Contralateral Delay Activity Reveals Life-Span Age Differences in Top-Down Modulation of Working Memory Contents

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Estimates of working memory (WM) capacity increase in children, peak in young adulthood, and decline thereafter. Despite this symmetry, the mechanisms causing capacity increments in childhood may differ from those causing decline in old age. The contralateral delay activity (CDA) of the electroencephalogram, an event-related difference wave with a posterior scalp distribution, has been suggested as a neural marker of WM capacity. Here, we examine 22 children (10–12 years), 12 younger adults (20–25 years), and 22 older adults (70–75 years) in a cued change detection paradigm. Load levels and presentation times were varied within subjects. Behaviorally, we observed the expected life-span peak in younger adults and better performance with longer presentation times. With short presentation times, task load increased CDA amplitude and decreased behavioral performance in younger adults. Both effects were less pronounced in older adults. Children showed a unique pattern: Their behavioral load effects were as strong as those of younger adults, but their CDA was unaffected by load. With long presentation times, task load modulated the CDA in children and older adults but not in younger adults. These findings suggest that age-related differences in CDA reflect changes in the top-down control over WM representations.

Keywords aging, contralateral delay activity, development, EEG, visual working memory

Introduction

Visual working memory (WM) capacity is generally assumed to be limited on average to about 3–4 items (Miller 1956; Luck and Vogel 1997; Cowan 2001) and to vary considerably across individuals (Vogel and Awh 2008). Currently, 2 perspectives dominate the discussion about the nature of WM capacity limits: The "discrete slot model" suggests an upper capacity limit for a fixed number of items, independent of their complexity (Luck and Vogel 1997; Vogel et al. 2001; Awh et al. 2007; Rouder et al. 2008). By contrast, the "flexible-resource model" suggests capacity limits to arise from over-taxing a shared resource. The latter view assumes that an increasing number of items can be stored at the cost of decreasing resolution for each single item (Wilken and Ma 2004; Bays and Husain 2008; Bays et al. 2009). Both models have gained support from behavioral (Alvarez and Cavanagh 2004; Eng et al. 2005; Awh et al. 2007; Zhang and Luck 2008) and neuroimaging studies (Todd and Marois 2004, 2005; Song and Jiang 2006; Xu and Chun 2006; Xu 2007), and the controversy is unresolved, in part due to conflicting findings (see, e.g., Bays and Husain 2008; Cowan and Rouder 2009).

The extent to which the discrete slot model and the flexible resource model of WM capture age-related differences in WM performance from childhood to old age has not been explored so far. Relating the 2 models to life-span data may help to clarify their relative strengths and shortcomings, and to delineate the differences and commonalities among the mechanisms that drive WM development from childhood to early adulthood, and from early adulthood to old age. At the aggregate performance level, WM shows a gradual increase up to young adulthood (Gathercole 1999), followed by monotonous decline that accelerates with advancing age (Park and Payer 2006). Thus, in cross-sectional comparisons, both children and older adults usually show lower WM performance than younger adults (Cowan et al. 2006). However, life-span psychological theorizing suggests that development in old age is not a mirror image of child development (Baltes et al. 2006; Craik and Bialystok 2006), raising the question of general processing differences between children and older adults. At the same time, process-oriented neural models of WM assume that performance in WM tasks depends on efficient neural communication within a widely distributed functional network including frontal, parietal, occipital, and temporal regions (Postle 2006; D'Esposito 2007; Zimmer 2008; Palva et al. 2010). In accordance with these views, we recently provided behavioral evidence that low-level feature binding and strategic control components contribute differentially to WM performance in children, younger adults, and older adults (Sander et al. forthcoming). For the present study, we complemented our behavioral approach with electroencephalography (EEG) of task-relevant neuronal activity.

The Contralateral Delay Activity in Change Detection Paradigms: Relation to Binding and Control Operations

In the past decade, the so-called change detection paradigm (Luck and Vogel 1997), has proven useful in probing WM capacity limits on behavioral and neuronal levels (e.g., Vogel et al. 2001; Wheeler and Treisman 2002; Todd and Marois 2004, 2005; Sauseng et al. 2009). In change-detection tasks, observers are presented with a memory array containing a variable amount of information to be retained (e.g., colored squares). After a retention interval, the observer has to compare the internally maintained representation of the memory array to a probe array in which one of the items has or has not been altered. By varying the number of presented items, this procedure yields an estimate of the individual WM capacity, the so-called k-score (Cowan 2001).

Combining change detection tasks with neuroimaging techniques has provided valuable insights into the neuronal correlates of WM capacity limits (e.g., Todd and Marois 2004, 2005; Song and Jiang 2006; Xu and Chun 2006). For example, studies relying on EEG of neuronal activity indicate that an

event-related difference wave occurring during the delay period in WM tasks can serve as an online marker of the current amount of WM contents (Vogel and Machizawa 2004; Vogel et al. 2005; McCollough et al. 2007). This difference has been designated as the contralateral delay activity (CDA), sometimes also referred to as the sustained posterior contralateral negativity, or SPCN (Jolicoeur et al. 2008). When studying the CDA in EEG paradigms, observers are cued to attend to only one hemifield of the memory array while maintaining fixation. The lateral presentation of items allows to separate specific WM-related activity from non-specific activity, given that the perceptual stimulation to both hemispheres is balanced (McCollough et al. 2007). Thus, any difference between attended and not-attended hemifield should be related to WM, attentional processes, or both (Luck 2005; McCollough et al. 2007).

Previous studies reported increasing CDA amplitudes with increasing load that levels off when the individual capacity limit is reached (Vogel and Machizawa 2004; McCollough et al. 2007). These observations suggest the CDA may qualify as an online marker of the number of currently maintained items. In addition, the posterior topography and a functional similarity to parametric changes in functional magnetic resonance imaging (fMRI) activity observed within the intraparietal sulcus (Todd and Marois 2005) suggest a source for the CDA in parietal regions (for corresponding magnetoencephalography results, see also Robitaille et al. 2009). Accordingly, the parietal cortex is often suggested to be the key locus of the WM capacity limit (Todd and Marois 2005; Xu and Chun 2006).

