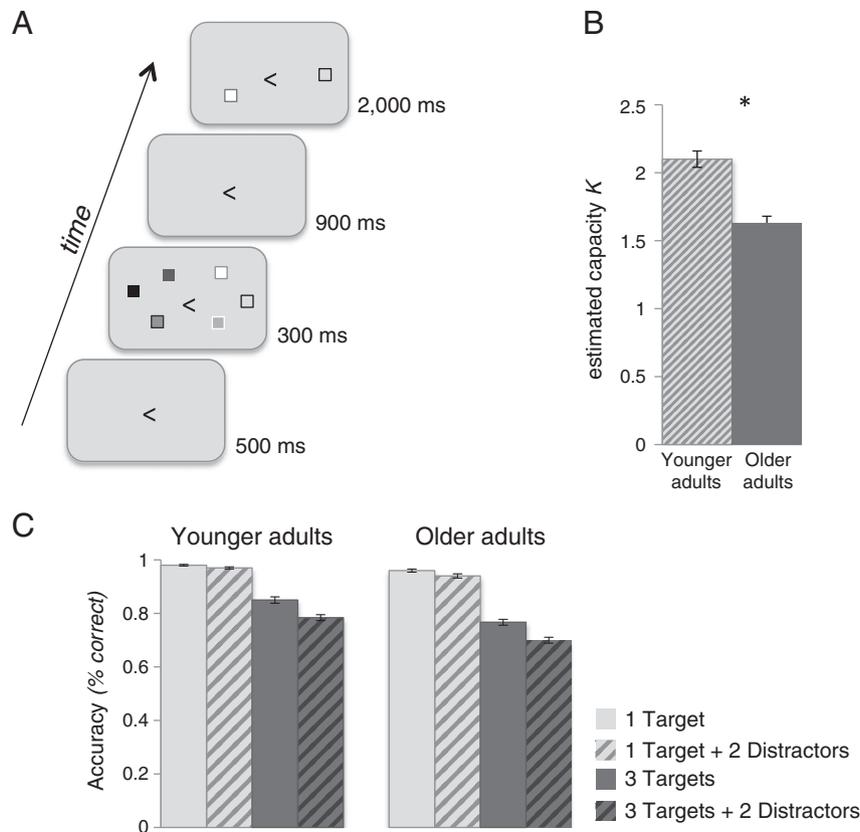


Fig. 1. Experimental procedure and behavioral results. (A) Illustration of the trial sequence with three target items and no interfering nontargets. Different shades of gray reflect different colors of the target squares. (B) Estimated WM capacity K for younger and older adults. K was estimated from the 3-target condition of the same task. (C) Accuracy (% correct) for the different conditions and age groups.

least two arrows pointing in the same direction on subsequent trials, but no more than four in a row.¹ The same pseudo-randomized sequence was used for both younger and older adults to ensure the same experimental precondition for all. The experiment consisted of 20 blocks of 32 trials each.

EEG recordings

Electrophysiological recordings were obtained from 64 Ag/AgCl electrodes placed according to a 10–10 system in an elastic cap (BrainAmp DC amplifiers, Brain Products GmbH, Gilching, Germany). All EEG signals were referenced to the right mastoid. The horizontal electrooculogram (HEOG) was recorded bipolarly using two electrodes positioned lateral to the external canthi; vertical electrooculogram (VEOG) was recorded using one electrode below the left eye. Electrode impedances were kept below 5 k Ω . All signals were recorded with a bandpass of 0.1–100 Hz and digitized at a rate of 1000 Hz.

Data analysis was performed with ERPSS (University of California, San Diego). The EEG and EOG epochs were segmented into 3-s epochs that started 1 s before onset of the memory display. A semi-automated procedure was used to remove epochs that contained horizontal eye movements, blinks, and amplifier blocking (c.f., Störmer et al., 2013). Horizontal eye movements were detected at HEOG channels, and blinks were detected at VEOG and FP1, located over the left eye. Artifact-free data were then used to create averaged ERP waveforms. Separate averages were created for the four memory displays. The averaged

waveforms were digitally low-pass filtered (-3 dB cutoff at 25 Hz) and digitally re-referenced to the average of the left and right mastoid.

Data analysis

Behavioral analysis

Visual-spatial WM performance (% correct) was analyzed using a repeated-measures analysis of variance (ANOVA) with age group as a between-subjects factor and set size of the memory display (1 target, 3 targets) and interference (irrelevant items absent, present) as within-subjects factors. Follow-up pairwise comparisons were conducted to test in which age group and at which level the effects were present. In addition, WM capacity was estimated with a standard formula (Cowan, 2001; Pashler, 1988) that is, $K = S * (\text{Hits} - \text{False alarms})$, where S is the number of items to be remembered. Similar to previous studies (e.g., Jost et al., 2011), we applied the formula for each subject in the 3-target condition (no interference).²

ERP analysis

Analysis of the underlying neural mechanisms of encoding and maintenance focused on lateralized ERP components elicited by the memory array. The analysis centered on the set size manipulation, as we only found age interactions with regard to set size (see Results).

