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Brain Activity Related to Working Memory and Distraction in Children and Adults

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In order to retain information in working memory (WM) during a delay, distracting stimuli must be ignored. This important ability improves during childhood, but the neural basis for this development is not known. We measured brain activity with functional magnetic resonance imaging in adults and 13-year-old children. Data were analyzed with an event-related design to isolate activity during cue, delay, distraction, and response selection. Adults were more accurate and less distractible than children. Activity in the middle frontal gyrus and intraparietal cortex was stronger in adults than in children during the delay, when information was maintained in WM. Distraction during the delay evoked activation in parietal and occipital cortices in both adults and children. However, distraction activated frontal cortex only in children. The larger frontal activation in response to distracters presented during the delay may explain why children are more susceptible to interfering stimuli.

Keywords: development, dorsolateral, event related, fMRI, prefrontal, visuospatial

Introduction

Working memory (WM) capacity (Gathercole 1999; Fry and Hale 2000; Luna and others 2004; Westerberg and others 2004) and the ability to ignore interference (Tipper and others 1989; Dempster 1992; Hale and others 1997; Ridderinkhof and others 1997) increase during childhood development. In order to retain information in WM during a delay, it is necessary to ignore interfering stimuli from the surroundings. Thus, high WM capacity is also essential for the ability to differentiate between relevant and irrelevant information (Lavie and others 2004, Vogel and others 2005). The increase in WM capacity during development occurs in parallel with prolonged maturation of the frontal lobes (Sowell and others 1999). Importantly, the neural correlates of the development of the ability to filter out distracters during a WM delay have not been identified.

Visuospatial WM relies on activation of the superior frontal sulcus, dorsolateral prefrontal cortex, and intraparietal sulcus (Klingberg and others 1997, 2002; Courtney and others 1998; Ungerleider and others 1998; Nelson and others 2000; Postle and others 2000; Rowe and others 2000; Pessoa and others 2002; Sakai and others 2002; Curtis and others 2004). Furthermore, development of visuospatial WM is related to increased activity in these cortical areas (Klingberg and others 2002; Kwon and others 2002; Olesen and others 2003) and maturation of frontoparietal white matter (Nagy and others 2004). However, none of these studies included evaluation of the effects of distraction on WM.

The importance of the prefrontal cortex for the ability to ignore distraction was first shown by Miller and others (1996). Neurons in the prefrontal cortex were found to have persistent activity during a WM delay, even in the presence of a distracter. Sakai and others (2002) used a visuospatial WM task with distraction during the delay to identify WM- and distracter-related brain activity in healthy adults. They showed that activity in the dorsolateral prefrontal cortex and higher order interactions between frontal and parietal areas were more important for correct performance on distracter trials than on trials without distraction. de Fockert and others (2001) used a verbal WM task with visual face distracters presented during the delay and found that activity in distracter-related areas was higher for high WM load trials compared with low load trials. This could mean that the effect of a distracter would be stronger in children than in adults because children have lower WM capacity and lower ability to suppress distracters.

Several previous studies have investigated developmental changes in brain activity using functional magnetic resonance imaging (fMRI) (Casey and others 1997; Bunge and others 2002; Tamm and others 2002; Booth and others 2003). However, none of these studies investigated the effect of distraction during the delay in a WM task.

In the present study, we used an event-related fMRI design to allow identification of changes in brain activity that were related to each WM phase. The distracter was defined as a separate event, and activity during distraction was compared with activity during the delay. To our knowledge, this is the first time that a distracter has been analyzed as a separate event in a developmental fMRI study. Furthermore, no previous study has used a WM task with distraction during the delay in order to study the developmental changes in brain activity related to distraction of goal-relevant information. Based on Sakai and others (2002), we expected that activation of an additional prefrontal area would be essential for ignoring distraction during the WM delay.

The WM task in the present study (Fig. 1) was adapted from Rowe and others (2000) and was modified to include a distracter. Brain activity was measured with fMRI in adults and 13-year-old children, reflecting a time point in childhood when WM capacity is still developing (Gathercole 1999; Luna and others 2004; Westerberg and others 2004) and the frontal lobes are still maturing (Sowell and others 1999). The event-related analyses of the imaging data included 4 events: cue presentation, delay, distraction, and response selection. Random effects analyses were performed to identify the main effects of each WM event for each group, as well as significant group differences.

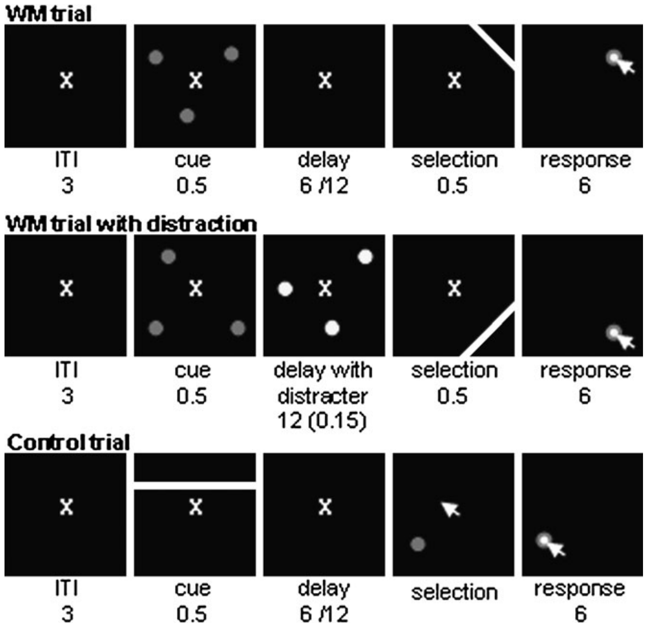

Figure 1. The WM task. The task was to remember the cues and to indicate with the cursor where the line intersected one of the previously presented cues. Accuracy was defined as the distance between the correct location of the cue and the location at which the participant clicked. Distracters were briefly presented during the delay for half of the WM trials. The task during control trials was to click on the circle that was presented after the delay.

