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Are Old Adults Just Like Low Working Memory Young Adults? Filtering Efficiency and Age Differences in Visual Working Memory

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While it is well known that working memory functions decline with age, the functional reasons for this decline are not well understood. A factor that has proven critical for general individual differences in visual working memory capacity is the efficiency of filtering irrelevant information. Here, we examine to what degree this factor is also responsible for age differences in working memory. Young and old participants performed a change-detection task where some items in the encoding display were marked as irrelevant. The contralateral delay activity of the electroencephalogram was used to assess individual participants' filtering efficiency (see Vogel EK, McCollough AW, Machizawa MG. 2005. Neural measures reveal individual differences in controlling access to working memory. Nature. 438:500–503.). Older adults showed smaller filtering scores than young adults, but only early in the retention interval, suggesting that efficient filtering was delayed. In contrast, age-independent individual differences in filtering were reflected primarily later in the retention interval. Thus, age and individual differences in filtering are reflected in different ways showing that old adults are not simply like less efficiently performing young adults.

Keywords: aging, contralateral delay activity, filtering efficiency, individual differences, visual working memory

Introduction

Complex cognition is constrained by our capacity to hold critical information online in working memory while at the same time keeping irrelevant information from intruding into our thoughts and actions. Working memory capacity varies widely across individuals and accordingly this variability accounts for a substantial portion of individual differences in tests measuring general intelligence (e.g., Süß et al. 2002; Conway et al. 2003; Ackerman et al. 2005; Kane et al. 2005; Oberauer et al. 2005). Working memory also declines with age (see e.g., Myerson et al. 2003; Chen et al. 2003 for span measures) and therefore may be a key factor behind widespread age-related decrements in those functions that can subsumed under the label fluid intelligence (e.g., Dobbs and Rule 1989; Verhaeghen and Salthouse 1997). In the present work, we build on recent progress in understanding general individual differences in visual working memory capacity to examine the nature of age deficits in working memory.

Vogel and colleagues recently described an event-related potential (ERP) effect, the contralateral delay activity (CDA), that can be utilized as an online measure of working memory during the retention interval (Vogel and Machizawa 2004). Using this method, they demonstrated that low working memory individuals actually represent more irrelevant information than high capacity individuals across the entire delay interval (Vogel et al. 2005), suggesting that "filtering efficiency" is a critical source of individual differences in working memory capacity.

Interestingly, according to the inhibitory deficit hypothesis, the inability to reduce interference from task-irrelevant information is also responsible for age differences in working memory (as well as in diverse other cognitive abilities; e.g., Hasher and Zacks 1988; Hasher et al. 1999; Zacks et al. 2000). A recent ERP study by Gazzaley et al. (2008) provided evidence for this theory. The authors used a paradigm that allowed tracking encoding of relevant and irrelevant information into working memory. They found that older adults exhibited a selective deficit in suppressing task-irrelevant information during visual working memory encoding, but only in the early stages of visual processing. According to the authors, this suggests that the suppression of irrelevant information in older adults may be slowed but not necessarily generally impaired.

While the paradigm by Gazzaley et al. (2008) allowed the fine-grained assessment of the effects of attention on initial perceptual encoding processes, the CDA tracks the actual fate of relevant versus irrelevant information in working memory across time. This allows us to ask the important question to what degree the mechanism that differentiates between high and low capacity individuals is the same as the one that differentiates between young and old individuals. Specifically, if old adults are like low capacity young adults, both groups should exhibit a generally increased tendency of representing irrelevant information across the entire delay interval. In contrast, if as suggested by Gazzaley et al. (2008) the primary deficit stems from a slowing of the selection mechanisms at the initial encoding stage, we should see age effects in the CDA filtering efficiency measure primarily during the early but not later phases of the memory retention interval.

Materials and Methods

Overview

In the present study, older and younger participants performed a visual working memory task (the change-detection task), and the CDA of the electroencephalogram (EEG) was measured during the retention interval (see Fig. 1). The CDA is a sustained negative wave recorded over the posterior cortex that is largest contralateral to the memorized hemifield. Its amplitude increases with the number of representations being held in visual working memory and reaches an asymptotic limit at each individual's specific memory capacity. Thus it provides an online measure of how many items are actively being represented in memory (see Vogel and Machizawa 2004). More importantly, via a filtering paradigm developed by Vogel et al. (2005), the CDA can also be used to