¹ Participants made a similar number of errors in arrow switch trials compared to no-switch trials (percent errors for younger adults: 9.7% for switch trials, 10.6% for no-switch trials; older adults: 15.9% for switch-trials, and 14.6% for no-switch trials; $p > .31$).

² Using the 3-target condition may possibly underestimate WM capacity, particularly in younger adults (applying the standard formula, WM capacity can never exceed the number of target items). We only used this K -value as an estimate, mainly for the neural-behavioral correlations, which makes our results more comparable to previous studies.

ERPs were collapsed across the visual field (left, right) and hemisphere of recording (left, right) to obtain waveforms recorded contra- and ipsilaterally with respect to the to-be-remembered side. Then, difference waveforms were computed by subtracting the ipsilateral waveforms from the contralateral waveforms for each condition and electrode pair separately. Mean amplitudes of the contralateral-minus-ipsilateral difference waveforms were measured with respect to a 100-ms prestimulus period for each participant and condition at four pairs of posterior electrodes (PO7/PO8, PO3/PO4, P3/P4, P7/P8), with three measurement windows based on the peaks in the difference waveforms: 170–190 ms (N1 component), 270–300 ms (N2pc component),³ and 500–1000 ms (CDA component) after onset of the memory array. The resulting mean amplitudes were analyzed in mixed between-within repeated-measure ANOVAs with factors age group (young, old) and set size (1 target, 3 targets). When necessary, follow-up ANOVAs and pairwise comparisons were performed. Greenhouse–Geisser corrected p -values were employed when appropriate. The alpha level was set to $p < .05$.

Spherical-spline-interpolated scalp maps of the contralaterally enlarged N1, N2pc, and CDA components are presented for the 3-target condition in Fig. 2B (scalp maps did not differ in topographical distribution between conditions). These scalp maps were created from the contralateral minus ipsilateral voltage differences for homologous left and right electrodes (e.g., PO7 and PO8), with the values at midline electrode sites (e.g., POz) artificially set to zero. This contra-minus-ipsilateral voltage topography could be projected to either side of the head, and we arbitrarily chose the right side (for a similar procedure, see Störmer et al., 2009).

Neural-behavioral relations

The relations between the different ERP components and estimated capacity K were analyzed. First, for each participant, a score for *perceptual processing* was calculated as the mean amplitude difference between 1 and 3 targets for the N1 component. Second, for each participant, a score for *attentional selection* was calculated as the mean amplitude difference between 1 and 3 targets for the N2pc component (Anderson et al., 2011; Drew and Vogel, 2008). Third, a *maintenance* score was calculated as the mean amplitude difference between 1 and 3 targets in the time interval of the CDA component (Vogel and Machizawa, 2004). Scores were computed on the mean ERP amplitudes at four electrode pairs PO3/PO4/PO7/PO8. The electrophysiological markers were then correlated with each individual's estimated WM capacity K . The correlational analysis was followed up with a performance group analysis to investigate individual differences in encoding in more detail. Such a follow-up group analysis can provide additional support for the continuous measure and enables the detection of small effects (Feldt, 1961; Preacher et al., 2005) and allows comparing individuals that perform at similar ranges across different age groups (for similar procedures, see Nagel et al., 2009; Papenberg et al., 2011). Based on their overall percent accuracy of performance, the 12 highest, the 11 intermediate, and the 12 poorest performers (tertile split) within each age group were sorted into subgroups. WM capacity as estimated by the K value and electrophysiological markers during encoding (N1, N2pc) was compared across the six groups.

³ The analysis was replicated using a larger, more common time window for the N2pc component, namely 200 to 300 ms. We chose a rather narrow time window in the main analysis to unambiguously dissociate the three components of interest (N1, N2pc, CDA).

