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# Distinct Neural Mechanisms of Individual and Developmental Differences in VSTM Capacity

**ABSTRACT:** Our ability to maintain visuo-spatial information increases gradually through childhood and is highly variable across individuals, although the cognitive and neural mechanisms underpinning these differences in capacity are unknown. We presented participants with arrays of to-be-remembered items containing two targets, four targets, or two targets and two distracters. The participants were divided into three groups: (i) high-capacity adults; (ii) low-capacity adults; and (iii) typically developing children. In addition to our behavioral methods we used electrophysiological scalp recordings to contrast the immature VSTM capacity of the children with the deficient VSTM capacity of the low-capacity adults. We also observed a relative negativity in the maintenance delay, over scalp contralateral to the original locations of the memoranda. For the low-capacity adults, this negativity was similarly modulated by target and distracter items, indicative of poor selectivity. This was not the case for the high-capacity adults; the response to memory arrays containing two target items and two distracters was equivalent to the response elicited by arrays containing only two target items. Importantly, the pattern of results in the children's ERP data was equivalent to that of the high-capacity adults, rather than to the performance-matched low-capacity adults. In short, despite their obvious differences in capacity, children are not specifically impaired at filtering out distractors, as characteristic of low-capacity adults. © 2013 Wiley Periodicals, Inc. Dev Psychobiol

**Keywords:** visual short-term memory; visual working memory; attention; top–down control; development; individual differences; event-related potentials

## INTRODUCTION

Many cognitive functions rely heavily on our ability to hold visual or spatial information in mind for brief periods of time. This ability is typically referred to as visual short-term memory (VSTM). This is particularly

true in childhood, with the ability of children to maintain information in mind for brief periods of time being a factor limiting their rate of learning (Bull, Espy, & Wiebe, 2008; Gathercole, Tiffany, Briscoe, & Thorn, 2005). For this reason, there has been a great deal of interest in the cognitive and neural mechanisms that underpin individual and developmental differences in VSTM capacity.

Differences in the number of items individuals can maintain in VSTM have been studied using a behavioural "capacity" index termed $K$ (e.g., Cowan, 2001; Vogel & Machizawa, 2004). In change-detection tasks, individuals view a briefly presented array and, after a delay in which they must maintain the array in mind, they are presented with a second array and have to judge whether any item has changed. $K$ is defined as the number of to-be-remembered items multiplied by

subjects' ability to detect a change in one of the items (hit rate − false alarm rate). The set size is varied across trials, and the asymptotic value of $K$ is given as a subject's capacity (Cowan, 2001).

The typical capacity of an adult is around three to four items (Cowan, 2001). However, there is a large degree of variability in capacity across adults of the same age (Awh & Vogel, 2008; Linke, Vicente-Grabovetsky, Mitchell, & Cusack, 2011). A number of recent studies have suggested that poor top–down control of attention might result in this apparent VSTM deficit: adults with low VSTM capacity perform poorly in tasks requiring them to resist attentional capture by irrelevant items (e.g., Fukuda & Vogel, 2009), and benefit to a greater extent than high-capacity individuals from stimulus properties that reduce the need for attentional control (e.g., Linke et al., 2011). Findings such as these have led some to argue that variability in VSTM capacity in adults stems primarily from an inability to use attentional control to select items to be stored and to suppress items to be ignored (Awh & Vogel, 2008). In short, adults with low VSTM might not have a lower *storage* capacity, but rather an impaired ability to use visual attention to select what ought to fill that capacity. The aim of this study was to explore the extent to which developmental differences may have the same underlying cause.

## Electrophysiological Measures of Capacity Differences in Adulthood

We made use of an electrophysiological marker that mirrors these individual differences in behavioral capacity to compare the influence of selective attention on storage capacity of adults and children. A lateralized sustained event-related potential, known as the contralateral delay activity (CDA) reflects the number of items an individual maintains from one side of a bilateral visual array (e.g., Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; Robitaille et al., 2010; Vogel & Machizawa, 2004). In adaptations of the change-detection task, participants are instructed to encode and maintain only items from one visual field according to a previously presented spatial cue, and to identify any changes that occur in items of the subsequent probe array on that side only. The CDA is a relative increase in negative voltage over lateral posterior electrodes, which develops and is sustained during the delay period. Importantly, the size of this contra-ipsilateral difference increases with VSTM load, and, like $K$, asymptotes at around three to four items (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). The CDA has been employed effectively to explore individual differences in VSTM capacity

(Vogel & Machizawa, 2004), with researchers arguing that it corresponds to $K$ because it too represents a direct measure of the number of items being maintained in VSTM (Fukuda, Awh, & Vogel, 2010).