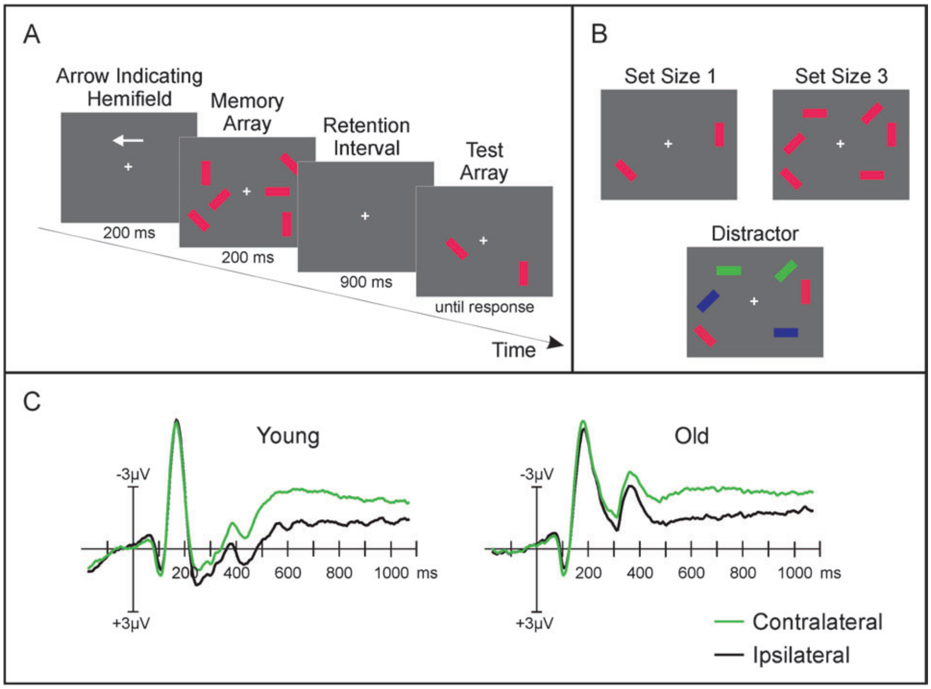

Figure 1. Stimulus sequence, experimental conditions, and ERPs during the retention interval. (*A*) Example of a trial in which the orientations of items in the left hemifield are to be stored. The test array displays a probe with changed orientation. (*B*) Three conditions for which amplitudes of the CDA are compared to investigate filtering performance. Critical will be the amplitude of the distractor condition because this indicates whether the irrelevant blue and green items are unnecessarily stored. (*C*) Grand average ERPs at occipital electrodes contralateral and ipsilateral to the memorized hemifield. The difference wave contralateral minus ipsilateral, that is, the CDA, represents the spatially specific hemispheric activity. Negative voltage is plotted upward in this and the following figure.

track the extent to which individuals represent irrelevant information in working memory. Here, we adapted this paradigm for our purpose.

On each trial, participants were presented with an array of colored rectangles of varying orientations, and the task was to remember the orientations of only the red items and to ignore the blue and green ones. In some trials, only red items were presented, either 1 or 3 (in the following named set-size 1 and set-size 3 conditions), and in the others, 2 distracting objects (green or blue) were added. As an indicator of filtering efficiency, we were mainly interested in the amplitudes of the CDA when the display contained 1 target and 2 distractor objects (set-size 1 plus 2 distractors) relative to the conditions in which the display contained either 1 or 3 target objects. The rationale is that if an individual is perfectly efficient at representing only the red items and excluding the irrelevant items from memory, then the CDA amplitude in the set-size 1 plus 2 distractors condition (in the following named distractor condition) should be equivalent to that observed in the set-size 1 condition. In contrast, if an individual is completely inefficient at excluding the irrelevant items, then the amplitude should be equal to the set-size 3 condition. Age differences were investigated by comparing these ERP filtering pattern between groups. If older participants do suffer from less efficiently working filtering mechanisms that in turn negatively affect working memory capacity, then their filtering scores (measured as CDA amplitude difference) should be smaller and their performance in the change detection weaker than in younger participants.

Participants

Twenty-five students (age: 19-38 years) and 30 older well-educated subjects (age: 64-92 years) participated in the study. All participants were healthy, had normal or corrected to normal vision, and gave informed consent according to procedures approved by the University of Oregon. Three younger and 4 older participants were excluded from the final sample because of extensive eye movements (>40% of the trials) resulting in too few trials for adequate ERP analysis. The final sample comprised data of 22 younger (age: 19-38 years; 7 female; mean age: 24.5 years) and 26 older (age: 64-92 years; 18 female; mean age: 72.88 years) participants. Education levels (i.e., years of education) did not differ (P = 0.444). The Digit Symbol Substitution test, which measures psychomotor speed, revealed the usual pattern for cognitive aging studies: Older adults' scores were significantly lower than those of younger adults (old = 48.99, SD 9.59; young = 67.31, SD 9.33; t_{40} = 6.266, P < 0.001; due to technical problems, digit symbol scores are not available for 2 young and 4 old adults).

Stimuli, Task, and Procedure

We utilized the change-detection paradigm that can be run in different variants, allowing to estimate working memory capacity as well as an online measurement of maintaining information by means of ERPs.

