

Age Group and Individual Differences in Attentional Orienting Dissociate Neural Mechanisms of Encoding and Maintenance in Visual STM

Andria Shimi¹, Bo-Cheng Kuo², Duncan E. Astle³,
Anna C. Nobre¹, and Gaia Scerif¹

Abstract

■ Selective attention biases the encoding and maintenance of representations in visual STM (VSTM). However, precise attentional mechanisms gating encoding and maintenance in VSTM and across development remain less well understood. We recorded EEG while adults and 10-year-olds used cues to guide attention before encoding or while maintaining items in VSTM. Known neural markers of spatial orienting to incoming percepts, that is, Early Directing Attention Negativity, Anterior Directing Attention Negativity, and Late Directing Attention Positivity, were examined in the context of orienting within VSTM. Adults elicited a set of neural markers that were broadly similar in preparation for encoding and during maintenance. In contrast, in children

these processes dissociated. Furthermore, in children, individual differences in the amplitude of neural markers of prospective orienting related to individual differences in VSTM capacity, suggesting that children with high capacity are more efficient at selecting information for encoding into VSTM. Finally, retrospective, but not prospective, orienting in both age groups elicited the well-known marker of visual search (N2pc), indicating the recruitment of additional neural circuits when orienting during maintenance. Developmental and individual differences differentiate seemingly similar processes of orienting to perceptually available representations and to representations held in VSTM. ■

INTRODUCTION

Multiple studies have shown that selective attention modulates the encoding and maintenance of information in visual STM (VSTM), both behaviorally and neurally (Gazzaley, 2011; Kuo, Yeh, Chen, & D'Esposito, 2011; Gazzaley & D'Esposito, 2007; Lepsien & Nobre, 2007; Postle, 2006; Postle, Awh, Jonides, Smith, & D'Esposito, 2004; Schmidt, Vogel, Woodman, & Luck, 2002; Awh & Jonides, 2001). Notably, in adults, biases applied to items held in VSTM elicit comparable behavioral benefit as biases applied to the encoding of perceptual items in VSTM (Griffin & Nobre, 2003). In contrast, recent findings indicate that, in childhood, the ability to use top-down attention to enhance encoding (i.e., prospective orienting) develops earlier than the ability to use top-down attention to enhance maintenance (i.e., retrospective orienting¹), suggesting that children and adults use attention cues differently to modulate a memory representation (Shimi, Nobre, Astle, & Scerif, 2013; Astle, Nobre, & Scerif, 2012). Yet, it remains largely unknown whether the equivalent efficiency of prospective and retrospective orienting that adults demonstrate is also dissociated at the neural level

in childhood. Here, we examined whether the neural correlates of attention biases in function of VSTM encoding and maintenance operate differentially in childhood compared with adulthood.

Extending the behavioral findings (Shimi et al., 2013), an understanding of the neurocognitive mechanisms that underlie the relation between selective attention and VSTM in childhood may have important implications for cognitive neuroscientists investigating the relation between attention and VSTM in adults (Chun, Golomb, & Turk-Browne, 2011; Gazzaley & Nobre, 2011; Awh, Vogel, & Oh, 2006) as well as during development (Jolles, Kleibeuker, Rombouts, & Crone, 2011; Craik & Bialystok, 2006; Casey, Tottenham, Liston, & Durston, 2005). This is because such knowledge can shed light on the neural mechanisms leading to the adult-end state: Seemingly similar neural processes before encoding and during maintenance in adulthood might be achieved via different neural pathways at different time points in development, suggesting their spatiotemporal dissociation, a hypothesis supported by their behavioral dissociation in childhood.

A substantial literature with adults also demonstrates a strong link between individual differences in selective attention and VSTM, with the suggestion that attentional selection abilities may underpin differences between individuals with low or high VSTM capacity (Jost, Bryck,

¹University of Oxford, ²National Taiwan University, ³Medical Research Council, Cambridge, UK

Vogel, & Mayr, 2011; Fukuda & Vogel, 2009; Awh & Vogel, 2008; Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Vogel, McCollough, & Machizawa, 2005). It remains unclear whether this is because individuals differ in their ability to bias encoding into memory, attend to information while maintaining it in memory, or both. To our knowledge, none of the currently published studies has examined how individual differences in childhood can elucidate the distinctions between selection for encoding and selection during maintenance, as well as their neural correlates. We therefore complemented our developmental questions with an individual differences approach, in both cases predicting a neural dissociation between processes of VSTM encoding and maintenance that are instead associated in adulthood.

Examining VSTM Encoding and Maintenance with Lateralized ERP Components of Attentional Orienting

Researchers have attempted to unravel the processing cascade and neural mechanisms by which attention operates on VSTM representations using paradigms in which participants search their memory for a specified target and/or feature (Dell'Acqua, Sessa, Toffanin, Luria, & Jolicoeur, 2010; Eimer & Kiss, 2010; Astle, Scerif, Kuo, & Nobre, 2009; Kuo, Rao, Lepsien, & Nobre, 2009) and under increasing memory loads (Kuo, Stokes, & Nobre, 2012; Nobre, Griffin, & Rao, 2008; Vogel & Machizawa, 2004). However, precise similarities and differences in attentional mechanisms gating encoding and maintenance in VSTM have received less attention so far (Gazzaley & Nobre, 2011). ERPs are an ideal method for investigating putative differences in attentional mechanisms supporting encoding versus maintenance of VSTM because they track brain responses on a millisecond-by-millisecond basis, allowing one to determine the multiple cognitive processing stages preceding a behavioral response along with their time course (Luck, Woodman, & Vogel, 2000; Hillyard & Anllo-Vento, 1998). In the current experiment, we asked participants to use a cue (before encoding or during maintenance) to modulate a VSTM representation and assessed this ability in both children and in adults. If attention selects stimuli from the memory array in a way that reflects their spatial layout, then we would expect to see differences in brain activity over the contralateral compared with the ipsilateral sites relative to the direction of the cue.

Griffin and Nobre (2003) investigated the extent to which shifts of spatial attention to upcoming perceptual representations engage similar neural processes to shifts toward representations held in VSTM and reported partially but not wholly overlapping neural processes for prospective and retrospective orienting in VSTM. However, these analyses focused on contrasting leftward or rightward shifts of attention, making them less directly comparable with the wealth of knowledge about the temporal dynamics of visuospatial orienting. Recently, Murray,

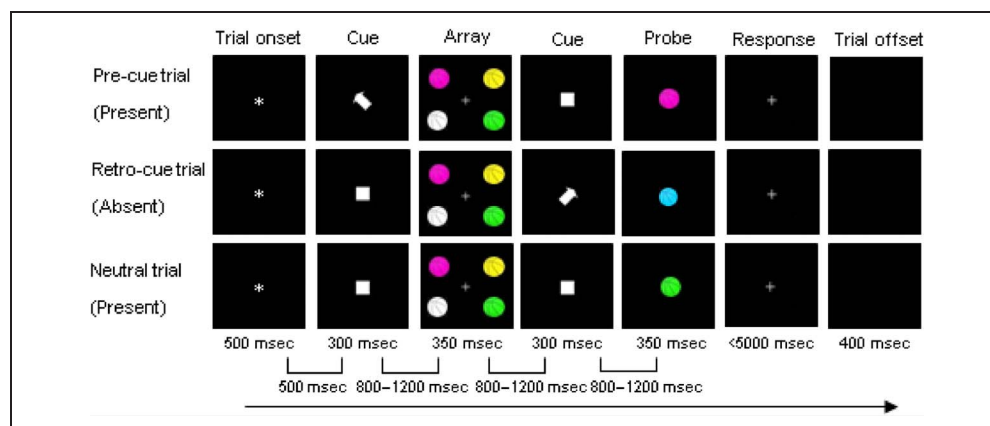
Nobre, and Stokes (2011) found that well-established lateralized components of visuospatial orienting, the Early Directing Attention Negativity (EDAN; thought to index the processing of the directional cue and the subsequent initiation of the attentional orienting), the Anterior Directing Attention Negativity (ADAN; associated with top-down attentional control), and the Late Directing Attention Positivity (LDAP; believed to tap the cortical excitability of the visual areas anticipating the upcoming stimulus in the array at the selected spatial location) underlie efficient encoding of information into VSTM. As this study focused on orienting in preparation for encoding, it remains to be explored, even in adults, whether lateralized neural modulations underlie attentional shifts triggered retrospectively during the maintenance period that are analogous to those supporting prospective attentional shifts.