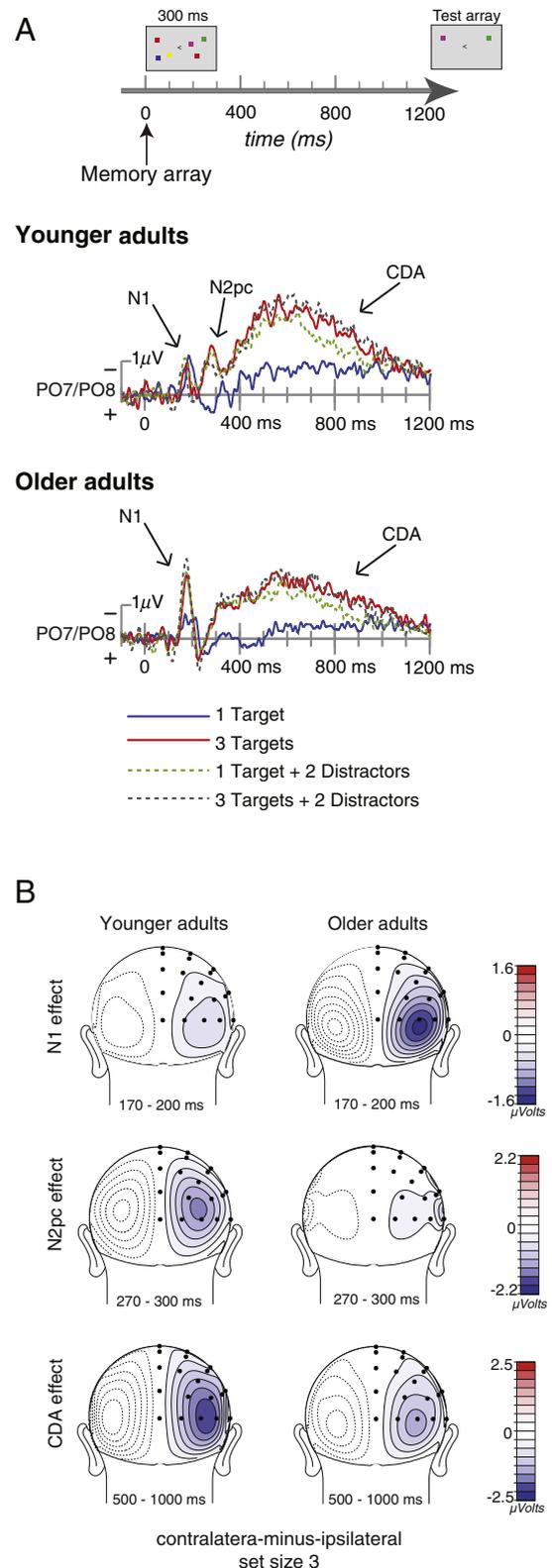


Fig. 2. Event-related potentials (ERPs) and scalp topographies of the voltage distributions. (A) Contralateral-minus-ipsilateral difference ERP waveforms for younger (top) and older (bottom) adults at parietal-occipital electrode sites PO7/PO8. Different colors and lining correspond to the four different conditions (see legend). On the top, the sequence of events of an example trial is depicted, illustrating the timing of the ERP components with regard to stimulus presentation. (B) Scalp topographies of the contralateral-minus-ipsilateral ERP voltage difference, projected on the right side of the scalp (see Methods for details). Topographical distributions of the enlarged contralateral ERP negativities in the time intervals of the N1 effect (170–190 ms), N2pc effect (270–300 ms) and CDA effect (500–1000 ms).

Results

In the following section, we focus on results that include age group as an interaction term.

Behavioral performance

Older adults performed less well than younger adults in the set size 3 condition (Fig. 1C). Statistical analysis confirmed this by revealing an age group \times set size interaction, $F(1,68) = 21.00$, $p < .05$, $\eta^2 = 0.02$. The K -scores also showed reliable age group differences in WM capacity: For the 3-target condition, younger adults' average capacity was estimated at 2.1 items, whereas older adults' average capacity was estimated at 1.6 items, $t(68) = 4.43$, $p < .05$, $\eta^2 = 0.57$ (Fig. 1B).

Overview of results of event-related potentials

Fig. 2A depicts the contralateral-minus-ipsilateral ERP waveforms for the different conditions and age groups separately at posterior electrode pairs. During the encoding phase (0 to 300 ms), two transient negative deflections are apparent in the difference waveforms. Peaking at about 180 ms post onset of the memory array a contralateral negativity (N1 component) was observed in both younger and older adults. Following this initial transient deflection, a second negative wave was observed in younger adults, which peaked about 280 ms post memory array (N2pc component). During the retention interval (~500–1000 ms) a sustained contralateral negativity (CDA component) is visible in both age groups. As depicted in Fig. 2B, topographical voltage maps of the contralateral-minus-ipsilateral voltage difference yielded similar scalp distributions between the age groups for the different ERP components.