Color Change-Detection Task

The experiment started with a standard behavioral version of the change-detection paradigm (see Luck and Vogel 1997). Participants were asked to maintain a varying number of colored squares (2, 4, 6, or 8 items) that were briefly displayed for 200 ms. After a retention interval of 900 ms, a test display was presented that either was identical to the memory display (in 50% of the cases) or differed in the color of one item. Participants indicated with a button press whether a change occurred or not. Stimulus arrays were presented within a centered 6.44° × 6.44° region on a gray background viewed at a distance of 80 cm. The size of each square was 1.16° × 1.16°, and the color was randomly selected from a set of highly discriminable colors (red, green, blue, yellow, purple, black, and white). A given color could appear no more than twice in an array. Trials were presented in 3 blocks each containing 20 trials for each set size (i.e., 80 trials in total). The first block was treated as practice and not analyzed. Accuracy rather than speed was stressed in the instruction.

The working memory capacity K was estimated with a standard formula (see Pashler 1988; Cowan 2001; Vogel and Machizawa 2004), that is, $K = S\,(H - F)$, assuming that, if K items can be held in working memory from an array of S items, the probed item would have been one of those held in memory on K/S of the trials such that performance will be correct on K/S of the change trials (= hit rate H). To correct for guessing, this procedure also takes into account the false alarm rate *F*. *K* was estimated as the mean of set-sizes 4, 6, and 8. Capacity measures with the task we have used here were found to correlate with measures of working memory span (see Cowan et al. 2005, 2006) as well as with fluid intelligence (Cowan et al. 2005; Fukuda et al., forthcoming; see also Gold et al., 2010) and broader measures of intellectual ability, such as scholastic aptitude (Cowan et al. 2005).

Estimation of Filtering Efficiency

Here, the task was not just to maintain information from the memory array but to distinguish between relevant and irrelevant information and to prevent the latter from being stored in working memory. On each trial, participants were presented with an array of colored rectangles (each 0.41° × 1.42°) of varying orientations (vertical, horizontal, 45°, and 315°), and the task was to remember the orientations of only the red items and to ignore the blue and green ones (see Fig. 1). In half of the trials, only red items were presented, in the other half, 2 distracting items were presented along with the task-relevant red ones. Set size, that is, the number of relevant red items was manipulated orthogonally and was either 1 or 3, resulting in 4 conditions. Note that our main focus here is on the set-size 1, the set-size 3, and set-size 1 plus 2 distractors conditions because these are sufficient to investigate filtering according to the rationale described above. The fourth condition, set-size 3 plus 2 distractors, was included to obtain equal numbers for distractor and no-distractor trials. Also, theoretically the set-size 1 plus 2 distractors condition can be solved without filtering by subjects with a working memory capacity of 3 objects and more because these can simply try to remember both target and distractor objects. However, by inclusion of the set-size 3 plus 2 distractors condition, which cannot be solved in this manner, we hoped to encourage adoption of a general "filtering set." Consistent with the notion that the CDA amplitude should asymptote when capacity limit is reached, the CDA for the set-size 3 plus 2 distractors condition did not differ from the CDA of the set-size 3 condition (see Supplementary Figure 2).

Considering that older adults are not able to hold the same number of items in short-term memory as younger adults (note that young adults can store about 3–4 items, see Luck and Vogel 1997), CDA amplitude increases should reach an asymptotic limit much earlier in older than in younger adults. In order to achieve sufficient set-size variation even in older adults, we used set sizes 1 and 3, instead of 2 and 4 as in the original study by Vogel et al. (2005). Moreover, the smaller number of to-be-stored items should also guarantee a sufficient number of trials with correct responses for the older adults' ERPs. This modification, however, results in a number of to-be-stored items that is smaller than the average short-term memory capacity. Therefore, we expect that behavioral distractor effects are generally small and that age differences in filtering may not become evident in the behavioral data but primarily in the ERPs measured during the retention interval.

Another modification concerns the colors of the irrelevant items. In the original study (Vogel et al. 2005), irrelevant items were always blue, whereas in the present study, one blue and one green item were presented in each distractor trial. Two colors for irrelevant items were used in order to prevent a perceptual "pop out" of the relevant item in the set-size 1 plus 2 distractors condition.

For the ERP part, the display was bilateral, that means, on both sides of the fixation cross a complete memory array was presented (i.e., two 3.62° × 6.18° rectangular regions centered 2.58° to the left and right of the central fixation cross) but only the items in one hemifield were to be remembered. This was indicated by an arrow presented in advance (see Fig. 1*A*). A bilateral display is essential because the CDA is a brain response from the posterior cortex that is most pronounced contralateral to the memorized hemifield. The CDA, calculated as amplitude difference between contralateral and ipsilateral activity, therefore allows isolating the lateralized effects of visual short-term memory from nonspecific bilateral activity. Inherent to this procedure and the related task is that participants are asked to focus attention on one hemifield while ignoring the other. As shown by several studies, deployment of spatial attention is comparable in older and younger adults (see e.g., Hartley 1993; for a review on attention and aging, see Kramer and Kray 2006). Therefore, we do not expect any age-related deficits regarding this aspect of the task.