Despite its posterior distribution, it is likely that neuronal activity reflected in the CDA component is influenced by both feedforward and feedback processes from more sensory posterior and frontal cortical regions (McCollough et al. 2007; Corbetta et al. 2008). In particular, "top-down" signals from prefrontal cortex (PFC) may bias processing in posterior cortical areas (Desimone and Duncan 1995; Miller and Cohen 2001). Recent evidence supports this assumption. For example, Woodman and Vogel (2008) investigated the modulation of the CDA by load using orientation bars of different colors. Participants had to either remember the color, the orientation, or both (conjunction condition). Thus, the sample items were always identical and only the instructions differed. Interestingly, when subjects were asked to memorize only the colors of the bars, the amplitudes of the CDA was smaller than when they were asked to memorize the orientations of the colored bars or the conjunction. This finding suggests that the amplitude of the CDA is modulated by the amount of top-down control required by the task. A recent patient study (Voytek and Knight 2010) provided further evidence on this issue: In patients with unilateral PFC lesions, load modulations of the CDA were only observed ipsilesional, but not contralesional—a finding that was interpreted as a loss in top-down facilitation by the authors. Furthermore, also in healthy subjects, interindividual differences in WM performance were related to "filter efficiency," or the control of WM contents, as reflected in corresponding CDA amplitude differences (Vogel et al. 2005; Fukuda and Vogel 2009).

In addition, the amplitude of the CDA varies generally across different stimulus attributes. For instance, amplitudes are larger for orientation bars than for colored squares (McCollough et al. 2007). Alternatively, this finding might indicate that more complex stimuli evoke larger sensory evoked response. However, 2 recent studies (Gao et al. 2009; Luria et al. 2009) reported that the CDA was not modulated by load for complex stimuli, such as random polygons. In these studies, the CDA already reached an asymptote at a load of only 2 items, in line with lower behavioral performance for more complex objects relative to simple objects (Alvarez and Cavanagh 2004; Eng et al. 2005). These results suggest that not only the number of objects may be the limiting factor of WM but that WM performance may also depend on the amount of resources needed for the representation of the objects, depending on their complexity (for similar fMRI results, see Song and Jiang 2006; Xu and Chun 2006). According to this interpretation, complex objects consume more storage capacity because they are made up of several features that have to be bound together in order to build up a coherent representation (e.g., Wheeler and Treisman 2002; Treisman and Zhang 2006; Luria et al. 2009).

Life-Span Age Differences in Behavioral and Neural Markers of WM Capacity

Surprisingly, the CDA has rarely been used to investigate the neuronal correlates of life-span age differences in WM performance (but see Jost et al. 2010). Based on discrete slot models and the conceptualization of the CDA as an online marker of WM contents (Vogel and Machizawa 2004; Vogel et al. 2005; McCollough et al. 2007), one would assume that the lower performance of children and older adults simply reflects a reduced storage space, which should result in lower CDA amplitudes compared with younger adults. However, when applied to an age-comparative setting, the current findings raise doubt whether a life-span parallelism between CDA amplitudes and WM performance can be expected.

Across the life span, different brain regions are differentially affected by maturation, learning, and senescence (Sowell et al. 2003; Raz et al. 2005; Raz and Rodrigue 2006; Toga et al. 2006). Taking into consideration that WM performance involves a distributed functional brain network (e.g., D'Esposito 2007; Zimmer 2008), age-related differences in the involvement of distributed cortical regions may constrain WM capacity in children and older adults relative to younger adults, but for different reasons (Shing et al. 2008, 2010; Park and Reuter-Lorenz 2009; Sander et al. forthcoming; Shing and Lindenberger forthcoming). In this vein, Werkle-Bergner et al. (2009) recently reported EEG evidence suggesting that low-level binding processes for simple stimuli such as circles and squares differ between children, younger, and older adults. This observation is consistent with behavioral finding suggesting that binding mechanisms differ in efficiency by age (Naveh-Benjamin 2000; Cowan et al. 2006; Shing et al. 2008).

With regard to the control of memory contents, Gazzaley and colleagues recently provided fMRI (Gazzaley et al. 2005) and electrophysiological (Gazzaley et al. 2008) evidence suggesting that older adults' lower WM performance reflects deficits in suppressing irrelevant information. In the later study (Gazzaley et al. 2008), older participants were characterized by a reduced ability to control WM contents as early as 100–200 ms after stimulus onset. However, later suppression processes were not impaired. In line with these results, Jost et al. (2010) provided evidence for reduced filtering efficiency in older adults compared with younger adults. These age differences

were particularly pronounced during early time windows of the CDA (350–500 ms after stimulus onset), suggesting that older adults show more attention to irrelevant information during early visual processing. Thus, several studies (Gazzaley et al. 2008; Jost et al. 2010) indicate that cognitive aging can be characterized by a combination of deficits in perceptual speed and suppression, such that inhibition processes are not absent but delayed. Along similar lines, we recently demonstrated that prolonged presentation times of memory arrays in a change detection task increase the possibility to exert top-down control over WM content and results in better performance in groups of children younger, and older adults (Sander et al. forthcoming).

Taken together, existing evidence suggests that life-span age differences in WM capacity may be brought about by age-differential recruitment of low-level binding and top-down control processes. Therefore, in the present study, we set out to test whether the CDA indeed reflects the amount of currently maintained items equally well in different age-groups and task conditions. If the CDA qualifies as an online marker of currently maintained information, we would assume reduced CDA modulations by increasing WM load in children and older adults compared with younger adults. The hypothesis is based on the observation that children and older adults usually show reduced WM capacity estimates in cross-sectional age-comparative studies.

However, if the CDA reflects the interplay of low-level feature binding and top-down control operations, we would expect age-differential patterns for the relation between behavioral and CDA measures. Therefore, to investigate whether CDA patterns in different age-groups would change depending on the possibility to control WM content, we asked children, younger adults, and older adults to perform a cued change detection task and varied within-subject load levels and presentation time of the memory array (see also Sander et al. forthcoming). We assumed that with short presentation times, the control of WM content would be constrained by the restricted amount of time, whereas the binding component would be heavily taxed. By contrast, longer presentation times would permit participants to increase control over WM contents, leading to enhanced performance due to the successful interaction of low-level binding and control processes.