Initial perceptual processing: the N1 component

Relative to younger adults, older adults showed an increased amplitude of the contralateral-minus-ipsilateral N1 component for conditions with three targets or with distractors (Fig. 2A). A between-within ANOVA confirmed this by disclosing an age group \times set size interaction, $F(1,68) = 21.94$, $p < .05$, $\eta^2 = .02$, and an age group \times interference interaction, $F(1,68) = 22.81$, $p < .05$, $\eta^2 = .02$. Follow-up analyses revealed a main effect of set size, $F(1,34) = 15.46$, $p < .05$, $\eta^2 = .12$, a main effect of interference, $F(1,68) = 27.17$, $p < .05$, $\eta^2 = .20$, and a set size \times interference interaction, $F(1,34) = 6.77$, $p < .05$, $\eta^2 = .04$, for older adults only. Follow-up pairwise comparisons revealed that the N1 effect in older adults depended only on the number of items, regardless of target and distractor (1 target + interference vs. 3 targets, $p > .05$, all other comparisons $ps < .05$). Thus, older adults showed an increase in amplitude of the contralateral N1 component with more items, regardless of stimulus type. No effects of set size or interference were significant for younger adults (all $ps > .05$).

Selecting target items during encoding: the N2pc component

Younger adults exhibited a clear N2pc component for all conditions except the 1-target condition, but this component appeared to be attenuated in older adults. In older adults, a negative-going wave contralateral to the to-be-remembered side is apparent (Fig. 2A). This negativity increased more slowly and was more sustained than the transient N2pc observed in younger adults (Fig. 2A). Statistical analysis revealed an age group \times set size \times interference interaction, $F(1,68) = 45.14$, $p < .05$, $\eta^2 = .024$, confirming that the N2pc in the group of older adults was smaller and less modulated relative to younger adults. For younger adults, a repeated-measures ANOVA revealed a main effect of set size, $F(1,34) = 22.08$, $p < .05$, $\eta^2 = .14$, and interference, $F(1,34) = 8.76$, $p < .05$, $\eta^2 = .05$, as well as a set size \times interference interaction,

$F(1,34) = 46.10$, $p < .05$, $\eta^2 = .23$. Subsequent pairwise comparisons showed that the amplitude of the N2pc component increased for all conditions relative to the 1-target condition ($ps < .05$; for all other comparisons $ps > .05$). Similarly, for older adults, a repeated-measures ANOVA revealed a main effect of set size, $F(1,34) = 15.82$, $p < .05$, $\eta^2 = .10$, and interference, $F(1,34) = 14.44$, $p < .05$, $\eta^2 = .13$, as well as a set size \times interference interaction, $F(1,34) = 5.38$, $p < .05$, $\eta^2 = .04$. These effects were driven by differences between the 1-target condition and all others, just like in younger adults ($ps < .05$; for all other comparisons: $ps > .05$). In sum, younger adults showed a clear N2pc component for multi-item displays, whereas older adults' showed a less clear N2pc component which was also much smaller in amplitude.

Maintaining items in WM: the CDA component

For the CDA component, we found an age group \times set size interaction, $F(1,68) = 4.35$, $p < .05$, $\eta^2 = .003$, and an age group \times interference interaction, $F(1,68) = 6.90$, $p < .05$, $\eta^2 = .004$. Follow-up pairwise comparisons revealed significant amplitude differences between all four conditions in younger adults (all $ps < .05$). For older adults, follow-up paired t -tests revealed that the mean amplitude differed between all conditions ($ps < .05$) except for the comparison of 3 targets vs. 3 targets plus distractors ($p > .05$). To summarize, the set size manipulation resulted in smaller amplitude modulations in older adults compared to younger adults. Regarding the interference manipulation, in younger adults, the CDA amplitude was larger when irrelevant items were present for both set sizes; in older adults, this effect was observed in the 1-target condition only.

N1 effect is differentially related to WM capacity in younger and older adults

In younger adults the magnitude of the N2pc effect (3 targets minus 1 target) predicted behaviorally assessed WM capacity,⁴ $r = .41$, $p < .05$, in line with previous findings (Anderson et al., 2011). The same correlation was not reliable in older adults ($r = .14$, $p > .05$). Instead, the magnitude of the N1 effect (3 targets minus 1 target) predicted WM capacity in older adults, $r = .40$, $p < .05$, but was not reliably associated with WM capacity in younger adults ($r = -.24$, $p > .05$; see Fig. 3). We tested whether the correlations differed significantly between the age groups. As for the N2pc and WM capacity correlations, there was no difference between the correlations observed in younger and older adults ($z = 1.18$, $p > .05$). However, the N1 and WM capacity correlations differed reliably between younger and older adults ($z = 2.67$, $p < .05$).