Each trial began with a 200-ms arrow cue presented above a fixation cross. After a variable interval of 200–400 ms, which should be sufficient to shift attention to the relevant hemifield, the memory array was presented for 200 ms. In contrast to the original study (Vogel et al. 2005), in which presentation time was 100 ms, we here increased presentation time in order to give older participants the opportunity to compensate for potentially slowed processing of the memory display. The following retention interval was 900 ms. Memory for the red items was tested with a single-item probe test array in which the probe was either identical to the object presented at the same location or differed in orientation. Again, participants responded by pressing one of 2 buttons, and accuracy was stressed. Moreover, they were instructed to keep their eyes fixated throughout a trial. Intertrial interval was 2 s.

Prior to the testing session, participants were familiarized with the task in a practice block of 40 trials that could be extended if required. This was often the case for older participants, who had more difficulty in keeping their eyes fixated. However, with more practice and feedback when eye movements occurred too frequently, most of the older adults managed the task. Testing consisted of 12 blocks with 80 trials each. Experimental condition, relevant side of the memory array, as well as match of memory and test arrays were completely balanced within a block.

EEG Recording and Analysis

The EEG was recorded from tin electrodes mounted in an elastic cap (Electro-Cap International), with 15 locations according to the International 10–20 System (F3, FZ, F4, T3, C3, CZ, C4, T4, P3, PZ, P4, T5, T6, O1, and O2) plus 5 nonstandard positions over the posterior cortex (OL and OR placed midway between T5 and O1 and T6 and O2, respectively; POz placed on the midline between Pz and O1/O2; and PO3 and PO4 placed halfway between POz and T5 and POz and T6, respectively). All sites were recorded with a left-mastoid reference and rereferenced off-line to the average of the left and right mastoids. The horizontal electrooculogram (EOG) was recorded from 2 electrodes placed approximately 1 cm to the left and right of the external canthi of the eyes. The vertical EOG was recorded from an electrode mounted beneath the left eye. Impedances of all electrodes were kept below 5 kΩ. Bandpass of the amplifier system was set to 0.01–80 Hz, and signals were digitized with 250 Hz.

The EEG was segmented into 1300-ms epochs starting 200 ms before the onset of the memory array and covered the whole retention interval. Only trials with correct responses were analyzed. Epochs containing blinks, eye movements (>1°), or amplifier saturation were excluded from further analysis. ERPs were based on average on 174 trials (minimum 73 trials). The CDA was computed by subtracting ipsilateral from contralateral activity (see Fig. 1*C*), averaged across hemispheres and 5 posterior electrode positions (i.e., P3/P4, PO3/PO4, O1/O2, OL/OR, T5/T6). A 100-ms interval preceding the onset of the memory array served as baseline.

CDA amplitudes, filtering scores, and their time courses were compared between young and old participants by means of analyses of variance (ANOVAs) and *t* tests. In order to achieve a high temporal resolution, analyses were run for consecutive time windows of 25 ms length, smoothed with a moving average of $n = 3$ time windows. Filtering scores were computed as amplitude difference between the set-size 3 and the distractor condition. This reveals negative values (because of the negative amplitude of the CDA), which were multiplied with −1 in order to obtain positive values for filtering scores. Consequently, a larger score indicates higher filtering efficiency. Note that computing filtering scores as difference between the distractor and the set-size 1 condition would be equally justifiable. However, the set-size 1 condition can be easily mastered without shifting attention to the relevant side. This might be the reason why in many of our subjects the difference contralateral minus ipsilateral is rather small or equal to zero, indicating that no lateralization took place. This, in turn, makes any comparison with the CDA of the set-size 1 condition difficult to interpret.

The time course of the filtering scores was compared for young and old participants. Moreover, the relation of filtering scores and working memory capacity was investigated with analyses of correlation. Note that we here used a different measure of filtering as in the studies by Vogel et al. (2005). There, filtering efficiency was computed as the ratio of 2 amplitude differences, that is, (set size 3 – distractor)/(set size 3 – set size 1). However, this procedure is highly susceptible to variations in amplitude when values are extracted from rather small time windows. The resulting extreme scores (outliers) could be problematic especially for correlations. We therefore decided in favor of simple difference scores to calculate filtering. However, this difference, in turn, depends on the set-size effect, that is, the amplitude increase from set size 1 to set size 3: Participants with large set-size 3 amplitudes will probably also have larger filtering scores. In order to correct for this confound, we reran the respective analyses with set-size effects partialed out. By means of this procedure, it was possible to maintain the more robust simple difference scores but without confounding filtering with set-size effects.

Results

Performance in the Change-Detection Task

Performance was measured as the percentage of correct responses in the change-detection task. Data from young and old adults are presented in Table 1. These show age differences in working memory performance, especially when the number of to-be-stored items increases. Performance of younger and older adults was near ceiling and did not differ significantly when only one item had to be stored. However, with increasing number of items, older participants performed significantly worse, $t_{46} = 4.96$, $P < 0.001$. Moreover, age differences were also present in the distractor condition, albeit less pronounced. Here, the percentage of correct responses was slightly but significantly smaller for older adults, $t_{46} = 2.12$, $P = 0.040$. These age effects also hold when hit and false alarm rates are examined separately. In comparison with young adults, older adults' hit rate was lower and the false alarm rate higher (with Ps < 0.05, except for the hit rate in the distractor condition where P was 0.073).