Materials and Methods

Participants

The effective sample comprised 22 children (*M* age = 11.9 years, range 10-13 years), 12 younger adults (*M* age = 24.2 years, range 20–25 years), 22 older adults (*M* age = 73.3 years, range 70–75 years). Since interindividual variation is usually larger in children and older adults relative to younger adults, we aimed at larger sample sizes for children and older adults. All participants were assessed on marker tests of verbal knowledge (Spot-a-Word; cf. Lehrl 1977) and perceptual speed (digit symbol substitution test; cf. Wechsler 1955) as well as on a marker test of sustained attention (d2; Brickenkamp 1994). Also, visual acuity was measured in Snellen decimal units at 2 different distances (30 and 5 m) using Landolt rings (Geigy 1977). Table 1 displays sample descriptives. The ethics committee of the Max Planck Institute for Human Development, Berlin, approved the study.

Experimental Paradigm

During the experimental procedure, participants were seated comfortably in a dimly lit as well as electromagnetically and

Table 1
Descriptive summary of covariate measures

| Measure	Children (*n* = 22), *M* (SD)	Younger adults (*n* = 12), *M* (SD)	Older adults (*n* = 22), *M* (SD)
Age	11.94 (0.52)	24.19 (1.57)	73.25 (1.54)
Digit symbol	50.73 (7.27)	66.92 (10.67)	49.77 (9.81)
Vocabulary	17.18 (3.45)	24.17 (3.69)	29.23 (3.13)
Close vision	0.85 (0.13)	0.82 (0.12)	0.45 (0.15)
Far vision	1.24 (0.42)	1.4 (0.55)	1.02 (0.38)

Note: SD, standard deviation.

acoustically shield room. The EEG measurement started with a 6-min relaxation phase (resting EEG), followed by the task. A hemifield version of the change detection task (Vogel and Machizawa 2004) was used to test the hypotheses (see Fig. 1). Memory arrays of colored squares were presented in 4 blocks to the participants. Presentation times of the memory array were set to 100 and 500 ms in 2 blocks each. The first 2 and the last 2 blocks were always presented with the same presentation time, and the order of the presentation time was counterbalanced across participants. Targets were defined as squares presented in one hemifield as indicated by a centrally placed hemifield cue before each trial. We presented memory arrays of 2, 4, or 5 targets to younger adults and memory arrays of 2, 3, or 4 targets to older adults and children. Set sizes were randomized within blocks. After a retention interval of 1000 ms, a probe array of colored squares was shown and participants had to indicate whether all the colors of the targets of the probe array were identical to the memory array or whether one of the squares had changed in color. Subjects answered by pressing buttons labeled as "same" (in German: "gleich") or "different" ("ungleich"). The mapping of response alternative on participants' hands was counter-balanced across individuals. Participants were encouraged to respond as accurate as possible and to guess if they were not sure of their response. Maximum response time was restricted to 5000 ms. Each block started with 12 practice trials to allow participants to get used to the current presentation time. Afterward, each participant completed 360 trials of varying set size per presentation time. Set size and change condition were equally distributed within each block. After each block, participants got feedback about the accuracy of their responses.

Given that we assumed that older adults and children may have additional difficulties with a cued hemifield presentation, we always presented the cue for 500 ms and showed it until the memory array was presented in order to avoid additional memory load. We also blocked the cue direction for 30 consecutive trials in order to prevent a task-switching situation that could differentially affect the age-groups (e.g., Kray and Lindenberger 2000; Davidson et al. 2006).

Stimuli

Stimulus presentation and recording of behavioral responses were controlled with Eprime v1.2 software (Psychology Software Tools Inc.). Stimuli consisted of colored squares (0.65° × 0.65° of visual angle) presented on gray background (RGB values: 200, 200, 200) within an area of 4° × 7.3° of visual angle right and left of the fixation cross (distance to the fixation cross was 1.5°). Spatial locations of the squares were random, with a minimum distance of 2° between the centers of the squares. Participants sat at a viewing distance of 70 cm. Colors were randomly selected from a set of 11 highly discriminable values, black (RGB values: 0, 0, 0), white (RGB: 255, 255, 255), gray (RGB: 126, 123, 126), blue (RGB: 0, 0, 255), green (RGB values: 0, 255, 0), red (RGB: 255, 0, 0), cyan (RGB: 0, 255, 255), violet (RGB: 255, 0, 255), brown (RGB: 153, 102, 51), orange (RGB: 255, 112, 1), and yellow (RGB: 255, 255, 0). The same color was not repeated more than twice per array. Pilot testing indicated that some color changes were difficult to detect for older adults. Hence, we excluded changes from black to blue or gray, from blue to black or gray, from red to orange, brown or magenta, from magenta to red, from brown to red or orange, from orange to red or brown, and from gray to black or blue.

| 700ms | 500ms | 100ms OR 500ms | 1000ms | max. 5000ms | 1000ms |
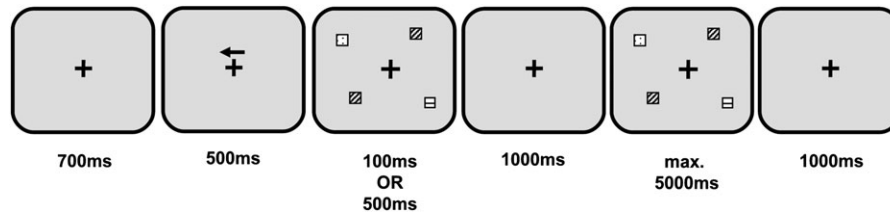
Figure 1. Trial structure of the change detection task. Different patterns of the squares represent different colors.

EEG Recording and Preprocessing

EEG was recorded continuously with BrainAmp amplifiers (BrainVision Products GmbH) from 61 Ag/Ag-Cl electrodes embedded in an elastic cap. Three additional electrodes were placed at the outer canthi (horizontal EOG) and below the left eye (vertical EOG) to monitor eye movements. During recording, all electrodes were referenced to the right mastoid electrode, while the left mastoid electrode was recorded as an additional channel. Electrode impedances were maintained below 5 kΩ before recordings. The EEG was recorded with a pass-band of 0.1–250 Hz and digitized with a sampling rate of 1000 Hz.