Critically, no study thus far has examined whether these neural markers are involved in spatial biases on encoding and maintenance of information in VSTM during childhood. EDAN and LDAP, but not ADAN, have been documented in children 6 to 9 years old in a study that required detection of incoming stimuli (Harter, Miller, Price, LaLonde, & Keyes, 1989). Here, we investigate these neural markers in the context of attentional orienting in service of VSTM. The three lateralized components (EDAN, ADAN, and LDAP) were derived by examining the electrical changes taking place after the cue onset and before target presentation by comparing the ERP waveforms that were ipsilateral and contralateral to the direction of the cue. The advantage of this methodological approach is that it provides direct evidence for attentional biases driven by visuospatial orienting before the onset of the attended stimuli, instead of inferring that the processing of the attended stimulus is because of a change in attentional biases on the basis of behavioral responses to the attended stimulus itself. This is particularly useful in the context of studying children, whose orienting before making behavioral responses may betray differentiable routes to memory performance.

Summary of Aims

We aimed to investigate three critical questions: First, by measuring EDAN, ADAN, and LDAP, we examined whether adults employ similar neural processes when allocating attention retrospectively to internal representations by means of retro-cues (i.e., visuospatial cues presented during the maintenance period) compared with when allocating attention prospectively in anticipation of perceptual input via pre-cues (i.e., visuospatial cues presented before encoding). Second, taking as a framework the neural markers observed in adults, we assessed whether children apply similar neural biases when encoding spatial information in VSTM (via pre-cues) and if so, whether they show similar neural biases when they orient their attention internally to VSTM (via retro-cues). Third, we explored whether neural markers of attentional control relate to individual

Figure 1. Schematic illustration of the task and the three different types of trials. In pre-cue and retro-cue trials, we used arrows as informative spatial cues to guide participants' attention to one of the array items. In neutral trials, we used filled squares as uninformative cues to prevent participants from directing their attention to one item only. Each trial began with an asterisk (500 msec) signaling the start of a new trial followed by a fixation point, which remained visible throughout the trial.



At 500 msec later, a cue appeared for 300 msec. In pre-cue trials, the cue was an arrow pointing to the item that participants should encode in memory, whereas in retro-cue and neutral trials, the cue was replaced by a spatially uninformative white square that nonetheless controlled for potential nonspatial alerting effects associated with the cue. After a randomly varied fixation interval (800–1200 msec), the memory array with the four colored items appeared for 350 msec, followed by a randomly varied fixation interval (800–1200 msec). Depending on the type of trial, participants had to store in memory either only one item of the four (pre-cue trials) or all four items (retro-cue and neutral trials). Subsequently, another stimulus appeared for 300 msec. In pre-cue and neutral trials, this stimulus was a spatially uninformative white square presented at that point to control for non-spatial alerting effects. In retro-cue trials, this stimulus was an arrow directing participants' attention to the mental representation of one of the already encoded items. After a randomly varied fixation interval (800–1200 msec), the probe appeared for 350 msec followed by a fixation point that remained on the screen until a response was made or until a maximum of 5000 msec elapsed (leading to minimal trial attrition across age groups). Participants had to respond whether the probe was present in the array or not by pressing mouse buttons.

differences in VSTM capacity in children. To do so, we computed correlations between behavioral measures of VSTM capacity and neural activity while children selectively allocated their attention before encoding and during maintenance in VSTM.

METHODS

Participants

Fifteen adults (eight men and seven women), aged 21–34 years ($M = 26.4$ years, $SD = 3.76$), were recruited among university students, and 17 children (5 boys and 12 girls), aged 10–11 years ($M = 10.2$ years, $SD = 0.39$), were recruited from local primary schools via an opt-in procedure. All participants were right-handed and had normal or corrected-to-normal vision. No neurological/psychiatric disorders were reported by adult participants or the parents of the children. One adult participant was excluded from the analyses because of significantly below-chance behavioral performance. The study received ethical approval from the Central University Research Ethics Committee of the University of Oxford. Before testing, adult participants and parents of child participants signed a consent form, and children also verbally assented to participate in the study. Adult participants received a monetary compensation for their time, and children received a certificate to thank them for their participation. We note that we chose 10- to 11-year-olds as our age comparison group to the adult group because a number of studies have shown that some cognitive control abilities reach the adult mature state around the age of 10–11 years, whereas other cog-

nitive control abilities continue to develop until later in adolescence (e.g., Huizinga, Dolan, & van der Molen, 2006). On the basis of this, 10- to 11-year-olds could either be similar to adults or still developing, making them thus an interesting target age group to study the developmental state of attention and memory processes. Also, we opted for a narrow age group to maximize the likelihood of separating age-related and individual differences. This would provide us with more statistical power (taking into account the large variability that may exist in children's data) than an alternative commonly used strategy, that is, collapsing ERP markers and behavioral performance within a wider age group (e.g., 6–11 years) with fewer participants per specific chronological age.

Apparatus

The task is presented schematically in Figure 1. Participants viewed arrays of four colored items, followed by a single colored probe item after a variable delay. They were instructed to indicate whether the probe was present among the initial four items by pressing a mouse button (left for present and right for absent). Arrays were either preceded or followed by central cues that were fully informative (100%) of the location of a target probe, should this appear in the memory array. In pre-cue trials, an informative centrally presented spatial cue (a white arrow) preceded the array and guided the participant's attention to one of the upcoming items of the array, and a spatially uninformative white-filled square was presented after the array. White squares served the purpose of controlling for the nonspatial alerting effects that spatial cues may

engender. In retro-cue trials, a white square was presented before the array, whereas an informative spatial cue was presented after the array and guided the participant's attention internally to the mental representation of one of the already encoded items of the array. In neutral trials, uninformative white squares were presented before and after the array.

Participants completed two practice blocks of six trials each to familiarize themselves with the task, followed by eight test blocks of 48 trials in each, totaling 384 experimental trials; 256 probe-present (67%) and 128 (33%) probe-absent trials. Half of all trials were cued (equally likely to point to one of the four possible locations), and half were neutral. Of the probe-present trials, 64 contained pre-cues, 64 contained retro-cues, and 128 were neutral. Of the probe-absent trials, 32 contained pre-cues and 32 contained retro-cues, to ensure that cues did not indicate a "present" response, and 64 were neutral trials. The task was split into four "pre-cue" blocks, containing pre-cue and neutral trials, and four "retro-cue" blocks, containing retro-cue and neutral trials. This helped prevent children from being confused by continually changing cue types across trials. Test blocks alternated throughout the task to ensure that participants would complete equal number of "pre-cue" and "retro-cue" blocks if they decided to terminate the task before they completed all eight test blocks and were counterbalanced across participants. Cued and neutral trials were intermixed randomly within each block.

Stimuli

Stimuli were presented on a black background with E-Prime 1.2 (Psychological Software Tools, Inc., Pittsburgh, PA). The items in the array were identical line drawings of objects (e.g., balls), but they were distinguished by their color, that is, they were drawn from a set of seven colors (white, red, magenta, orange, yellow, green, and blue), and they were symmetrically arranged, each centered at 2.87° lateral and 2.87° azimuthal eccentricity from a central fixation point. Each item subtended $1.64^\circ \times 2.05^\circ$ of visual angle from a distance of 100 cm. The fixation point subtended a visual angle of 0.16° . All cues (white arrows and white filled squares) were centrally presented at the location of the fixation point and subtended $0.82^\circ \times 0.82^\circ$ of visual angle.

Procedure

Participants were comfortably seated in a dimly illuminated, electrically shielded room. They were given written and verbal instructions along with examples on cards. They were recommended and reminded before the beginning of each block to pay attention to the cue, as this would help them decide whether the probe item reappeared. Participants held the mouse with their right hand and were advised to respond as quickly and accu-

rately as possible while maintaining their gaze on the fixation point throughout the trial. They were also asked to blink as little as possible, preferably after they responded, and to try to remain still during task performance. On practice trials, participants received verbal feedback from the experimenter and visual feedback (correct, incorrect, no response) on the screen after each trial, whereas on experimental trials, participants received feedback about the number of correct responses every 16 trials and at the end of each block. Breaks between blocks were self-paced. All participants were monitored throughout the task via a camera to ensure that they were engaged in the task and that they were not moving or blinking excessively during the test blocks. All participants but a child completed all eight test blocks, whereas one child completed six blocks, three pre-cue and three retro-cue blocks, because of fatigue and loss of interest to the task.

EEG Recording and Data Processing

EEG was recorded continuously from 19 sites according to the International 10–20 system, using a NuAmp (Neuroscan, Inc., El Paso, TX) amplifier and Ag/AgCl electrodes mounted on an elastic cap (Easy Cap, Electro-Cap, Inc., Eaton, OH). EEG data were stored and processed using the NeuroScan 4.3 software. The montage included four midline scalp sites (Fz, FCz, Cz, Pz) and five scalp sites over each hemisphere (F3/F4, C3/C4, P3/P4, PO7/PO8, O1/O2). The horizontal EOG was recorded bipolarly with electrodes placed on the outer canthi of both eyes, and the vertical EOG was measured with one electrode placed below the right eye. Additional electrodes were used as ground and reference sites. The electrode placed at AFz on the midline served as the ground. Electrode impedances were kept below 5 k Ω . The ongoing brain activity at all scalp sites was sampled every 1 msec (1000 Hz analogue-to-digital sampling rate) and filtered with a band pass of 0.50–70 Hz. The EEG was referenced on-line to the FCz electrode and then rereferenced off-line to the algebraic average of the left and the right mastoids.