Reduced Working Memory Capacity for Older Adults

The group differences in working memory capacity also become evident when capacity *K*—an estimation of how many items an individual can store in working memory—is estimated from performance using a standard formula (Pashler 1988; Cowan 2001; Vogel and Machizawa 2004, see Materials and Methods for detail). The estimation from the set-size 3 condition revealed a mean capacity of 1.46 items for older and of 2.14 items for younger adults, $t_{46} = -4.938$, $P < 0.001$. Because this procedure can underestimate capacity (note that the estimated capacity *K* can never exceed the number of to-be-stored items, which in this case was 3), we also established capacity with a task in which up to 8 items had to be maintained and thus is less susceptible to such ceiling effects. This behavioral part of the study did not include distractor trials. Moreover, the to-be-remembered feature here was the color of the objects (instead of orientation as in the EEG part). This procedure provides the opportunity to validate the measures under different conditions. From this, capacity for young adults was estimated at 2.99 items (similar to previous studies, see e.g., Vogel and Machizawa 2004) and for old adults at 2.05 items, again significantly different, $t_{46} = -3.325$, $P = 0.002$. Moreover, the *K* estimates from the behavioral and the EEG part correlated significantly with $r = 0.658$ ($P < 0.001$) and 0.484 ($P = 0.022$) for the groups of old and young adults, respectively, which is in the general ballpark of correlations between different measures of *K* (see Fukuda et al., forthcoming) and correlations between other visual working memory tasks (e.g., Oberauer et al. 2000). For more information and different measures of *K*, see the Supplementary Material. Note that for the correlations with ERP measures (described below), we used the capacity estimate from the EEG part.

Table 1
Performance in the change-detection task

	Condition					
	Set-size 1		Set-size 3		Distractor	
	M	SD	M	SD	M	SD
Old						
% Correct	96.89	2.46	74.31	8.26	95.18	5.66
% Hit	95.13	4.39	70.79	12.53	93.18	7.82
% FA	1.35	1.51	22.17	15.39	2.82	3.92
Young						
% Correct	97.77	1.49	85.91	7.43	97.77	1.78
% Hit	97.08	2.16	83.18	7.42	96.43	3.12
% FA	1.55	1.61	11.36	11.60	0.91	0.99

Note: Percent correct responses, hits, and false alarms for set-sizes 1 and 3 and the distractor condition. Differences between young and old participants emerge in the set-size 3 and the distractor conditions. M, mean; SD, standard deviation.

Filtering Efficiency in Young and Old Adults

In order to test whether filtering performance is a critical factor for the age differences in working memory capacity and performance in the change-detection task, we compared ERPs measured during the retention interval. The direct comparison of amplitude effects between age groups should help to delineate whether older participants tend to unnecessarily store irrelevant items.

Figure 2*A* shows the respective CDAs for the 3 critical conditions, obtained by computing the differences of the contralateral and ipsilateral activities measured over the posterior cortex (cf. Fig. 1*C*). The CDA shows the characteristic amplitude increase with increasing number of items in the memory display. Moreover, this increase varied substantially across subjects and correlated significantly with individual working memory capacity (for details, see the Supplementary Material). These findings replicate previous ones and suggest that the CDA directly indexes the number of active representations in visual working memory. The direct comparison of the distractor with the no-distractor conditions, therefore, will indicate whether irrelevant items are unnecessarily stored.

As obvious from Figure 2*A*, in early time windows, that is, between 200 and 300 ms, the distractor condition is equal to the set-size 3 condition, whereas later in the retention interval, the distractor condition converges toward set-size 1. This holds for both groups. However, a closer look at the time courses revealed that young and old adults differ in the onset of efficient filtering. The vertical lines in Figure 2*A* indicate the "reversal points," that is, when the difference between the distractor condition and set-size 1 is smaller than between the distractor condition and set-size 3. For the grand averages, this was at 350 ms for young adults and at 475 ms for old adults. For the statistics, we tested in which time windows the difference between distractor and set-size 3 condition was larger than the difference between distractor and set-size 1 condition. For young adults, filtering started in the time window 375–400 ms,