For preprocessing, the EEG was re-referenced to mathematically linked mastoids, downsampled to 256 Hz, and band-pass filtered between 0.5 and 100 Hz. Four-second data epochs were extracted from –2 to 2 s with respect to the memory array onset. The extracted segments were visually inspected and trials with eye movements (especially saccades) and excessive muscle activity were rejected from analysis. Only trials with correct responses were kept for analysis. Mean numbers of correct, artifact-free trials were 257 [standard error (SE) = 11.0] for children, 259 (SE = 10.0) for younger adults, and 268 (SE=7.0) for older adults in the 100-ms presentation time condition, and 262 (SE = 9.5) for children, 265 (SE = 9.3) younger adults, and 283 (SE = 5.8) for older adults in the 500-ms presentation time condition. Afterwards, an independent component analysis (ICA) was used to correct for remaining eye blink, noise, and muscle activity (Jung et al. 2000). Independent components representing artifactual sources were visually identified and removed from the data.

Analysis of Behavioral Data

In line with the literature, we calculated the individual memory capacity for each presentation time and set size according to Cowan (2001) as $k =$ (hit rate false alarm rate) × set size. Generally, k is assumed to increase with increasing set size and to reach an asymptote at the individual maximum performance level.

Analysis of Event-Related Potentials

All analyses were performed with the Fieldtrip software package (developed at the F. C. Donders Centre for Cognitive Neuroimaging, Nijmegen, The Netherlands; http://fieldtrip.fcdonders.nl/) supplemented with custom-made MATLAB code (The MathWorks Inc.). For event-related potential (ERP) analyses, ICA-cleaned, artifact-free EEG epochs were downsampled to 256 Hz and band-pass filtered between 0.5 and 20 Hz. Only trials with correct responses were included in the analyses.

Comparing ERPs between different age-groups always poses particular difficulties such that 1) the same component might show a different topography (e.g., Müller et al. 2008) or 2) the same component might show a different latency (e.g., Gazzaley et al. 2008) or 3) additional, related components may be present (e.g., Talsma et al. 2006). To enhance the validity of our age-group comparisons, we followed a data-driven approach instead of specifying regions and time windows of interest a priori. First, we identified a suitable time window to quantify the CDA effects within each age-group. The CDA generally reflects the difference in EEG activity between contralateral and ipsilateral sites as a function of cue direction. Therefore, we conducted t-tests within each subject comparing the contralateral and ipsilateral activity across trials of all load levels but separately for each presentation time condition. Individual t-values were transformed into z-values (Hughett 2007), pooled across parietal

electrodes within one hemisphere (P1/2, P3/4, P5/6, P7/8, PO3/4, PO7/8), and averaged across subjects, separately for each age-group. Note that the resulting z-values reflect the normalized contra–ipsi difference within subjects, thereby reducing intersubject variability (cf. van Dijk et al. 2010). The cluster of electrodes to determine the time window for the CDA effects was chosen based on prior studies, indicating that the peak of ipsi–contra differences is found over parietal regions (Vogel and Machizawa 2004; McCollough et al. 2007; Jolicoeur et al. 2008).

Second, for each time point, we used a bootstrap procedure to estimate a 95% confidence interval (CI) around the mean z-value within age-group. For this purpose, 10 000 random samples from the original distribution of z-values were drawn with replacement. Time windows later than 200 ms after stimulus onset for which the CI did not include zero for a minimum length of 10 consecutive points were considered reliable time points of interest (TOI). To determine the topographical distribution of the CDA effects, cluster-based permutation tests (Maris and Oostenveld 2007) were conducted based on all electrodes from one hemisphere. This analysis allowed to define age-specific regions of interest (ROI) and to check whether observed effects were indeed specific to posterior regions. Specifically, dependent sample t-tests were conducted for the ipsi–contra contrast within each age-group, separately for each time condition. The permutation null distribution for the resulting t-values was determined by randomly switching the ipsi–contra labels 1000 times and recomputing the t-tests. The threshold for electrodes to be included into a cluster was set to $P = 0.01$. Clusters were defined as a minimum of 2 neighboring electrodes showing reliable differences in activity. These statistics yielded significant ($P < 0.05$) clusters of electrodes that were considered as ROI in subsequent analyses (see Fig. 2).

We computed difference waves (i.e., contralateral minus ipsilateral activity) to quantify age- and load-dependent effects on CDA amplitudes. Given that the CDA reflects a sustained effect during the retention interval, detailed analyses were based on the mean amplitude of the difference wave within statistically identified time and electrode ROI. Mean amplitude values were calculated separately for each subject, load, and presentation time condition.

Statistical Analysis

Main analyses of age differences in estimated capacity parameters and the mean CDA amplitudes were conducted with the Proc Mixed Procedure in SAS (SAS 9.1 for Windows). The Proc Mixed model allows for heterogeneous variance and covariance structures across age-groups and conditions in a repeated measures design. To constrain the data as little as possible, we fitted an unstructured covariance matrix to the data (for a similar approach, see Shing et al. 2008; Werkle-Bergner et al. 2009). Statistical analyses included only load conditions that were tested across all 3 age-groups, thus set sizes of 2 and 4 items, if not stated otherwise. The alpha level for all statistical analyses was set to $\alpha = 0.05$. For reliable effects and trends ($0.1 > P > 0.05$), effect sizes are indicated by reporting the intraclass correlation coefficient ρ_I or Cohen's d.