The EEG data were then filtered off-line with a low-pass filter of 40 Hz to exclude high-frequency noise. Bipolar EOG signals were derived by computing the difference between the voltages at electrodes placed to the side of the left and right eyes (horizontal EOG) and between F4 and below the right eye (vertical EOG). The continuous EEG was further processed to segment ERPs for each stimulus type (i.e., pre-cue, retro-cue). Epochs started 100 msec before stimulus onset and ended 600 msec after stimulus onset. ERP amplitude values were baseline-corrected relative to a -100 to 50 msec stimulus interval. Artifacts were removed using a two-step protocol. First, EOG deflections exceeding ± 50 μ V for adults and ± 100 μ V for children as well as any other artifacts in all other scalp sites exceeding ± 100 μ V for adults and ± 150 μ V for children were automatically rejected. The thresholds for each age group were chosen based on previous ERP

parameters used with adults (cf. Murray et al., 2011) and with children (cf. Melinder, Gredeback, Westerlund, & Nelson, 2010). Second, three researchers visually inspected all epochs for any residual artifacts, which were all manually eliminated, an additional check that was especially important for lateralized eye movements, as these may capture overt rather than covert orienting. This two-step artifact rejection procedure resulted in retaining approximately 82% of overall trials for adults and 85% of overall trials for children. Only ERPs from artifact-free and trials with correct behavioral responses were included in the analyses. To maintain an acceptable signal-to-noise ratio, we set the accepted lower number of trials in each trial type condition (pre-cue, retro-cue) per participant to 20 trials, again in agreement with previous adult work (e.g., Nobre et al., 2008), and on average retained 70 trials per condition for adults and 65 trials per condition for children.

ERP Analyses

The aim of this experiment was to investigate whether the orienting of attention internally to mental representations held in VSTM (retro-cue trials) elicits well-established lateralized components that have been observed in tasks focused on detection and discrimination of incoming stimuli, and the extent to which these neural processes, if any, resemble those observed in VSTM encoding (pre-cue trials). For this reason, the ERP analyses focused on epochs locked to cues presented before VSTM encoding (pre-cues) and during maintenance (retro-cues). Pre-cue and retro-cue ERP conditions were derived by averaging the cue-locked epochs for pre-cue and retro-cue trials, respectively. Because in this experiment we targeted known preparatory components such as EDAN, ADAN, and LDAP, we investigated lateralized neural activity relative to the direction of the cue. Epochs from leftward and rightward cue trials were combined with an averaging procedure that preserved the spatial location of the electrode relative to the direction of the cue (i.e., contralateral or ipsilateral). EDAN, ADAN, and LDAP were then quantified as the mean voltage difference between contralateral and ipsilateral sites. On the basis of previous findings, EDAN was expected to occur and therefore measured at posterior electrodes, P3/4, PO7/8, and O1/2 (e.g., Praamstra & Kourtis, 2010; McDonald & Green, 2008; Jongen, Smulders, & Van der Heiden, 2007; Van der Stigchel, Heslenfeld, & Theeuwes, 2006; Hopf & Mangun, 2000; Harter et al., 1989). Given the results of Harter et al. (1989) with children, EDAN was also measured at central electrodes, C3/4; ADAN was measured at frontal and central electrodes, F3/4 and C3/4 (e.g., Jongen et al., 2007; Van der Stigchel et al., 2006; Eimer, Van Velzen, & Driver, 2002; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000); and LDAP was measured at posterior electrodes, P3/4, PO7/8, and O1/2 (e.g., Jongen et al., 2007; Harter et al., 1989). Although LDAP has been tradi-

tionally reported in time windows that extend beyond 600 msec (e.g., Murray et al., 2011; Seiss, Driver, & Eimer, 2009; Hopf & Mangun, 2000), we segmented smaller ERP epochs to 600 msec poststimulus onset to limit trial loss because of blinks, especially for children, and we note that this is also equivalent to the procedure used by Jongen et al. (2007) and Harter et al. (1989). We examined the presence of LDAP only for pre-cues as there was no lateralized upcoming target for selection following retro-cues in this experiment. Two-tailed paired sample *t* tests on each electrode pair were conducted on the mean voltage difference of each component separately for pre-cues and retro-cues.

Statistical Design, Statistical Power, and Behavioral Analyses

Separate 2 (Block: pre-cue vs. retro-cue) \times 2 (Trial Type: cued vs. neutral) \times 2 (Age Group: adults vs. children) repeated-measures ANOVA were performed on d' , K , and median RT scores. d' is a sensitive discrimination measure that reflects the degree to which participants accurately report the presence or absence of the probe in the preceding array. d' was calculated using the formula: $d' = z(\text{hit rate}) - z(\text{false alarm rate})$. K is a memory capacity measure that reflects the number of stored items in memory (Cowan, 2001; Pashler, 1988). K was calculated using the formula: $K = S(\text{set size of the initial array}) \times (\text{hit rate} - \text{false alarm rate})$. Extreme scores (e.g., perfect hit rate) in both calculations were adjusted using the formula $1 - (1/2N)$ as recommended by Macmillan and Creelman (2005) where N = the number of total trials in a condition. RTs were computed for probe-present trials and for correct responses only because incorrect responses and absent trials maybe influenced by multiple nonattentional processes (as discussed in Griffin & Nobre, 2003). Significant findings were subsequently followed by Bonferroni-corrected analyses of simple main effects. Difference scores were also calculated to assess the size of cueing effects in accuracy and latency. Finally, we explored functional links between electrophysiological activity and behavioral performance in children, via Spearman's rho correlations and split-half paired-sample *t* tests on high- and low-memory capacity groups separately.

To ensure that our sample sizes for both children and adults afforded sufficient statistical power, we carried out power analyses using G*Power 3 (Faul, Erdfelder, Lang, & Buchner, 2007). We calculated effect sizes from the most influential adult ERP studies investigating our target ERP components (e.g., Dell'Acqua et al., 2010; Kuo et al., 2009). The analysis revealed that, even taking the lowest calculated effect size from these studies ($d = 0.81$), we had adequate statistical power to detect significant lateralized differences for our group of adults ($N = 14$, power = 0.79) and children ($N = 17$, power = 0.88). In addition, our study also investigated the role of individual differences in our sample of children. For that analysis, we

had a power of 0.60 to detect a significant correlation, with a large effect size.

RESULTS

Behavioral Results: Developmental Differences across Age Groups

d' , K , and median RT scores are reported in Table 1. As d' and K analyses converged, for brevity here we report statistics for K alone. There were significant main effects of Age Group, $F(1, 29) = 20.40, p < .001$, block, $F(1, 29) = 7.51, p = .01$, and Trial Type, $F(1, 29) = 79.94, p < .001$, and a significant interaction of Block \times Trial Type, $F(1, 29) = 37.41, p < .001$. There were interaction effects of Age Group \times Block, $F(1, 29) = 57.49, p = .026$, and Age Group \times Block \times Trial Type, $F(1, 29) = 7.91, p = .009$. Analyses of simple main effects for the latter showed that the interaction was driven by the children benefiting more from cues presented before encoding compared with those presented during maintenance ($p < .001$), although both groups benefited from cues across blocks ($ps < .01$). Adults performed equally well across the two blocks ($p = .18$). These results were supported by a difference-scores analysis that investigated cueing benefits independently of baseline differences on neutral trials, revealing an interaction between Age Group \times Cue Benefit, $F(1, 29) = 7.91, p = .009$, driven by bigger benefits drawn from pre-cues compared with retro-cues for children ($M = 1.54$ and $M = .61$) than for adults ($M = 1.17$ and $M = .83$; see Figure 2).