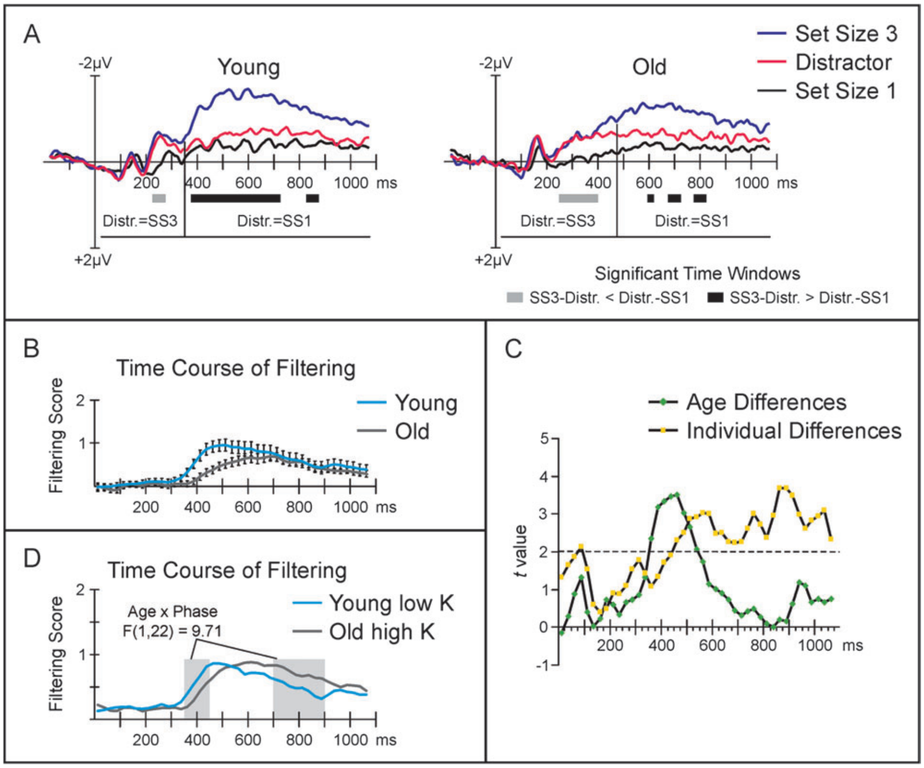

Figure 2. Age and individual differences in filtering performance during the retention interval. (*A*) Grand average ERP difference waves (contralateral minus ipsilateral) averaged across 5 posterior electrode positions. The distractor condition indicates how good old and young adults prevent irrelevant information from being stored in short-term memory. The vertical line shows the time point of efficient filtering, that is, when the amplitude of the distractor condition (distr.) is more similar to the amplitude of the set-size 1 condition (SS1). (*B*) Filtering scores computed as amplitude differences between distractor and set-size 3 condition. The values are computed from the mean of the 25-ms time windows. The larger the score the better is the filtering. Error bars reflect standard errors of the mean. Age differences are prominent in the rising flank of the CDA, suggesting an "early" filter deficit for older adults. (*C*) Age and individual differences showing distinct time courses. Presented are *t* values for the 2 contrasts. The horizontal line indicates the critical *t* value. (*D*) Time course of filtering for high-*K* old participants in comparison with low-*K* young participants. Although mean *K* is the same, the waveforms are completely different indicating that filtering deficits in early as well as in later time windows of the retention interval could be responsible for reduced working memory capacity.

t_{21} = 2.268, P = 0.0340, whereas for older adults filtering was not efficient before time window 600–625 ms, t_{25} = 2.100, P = 0.0459.

Age and Individual Differences in Filtering

In order to investigate the age effect in filtering in more detail, we directly compared the 2 groups' filtering scores (set-size 3 minus distractor, see Fig. 2*B*). Age effects are significant between 350 and 550 ms, with t_{46} values ranging from 2.06 (P = 0.0453) to 3.51 (P = 0.0010, see also Fig. 2*C*). This indicates that older participants start to filter out the irrelevant information later in time, which could be the reason for the worse performance of the elderly and their decline in memory capacity. Note that age effects are also present in the early time windows of the CDA (between 300 and 450 ms) when filtering efficiency is calculated as difference between distractor and set-size 1 condition (but see Materials and Methods section for arguments against this difference score).

To investigate whether age-related working memory deficits result from the same underlying sources as individual differences, we directly compared how filtering efficiency behaves across time as a function of age on the one hand and as a function of individual differences irrespective of age on the other. As in previous studies, filtering scores correlated with memory capacity: Participants who were good in filtering out irrelevant information also scored high in working memory capacity (for details, see the Supplementary Material). In order to investigate the time course of this relation, we computed the correlation between filtering scores and capacity for each time window. As we are interested in pure individual differences, we partialed out the age effects. In particular, we computed for each time window a hierarchical regression analysis with K as criterion. In a first step, age was included as predictor and was therefore controlled statistically. In a second step, filtering score was included. The time course of the relation between filtering score and capacity (in terms of t values) is plotted in Figure 2*C*; t values larger than 2.01 reach significance with $P < 0.05$ (see horizontal line in the graph), which was the case from 450 ms until the end of the retention interval; t values ranged from 2.25 (P = 0.0297) to 3.69 (P = 0.0006). This indicates that filtering scores as of 450 ms are reliable predictors of individual differences in working memory capacity. A direct comparison of these individual differences with age effects (see the t values for the contrast old vs. young participants regarding filtering scores in Fig. 2*C*) indicates that age-related differences are represented in the CDA much earlier than individual differences. This dissociation suggests that low working memory capacity can arise from 2 different patterns of filtering deficits.