In one particular study of adults using the CDA measure, arrays containing both target and distracter items were presented to subjects (Vogel et al., 2005; see also McCollough, Machizawa, & Vogel, 2007). Importantly, whilst both high- and low-capacity subjects showed an increasing CDA with increasing target items, the low-capacity group also showed an increasing CDA effect with the number of distracters. This was an important result for two reasons: (i) it supported the argument that the CDA indexes the number of items maintained—in the high-capacity subjects the CDA effect did not increase with the number of distracters, just with the number of targets; (ii) it implied that low-capacity subjects are less able to select efficiently the appropriate items from an array containing distracter items than are high-capacity adults (i.e., low-capacity adults hold representations of targets and distracters, whereas high-capacity adults are able to suppress distracters and maintain target stimuli only). In this case, the CDA directly reflects the number of items in VSTM, but testing whether the CDA increases with increasing targets or distracters can provide an indirect measure of the number of distractors also encoded into VSTM, due to poor top–down attentional selection. In short, this finding supported both the view that the CDA indexes the number of items maintained and the view that poor VSTM capacity stems from a failure of selection.

## Electrophysiological Measures of Capacity Differences in Childhood

In addition to differing across individuals of the same age, VSTM capacity differs greatly across individuals of different ages (see Astle & Scerif, 2011, for a review). Capacity estimates for children vary across studies. For example, 11-year olds have been reported to have a capacity of almost 4 (Riggs, Simpson, & Potts, 2006) or around 2 (Astle & Scerif, 2011; see also Cowan, Morey, AuBuchon, Zwilling, & Gilchrist, 2010; Cowan, AuBuchon, Gilchrist, Ricker, & Saults, 2011). Nevertheless, despite these discrepancies in absolute capacity, multiple studies converge on the gradual increase in $K$ from early childhood to adulthood.

Sander, Werkle-Bergner, and Lindenberger (2011) found significantly different patterns of CDA effects across children (aged 10–13 years old) and adults. Only adults showed a CDA effect that scaled with VSTM load. However, the authors found no significant differ-

ence in *K* scores across the groups, making this result difficult to interpret (one possibility is that adults were not provided with large enough set-sizes to demonstrate their superior VSTM capacity). This notwithstanding, Sander et al. demonstrated an important dissociation between the number of items maintained (K) and the CDA. As the adults maintained more items their CDA increased, as we would expect if the CDA indexed the number of items. However, this was not true of the children; like adults they certainly stored more items in the 4 than in the 2-target condition, but they did not show the significantly increased CDA effect that ought to mirror this. Sander et al. suggest that the CDA reflects the top–down control of items in VSTM, rather than the number of items stored per se, and that ultimately some form of failure of top–down control underpins poor VSTM performance in children.

Interestingly, this seems to contradict recent behavioural studies by Cowan et al. (2010, 2011). In these behavioral studies, children are shown arrays of different shapes in different colors to be remembered. Cowan et al. (2010) presented children and adults with a simple change-detection task in which they had to monitor items of a specific shape. The to-be-remembered shape was cued, and varying the relative validity of this cue enabled the researchers to test the subjects' ability to bias the storage of targets relative to distracters. Children displayed adult-like attentional control when the VSTM storage load was small, but at higher VSTM loads the children showed disproportionately poor attentional control. At a minimum, therefore, attentional control differences alone do not account for the capacity differences across children and adults.

The present study tested directly whether children, like low-capacity adults, suffer from an attention deficit, that is, a particular difficulty in ignoring distracters. We compared a group of high-capacity adults, low-capacity adults, and 10-year-old children. Importantly, the performance of the children and low-capacity adults was matched, with both groups displaying an equivalent mean VSTM capacity and performing equivalently well on our experimental VSTM task. It is important to note that this performance matching was somewhat different to that of Sander and colleagues. In the current experiment we used large set sizes for the adults, meaning that our LC adults had every opportunity to store more items but were unable to.

Our procedures enabled us to test directly, for the first time, whether individual and developmental differences in VSTM capacity stem from a common underlying mechanism related to attentional selection. We presented participants with arrays containing only targets (two or four items) or containing a mixed set of targets and distracters (two of each, as in McCollough

et al., 2007; Vogel et al., 2005), and examined the CDA effects across these conditions for each group. We predicted that the low-capacity adults would show poor attention selection and treat distracters like targets, and that this would be reflected in the CDA amplitudes (as in Vogel et al., 2005). Accordingly, this group should show a CDA effect on distracter-present trials resembling that on 4-target trials, but significantly larger than on 2-target trials. We predicted that for high-capacity adults distracter items would have no effect on CDA amplitudes (also as in Vogel et al., 2005). Accordingly, this group should show a CDA amplitude on distracter-present trials that is equivalent to that on 2-target trials, and significantly smaller than that on 4-target trials. Finally, we predicted that if developmental differences are underpinned by the same variation in attentional mechanisms that contribute to individual differences in adults, then the pattern of CDA effects in the children ought to align with that of the LC adults.