Results

Electrophysiological Markers of WM Capacity

For all age-groups and time conditions, the statistical procedures identified more negative-going contralateral activity
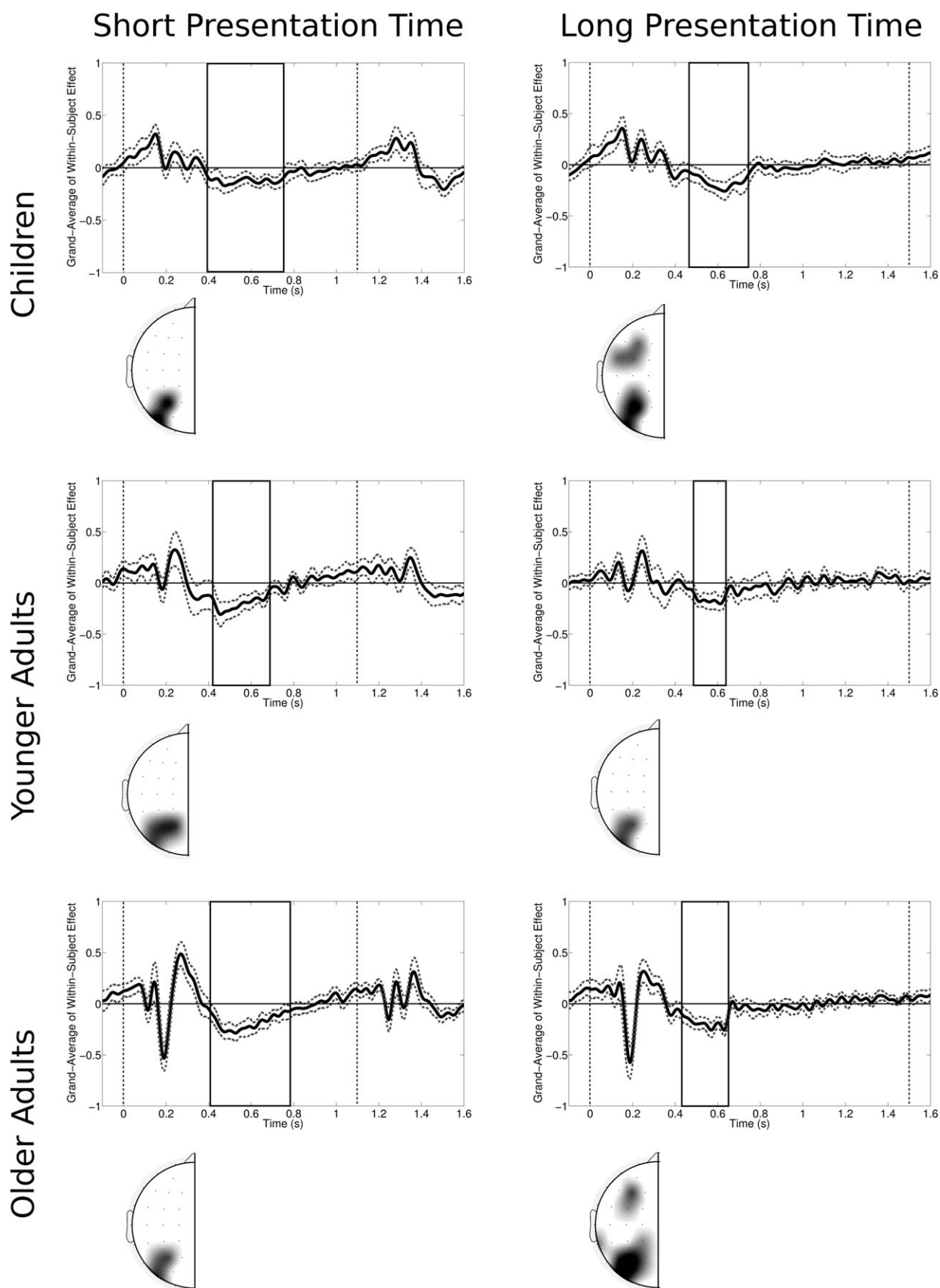
Figure 2. Grand averages of *z*-values of the within-subject effect of hemispheric differences averaged over all posterior electrodes. The entire trial length is shown. Stimulus onset and probe onset are indicated by vertical dotted lines. The black line represents the average of the *z*-transformed within-subject statistics, and the gray dotted lines represent the bootstrapped 95% CI. TOIs taken for analysis are indicated by rectangles. The corresponding ROI is displayed below.

(compared with ipsilateral recordings) during the retention interval within a cluster of electrodes with a posterior parietal distribution. We therefore refer to this effect as the CDA (see Fig. 2). Time windows and electrode clusters were overlapping across age-groups and time conditions (see Table 2). Note that in both time conditions, the effects were observed between 400 and 600 ms. This finding is remarkable, as for the 500-ms presentation time condition, the stimulus was still present on the screen, whereas for the 100-ms presentation time condition, it was not. This result implies that the observed CDA effects are not just reflections of sensory evoked activity.

As an unexpected finding, for children as well as older adults, a second frontally distributed cluster of electrodes with a reliable ipsi–contra difference emerged for the 500-ms presentation time condition (see Fig. 2 and Table 2). These clusters were independent from the posterior electrode clusters. For younger adults, no such effect was observed.

The mean CDA amplitudes were subjected to an overall mixed model with age-group as between-subject factor (3), and set size (2) and presentation time (2) as within-subjects factors. The analysis resulted in a main effect of age-group, $F_{2,32.8} = 10.46$, $P < 0.05$, $\rho_I = 0.62$; a main effect of set size, $F_{1,36} = 9.38$, $P < 0.05$, $\rho_I = 0.45$; and the expected 3-way interaction of age-group, presentation time, and set size, $F_{2,18.4} = 5.63$, $P < 0.05$, $\rho_I = 0.62$. All other effects were not significant, $Fs < 1.71$, all $Ps > 0.19$. To break down the 3-way interaction, we defined contrasts that compared load 2 and load 4 conditions separately in the 3 age-groups for each of the 2 presentation time conditions. For the 100-ms presentation time condition, this set of analyses revealed a set size effect in younger adults, $t_{11} = 3.65$, $P < 0.05$, $d = 1.31$; as well as a small yet reliable effect in older adults, $t_{21} = 2.69$, $P < 0.05$, $d = 0.38$; and no reliable set size effect in the children, $t_{21} = 0.16$, $P > 0.87$. Evaluating the set size modulation of CDA amplitudes separately for each age-group for the 500-ms presentation time condition revealed a reliable difference between set size 2 and set size 4 in children, $t_{21} = 2.67$, $P < 0.05$, $d = 0.61$; a smaller but still reliable effect in older adults, $t_{21} = 2.09$, $P < 0.05$, $d = 0.54$; and no reliable effect in younger adults, $t_{11} = 0.8$, $P > 0.05$. Estimated means and SEs of both analyses are displayed in Figure 3, and the corresponding grand-average difference waves are shown in Supplementary Figure S1. Analyses using the more standard ROI-based approach with fixed TOI for all age-groups led to similar results (see Supplementary Material).