If individual differences and age differences in working memory can be attributed to different periods during the encoding-retention sequence, then we should be able to find young adults and old adults with identical *K*, but distinct filtering profiles. In fact, a direct comparison of old participants with above-median *K* (mean $K = 1.84$) and young participants with below-median *K* (mean $K = 1.79$) revealed different ERP pattern (see Fig. 2*D*) for these 2 groups with equivalent levels of *K* ($P = 0.753$). In early time windows, older participants showed smaller filtering scores, whereas in later time windows, they showed larger filtering scores than young participants. An ANOVA with a group factor and the repeated measurement factor time window (350–450 ms vs. 700–900 ms) revealed a significant interaction, $F_{1,22} = 9.71$, $P = 0.005$. This result clearly demonstrates that old participants are not simply like less efficiently performing young participants, and complements the above described distinction between age and individual differences.

Additional Analyses

Note that the filtering score we have used here is not independent of the set-size effect. We therefore ran the statistics for the age and individual differences reported in Figure 2*C* again but now with set-size effects on CDA amplitude partialed out. This did not change the results. Age and individual differences were still present and differed in their time courses (see the Supplementary Material for detail, Supplementary Fig. 4). The results with set-size effects partialed out therefore validate the assumption that it is indeed filtering efficiency that is responsible for the observed differences between the 2 groups.

The current results suggest that the time course of filtering differs between older and younger adults. However, rather than being due to slower attentional filtering, it is still possible that this effect instead results from a nonspecific age difference in processing speed (e.g., Salthouse 1996). In order to examine this aspect in more detail, we investigated early stages of perceptual processing by means of the latencies of the initial visual ERP components: P1 and N1. In a first step, we investigated whether the latencies of the P1 and N1 evoked by the memory array differed for old and young subjects. Individual's latencies were determined at lateral occipital and for these components typical electrodes (i.e., OL/OR, T5/T6, O1/O2. Note that these are also the electrodes where the components were maximal in our study) in time windows 75–137 ms and 130–200 ms for P1 and N1, respectively. There was a small but not significant tendency for longer N1 latencies for older subjects in the set-size 3 (174 and 168 ms, for older and younger subjects, respectively; $P = 0.102$) and the distractor conditions (173 and 169 ms, for older and younger subjects, respectively; $P = 0.338$). Interestingly, P1 latency was actually slightly but not significantly shorter for older than for younger subjects (104 vs. 109 ms, averaged across the 3 conditions; $P = 0.152$). Moreover, N1 latencies neither correlated substantially with memory capacity *K* nor with individually defined time points of efficient filtering (i.e., for each participant's CDA differences, the first time window in which the difference set size 3 minus distractor is larger than the difference distractor minus set size 1). This holds regardless of whether correlations were calculated separately for age groups or across age groups and also regardless of whether N1 values were calculated separately for conditions or pooled over conditions. Thus, there is no evidence that older adults' delayed onset of efficient filtering is associated with a general slowing of early processing. Nevertheless, we partialed out the N1 latencies from the analysis of age effects in filtering scores. The results revealed that the early age effects in filtering were independent from N1 latency effects.

In a second step, we ran a similar set of analyses but instead of examining the latency of these initial components, we examined the latency of the influence of spatial attention on the P1 and N1. That is, because the subject was cued to which hemifield was relevant well in advance of the onset of the memory array, there was sufficient time to orient spatial attention to that side of the visual display, resulting in a modulation of the amplitude of the P1 and N1 components. Spatial attention effects of this form have been reported many times previously and can be measured directly by calculating a difference wave between the contralateral and ipsilateral electrode sites with respect to the attended hemifield (e.g., Mangun and Hillyard 1991; Luck et al. 1994). Latencies of these early spatial attention effects were determined again at lateral posterior electrodes but with time windows 60–137 ms and 115–200 ms for P1 and N1 attention effects. Although these analyses revealed reliable differences in the latency of the N1 attention effect (latencies averaged across conditions were 162 vs. 150 for old and young participants, respectively; $P = 0.002$), there was no evidence for a direct relation between older adults' N1 latency increase on the one side and CDA filtering efficiency and memory capacity on the other. In particular, the latency of the N1 attention effect was not correlated with memory capacity nor was it correlated with the time point of efficient filtering. Furthermore, partialing out the latency of N1 attention effects did not change the findings of age differences in filtering. Taken together, these results suggest that the observed age-related delay in efficient filtering is not caused by delayed early attentional processes. Moreover, it also seems to be specific to filtering. The onset of the set-size effect, which can be taken as a marker for the onset of memory encoding, started around 200 ms in both groups (see Supplementary Material for details). Thus, the age-related delay in filtering was not accompanied by a general delay in working memory encoding.