## METHODS

### Participants

Fifty-two subjects completed an EEG recording session and a subsequent session comprising a number of standardized short-term and working memory (STM and WM, respectively) assessments. Thirty-four of these participants were adults (mean age 20.5, SD 1.62 years, of which 30 were female), and 18 were children (mean age 10.3, SD 1.48, 8 were female). We used a subtest that measures VSTM capacity (the Dot Matrix task) from the Automated Working Memory Assessment in order to provide some indication of the standardized performance of these children on VSTM tasks (Alloway, Gathercole, Kirkwood & Elliot, 2008); the mean performance was 100, with a standard deviation of 15 standard points, suggesting that the VSTM ability of our children was typical for children of their age. The adults were subsequently split into two groups, using a median split, on the basis of their VSTM capacity (*K* estimates). We subsequently refer to the three groups as low-capacity adults (LC), high-capacity adults (HC), and Children. We also excluded one LC adult, two HC adults, and three children, because they had a number of bad channels around the sites that the CDA is usually maximal. The EEG/ERP analysis included 16 subjects in the LC group, 15 in the HC group, and 15 children. The study was approved by the ethical review panel at Royal Holloway, University of London. All subjects had normal or correct-to-normal vision. Adult subjects provided written informed consent, as did the parents of the children; the children themselves provided verbal assent. Each adult was paid £20 for participating in the study. The children were all recruited through the Royal Holloway Summer Science Camp.

### Behavioral Task

A trial schematic can be seen in Figure 1. A central fixation cross was present throughout each trial. On every trial
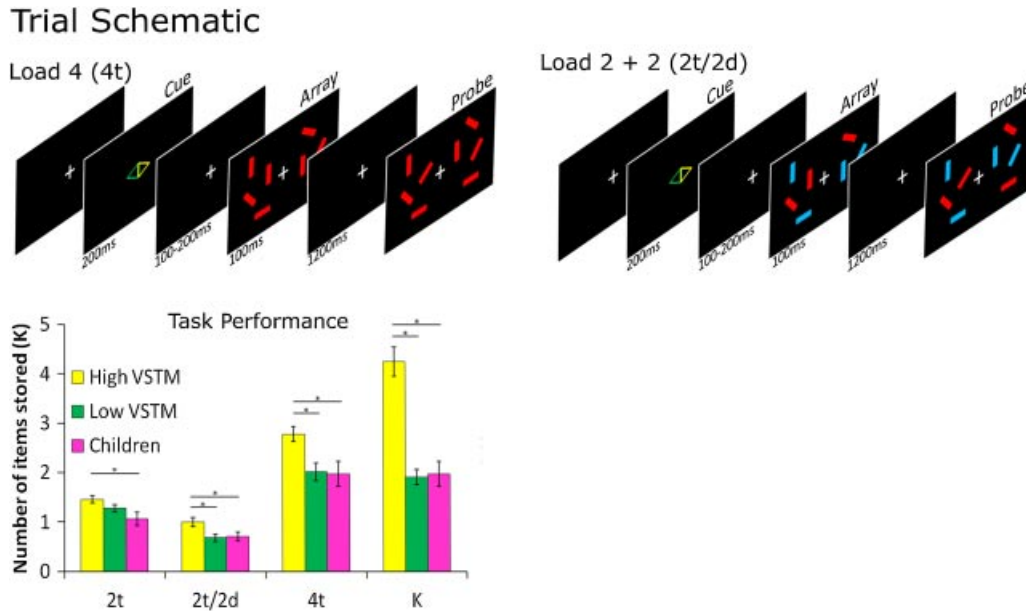
## Trial Schematic



**FIGURE 1**  The top two panels show trial schematics for a load 4-trial (left) and a load 2 plus 2 distracters trial (right). The bottom left panel shows performance across the three groups for each condition, as well as their VSTM capacity estimates (*K*). In each case the error bars show the standard error of the mean.

subjects were presented briefly with a directional cue at fixation. This was formed from a green triangle pointing to one hemifield and a yellow triangle pointing to the other hemifield, with each subject using a pre-designated cue color to orient their attention to one hemifield. A bilateral array of colored bars was then presented; subjects were instructed to remember the location and orientation of the items in the cued hemifield. These bars then disappeared for 1,200 ms, after which they reappeared in the same locations, in the form of a probe array. Subjects had to respond as to whether any of the bars in the cued hemifield had changed orientation. After subjects had responded the next trial started.

### Task Design

Timings for all events and intervals in trial sequences are provided in Figure 1. The design was modeled very closely on that of Vogel et al. (2005). Subjects were presented with a spatial cue for 200 ms, followed by a further interval of 100–200 ms. The array of bars was presented after this, for 200 ms, and there were always equal numbers of bars appearing in each hemifield, though not necessarily in the same location. The bars were colored either red or blue, with one color being designated targets and the other distracters. After this memory array there was a maintenance delay of 1,200 ms, followed by the probe array, presented until subjects made their response.