Consistent with previous studies (Vogel and Machizawa, 2004), the increase in CDA amplitude from 1 target to 3 targets was a reliable predictor of WM capacity in younger adults, $r = .40$, $p < .05$. In older adults, however, no correlation between CDA amplitude increase from 1 target to 3 targets and capacity K was observed ($r = .05$, $p > .05$). The correlations between CDA and WM capacity did not differ statistically between the age groups ($z = 1.49$, $p > .05$). To explore to what extent the N2pc and the CDA contribute to WM capacity, we conducted a multiple regression analysis with both components as predictors in younger adults. The two predictors showed a trend of a moderate correlation, $r = .31$, $p = .062$. When entered simultaneously into the regression equation, both semipartial correlation coefficients were reliable, $\beta_{N2pc} = 0.30$, $\beta_{CDA} = 0.34$, both $ps < .05$, indicating that N2pc and CDA yielded independent contributions to

⁴ Note that given the ERP negativities, the scale of the correlations is reflected to show that larger amplitude modulations (i.e., more negative values) are associated with better WM performance.

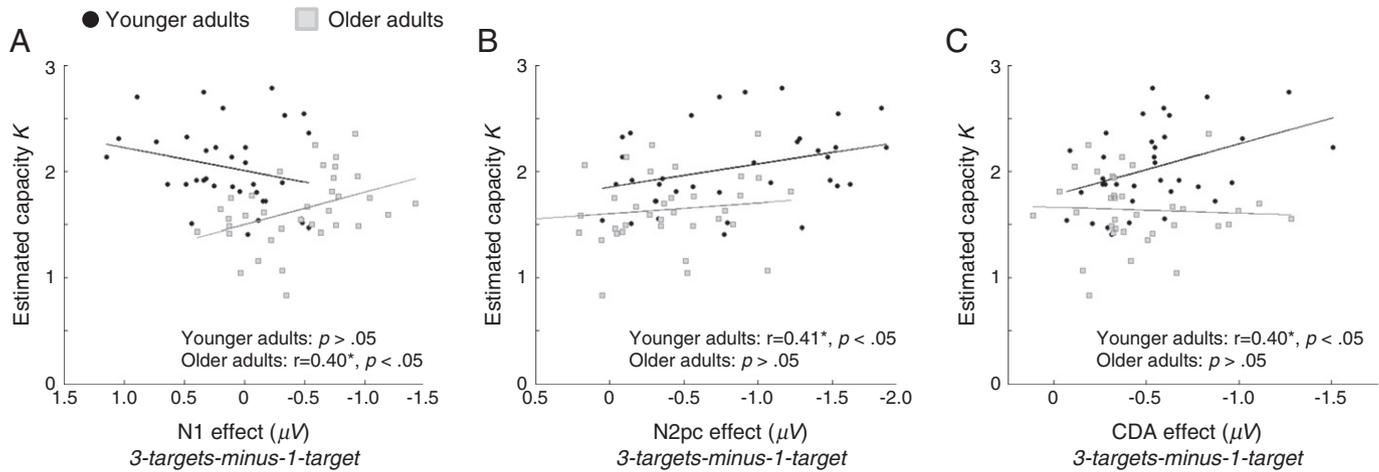


Fig. 3. Correlations between individual's WM capacity K and the magnitude of the ERP effects at parietal–occipital electrode sites (PO3/PO4/PO7/PO8) at different time intervals. Note that the scale of the correlations is reflected to show that larger amplitude modulations (i.e., more negative values) are associated with better WM performance. (A) The magnitude of the N1 effect was predictive of WM capacity in older adults, but not in younger adults. (B) The magnitude of the N2pc effect was predictive of WM capacity in younger adults. (C) The magnitude of the CDA effect was predictive of WM capacity in younger adults.

individual differences in younger adults' WM performance.⁵ The two predictors together accounted for 26% of the variance. In older adults, there was no association between the N2pc and the CDA component ($p > .05$).

Dissociating effects of age group from differences in performance level during WM encoding

We formed subgroups based on overall performance within each age group. Fig. 4A illustrates the K -scores for each group, with high-performing younger adults as the best group, followed by high-performing older adults and intermediate-performing younger adults, then low-performing younger adults together with intermediate-performing older adults, and finally low-performing older adults. Statistical analyses revealed that intermediate-performing younger adults and high-performing older adults, as well as low-performing younger adults and intermediate-performing older adults did not differ in their WM capacity K ($ps > .05$). All other pairwise comparisons were reliable (all $ps < .05$).