Discussion

In this study, we used an ERP component that is sensitive to the amount of information stored in visual working memory in order to assess how efficiently older and younger adults regulate visual working memory content. We found that the age-dependent drop in working memory capacity is accompanied by reduced filtering scores. This general result is consistent with previous observations that low working memory capacity within young adults is associated with reduced filtering efficiency (Vogel et al. 2005). This result is also generally consistent with the inhibition-deficit theory (Hasher and Zacks 1988), which holds that as we age our ability to suppress irrelevant representations or response tendencies declines. However, we also found that the filtering inefficiency exhibited in old adults is not identical to the filtering inefficiency exhibited in young adults with low working memory capacity. Age-related differences in filtering efficiency are predominantly expressed during the early moments (between 350 and 550 ms) of the retention interval, possibly during initial encoding of information into working memory; thereafter, the CDA effects for old and young adults are virtually indistinguishable (see Fig. 2*B*). In contrast, individual differences in filtering become more strongly represented in the CDA as the retention interval unfolds (see Fig. 2*C*). The pattern of early age differences that are not present later in the retention interval suggest that older adults' filtering is delayed.

The early age difference in filtering is generally consistent with results by Gazzaley et al. (2005, 2008), who concluded on the basis of both functional magnetic resonance imaging and EEG evidence that old adults show more attention to irrelevant information during early visual processing. In their study, participants were presented faces and scenes in randomized sequences and had to remember either just the faces or just the scenes. This procedure allowed them to compare the early visually evoked potentials (i.e., P1 and N1) for stimuli that were either to be attended or ignored on a given trial as a means of assessing how effectively attention was operating during the initial processing of the stimuli. They found that older adults were less effective at suppressing irrelevant items. Similar findings were also reported in a study by Fabiani et al. (2006) with a passive listening task.

However, the results from Gazzaley et al. (2008) also indicate that only early stages of visual processing are affected. In contrast, the paradigm we have used is suited to investigate ERPs during the retention interval, and the CDA is assumed to reflect encoding and maintenance. Therefore, it is unclear whether the filtering deficits observed in our and the Gazzaley study are the same. Moreover, in the Gazzaley et al. study relevant and irrelevant information was presented in distinct successive displays. This implies that the complete information is either to be attended or to be ignored—a situation that may allow for indiscriminant, early filtering, at least in individuals with functional filtering efficiency (i.e., young adults). In contrast, in the present experiment, relevant and irrelevant information was presented simultaneously. In such a situation, filtering may have to occur at a somewhat later stage, after determining which aspects in the display need to be encoded and which need to be ignored.

Despite the subtle differences in paradigms and results between Gazzaley et al. (2005, 2008) on the one hand and the current work on the other, the emerging pattern regarding age differences in working memory is that it results from slowed selection against irrelevant information. The additional novel finding from the present work is that the pattern of filtering deficits behind reduced working memory performance is not the same for old adults and low working memory young adults. For the question of age differences in working memory, it is important to know that old adults are not just like young adults with low working memory capacity. For example, recent attempts to use working memory interventions in old adults that have shown some success in young adults and children (e.g., Klingberg et al. 2002) seem to have only very limited success in old adults (see Mayr 2008). Possibly the specific filtering deficit found in old adults requires an intervention that targets exclusion of irrelevant information during encoding of information into working memory in a more focused manner than existing interventions.

There is evidence that filtering of information into working memory depends on signals from the basal ganglia and the prefrontal cortex that help to control which items will ultimately be represented in the posterior parietal cortex (Chao and Knight 1998; Rainer et al. 1998; Yago et al. 2004; Buschman and Miller 2007). Low capacity individuals appear to be less capable of engaging these frontal control mechanisms, and consequently, they unnecessarily store irrelevant items in working memory (McNab and Klingberg 2008). Given the present results, we might expect that when compared with low capacity young adults, old adults may still be able to engage the critical frontal–striatal network, but would be slower to do so.

The finding that age and individual differences in working memory capacity relate to filtering efficiency in different ways is important beyond the question of age differences in working memory. Cognitive psychologists and neuroscientists are interested in uncovering the "cognitive primitives" that account for complex behavior and individual differences therein but that cannot be further decomposed into constituent processes. The number of elements people can maintain over short periods of time is one candidate for such a "cognitive primitive." For example, consistent with this view, in psychometric space, simple short-term memory tasks and fluid intelligence assume overlapping regions (e.g., Cowan et al. 2005). However, the present finding that the same low working memory score can be the result of qualitatively different types of filtering problems (i.e., early vs. late) suggests an interesting complication of this picture. Looking at it from the perspective of complex cognitive tasks that are typically used to assess fluid intelligence, working memory capacity may still be considered as a cognitive primitive in the sense that it represents an important source of individual differences in a parsimonious manner. However, on the level beneath, we need to consider distinct neurocognitive processes that each contribute to an individual's working memory capacity.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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