The spatial cue was made up of a composite of two colored triangles, each pointing to one hemifield. Subjects were assigned one color as their spatial cue, using that color to select the side of items to be remembered throughout the

entire experimental session. The color triangle that subjects used as a directional cue was counterbalanced across subjects, but always consistent throughout for any one subject. This is a change from the original design. Having a bidirectional colored cue, with the color corresponding to the cue being counterbalanced across subjects, equates the physical appearance of the cues between spatial conditions, and makes it easier to interpret contra-ipsilateral differences that we observe following the cue (see Murray, Nobre, & Stokes, 2011; Nobre, Sebestyen, & Miniussi, 2000). The colors used to designate targets and distracters were also counterbalanced across subjects, such that any target versus distracter comparison was not confounded by any perceptual differences at the group level. There were three different types of trial, those with two target bars in each hemifield (2T), four target bars in each hemifield (4T) and two targets and two distracters in each hemifield (2T2D). The bars were presented within two rectangular regions, one per hemifield (4° × 7.3°, and 3° from fixation). Each bar (.65° × .65°) was always presented at 0°, 45°, 90°, or 315° orientations. These aspects of the design were chosen in order to replicate the stimuli of Vogel et al. (2005). On half of all trials, at the onset of the probe array, one of the bars in the cued hemifield changed by 45°, this could be in either a clockwise or anti-clockwise direction. Subjects used their right hand to respond, using the index finger for change and their middle finger for no-change responses. The order of the trials was randomized. All adults performed 410 experimental trials, and the children performed an average of 263 experimental trials (minimum of 220 trials). Immediately prior to the experimental trials, all participants (adults and children) completed a block of

practice trials, which were identical in design to the experimental trials. Feedback was given on practice trials but not on experimental trials. Children were given more practice trials, and for some of the children we slowed the trial events down for the practice trials.

### K Estimates

We split the adults into two groups on the basis of a *K* estimate taken during a task very similar to that used during the EEG recording. This additional task was identical to the main experiment, but had a wider range of set sizes (2, 3, 4, 6, and 8 target items) and no distracters. Participants were presented with 20 trials of each set size (10 change and 10 no-change trials per set size); and the order of these trials was fully randomized. We took the *K* estimate for each subject as the peak in *K* across these different array sizes. We used this pre-task assessment to allocate the adult subjects to the two groups in the majority of cases. However, for four subjects (for whom we did not have a *K* estimate from this extra task because of a technical failure), we simply used their main task performance (as in Sander et al., 2011). We used these estimates to form two groups based on a median split; our two adult groups had a mean capacity of 4.25 ($\pm$1.14 SD) and 1.9 ($\pm$.63 SD) items, respectively. For the group of children we took their *K* estimate from their performance on the 4T condition in the task, giving them a mean capacity of 1.98 ($\pm$1.07 SD) items. A one-way ANOVA revealed that the these capacity differences across the groups were indeed significant [$F(2, 51) = 26.944$, $p < .001$, $d = 2.36$]. This difference was driven by a difference between the high and low capacity adults [$t(32) = 6.726$, $p < .001$, $d = 2.38$] and by a difference between high capacity adults and children [$t(33) = 5.608$, $p < .001$, $d = 1.95$], but there was no difference between the children and the low capacity adults [$t(33) = .094$, $p = .926$].

### EEG Acquisition and Pre-Processing

EEG data were acquired using a 64-channel Mark II Biosemi ActiveTwo system, sampled at 2,016 Hz. Additional electrodes were placed at the outer canthi of each eye and above and below the right eye; these were used to form bipolar HEOG and VEOG channels, respectively. Offline, the data were down-sampled to 300 Hz and re-referenced to the average of the left and right mastoid recordings and high-pass filtered at 1 Hz. To remove ocular-related artefacts, we used an Independent Component Analysis (ICA) approach. We split the data into 64 independent components, and correlated the time course of each with the HEOG and VEOG channels. Components highly correlated with either channel were removed. In the majority of cases, a single component reflected saccades and a separate single component reflected blinks. Components carrying ocular artifacts were then regressed from the original data. We then applied a low-pass 30 Hz filter and epoched the data from −200 to 1200 ms relative to the onset of the spatial cue. The recordings were baseline corrected from −200 to 0 ms, relative to the onset of the cue. The trials were averaged according to load and the side of the relevant target array. These averages included both correct and incorrect trials. Whilst it is usual practise to use only trials with correct responses (e.g., Murray et al., 2011), in this study, we are interested in the brain signals that differ between performance groups, therefore it is important not to discard the variance due to behavioral error. These measures were then combined using an averaging procedure that preserves the location of the electrode relative to the remembered hemifield of the screen (contralateral or ipsilateral, as in Vogel & Machizawa, 2004). All of these steps were performed using SPM8 (Wellcome Trust Centre for Neuroimaging, London). There was an average of 110 trials per condition for the adults, and 75 trials per condition for the children.