The analysis on median RTs to probes accurately reported as present in the memory array showed significant main effects of Block, $F(1, 29) = 5.91, p = .02$, Trial Type, $F(1, 29) = 53.15, p < .001$, and Age Group, $F(1, 29) =$

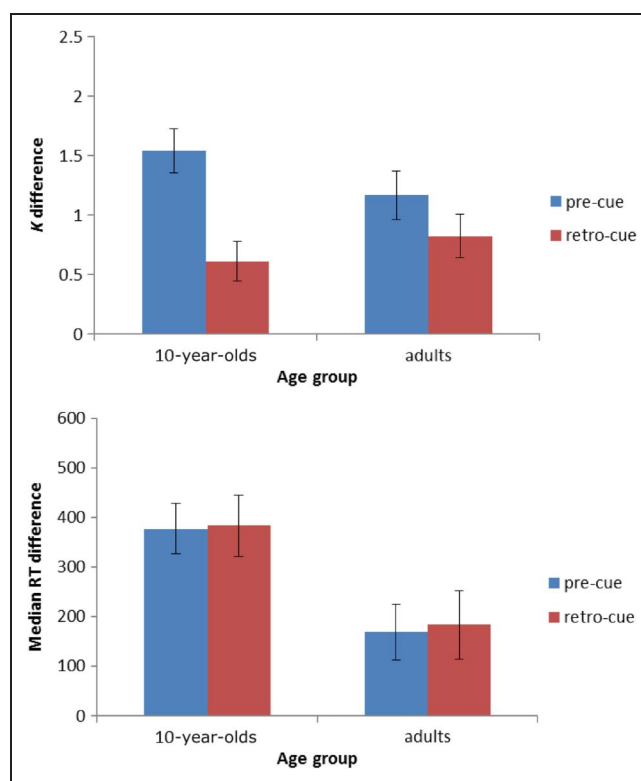


Figure 2. K and median RT difference scores from neutral baseline, comparing pre-cue and retro-cue blocks, for 10-year-olds and adults. Error bars represent SEMs.

39.51, $p < .001$, as well as significant interactions of Age Group \times Block, $F(1, 29) = 9.87, p = .004$, and Age Group \times Trial type, $F(1, 29) = 7.10, p = .01$. Analyses of simple main effects for the Age Group \times Block interaction showed that it was driven by children performing faster

Table 1. Mean d' , K , and Median RTs for Pre-cue, Retro-cue, and Neutral-cue Trials for Children and Adults

	Pre-cue Block		Retro-cue Block	
	Cued	Neutral	Cued	Neutral
d'				
10-year-olds	3.11 (0.25)	1.14 (0.16)	1.79 (0.21)	1.19 (0.18)
Adults	4.22 (0.28)	2.10 (0.18)	3.50 (0.23)	2.26 (0.20)
K				
10-year-olds	3.10 (0.20)	1.56 (0.17)	2.25 (0.20)	1.63 (0.20)
Adults	3.83 (0.22)	2.66 (0.19)	3.62 (0.22)	2.80 (0.21)
Median RT (msec)				
10-year-olds	838.71 (45.81)	1216.35 (54.88)	919.68 (57.05)	1303.18 (62.07)
Adults	557.36 (50.48)	727.00 (60.47)	539.46 (62.87)	723.50 (68.40)

SEMs are reported in brackets.

in the pre-cue than in the retro-cue block ($p < .001$), whereas adults did not differ in speed across the two blocks ($p = .64$). In addition, simple main effects for the Age Group \times Trial Type interaction revealed that the interaction was driven by a smaller RT benefit drawn from cues by adults ($M = 548.41$ and $M = 725.25$ for cued and neutral trials, respectively, $p = .004$) than children ($M = 879.19$ and $M = 1259.77$ for cued and neutral trials, respectively, $p < .001$). A subsequent difference-scores analysis was carried out to interpret the interaction independently of baseline differences on neutral trials and taking overall slowing in RT into account by treating RT differences as proportions of neutral RTs [(neutral - cued)/neutral]. Neither the interaction of Age Group \times Cue Benefit nor the main effect of Age Group on scaled RTs remained significant ($p = .32$ and $p = .47$, respectively), thus suggesting that the larger RT benefits in children depended on overall slowing in baseline responses by the children.

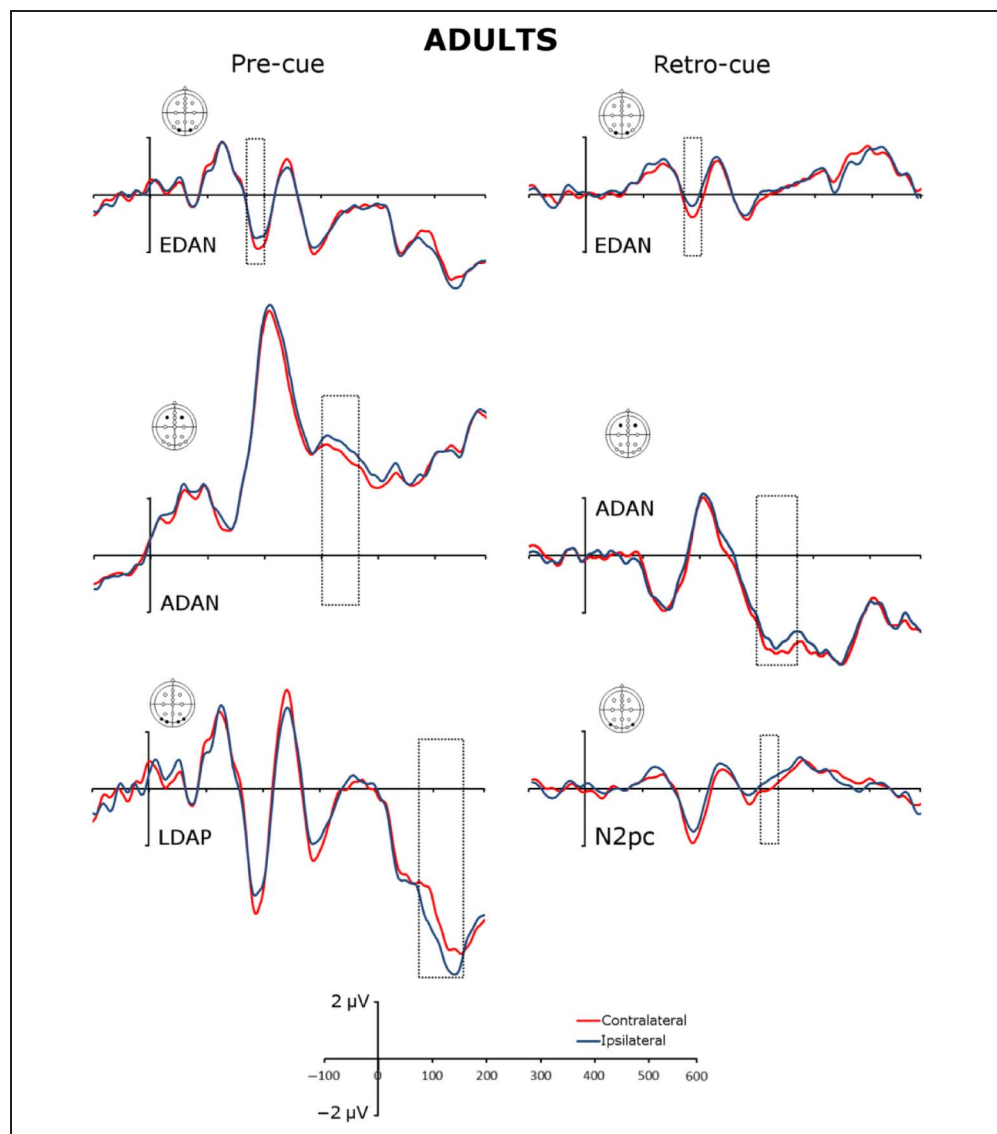
ERP Results

Because of the difficulties inherent in comparing directly electrophysiological data across age groups (e.g., differences depending on scalp thickness and other anatomical, rather than functional differences; see Scerif, Kotsoni, & Casey, 2006, for a discussion; as well as potential topographical and latency differences, e.g., Gazzaley et al., 2008; Mueller, Brehmer, Von Oertzen, Li, & Lindenberger, 2008), we first analyzed spatial biases at the neural level in adults separately from children and then followed with a comparison.

Adults

As predicted, EDAN, ADAN, and an LDAP-like component were observed for pre-cues (Figure 3). There was a significant enhanced negativity contralateral to the direction of the cue between 180 and 200 msec at O1/2

Figure 3. Grand-averaged waveforms elicited by pre-cues and retro-cues in adults. Red lines indicate neural activity contralateral to the side directed by the cue and blue lines indicate neural activity ipsilateral to the side directed by the cue. Positive voltage is plotted upwards. The montage used for the experiment and the electrode sides that were found significant for each component are shown next to each ERP waveform panel. Boxes highlight the time windows during which the mean voltage difference of each component was found significant.



sites, $t(13) = -2.64, p = .02$, signifying EDAN; followed by a significant enhanced negativity contralateral to the direction of the cue between 300 and 370 msec at F3/4 sites, $t(13) = -2.34, p = .036$, signifying ADAN. Finally, a significant enhanced positivity contralateral to the direction of the cue between 480 and 560 msec at PO7/8 and O1/2, $F(1, 13) = 9.29, p = .009$, was observed, signifying an LDAP-like component.