The electrophysiological data of the six groups shows that the N1 effect remained specific to the group of older adults (see Fig. 4B). Pairwise comparisons between all groups revealed that the N1 effect was larger for high-performing older adults compared to all other groups (all $ps < .05$), except the intermediate-performing older adults ($p > .05$); similarly, the N1 effect was larger for intermediate-performing older adults than for all groups of younger adults ($ps > .05$), but did not differ from the low-performing older adults ($p > .05$). As illustrated in Fig. 4C, high-performing younger adults had a larger N2pc effect relative to any of the groups in older adults ($ps > .05$), and intermediate-performing younger adults differed reliably from intermediate- and low-performing older adults ($ps < .05$), but not from high-performing older adults ($p > .05$). In younger adults only, the difference between high- and low-performers was statistically reliable ($p < .05$), whereas the differences between high- and intermediate performers as well as intermediate- and low-performers were not ($ps > .05$). In older adults, the N2pc effect did not differ between any of the performance groups (all $ps > .05$).

⁵ When also including the N1 component in the regression analysis in addition to N2pc and CDA, its semipartial correlation coefficient is not reliable, $\beta_{N1} = -.13$, $p > .05$, further supporting the finding that the N1 effect did not contribute to individual differences in WM performance in younger adults.

Further, the N2pc effect did not differ between any of the groups of older adults relative to low-performing younger adults ($ps < .05$).

Discussion

The aim of the present study was to investigate how differences in cortical mechanisms of visual–spatial WM encoding relate to individual differences in WM capacity. We tested healthy younger and older participants in a visual–spatial WM task and manipulated memory load (1 target vs. 3 targets) and interference (distractors present vs. absent). Our results indicate that healthy aging modulates cortical mechanisms of visual–spatial WM encoding at early processing stages and additionally show that these modulations are functionally relevant for age differences in WM capacity.

Limits of WM capacity in younger and older adults

In good agreement with previous studies on WM performance and aging (Babcock and Salthouse, 1990; Borella et al., 2008; Cowan et al., 2006; Li et al., 2008), older adults performed less well in the high-load memory condition (3 targets) than younger adults, indicating that older adults were—on average—more limited in their WM capacity than younger adults. The presence of irrelevant items, however, produced a similar interference effect in younger and older adults. This finding might appear surprising in light of inhibition deficit accounts of cognitive aging (e.g., Dempster, 1992; Hasher and Zacks, 1988). The lack of an age group \times interference interaction is, however, consistent with another recent visual–spatial WM study that used similar stimuli (Jost et al., 2011). Although the interference manipulation did not affect performance in the low-load memory condition (1 target), it showed clear modulations of the lateralized delay activity. In both younger and older adults, the CDA amplitude became larger when irrelevant items were present in the 1-target condition, suggesting that irrelevant items were stored to some extent in both age groups. This suggests that irrelevant items were not completely filtered out when WM load was low, and that this was not detrimental to WM performance. This is consistent with recent studies, which report a close relationship between WM load and filtering efficiency (Arend and Zimmer, 2011, 2012). In younger adults, the CDA amplitude in the condition with distractors was also enlarged when WM load was high (3 targets). Perhaps, the WM capacity of some younger adults was still not overtaxed in the high load condition, such that irrelevant items could still be processed

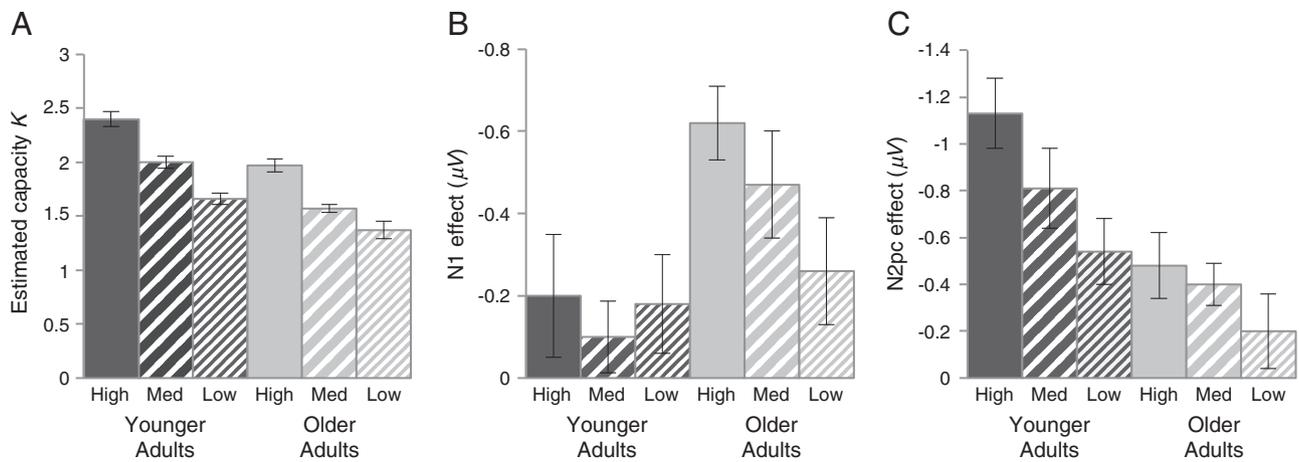


Fig. 4. Results from the performance group analysis. Different patterns denote the different performance groups: 'High' = high-performers, 'Med' = intermediate-performers, 'Low' = low-performers, and different shades of gray denote the two age groups: dark = younger adults, light = older adults. (A) Estimated WM capacity K for the six groups. (B) Magnitude of the N1 effect with respect to the six different groups. (C) Magnitude of the N2pc effect with respect to the six different groups.