### ERP Analyses

Across the 46 subjects included in the ERP analysis, we compared the difference between contralateral and ipsilateral scalp recordings across different trials types and subject groups during the maintenance-related CDA (Murray et al., 2011; Vogel & Machizawa, 2004). In previous studies, researchers have chosen particular posterior pairs of electrodes, or a cluster of pairs, across which to look for the effect (Murray et al., 2011; Vogel & Machizawa, 2004). However, this approach could favour one group over another (i.e., the distribution of the CDA might differ across the groups). For this reason, we first carried out an orthogonal contrast in each group, including a number of posterior electrodes, to identify which electrodes best revealed any contralateral–ipsilateral differences in the maintenance delay for each particular group (as in Sander et al., 2011). We averaged across all three conditions, and identified which electrodes best showed a significant CDA effect. For the HC adults this was CP3/4, CP1/2, P1/2, P3/4, P5/6, P7/8, and 01/2; for the LC adults this was CP3/4, CP1/2, P1/2, P3/4, P5/6, P7/8, and PO3/4; for the Children this was CP3/4, CP5/6, P1/2, P5/6, and PO7/8. We then averaged across these electrodes for each group in order to look for differences in CDA across our conditions and group. We consider this to be the most conservative approach; any difference across the groups cannot be driven by a failure to capture the CDA maximally in any group.

The CDA was calculated by subtracting ipsilateral from contralateral voltages in the maintenance window, and comparing these across conditions (2T, 4T, and 2T2D). For consistency with previous comparisons performed by Vogel et al. (2005), we compared the CDA size on 2T2D trials, relative to that on 2T and relative to 4T trials. Finally, to explore the group differences in attentional filtering using the CDA measures, we also compared between groups the difference in CDA across the 2T and 2T2D trials (which should be large for LC adults but small for HC adults), and the differences in CDA across the 4T and 2T2D trials (which should be small for LC adults but large for HC adults).

## RESULTS

### Behavioral Results

***Task performance.*** We entered the *K* scores taken from the main experimental task to a mixed-effects

ANOVA, with the three memory array types (2T, 4T, and 2T2D) as a within-subject factor, and Group as a between-subject factor. These data can be seen in Figure 1. There was a significant two-way interaction [$F(4, 98) = 3.884$, $p = .006$]. We followed up this result by performing a one-way ANOVA on each condition. This was significant at the 2T condition [$F(2, 51) = 3.622$, $p = .034$, $d = .69$], the 2T2D condition [$F(2,51) = 3.801$, $p = .029$, $d = .72$] and the 4T condition [$F(2,51) = 4.179$, $p = .021$, $d = .78$]. For the 2T condition, this effect was driven by a difference between the HC adults and the Children [$t(33) = 2.412$, $p = .022$, $d = .84$], with there being no significant difference between the two adult groups [$t(32) = 1.366$, $p = .181$] or between then the LC adults and the Children [$t(33) = 1.482$, $p = .148$]. For the 2T2D condition, the HC adults out-performed both the Children [$t(33) = 2.139$, $p = .040$, $d = .74$] and the LC adults [$t(32) = 2.616$, $p = .013$, $d = .92$], but the LC adults did not differ significantly from the Children [$t(33) = .298$, $p = .768$]. For the 4T condition, the HC adults out-performed both the children [$t(33) = 2.426$, $p = .021$, $d = .84$], and the LC adults [$t(32) = 2.961$, $p = .006$, $d = 1.05$]; again, the children and LC adults did not differ significantly [$t(33) = .067$, $p = .947$]. This can be most clearly seen in Figure 1.

## ERP Results

***Contralateral Delay Activity (CDA).*** The corresponding waveforms can be seen in Figure 2, which shows contra and ipsilateral voltages across the three conditions for each group. They show that contralateral recordings were more negative than the ipsilateral recordings. We calculated the relative contra-ipsilateral difference during the maintenance delay, between 700 and 1,100 ms post-cue-onset, and defined this as our CDA effect in adults (as in Murray et al., 2011). We shifted the window by 100 ms for the children (800–1,200 ms), because our examination of the CDA plots (see Fig. 3) suggested that this slightly later window was more appropriate for capturing the CDA in this group. We started by attempting to replicate the within-group pattern of results shown by Vogel et al. (2005) by making their exact pair-wise comparisons, before comparing the groups with our own cross-group CDA comparison.

***CDA effects in high-capacity adults.*** We replicated the pattern shown by Vogel et al. (2005) in our HC adult group: the HC adults showed no significant difference between the size of the CDA on 2T2D trials relative to 2T trials [$t(14) = .284$, $p = .780$], but did relative to

4T trials [$t(14) = 2.149$, $p = .050$, $d = .63$].This pattern can be most clearly seen in Figure 3 (top panel). This implies that for the HC adults, distracters and targets do not have an equivalent effect on CDA amplitudes.

***CDA effects in low-capacity adults.*** We also replicated the pattern shown by Vogel et al. (2005) for the LC group: the CDA was significantly larger on 2T2D trials, relative to 2T trials [$t(15) = 3.137$, $p = .007$, $d = .91$], but there was no difference relative to 4T trials [$t(15) = 1.185$, $p = .254$]. This pattern can most clearly be seen in Figure 3 (middle panel). This implies that for the LC adults, distracters and targets have an equivalent effect on CDA amplitudes.