For retro-cues, both the EDAN and the ADAN were observed indicating similar neural activity across pre-cues and retro-cue blocks (Figure 3). As with pre-cues, there was a significant enhanced negativity contralateral to the direction of the cue between 180 and 200 msec at O1/2 sites, $t(13) = -2.76, p = .016$, indexing EDAN; followed by a significant enhanced negativity contralateral to the direction of the cue between 300 and 370 msec at F3/4 sites, $t(13) = -2.12, p = .05$, signifying ADAN. Unexpectedly, with retro-cues a second later negativity contralateral to the direction of the cue reached significance at posterior sites (PO7/8) at 310–330 msec, $t(13) = -2.32, p = .038$. This second posterior contralateral negativity resembled the N2pc component that has been linked to visual search and attentional selection activity both in service of perception and VSTM (e.g., Dell’Acqua et al., 2010; Kuo et al., 2009; Eimer, 1996) and suggested recruitment of additional parietal-occipital sites when orienting attention to representations held in VSTM. As already explained in the ERP analyses section, LDAP was not tested for retro-cues.

Children

The statistical analyses on the children’s ERP amplitudes showed a different pattern of results compared with adults, both in terms of topography of the effects and their timing (Figure 4). For pre-cues, there was a significant enhanced negativity contralateral to the direction of the cue between 180 and 200 msec at C3/4 sites, $t(16) = -2.32, p = .034$, signifying EDAN at central sites (cf. Harter et al., 1989) rather than at posterior sites. In contrast, there was only a trend for significance for an enhanced negativity contralateral to the direction of the cue between 180 and 200 msec at PO7/8 sites, $t(16) = -1.90, p = .075$, indexing a weak EDAN at posterior sites. Also, a significant enhanced positivity contralateral to the direction of the cue was observed between 540 and 600 msec at PO7/8 and O1/2, $F(1, 16) = 5.38, p = .034$, signifying an LDAP-like component. No significant ADAN was observed in children at the group level, $t(16) = -1.03, p = .32$, although we report on significant individual differences for this component in the upcoming section.

For retro-cues, there was only a trend toward significance for an enhanced negativity contralateral to the direction of the cue between 180 and 200 msec at PO7/8 sites, $t(16) = -1.89, p = .077$, reflecting a weak EDAN at posterior sites similar to pre-cues (Figure 4). In contrast to

the pre-cue condition, no significant EDAN was observed at central sites, $t(16) = -1.04, p = .32$. Like in adults, with retro-cues a second later negativity was observed contralateral to the direction of the cue between 280 and 320 msec at posterior sites (PO7/8) that reached significance, $t(16) = -2.24, p = .04$. Similarly to adults, this contralateral negativity resembled the N2pc component and suggested the recruitment of additional parietal-occipital areas when orienting attention to mental representations held in VSTM in children as well. However, like in their pre-cue condition ERPs, ADAN did not emerge at the group level for the children in the retro-cue condition, $t(16) = -1.17, p = .26$. As with adults, LDAP was not tested for retro-cues.

Developmental Comparison for EDAN and ADAN

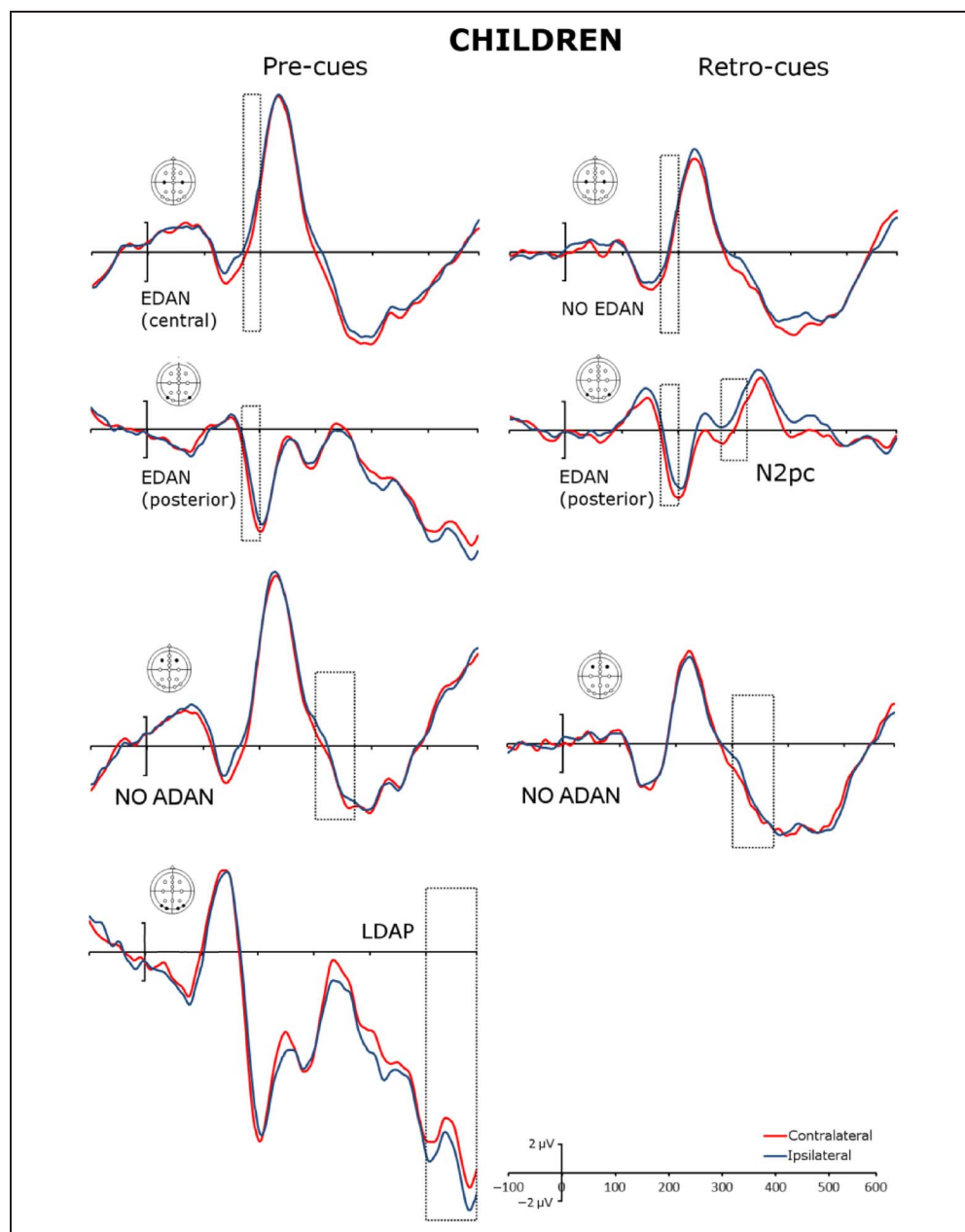
We compared directly adults and children’s ERP amplitudes for the two lateralized components that were found in adults but not reliably so in children, that is, EDAN and ADAN, by computing difference scores between ipsilateral and contralateral waveforms. There were no statistically significant age-related effects on the mean amplitude of either EDAN, $t(29) = .44, p = .66$ and $t(29) = .75, p = .46$ for pre-cue and retro-cue, respectively, or ADAN, $t(29) = .28, p = .78$ and $t(29) = .41, p = .68$ for pre-cue and retro-cue, respectively. This remained the case even after scaling these difference scores with multiple accepted normalization procedures (all $ps > .05$). We attribute this finding to the large variability observed in children’s (EDAN: $SD = 1.74$ for pre-cue and $SD = 1.91$ for retro-cue; ADAN: $SD = 1.97$ for pre-cue and $SD = 1.86$ for retro-cue) compared with adults’ data (EDAN: $SD = .40$ for pre-cue and $SD = .51$ for retro-cue; ADAN: $SD = .54$ for pre-cue and $SD = .55$ for retro-cue). This further justified our third main goal: to investigate whether null effects at the level of the group depended on individual differences in the sample of children (see next section).

Electrophysiological Predictors of VSTM Capacity in Children

Our next goal was to examine whether children’s ability to orient attention related to their VSTM capacity. For this reason, we carried out Spearman’s rho correlation analyses between the neural activity elicited in children, in the time windows and at scalp sites where EDAN and ADAN were observed in adults, and the difference scores (cued-neutral) in K . This allowed us to investigate whether the magnitude of “adult-like” neural activity of attentional control in children related to variation in VSTM capacity. Figure 5 plots these individual scores as a function of children’s memory capacity.

Results showed that individual differences in the magnitude of lateralized differences within these time windows correlated with individual differences in behavior.