A separate set of analyses was run for the frontal cluster of electrodes that displayed reliable differences between contra-

lateral and ipsilateral activity among children and older adults in the 500-ms presentation time condition. As load conditions were identical in children and older adults (2, 3, and 4 items), this analysis made use of all available data. The mixed model with set size (3) as within-factor and age-group (2) as between-factor yielded a reliable effect of age-group, $F_{2,29.1} = 10.2$, $P < 0.05$, $\rho_I = 0.96$, reflecting a larger average amplitude of the difference waves in children than in older adults. Neither the effect of set size, $F_{2,25.5} = 1.26$, $P > 0.30$, nor the interaction of age-group and set size, $F_{2,25.5} = 0.92$, $P > 0.41$, was reliable. Estimated means and SEs are displayed in Table 3.

Behavioral Markers of WM Capacity

In a first step, we characterized age differences in overall WM capacity, by comparing k-score estimates for set size 4 across age-groups (between-subjects factor, 3 levels) and presentation time (within-subjects factor, 2 levels). [We chose set size 4 because it is the largest set size that was administered to all age-groups. Especially in YA, the k estimates might have been artificially restricted. Therefore, we also compared the maximum k-scores across all load conditions (including set size 5 for YA). These analyses essentially resulted in the same pattern of results, and the main effect of age-group reached significance, $F_{2,33.1} = 6.1$, $P < 0.05$, $\rho_I = 0.52$.] The mixed model analysis revealed a trend for a main effect of age-group, $F_{2,35.9} = 2.76$, $P = 0.076$, $\rho_I = 0.37$, reflecting reliably larger k-score estimates for YA than OA, $t_{21.4} = 2.3$, $P < 0.05$, $d = 0.84$, whereas children's estimates did not reliably differ from YA, $t_{18.6} = -1.29$, $P > 0.20$, $d = 0.5$, and OA, $t_{40.9} = -1.44$, $P > 0.15$, $d = 0.43$. Furthermore, all age-groups profited from additional encoding time as reflected in a reliable main effect of presentation time, $F_{1,31.8} = 16.28$, $P < 0.05$, $\rho_I = 0.58$. However, the interaction between age-group and presentation time did not reach significance, $F_{2,35.7} = 0.49$, $P > 0.61$.

In a second step, we investigated whether the experimental manipulation of presenting different numbers of items influenced the number of remembered items, resulting in a modulation of the k-score estimate with set size. To this end, we compared the difference in k-scores achieved under set size 2 and set size 4 conditions across age-groups and presentation times. The mixed model analysis resulted in a main effect of age-group, $F_{2,35.8} = 3.44$, $P < 0.05$, $\rho_I = 0.40$, reflecting that the presentation of additional items increased the number of remembered items to a greater extent in CH and YA than in OA, $t_{38.8} = 2.18$, $P < 0.05$, $d = 0.66$, and $t_{21.2} = 2.29$, $P < 0.05$, $d = 0.84$, whereas CH and YA did not reliably differ from each other, $t_{16.8} = 0.84$, $P > 0.42$. In all age-groups, the difference between the conditions was larger at longer presentation time as reflected in a main effect of time condition, $F_{1,32.8} = 10.85$, $P < 0.05$, $\rho_I = 0.50$. The interaction between age-group and presentation time condition did not reach significance, $F_{2,35.8} = 1.36$, $P > 0.27$. Estimated means and SEs are displayed in Figure 3.

Discussion

We used behavioral and electrophysiological markers to investigate life-span differences in WM functioning from childhood over early adulthood to old age. Age-group differences in performance levels and CDA differed markedly by presentation time. The resulting overall pattern of findings is

Table 2
Final time windows (TOIs) and electrode ROIs for CDA estimation

	100-ms presentation time		500-ms presentation time	
	TOI	ROI	TOI	ROI
Children	0.395–0.754	P3, P5, PO7	0.473–0.742	CP3, P3, P5, PO7 (F3, FC3, FC5)
Younger adults	0.422–0.688	P1, P3, P5, PO3, PO7	0.484–0.640	P3, P5, PO7
Older adults	0.410–0.785	P3, P5, PO3, PO7	0.426–0.652	CP1, P1, P3, P5, PO3, PO7, TP7 (F3, FC3)

Note: Additional frontal clusters (not included in CDA estimation) presented in parentheses.
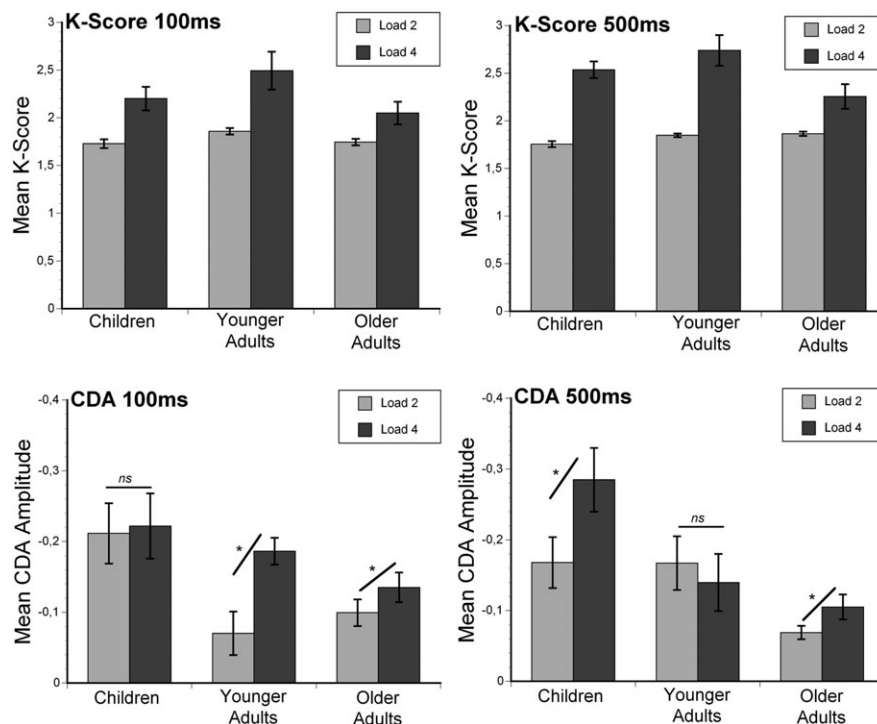
Figure 3. Mean *k*-scores (upper 2 panels) and CDA amplitudes (lower 2 panels) for the 2 presentation time conditions (left panels: 100 ms; right panels: 500 ms). Error bars indicate the SE of the mean. In the lower 2 panels, the sign of the *y*-axis is inverted to facilitate rendition of the CDA effect.