***CDA effects in children.*** Unlike the LC adults, the CDA on the 2T2D condition did not differ significantly from that on 2T trials [$t(14) = 1.279$, $p = .222$], although the difference between 2T2D and 4T trials did not reach significance either [$t(14) = 1.779$, $p = .097$]. Whilst the pattern is clearly not the same as for LC adults, we wanted to test more directly the pattern in CDA effects across the groups. The Children's CDA amplitudes can be seen in Figure 3 (bottom panel).

***Cross group CDA comparison.*** We wanted to compare directly the relative changes in CDA amplitude across the three conditions and the three groups. Before we did this we normalized the values within each group, enabling us to test for relative changes in the pattern of the CDA across the groups, without this being influenced by any potential main effect of group on the CDA amplitudes (McCarthy & Wood, 1985). There was a significant interaction between group and condition [$F(4,86) = 2.810$, $p = .030$], indicating that the relative changes in CDA amplitude across the three conditions differed significantly across the three groups. Follow-up comparisons were made by comparing the relative difference between 2T2D and 2T, and the relative difference between 4T and 2T2D trials (as in Vogel et al., 2005). The relative change in CDA between the 2T2D and 2T conditions should be more negative for the LC adults than for the HC adults, as the LC adults process distracters like targets; conversely, the relative change in CDA between the 4T and the 2T2D conditions should be more negative for the HC adults than the LC adults, as the HC adults do not process distracters like targets; in our case the children were included in this comparison to test whether their pattern of CDA amplitudes aligned with that of the LC adults. Both of these follow-up tests were (or approaching) significant [$F(2, 45) = 4.366$, $p = .019$, $d = 1.09$; $F(2, 45) = 3.116$, $p = .054$, $d = .92$, respectively]. As
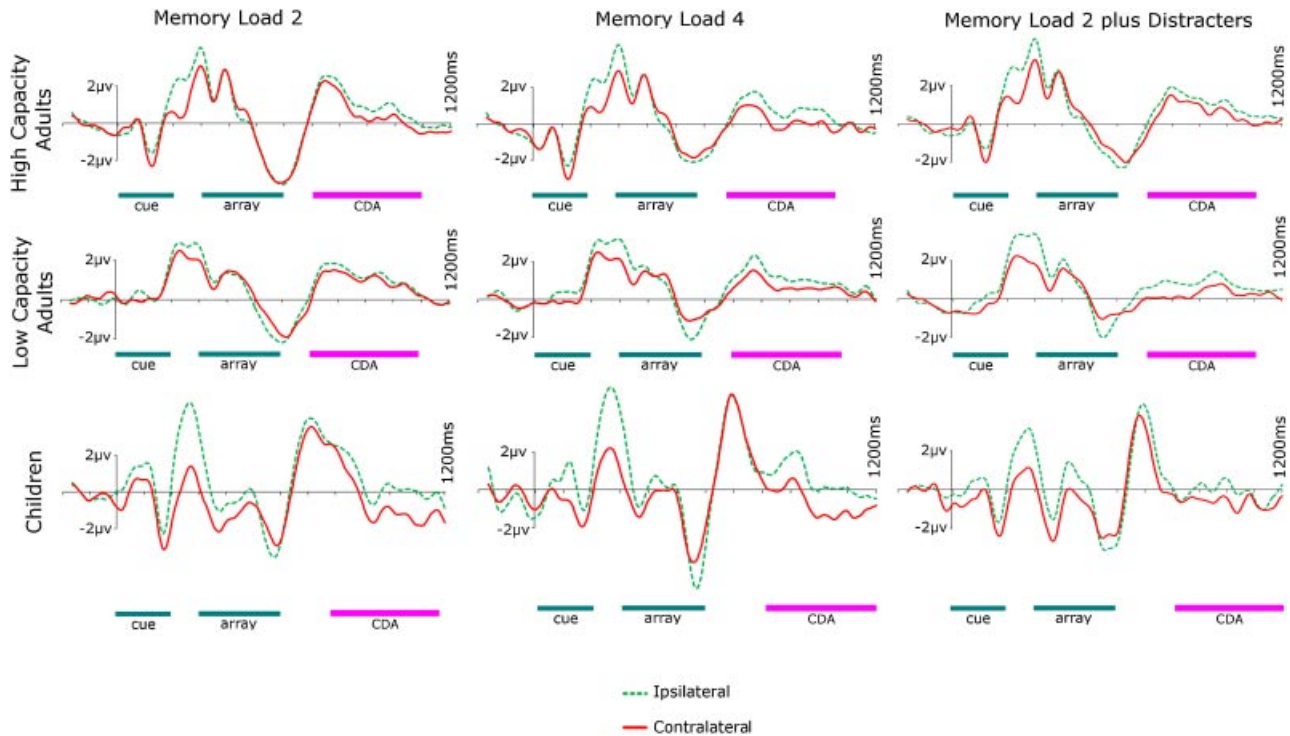
**FIGURE 2** ERPs recorded contra and ipsilateral to the memoranda hemifield, time locked to the onset of the directional cue at 0 ms. The dark green bars show the onset and offset of the cue and the memory array. The pink bars show the time window for the CDA. The top line of waveforms are taken from the HC adults, for the three conditions; the second line of waveforms are taken from the LC adults; the bottom line of waveforms are taken from the Children. In all cases, the waveforms are collapsed across the electrodes that best show the CDA effect (as described in the Methods Section).