Figure 4. Grand-averaged waveforms elicited by pre-cues and retro-cues in children. Red lines indicate neural activity contralateral to the side directed by the cue and blue lines indicate neural activity ipsilateral to the side directed by the cue. Positive voltage is plotted upwards. The montage used for the experiment and the electrode sides that were found significant for each component are shown next to each ERP waveform panel. Boxes highlight the time windows during which the mean voltage difference of each component was found significant.



Specifically, EDAN in the pre-cue block, measured at O1/2 at 180–200 msec, and ADAN in the pre-cue block, measured at F3/4 at 300–370 msec, correlated with K pre-cue benefit, $r(15) = .50, p = .02$ and $r(15) = .47, p = .028$, respectively. We then complemented these analyses by performing median-split analyses and dividing children into high- and low-capacity groups (on the basis of K) and carrying out paired-sample t tests between contralateral and ipsilateral ERP amplitudes to explore the presence of EDAN and ADAN in each capacity group separately. Splitting the children into those who showed a large versus small cue benefit following pre-cues in terms of K revealed a significant enhanced negativity contralateral to the direction of the cue between 180 and 200 msec at O1/2 sites, $t(8) = -2.43, p = .04$, that is, EDAN, for the large cue

benefit group. In contrast, there was no EDAN in the small cue benefit group, $t(7) = .63, p = .55$. Splitting the children into high versus low pre-cue K capacity groups revealed a significant enhanced negativity contralateral to the direction of the cue between 300 and 370 msec at F3/4 sites, $t(7) = -2.36, p = .05$, signifying ADAN for the high-capacity group. In contrast, there was no ADAN in the low-capacity group, $t(8) = -.09, p = .93$. Finally, there were no reliable correlations between ERPs for retro-cues and capacity measures.

DISCUSSION

This study revealed that the processes of orienting attention in anticipation of perceptual input and to

representations held in memory are achieved through different temporal dynamics in childhood, whereas they align in adulthood. All participants benefited from cues before encoding and during maintenance, corroborating the suggestion that prospective and retrospective orienting modulate VSTM in adulthood (Makovski, Sussman, & Jiang, 2008; Sligte, Scholte, & Lamme, 2008; Griffin & Nobre, 2003; Landman, Spekreijse, & Lamme, 2003; Schmidt et al., 2002) and in childhood (Shimi et al., 2013; Astle et al., 2012). However, the underlying pattern of neural activity differed across age groups. Adults elicited EDAN, ADAN, and LDAP during prospective orienting and EDAN and ADAN during retrospective orienting. Children elicited reliably only EDAN and LDAP during prospective orienting. Furthermore, EDAN's spatial distribution and LDAP's latency differed compared with the adults' components. Following retro-cues, children's EDAN only reached a trend, and no significant ADAN was found in conjunction with either prospective or retrospective orienting. An N2pc was observed during both children's and adults' retrospective orienting but differed in latency across age groups. Finally, individual differences in the extent to which neural markers of attentional orienting were "adult-like" related to variation in VSTM capacity in children.

The finding of similar neural modulations for adults across prospective and retrospective orienting suggests that biases to perceptual input and to internal representations in adulthood share a sequence of neural markers, each reflecting a different processing stage. In both orient-

ing conditions we observed EDAN, indicating the decoding of cue meaning and the subsequent initiation of orienting. ADAN followed, indicating attentional orienting via top-down control in both conditions. The two conditions were then differentiated: during prospective orienting, LDAP followed, indicating lateralized preparatory activity of visual areas for processing the upcoming item at the selected location. In contrast, during retrospective orienting, we observed an N2pc, indicating search of the target item within memory and its selection for maintenance.

The adult findings during prospective orienting are in line with those from a study that identified these preparatory markers (EDAN, ADAN, and LDAP) during selective encoding into VSTM (Murray et al., 2011) and therefore extend previous findings relating these markers with perceptual biases (Jongen et al., 2007; Hopf & Mangun, 2000; Nobre et al., 2000; Harter et al., 1989) to the memory domain. Focusing on attentional orienting within VSTM, we revealed for the first time the involvement of EDAN, ADAN, and N2pc in the selective maintenance of information in VSTM in adults. Many studies have targeted the cognitive mechanisms through which cues during maintenance enhance internal representations and facilitate memory performance (Astle, Summerfield, Griffin, & Nobre, 2011; Makovski & Jiang, 2008; Makovski et al., 2008; Lepsien & Nobre, 2007; Matsukura, Luck, & Vecera, 2007). However, none has examined whether retrospective attentional shifts are characterized by conventional lateralized neural markers that index cognitive processes such as the decoding of the cue and the

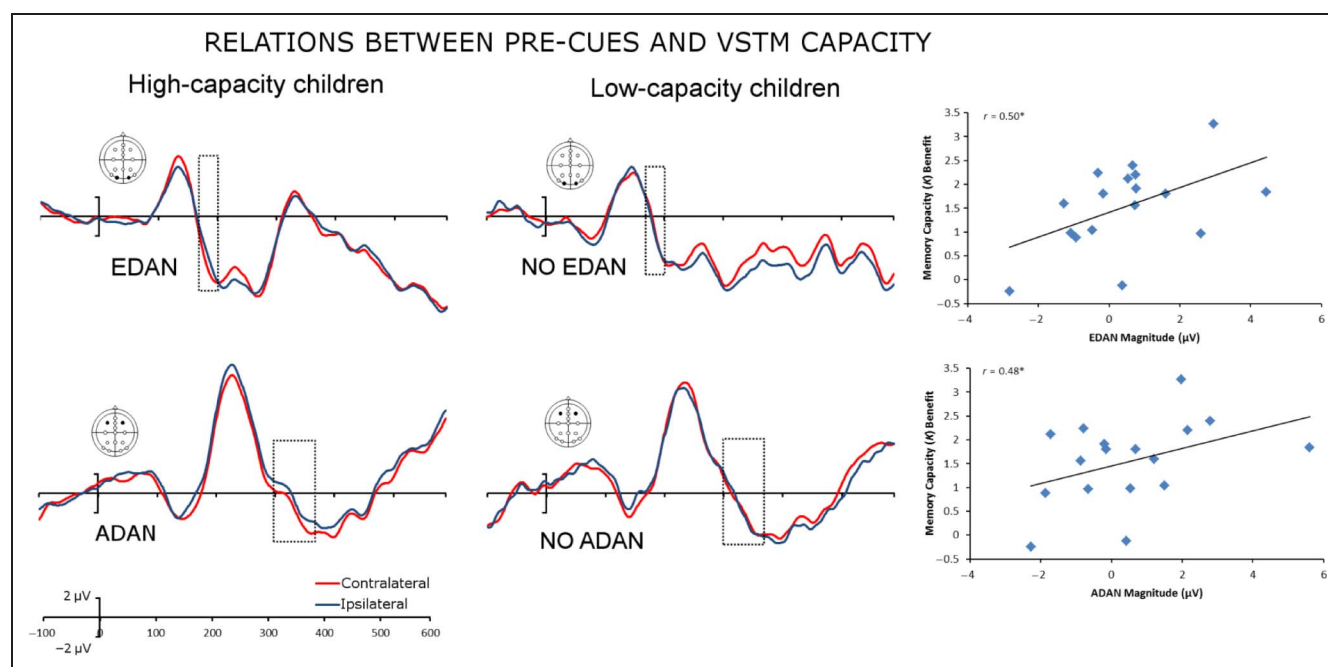


Figure 5. Grand-averaged waveforms for EDAN (on top) and ADAN (on bottom) elicited by pre-cues and divided between high- and low-memory capacity children. Red lines indicate neural activity contralateral to the side directed by the cue, and blue lines indicate neural activity ipsilateral to the side directed by the cue. Positive voltage is plotted upwards. Correlations between the ERP magnitudes (EDAN on top row and ADAN on the bottom row) and benefit in VSTM capacity measured with K are shown next to the relevant ERP waveforms.

subsequent initiation of the attentional orienting (EDAN), top-down attentional control (ADAN), and search through attentional templates (N2pc).

The N2pc has been associated with visual search and spatial selection of targets among distractors in incoming percepts (Hickey, Di Lollo, & McDonald, 2009; Kiss, Van Velzen, & Eimer, 2008; Hopf et al., 2000; Luck, Girelli, McDermott, & Ford, 1997; Eimer, 1996; Luck & Hillyard, 1994). More recently, it has been identified in the search and detection of targets held in VSTM (Dell'Acqua et al., 2010; Kuo et al., 2009). Obtaining an N2pc here suggests that retrospective orienting employs additional processes besides cue processing and directing attention, such as searching and spatially selecting the critical item from the memory array for later recognition (Kuo et al., 2012). Overall, adult findings here corroborate the suggestion that the electrophysiological correlates of the processes underlying pre-cues and retro-cues are characterized by both similarities and differences (Griffin & Nobre, 2003). The novelty is that the conventional lateralized markers of attentional orienting and the N2pc provide a medium for conceptualizing how these two processes may differ by identifying the specific cognitive steps needed to bias incoming input and maintain information internally.