Table 3

Mean amplitudes averaged over frontal electrode clusters separated for age-group and set size

	Children (*n* = 22), *M* (SD)	Older adults (*n* = 12), *M* (SD)
Set size 2	−0.08 (0.05)	−0.04 (0.01)
Set size 3	−0.18 (0.04)	−0.05 (0.02)
Set size 4	−0.14 (0.05)	−0.06 (0.02)

Note: SD, standard deviation.

at odds with the view that the CDA is a direct expression of the currently maintained WM contents (Vogel and Machizawa 2004; Vogel et al. 2005; McCollough et al. 2007). Instead, it is consistent with the proposition that the CDA reflects the degree to which contents held in WM memory are under top-down control. According to this alternative view, the CDA is intimately linked to attentional processes (Drew and Vogel 2008; Emrich et al. 2009; Eimer and Kiss 2010). In the following, we first recapitulate the results for short and long presentation times, and then elaborate this interpretation.

Age Differences in the Modulation of Performance and CDA by Load: Short Presentation Times

With a presentation time of 100 ms, younger adults showed the highest levels of performance, followed by children and older adults, who performed most poorly. In younger adults and children, *k*-score estimates were modulated by set size. This effect was less pronounced in older adults, suggesting that they reached upper levels of performance with a smaller set size than younger adults and children. The age differences observed

in the present study were relatively small (in particular those between children and younger adults), presumably reflecting the restricted range of tested set sizes. Behavioral studies suggest that observed capacity differences between age-groups are greater when a wider range of load conditions is used, as individual differences are assessed more reliably under these conditions (e.g., Cowan et al. 2006; Sander et al. forthcoming). Nevertheless, our results were consistent with the expected pattern of age-group differences in WM performance.

At the neural level, we observed reliable differences between contralateral and ipsilateral activity, with a posterior distribution in all 3 age-groups. If participants would have encoded the whole memory array at once, differences between contralateral and ipsilateral activity would have been absent (Luck 2005; McCollough et al. 2007). Therefore, this finding demonstrates that participants of all ages were able to shift their attention to the cued hemifield. Children showed a larger CDA than younger and older adults, who did not differ in overall amplitude.

Importantly, the relation between CDA and load differed markedly between adults and children. In younger adults, we observed the previously reported pattern (Vogel and Machizawa 2004), reflecting a monotonically increasing relation between the CDA and the number of items held in WM. Older adults showed a smaller effect of load on performance, and a smaller load modulation of the CDA, again in line with earlier evidence (Jost et al. 2010). In contrast, children revealed a behavioral pattern more similar to younger adults without showing a reliable modulation of the CDA with load. With short presentation times, the decoupling between behavioral performance and CDA was a specific characteristic of the group of children.

Age Differences in the Modulation of Performance and CDA by Load: Long Presentation Times

In all 3 age-groups, load-dependent performance differences were more pronounced with long presentation times. Load effects did not differ reliably between younger adults and children, and were smaller in older adults. Again, the pattern of CDA amplitudes did not always follow the behavioral pattern. Younger adults did not show any load-dependent modulation of the CDA, whereas children, whose CDA was unaffected by load at short presentation times, now showed a positive relation between load and CDA amplitude. Older adults again showed a smaller load effect than children and younger adults, and a smaller but expected load-dependent modulation of the CDA.

CDA Amplitude and Top-Down Control: A Life-Span Dissociation?

Previous studies documented the dependence of CDA amplitudes on stimulus characteristics (McCollough et al. 2007; Gao et al. 2009; Luria et al. 2009), individual differences (Vogel and Machizawa 2004), and top-down control (Voytek and Knight 2010). Together with the study by Jost et al. (2010), the present findings add to this picture by showing that the CDA varies in relation to participants' age. This age-dependent nature of the CDA is in need of explanation. According to a recently introduced 2-component model of WM development across the life span (Sander et al. forthcoming; cf. Shing et al. 2008, 2010; Shing and Lindenberger forthcoming), the relative contributions of low-level feature binding and strategic top-down control to WM are not invariant across age but evolve across the life course, reflecting differences in the relative efficiency and integrity of the corresponding brain areas and their interconnections (Sowell et al. 2003; Gogtay et al. 2004; Bunge and Wright 2007). In 12-year-old children, the posterior and temporal regions of the brain can be considered to be relatively mature (Ofen et al. 2007; Ghetti et al. 2010); hence, most of the mechanisms supporting low-level feature binding, which critically depend on these regions, are fully functional. In contrast, the top-down (e.g., strategic) control of WM contents critically involves frontal regions (Desimone and Duncan 1995; McNab and Klingberg 2008; Edin et al. 2009), which are known to show a protracted maturational course extending well into early adulthood (Casey et al. 2000; Gogtay et al. 2004; Paus 2005). According to this view, children are less efficient in implementing top-down control over WM contents than younger adults, but their low-level binding mechanisms operate close to adult levels. In older adults, however, both the low-level feature binding component and the strategic component of WM are impaired relative to younger adults.