predicted, the 2T2D versus 2T difference was significantly more negative for the LC adults, relative to HC adults [$t(29) = 2.419$, $p = .022$, $d = .90$]; interestingly this was also significantly more negative than in the group of children [$t(29) = 2.639$, $p = .013$, $d = .98$], whereas there was no difference between the children and the HC adults [$t(28) = 1.000$, $p = .326$]. Also as predicted, the 4T versus 2T2D difference was significantly more negative for the HC adults, relative to the LC adults [$t(29) = 2.350$, $p = .026$, $d = .87$]; interestingly, this was also significantly more negative in the children, relative to the LC adults [$t(29) = 2.167$, $p = .039$, $d = .80$], with the children and HC adults not differing significantly [$t(28) = .532$, $p = .599$]. In short, with regards to the effect of distracters on CDA amplitudes, the children align with the HC adults and differ significantly from the LC adults.

This pattern of effects is also apparent if the follow-up comparisons are performed on the raw (non-normalized) data (as in Vogel et al., 2005). There was a more negative CDA effect for 2T2D versus 2T trials in the LC adults relative to the HC adults [$t(29) = 2.214$,

$p = .035$, $d = .82$; $-.35$ μV $\pm$ .10 (SE) vs. .02 μV $\pm$ .10 (SE), respectively], and for LC adults relative to Children [$t(29) = 2.114$, $p = .044$, $d = .79$; .53 μV $\pm$ .43 (SE)], with no significant difference between the HC adults and the children [$t(28) = 1.211$, $p = .236$]. Likewise the 4T versus 2T2D CDA difference was significantly more negative for the HC adults relative to the LC adults [$t(29) = 2.120$, $p = .043$, $d = .79$; $-.19$ μV $\pm$ .09 (SE) vs. .11 μV $\pm$ .09 (SE)], and for children relative to the LC adults [$t(29) = 2.095$, $p = .045$, $d = .78$; $-.62$ μV $\pm$ .26 (SE)], with the HC adults and children not differing significantly [$t(28) = 1.182$, $p = .247$].

## DISCUSSION

Low-capacity adults showed poor attention selection and treated distracters like targets, this was reflected in the CDA amplitudes: this group showed a CDA effect on distracter-present trials resembling that on 4-target trials, but significantly larger than on 2-target trials. By
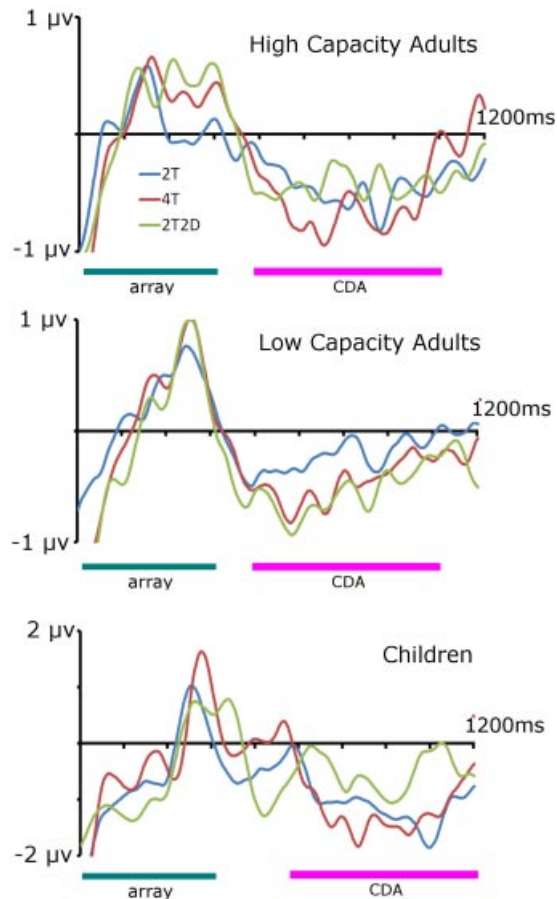
**FIGURE 3** Contralateral delay activity (CDA) in the form of difference waves (contralateral minus ipsilateral), shown for the three conditions, time-locked to the onset of the array. The top panel shows these for the high-capacity adult group, the middle panel for the low-capacity adult group and the bottom panel for the children.

contrast, for high-capacity adults distracter items had no significant effect on CDA amplitudes: this group showed a CDA amplitude on distracter-present trials that was equivalent to that on 2-target trials, and significantly smaller than that on 4-target trials. This pattern replicates that previously shown by Vogel et al. (2005). We had predicted that children would show a pattern of effects similar to that of the low-capacity adults, because the two groups had a similar VSTM capacity. However, contrary to our predictions, the ERP results suggested that the lower VSTM capacity of children relative to adults does not stem exclusively, or perhaps even primarily, from a difficulty in ignoring distracters. When we compared the pattern of CDA effects across the groups, the children differed significantly from the low-capacity adults, but not from the high-capacity adults. The low capacity adults showed a significantly bigger CDA difference between the

2-target and 2-target with 2-distracters conditions than either the high capacity adults or the children. Both the high capacity adults and children showed a significantly bigger CDA difference between the 4-target and 2-target with 2-distracter trials. Whilst the low capacity adults treated distracters like targets, neither the high capacity adults nor the children did.