In contrast to the adult findings, children's results across prospective and retrospective orienting suggest more marked differences in how biases to perceptual input and to internal representations dissociate: prospective orienting in children elicited a significant central EDAN indicating the decoding of the cue meaning, whereas no such neural activation in central areas was found in retrospective orienting. There was a trend toward a posterior EDAN in both orienting conditions, possibly implying the presence of a developing adult-like EDAN in prospective and retrospective orienting in VSTM, as it shared the typical spatiotemporal characteristics reported for this component in adult perceptual studies (e.g., McDonald & Green, 2008; Van der Stigchel et al., 2006; Nobre et al., 2000). Yet, in children, these two adult-like posterior components did not reach statistical significance at the group level, and neither did ADAN. EDAN in prospective orienting was followed by LDAP indicating preparatory activity of visual areas for processing the upcoming stimulus at the selected location. In contrast, during retrospective orienting, we observed an N2pc indicating the visual search and the selection of the item to be maintained.

Children's differences across orienting conditions point to differential processing of the cue during prospective and retrospective orienting. For example, the fact that EDAN was reliably present with pre-cues but not with retro-cues suggests that processing of the cue before encoding and during maintenance follows a different developmental trajectory before reaching the adult end-state: Our findings demonstrate that in children this activation is greater during prospective than retrospective orienting and is characterized by a central rather than a posterior topography. It has been proposed that symbolic

cues are overlearned stimuli in adulthood, with cue processing becoming automatic only gradually (Ristic, Friesen, & Kingstone, 2002; Eimer, 1997). It is possible that with development, this decoding process and the initiation of orienting shift from central to more posterior brain areas. In other cognitive domains, similar developmental shifts have been reported and interpreted as children progressing from effortful processing to more automatic mechanisms and with parietal areas becoming functionally specialized to a given process (Ansari, Garcia, Lucas, Hamon, & Dhital, 2005). It should be noted that the presence of a central rather than posterior EDAN is also consistent with the child data published by Harter et al. (1989), in which the EDAN in children also emerged over central sites.

Furthermore, the difference in neural substrates underlying prospective and retrospective orienting in children may well be related to how children implement orienting to support VSTM encoding and maintenance. Indeed, the evidence of a similarly reliable N2pc across age groups with retro-cues is in stark contrast with what we found for other components and suggests that children oriented their attention within VSTM in a different manner compared with adults. Children seem to have understood that they needed to search their memory to select an item from those encoded in VSTM and maintain it for later comparison (as indexed with N2pc), but this process was not paired with markers of cue processing (EDAN) and of recruiting top-down attentional control accordingly (ADAN) as it was in adults. Indeed, at the group level, there was no clear evidence of ADAN in children, either before encoding or during maintenance, which is consistent with prefrontal circuits being slow to develop from childhood into adulthood (e.g., Casey, Giedd, & Thomas, 2000) to allow for sophisticated voluntary attentional allocation. This finding is also consistent with Harter et al.'s (1989) result in which no ADAN was observed in service of incoming perceptual input and extends it by demonstrating its gradual development for selective encoding and maintenance in VSTM. The absence of ADAN might also justify the latency and duration difference of the N2pc across the age groups; that is, children elicited the N2pc earlier and for longer than adults, possibly because adults first directed their attention to a spatial location by recruiting frontal brain areas and then briefly selected the item to be remembered from the remaining array items by recruiting posterior brain areas, in agreement with how the frontoparietal network may be involved in selective attention and visual working memory in adults (Postle & D'Esposito, 1999; Corbetta, 1998).

Despite the limited presence of clear neural markers of orienting in VSTM in children at the group level, our second most prominent finding is the demonstration of an "adult-like" neural modulation before the encoding of perceptual input in VSTM by high-capacity children. Although children failed to demonstrate neural modulations as a

group, individual differences discriminated children of high versus low VSTM capacity. High-capacity children elicited both EDAN and ADAN, sharing the same spatio-temporal characteristics of the components observed in adults, whereas low-capacity children did not. For high-capacity children, this was the case during prospective orienting only, not for retrospective orienting, demonstrating again that both developmental and individual differences in childhood dissociate neural mechanisms of encoding and maintenance in VSTM. To our knowledge, this is the first study to show correlations between the mechanisms of attentional orienting and VSTM capacity in childhood, extending the plethora of adult findings (Fukuda & Vogel, 2009; Zanto & Gazzaley, 2009; Gazzaley et al., 2005; Todd & Marois, 2005; Vogel & Machizawa, 2004) to younger individuals.

In conclusion, we showed that investigating the development and individual differences of attentional orienting can throw light onto the neural mechanisms of attentional orienting in preparation for encoding and during maintenance in VSTM and onto the relations between attentional orienting and VSTM capacity.

Acknowledgments

A. S. was supported by a Bodossaki Foundation scholarship, St. Peter's College, University of Oxford, and by an A.G Leventis Foundation scholarship. G. S. was supported by a Scholar Award of the James S. McDonnell Foundation. This work was supported by the Wellcome Trust (grant WT082791MA to A. C. N.) and the National Institute for Health Research (NIHR) Oxford Biomedical Research Centre.

Reprint requests should be sent to Andria Shimi, Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford, OX1 3UD, United Kingdom, or via e-mail: andria.shimi@psy.ox.ac.uk.

Note

1. With the term prospective orienting, we refer to the ability to orient attention spatially to select and bias one item (out of multiple) for encoding. With the term retrospective orienting, we refer to the ability to orient attention spatially to information already encoded in VSTM to select and bias the maintenance of one (out of multiple) VSTM representations.

REFERENCES

- Ansari, D., Garcia, N., Lucas, E., Hamon, K., & Dhital, B. (2005). Neural correlates of symbolic number processing in children and adults. *NeuroReport*, *16*, 1769–1773.
- Astle, D. E., Nobre, A. C., & Scerif, G. (2012). Attentional control constrains visual short-term memory: Insights from developmental and individual differences. *The Quarterly Journal of Experimental Psychology*, *65*, 277–294.
- Astle, D. E., Scerif, G., Kuo, B.-C., & Nobre, A. C. (2009). Spatial selection of features within perceived and remembered objects. *Frontiers in Human Neuroscience*, *3*, 1–9.
- Astle, D. E., Summerfield, J., Griffin, I., & Nobre, A. C. (2011). Orienting attention to locations in mental representations. *Attention, Perception & Psychophysics*, *74*, 146–162.
- Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, *5*, 119–126.
- Awh, E., & Vogel, E. K. (2008). The bouncer in the brain. *Nature Neuroscience*, *11*, 5–6.
- Awh, E., Vogel, E. K., & Oh, S.-H. (2006). Interactions between attention and working memory. *Neuroscience*, *139*, 201–208.
- Casey, B. J., Giedd, J. N., & Thomas, K. M. (2000). Structural and functional brain development and its relation to cognitive development. *Biological Psychology*, *54*, 241–257.
- Casey, B. J., Tottenham, N., Liston, C., & Durston, S. (2005). Imaging the developing brain: What have we learned about cognitive development? *Trends in Cognitive Sciences*, *9*, 104–110.
- Chun, M. M., Golomb, J. D., & Turk-Browne, N. B. (2011). A taxonomy of external and internal attention. *Annual Review of Psychology*, *62*, 73–101.
- Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *Proceedings of the National Academy of Sciences, U.S.A.*, *95*, 831–838.
- Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *The Behavioral and Brain Sciences*, *24*, 87–185.
- Craik, F. I. M., & Bialystok, E. (2006). Cognition through the lifespan: Mechanisms of change. *Trends in Cognitive Sciences*, *10*, 131–138.
- Dell'Acqua, R., Sessa, P., Toffanin, P., Luria, R., & Jolicoeur, P. (2010). Orienting attention to objects in visual short-term memory. *Neuropsychologia*, *48*, 419–428.
- Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, *99*, 225–234.
- Eimer, M. (1997). Uninformative symbolic cues may bias visual-spatial attention: Behavioral and electrophysiological evidence. *Biological Psychology*, *46*, 67–71.
- Eimer, M., & Kiss, M. (2010). An electrophysiological measure of access to representations in visual working memory. *Psychophysiology*, *47*, 197–200.
- Eimer, M., Van Velzen, J., & Driver, J. (2002). Cross-modal interactions between audition, touch, and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *Journal of Cognitive Neuroscience*, *14*, 254–271.
- Paul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*, 175–191.
- Fukuda, K., & Vogel, E. K. (2009). Human variation in overriding attentional capture. *Journal of Neuroscience*, *29*, 8726–8733.
- Gazzaley, A. (2011). Influence of early attentional modulation on working memory. *Neuropsychologia*, *49*, 1410–1424.
- Gazzaley, A., Clapp, W., Kelley, J., McEvoy, K., Knight, R. T., & D'Esposito, M. (2008). Age-related top-down suppression deficit in the early stages of cortical visual memory processing. *Proceedings of the National Academy of Sciences, U.S.A.*, *105*, 13122–13126.
- Gazzaley, A., Cooney, J. W., Rissman, J., & D'Esposito, M. (2005). Top-down suppression deficit underlies working memory impairment in normal aging. *Nature Neuroscience*, *8*, 1298–1300.
- Gazzaley, A., & D'Esposito, M. (2007). Top-down modulation in visual working memory. In N. Osaka, R. H. Logie, & M. D'Esposito (Eds.), *The cognitive neuroscience of working memory* (pp. 197–212). Oxford: Oxford University Press.