When we apply this framework to the present data, the observed age differences in load- and time-dependent CDA modulations can be interpreted as signatures of life-span changes in the interplay between binding and control processes. At short presentation times, children showed a marked decoupling between behavioral performance and CDA amplitude. Others have observed that lower performance in a perceptually more challenging condition was not reflected in a higher CDA (Luria et al. 2009; Ikkai et al. 2010). In that case, the reported decoupling may reflect a greater number of errors during the comparison phase of the task. In our case, however, children's higher amplitude at conditions of lower load cannot be explained by comparison errors. Instead, we propose that children were not able to exert control over WM content at short presentation times, so that their performance was highly dependent on low-level binding processes. In contrast, children's CDA increased with load at long presentation times because strategic control processes had sufficient time to influence WM.

According to the 2-component model, the lower performance of older adults at shorter presentation times reflects senescent changes in both binding and control processes, resulting in smaller overall CDA amplitudes and smaller CDA modulations with load. With longer presentation times, also older adults were able to increase their performance. The degree of load modulation of the CDA increased as well again, in line with the assumption that the amplitude of the CDA is influenced by the degree of top-down control over WM.

Younger adults' data at short presentation times were well in agreement with earlier findings (Vogel and Machizawa 2004; McCollough et al. 2007), with larger CDA amplitudes at higher load. However, with longer presentation times, the CDA amplitude did not increase with load in this age-group. We suggest that younger adults were fully able to control WM content at short presentation times (Luck and Vogel 1997). With increased presentation times, the difficulty of the task decreased. As a consequence, younger adults were less likely to recruit demanding control operations, and the CDA was no longer modulated by load.

In summary, we suggest that the CDA amplitude is strongly modulated by load and related to behavioral performance when both low-level binding processes and top-down control successfully interact. However, if top-down control is not possible or not necessary, CDA amplitudes do not vary with load. Given that individuals of different age-groups differ in the relative contribution of strategic control to WM performance, the CDA may provide a useful indicator for studying age differences in the strategic contribution to WM performance.

Capacity Limits in Visual WM: Fixed Objects versus Flexible Resources

The results of the present study also contribute to the ongoing discussion about the nature of capacity limits in visual WM. Two viewpoints are currently under debate, namely the "discrete source" or "slot" model of WM (Luck and Vogel 1997; Vogel et al. 2001; Vogel and Machizawa 2004; Rouder et al. 2008; Zhang and Luck 2008; Barton et al. 2009) and the flexible resource model (Bays and Husain 2008) of capacity. Whereas the discrete source model suggests that the capacity limit is defined by the maximum number of items that can be held in memory, the flexible resource model accounts for the capacity limit by assuming a reduced resolution of the single item with increasing set size, given that a common resource has to be shared across more items. The debate has not been settled so far, as evidence in favor of either view has been reported (Bays and Husain 2008; Cowan and Rouder 2009).

In principle, the 2 views may not be mutually exclusive. It is possible that a limited number of slots determines the maximum number of representations held in memory. At the same time, resources that are more or less independent of the mechanisms that limit the number of slots may influence the representational resolution of items held in memory in a continuous fashion (Awh et al. 2007; Zhang and Luck 2008;

Barton et al. 2009; Fukuda et al. 2010). This intermediate view is consistent with recent neuroimaging studies reporting dissociable neural mechanisms that contribute to WM performance (Song and Jiang 2006; Xu and Chun 2006; Xu 2007, 2009; Palva et al. 2010).

These considerations are fully consistent with the 2-component framework of WM that motivated the present study. First, the upper limit of the number of items held in WM may reflect the potential for successful binding of within-object features (e.g., Lisman and Idiart 1995; Sauseng et al. 2009). This set of mechanisms may be fully functional in late childhood but compromised in older adults. Second, the amount of available resources may reflect the successful implementation of top-down control over WM representations. In children, this ability is not yet operating as optimal as in younger adults, and in older adults, it is compromised by normal aging.

Admittedly, the proposed 2-component model of life-span changes in WM performance is empirically underidentified in the present study. Specifically, from the perspective of this model, we lack direct neural measures of the low-level feature binding component. This is seen most clearly in children at short presentation times, where the observed increase in performance with larger set sizes is not accompanied by greater amplitudes of the CDA. Future work should therefore aim at varying the effects of intraitem complexity as well as the participant's possibility to exert top-down control in order to better understand the effects on the CDA.

Additional Frontal Activations in Children and Older Adults: Evidence for Cortical Recruitment?

In addition to the posterior CDA effects, we observed a frontal cluster of electrodes that displayed hemispheric differences in children and older adults at long presentation times. This frontal activity was larger over the contralateral hemisphere, but, unlike the CDA, it was not modulated by load. We cannot offer a firm interpretation of this unexpected finding. In aging research, several WM studies have reported that older adults tend to activate regions of PFC that are not significantly activated in younger adults (for a review, see Reuter-Lorenz 2002; Reuter-Lorenz and Jonides 2007). These activations have been interpreted as additional recruitment of control processes, counteracting age-related neurocognitive decline and supporting the WM maintenance (Cabeza et al. 2002; Madden et al. 2007; Nagel et al. 2009; Reuter-Lorenz and Park 2010). These results suggest that the frontal activations observed in our study may reflect a greater engagement of prefrontally mediated control processes in children and older adults relative to younger adults when demands on perceptual speed are relatively low. Note, however, that this additional prefrontal activity was not modulated by load. We conclude that the functional significance of the prefrontal cluster is unclear and needs to be evaluated in future research.

Summary

The CDA and its relation to behavioral performance were investigated under different presentation time conditions in children, younger adults, and older adults. Our results suggest that the CDA should not be understood as a neural marker of currently maintained memory contents in the strict sense (McCollough et al. 2007) since this assumption did not hold across age-groups and time conditions. In the absence of behavioral differences, we found differences between children and younger adults on CDA measures, whereas in the presence of behavioral differences between younger adults and older adults, we only found minor differences in the neural response. We therefore rather suggest that the CDA is reflecting the amount of top-down controlled memory content and is closely related to attentional processes (Drew and Vogel 2008; Woodman and Vogel 2008; Fukuda and Vogel 2009; Eimer and Kiss 2010). In conditions when either top-down control is constraint (e.g., due to short presentation times) or less needed (e.g., with very long presentation times in younger adults), the CDA is not related to behavioral performance. Accordingly, the CDA may only be related to behavioral performance under conditions requiring top-down control of internal representations and may therefore not always be a strict marker of WM content when comparing different age-groups.

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