and stored to some extent. At the same time, irrelevant items affected performance negatively in both younger and older adults. In the present paradigm, the interference manipulation was rather subtle, as the irrelevant items were perceptually very similar to the relevant target items (i.e., they differed only in shape). Therefore, the observed CDA amplitude increases might in part reflect inefficient filtering regardless of memory load.

Dissociating mechanisms of WM encoding by age

Two ERP components served as markers of distinct WM encoding processes. Attentional selection was quantified as the magnitude of the N2pc component, a well-established ERP component that reflects the focusing of attention onto multi-stimulus arrays. The N2pc reflects a process of object individuation, or more precisely, the attentional mechanism that forms temporal representations of distinct objects from multi-stimulus arrays (Ester et al., 2012; Mazza and Caramazza, 2011; Pagano and Mazza, 2012). Younger adults showed a clear N2pc component for the high-load memory condition (i.e., 3 targets), consistent with the account of attentional object individuation, and hence, more distinct target representation. In older adults, the load-dependent modulations of the attentional focus were attenuated, suggesting that target representations were assembled comparatively sparsely in older relative to younger adults. It should be noted that the ERP wave during the time interval of the N2pc showed a very different pattern in older relative to younger adults. In older adults, during the time range of the N2pc, the waveform gradually became more negative and did not show a clear transient negative deflection, as it did in younger adults. Thus, any effects during the time window of the N2pc ought to be interpreted with caution in older adults, as they may not reflect the same component as in younger adults.

In the absence of a clear selection mechanism during encoding, older adults showed a load-dependent increase of perceptual stimulus processing. Perceptual processing of the to-be-remembered memory array—as reflected in the contralateral N1 component—increased parametrically, irrespective of targets and nontargets. This nonspecific (i.e., nonspecific to the discrimination between targets and distractors) load-dependent increase of the N1 component was absent in younger adults. This N1 effect cannot be attributed to differences in sensory stimulation, as it reflects the contralateral-minus-ipsilateral amplitude difference of a sensorily balanced memory array. Rather, the N1 component seems to be sensitive to item numerosity in older adults, regardless of stimulus type. Importantly, different from the N2pc component, the N1 component is not related to selection of individual items, but reflects

the more global perceptual processing of incoming visual stimuli (Heinze et al., 1990; Mangun, 1995). Thus, it seems as if the N1 amplitude enhancements observed here reflect a rather coarse boost in perceptual processing of to-be-remembered memory arrays in the attended hemifield, in the absence of item individuation and selection. Surprisingly, this rather coarse mechanism of stimulus enhancement was beneficial for older adults' WM performance in the current task, indicating that a simple increase in perceptual processing improved WM representations. However, as highlighted in the performance group analysis, older adults who showed a large increase in perceptual processing did not reach the performance level of younger adults who showed large attentional selection (N2pc). This indicates that even though the increase in perceptual processing helps WM performance in older adults, older adults are still at a disadvantage without the later more specific selection mechanism relative to younger adults. Most important is the observation that mechanisms of encoding are dissociable between the younger and older adults. Younger adults showed selective processing of individual items, whereas older adults boosted perceptual processing of all items in the memory array.

We correlated the magnitude of the N2pc effect—as an indicator of attentional selection—with individual WM capacity and found that stronger attentional selection was associated with better WM performance in younger, but not in older adults. The correlation between increases in perceptual processing—reflected in the magnitude of the N1 effect—was only reliable in the group of older adults, but absent in the group of younger adults. The dissociation on the mean level as well as in the correlational patterns expedites that the neural mechanisms that support WM encoding shift from young to old age. This suggests that during WM encoding, different cortical circuitries were recruited in younger and older adults. The N2pc has been localized to the posterior parietal and occipito-temporal cortex (Hopf et al., 2000), whereas the posterior N1 component is thought to originate in the occipito-temporal cortex (Di Russo et al., 2003). One might speculate that during encoding, younger adults recruited parietal-occipital areas, whereas older adults largely relied on activation in the occipital cortex. Future research will have to delineate the exact cortical circuitries underlying the differential neural activation patterns and the specific mechanisms that may lead to these age-related differences during encoding.