- Gazzaley, A., & Nobre, A. C. (2011). Top-down modulation: Bridging selective attention and working memory. *Trends in Cognitive Sciences*, *16*, 129–135.
- Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience*, *15*, 1176–1194.
- Harter, R. M., Miller, S. L., Price, N. J., LaLonde, M. E., & Keyes, A. L. (1989). Neural processes involved in directing attention. *Journal of Cognitive Neuroscience*, *1*, 223–237.
- Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, *21*, 760–775.
- Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences, U.S.A.*, *95*, 781–787.
- Hopf, J. M., Luck, S. J., Girelli, M., Hagner, T., Mangun, G. R., Scheich, H., et al. (2000). Neural sources of focused attention in visual search. *Cerebral Cortex*, *10*, 1233–1241.
- Hopf, J. M., & Mangun, G. R. (2000). Shifting visual attention in space: An electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology*, *111*, 1241–1257.
- Huizinga, M., Dolan, C. V., & van der Molen, M. W. (2006). Age-related change in executive function: Developmental trends and a latent variable analysis. *Neuropsychologia*, *44*, 2017–2036.
- Jolles, D. D., Kleibeuker, S. W., Rombouts, S. A. R. B., & Crone, E. A. (2011). Developmental differences in prefrontal activation during working memory maintenance and manipulation for different memory loads. *Developmental Science*, *14*, 713–724.
- Jongen, E. M. M., Smulders, F. T. Y., & Van der Heiden, J. S. H. (2007). Lateralized ERP components related to spatial orienting: Discriminating the direction of attention from processing sensory aspects of the cue. *Psychophysiology*, *44*, 968–986.
- Jost, K., Bryck, R. L., Vogel, E. K., & Mayr, U. (2011). Are old adults just like low working memory young adults? Filtering efficiency and age differences in visual working memory. *Cerebral Cortex*, *21*, 1147–1154.
- Kiss, M., Van Velzen, J., & Eimer, M. (2008). The N2pc component and its links to attention shifts and spatially selective visual processing. *Psychophysiology*, *45*, 240–249.
- Kuo, B.-C., Rao, A., Lepsien, J., & Nobre, A. C. (2009). Searching for targets within the spatial layout of visual short-term memory. *Journal of Neuroscience*, *29*, 8032–8038.
- Kuo, B.-C., Stokes, M. G., & Nobre, A. C. (2012). Attention modulates maintenance of representations in visual short-term memory. *Journal of Cognitive Neuroscience*, *24*, 51–60.
- Kuo, B.-C., Yeh, Y.-Y., Chen, A. J.-W., & D’Esposito, M. (2011). Functional connectivity during top-down modulation of visual short-term memory representations. *Neuropsychologia*, *49*, 1589–1596.
- Landman, R., Spekreijse, H., & Lamme, V. A. F. (2003). Large capacity storage of integrated objects before change blindness. *Vision Research*, *43*, 149–164.
- Lepsien, J., & Nobre, A. C. (2007). Attentional modulation of object representations in working memory. *Cerebral Cortex*, *17*, 2072–2083.
- Luck, S. J., Girelli, M., McDermott, M. T., & Ford, M. A. (1997). Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. *Cognitive Psychology*, *33*, 64–87.
- Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 1000–1014.
- Luck, S. J., Woodman, G., & Vogel, E. (2000). Event-related potential studies of attention. *Trends in Cognitive Sciences*, *4*, 432–440.
- Macmillan, N. A., & Creelman, C. D. (2005). *Detection theory: A user’s guide* (2nd ed.). Mahwah, NJ: Erlbaum.
- Makovski, T., & Jiang, Y. V. (2008). Proactive interference from items previously stored in visual working memory. *Memory & Cognition*, *36*, 43–52.
- Makovski, T., Sussman, R., & Jiang, Y. V. (2008). Orienting attention in visual working memory reduces interference from memory probes. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*, 369–380.
- Matsukura, M., Luck, S. J., & Vecera, S. P. (2007). Attention effects during visual short-term memory maintenance: Protection or prioritization? *Perception & Psychophysics*, *69*, 1422–1434.
- McDonald, J. J., & Green, J. J. (2008). Isolating event-related potential components associated with voluntary control of visuo-spatial attention. *Brain Research*, *1227*, 96–109.
- Melinder, A., Gredeback, G., Westerlund, A., & Nelson, C. A. (2010). Brain activation during upright and inverted encoding of own- and other-age faces: ERP evidence for an own-age bias. *Developmental Science*, *13*, 588–598.
- Mueller, V., Brehmer, Y., Von Oertzen, T., Li, S.-C., & Lindenberger, U. (2008). Electrophysiological correlates of selective attention: A lifespan comparison. *BMC Neuroscience*, *9*, 1–21.
- Murray, A. M., Nobre, A. C., & Stokes, M. G. (2011). Markers of preparatory attention predict visual short-term memory performance. *Neuropsychologia*, *49*, 1458–1465.
- Nobre, A. C., Griffin, I. C., & Rao, A. (2008). Spatial attention can bias search in visual short-term memory. *Frontiers in Human Neuroscience*, *1*, 1–9.
- Nobre, A. C., Sebestyen, G. N., & Miniussi, C. (2000). The dynamics of shifting visuospatial attention revealed by event-related potentials. *Neuropsychologia*, *38*, 964–974.
- Pashler, H. (1988). Familiarity and visual change detection. *Perception & Psychophysics*, *44*, 369–378.
- Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, *139*, 23–38.
- Postle, B. R., Awh, E., Jonides, J., Smith, E. E., & D’Esposito, M. (2004). The where and how of attention-based rehearsal in spatial working memory. *Cognitive Brain Research*, *20*, 194–205.
- Postle, B. R., & D’Esposito, M. (1999). “What-then-where” in visual working memory: An event-related fMRI study. *Journal of Cognitive Neuroscience*, *11*, 585–597.
- Praamstra, P., & Kourtis, D. (2010). An early parietal ERP component of the frontoparietal system: EDAN not = N2pc. *Brain Research*, *1317*, 203–210.
- Ristic, J., Friesen, C. K., & Kingstone, A. (2002). Are eyes special? It depends on how you look at it. *Psychonomic Bulletin & Review*, *9*, 507–513.
- Scerif, G., Kotsoni, E., & Casey, B. J. (2006). The functional neuroimaging of development. In R. Cabeza & A. Kingstone (Eds.), *Functional neuroimaging of cognition* (pp. 351–378). Cambridge, MA: MIT Press.
- Schmidt, B. K., Vogel, E. K., Woodman, G. F., & Luck, S. J. (2002). Voluntary and automatic attentional control of visual working memory. *Perception & Psychophysics*, *64*, 754–763.
- Seiss, E., Driver, J., & Eimer, M. (2009). Effects of attentional filtering demands on preparatory ERPs elicited in a

- spatial cueing task. *Clinical Neurophysiology*, *120*, 1087–1095.
- Shimi, A., Nobre, A. C., Astle, D. E., & Scerif, G. (2013). Orienting attention within visual short-term memory: Development and mechanisms. *Child Development*, doi: 10.1111/cdev.12150.
- Sligo, I. G., Scholte, H. S., & Lamme, V. A. F. (2008). Are there multiple visual short-term memory stores? *PLoS ONE*, *3*, e1699.
- Todd, J. J., & Marois, R. (2005). Posterior parietal cortex activity predicts individual differences in visual short-term memory capacity. *Cognitive, Affective & Behavioral Neuroscience*, *5*, 144–155.
- Van der Stigchel, S., Heslenfeld, D. J., & Theeuwes, J. (2006). An ERP study of preparatory and inhibitory mechanisms in a cued saccade task. *Brain Research*, *1105*, 32–45.
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*, 748–751.
- Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature*, *438*, 500–503.
- Zanto, T. P., & Gazzaley, A. (2009). Neural suppression of irrelevant information underlies optimal working memory performance. *Journal of Neuroscience*, *29*, 3059–3066.