## Children Align With High-Capacity Rather Than Low-Capacity Adults

To our knowledge this is the first study to include groups of performance-matched children and LC adults. This is important because many developmental comparisons are confounded by differential success rates, different levels of required effort, or different test materials (needed to match performance across the groups); a performance-matched LC group is instrumental for disentangling developmental and individual differences. Unlike LC adults, children were not disproportionately poor performers in the presence of distracting stimuli. This conclusion might seem to contradict previous demonstrations that attentional control can constrain children's working memory capacity, revealed by significant relationships between attentional control and memory capacity across children of the same age (Astle, Nobre, & Scerif, 2012). However, we draw a clear distinction between individual differences in children (the large differences in VSTM capacity that exist across children of the same age) and developmental differences (the large differences in VSTM capacity that exist across children of different ages). Children, just like adults, can use attentional control processes to optimize their limited VSTM capacity, but there are differences in capacity across individuals of different ages that cannot be accounted for purely by the increasing ability to ignore distracters. Of course there could be other attentional mechanisms that might contribute directly to developmental improvements in VSTM, for instance the allocation of attention at the point of VSTM retrieval. Indeed there are likely multiple factors that will constrain performance on VSTM tasks, and these could change with age. Logically roughly half of our children sample might go on to be characterized as having low capacity in adulthood (if we used a median split criteria as with the current adult sample), but these individual differences in adulthood could be influenced by multiple underlying factors (e.g., motivation), that are not the same factors that constrained performance in childhood. The point we make here is that whilst differences in attentional filtering (ignoring distracters) might account for *individual* differences, they do not account for *developmental* differences in VSTM capacity.

***CDA as a marker of item representation or attentional control.*** Importantly, CDA amplitudes scale with individual differences in VSTM capacity; the larger the subject's VSTM capacity the greater the CDA difference between two and four items (Vogel & Machizawa, 2004). The asymptote of these CDA increases occurs at around four items, roughly corresponding to the supposed capacity of VSTM (Cowan, 2001). Thus, the CDA is thought by some to reflect directly the number of items maintained in VSTM (Vogel & Machizawa, 2004), and has been interpreted to provide persuasive evidence that there is an item-based limit to VSTM capacity, and that the CDA amplitude reflects item representation per se (Fukuda et al., 2010). An alternative possibility is that the CDA reflects the spatial allocation of attention, corresponding to contralateralized decreases in alpha-band power (van Dijk, van der Werf, Mazaheri, Medendorp, & Jensen, 2010). There are now a number of demonstrations that subjects can recruit attentional control mechanisms during VSTM maintenance (Astle, Nobre, Scerif, 2009) and retrieval (Astle, Nobre, & Scerif, 2010; Astle, Scerif, Kuo, & Nobre, 2009). In particular, directing spatial attention during the maintenance delay produces a substantial contralateral negativity (e.g., Griffin & Nobre, 2003), and substantially attenuates the CDA effect (Kuo, Stokes, & Nobre, 2011). Furthermore, orienting attention within the spatial layout of VSTM yields substantial capacity benefits (Astle, Summerfield, Griffin, & Nobre, 2012) and the ability to do so constrains individual differences in maintenance capacity (Astle, Nobre, et al., 2012). In support of this spatial attention account, a recent study demonstrated that it was the preparatory allocation of spatial attention that best predicted VSTM capacity differences, rather than the CDA effect (Murray et al., 2011). One possibility is that those with high VSTM use the spatial attention in the maintenance window to enhance the representation of the array in VSTM, such that it survives the onset of the probe array. Being able to selectively encode targets and ignore distracters is clearly advantageous, allowing the targets to be preserved and the distracters wiped at the onset of the probe array. This account of the CDA may be very similar to that proposed by Sander et al. (2011), with the CDA reflecting the allocation of top–down control rather than the representation of items per se. Our findings are compatible with the CDA indexing a change in the number of representations or with a top–down control mechanism required to maintain target items selectively.

In summary, our data support the view that adults with low VSTM capacity have a relative inability to use selection mechanisms necessary to resist distraction. However, rather than aligning to their capacity-matched controls, the children aligned with adults with high VSTM capacity. Whatever the reason for children's immature VSTM capacity, our data argue that it cannot be explained via the same route as deficient VSTM capacity in adulthood.

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