Separating age differences from performance differences

In the presence of mean differences in performance between age groups, any observed differences in indicators of encoding could, in principle, reflect differences that are unrelated to age (Kliegl et al.,

1994; Rogers et al., 2000). To directly test whether performance level can account for the differences in neurocognitive functions, we conducted a subgroup analyses and separated individuals based on their overall performance in 'high-', 'intermediate', and 'low'-performers in order to compare groups of different age but same performance level (see also Nagel et al., 2009). Only older adults showed a boost in perceptual processing (N1 effect), and the N2pc remained to be specific to younger adults. Within each age group, the magnitude of each effect scaled with WM capacity (Fig. 4). These results confirm that the differences in WM encoding were indeed driven by differences in age and cannot be explained by differences in performance level. Interestingly, 'high'-performing older adults (who also showed the largest N1 effect) performed above the level of 'low'-performing younger adults, but they did not reach the performance level of 'high'-performing younger adults. WM capacity was estimated to 2.4 items for 'high'-performing younger adults, but only to 2 items for 'high'-performing older adults. Possibly, this difference in capacity reflects efficiency differences in the neural mechanisms associated with the N2pc and N1 components.

Together, these results show that the age group differences in the pattern of N1 and N2pc components cannot be portrayed as a mere byproduct of lower levels of WM capacity in old age. In younger adults, subgroups with higher overall performance showed a larger N2pc effect. In older adults, subgroups with higher overall performance showed a larger N1 effect. At the same time, the performance group analysis illustrates that individuals with the largest N1 effect (i.e., high-performing older adults) reached the same performance as intermediate-performing younger adults exhibiting an N2pc effect.

Relation of encoding, maintenance, and age

We found that older adults showed less load-dependent modulation of neural activity during the retention interval relative to younger adults, consistent with previous research (Mattay et al., 2006; Nagel et al., 2009; Nyberg et al., 2009; Sander et al., 2011). In younger adults, the amplitude increase of the CDA component was related to WM performance, but there was no reliable association in the group of older adults. In younger adults, the N2pc and CDA effects uniquely predicted WM capacity, documenting their independent contributions to stimulus encoding and stimulus maintenance. At the same time, the two components tended to correlate with each other.

Both components are most likely generated in the parietal cortex (Hopf et al., 2000; McCollough et al., 2007). This brain region has been proposed to reflect a system that is sensitive to the individuation of items and representations (Drew and Vogel, 2008; Mazza and Caramazza, 2011) as well as the number of stored representations (Todd and Marois, 2004, 2005; Vogel and Machizawa, 2004). Recent findings suggest that there is a direct link between the limits of how many items can be selected for further processing and how many representations can be actively maintained, reflected in similar modulation limits of the N2pc and CDA components (Anderson et al., 2011). It is not within the scope of this paper to address the overlaps or disparities of the two ERP components. Note, however, that younger adults exhibited both components in close interplay, whereas older adults only expressed the CDA effects, suggestive of at least partly independent underlying processes. Furthermore, in the group of older adults, there was no hint of a correlation between the two components.

Conclusion

Capacity limits of WM can derive from processing limitations during stimulus encoding, maintenance, or retrieval. Measures of behavioral outcomes reflect the cumulative result of these processes, rendering it difficult to determine at what stage age-related impairments are generated, exacerbated, or perhaps attenuated. The

present results indicate that aging alters attentional processes during stimulus encoding already and show that these age differences are functionally relevant for WM performance. When attentional control processes operate suboptimally during encoding, item representations will be less accurate and of lower fidelity, and hence lead to lower WM performance.

Prior work has suggested that during WM and visual attention tasks similar mechanisms are applied in younger and older adults, but often these mechanisms seem to be less efficient in the elderly. Such inefficiencies may be reflected in latency shifts of selective processing (Jost et al., 2011; Störmer et al., 2013; Zanto et al., 2010), or decreases of load-sensitive modulations of neural activity during the retention interval (e.g., Mattay et al., 2006; Nagel et al., 2009; Sander et al., 2011). Here we show that healthy aging constrains cortical mechanisms during stimulus encoding already. We found that younger and older adults exert different mechanisms during WM encoding, and that each of them aids individual memory performance. Whereas younger adults are likely to activate an attentional selection mechanism during encoding, many older adults appear to rely on a rather general stimulus-driven perceptual facilitation process. The results point to a normative shift in the mechanisms supporting visual-spatial WM encoding with advancing adult age and emphasize the importance of early cortical processes for adult age differences in WM capacity.

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