Materials and Methods

Subjects

Thirteen children (10 males, 13.1 ± 0.5 years) and 11 adults (4 males, 22.8 ± 3 years) participated in the scanning. The children were recruited from a school in Solna, Sweden. The adults were recruited through an advertisement on the hospital website and through friends. All subjects were healthy and right handed. Written consent was obtained from all subjects and from the parents of the children. The study was approved by the ethical committee at Karolinska Institute.

WM Task

The task performed during scanning (Fig. 1) was adapted from a previous study (Rowe and others 2000). It was a visuospatial WM task created with the E-prime® software (Psychology Software Tools, Inc., Pittsburgh, PA). An easy task was chosen so that both children and adults would perform at a high level. All trials started with a fixation cross and a 3-s intertrial interval (ITI). For WM trials, 3 blue circles (gray in the figure) appeared for 0.5 s, followed by a delay that varied pseudorandomly between 6 and 12 s. After the delay, a line flashed on the screen for 0.5 s and crossed the location of one of the previously presented circles. The task was to move the cursor to the location of the cue intersection and click on it. A red circle (displayed as white with a gray border in the figure) appeared to indicate that the participant had made a response. Distracter trials included the presentation of 3 yellow circles (white in the figure) for 0.15 s during the delay. The distracters appeared after 3, 6, or 9 s during half of the 12-s delay periods in the WM trials. Every second trial was a control trial, designed to control for activity related to motor and visual functions. In the control trials, a line crossed the screen for 0.5 s, followed by a delay of 6 or 12 s. After the delay, a blue circle (gray in the figure) appeared and the task was to click on this circle. For both WM and control trials, the maximum response time was 6 s. Half of the trials were no-response trials. In these trials, a pink circle, presented for 0.5 s after the delay, indicated the end of the trial.

Accuracy scores and reaction times (RTs) were collected during scanning (defined in Results). Behavioral data from 3 children and 2 adults could not be collected due to mechanical problems with the optic trackball. Also, the tracking function was not working optimally, which made the RT scores during scanning less reliable. Each scan included 3 sessions, and each session included 12 WM trials (6 WM trials with 6 s delay and 6 trials with 12 s delay including 3 trials with distraction) and 12 control trials (6 control trials with 6-s delay and 6 trials with 12-s delay). One session was 7 min and 5 s long.

Analysis of Behavioral Data

Significant effects of task and group, and the interaction between these factors, were calculated using a repeated measures analysis of variance (ANOVA). This test was applied using the multivariate analysis of variance (MANOVA) option in the statistical package JMP (JMP®, SAS Institute Inc., Cary, NC, version 4.0.4). In this analysis, only long delay trials were included. To get more reliable results for the interaction effect, additional data were included in the MANOVA. These data were collected outside the scanner from 18 adults (8 males, 23.7 ± 1.9 years) and 9 children (6 males, 12 ± 0.9 years). The behavioral data collected during scanning were analyzed together with these data and separately. Behavioral data was successfully collected from 9 adults and 10 children during scanning. Thus, the main performance analysis was based on data from 27 adults (11 males, 23.3 ± 2.4 years) and 19 children (13 males, 12.7 ± 0.9 years).

Scanning Procedure

The subjects were informed about the scanning procedure and practiced the WM task before entering the scanner. The head was fixated with foam pads and tape on the nose and forehead to reduce motion during image acquisition. Headphones were used against scanner noise. The WM stimuli were projected onto a screen placed on the scanner bed. Mirrors were mounted on the scanner head coil such that the subject could see the screen from the bed. Responses were collected using a nonmagnetic fiber-optic trackball (Current Designs, Philadelphia, PA). Each participant spent approximately 30 min in the scanner.

Data Acquisition

Scanning was performed on a 1.5-T Signa Excite General Electric magnetic resonance scanner. T_2-weighted fast spin echo XL anatomical images were acquired (echo time [TE] = 85 ms, repetition time [TR] = 4500 ms, echo train length = 16) followed by functional T_2*-weighted gradient echo echo-planar images (TE = 40 ms, TR = 2000 ms, flip angle = 76) sensitive to the blood oxygenation level–dependent (BOLD) contrast. For each volume, twenty-two 4.5-mm-thick slices were collected with 0.1 mm interleave. The field of view was 220 mm, and matrix size was 256 × 256 voxels for anatomical images and 64 × 64 voxels for functional images. This resulted in a voxel size of 0.859 × 0.859 × 4.6 mm for the anatomical images and 3.4 × 3.4 × 4.6 mm for the functional images. The functional images were collected at the same localizations as the anatomical images. For each session, 213 volumes were acquired.

Image Preprocessing and Statistical Analysis

The image preprocessing and statistical analysis were performed using SPM2 (http://www.fil.ion.ucl.ac.uk/spm/software/spm2/). Functional images were realigned to the first image in each time series. Variance due to movement artifacts was removed using the unwarp toolbox (Andersson and others 2001). The anatomical images were coregistered with the mean functional image. To correct for differences in acquisition time, the functional images were slice-time corrected by interpolation to the middle slice. The anatomical images were normalized to a T_2 template, and the normalization parameters were applied to the functional images. Finally, the functional images were smoothed with an isotropic Gaussian kernel of 8 mm. All images were included in the statistical analysis as the within-session head movement did not exceed 2 mm for any subject. Also, there were no differences in head motion between the groups either in translation (P = 0.16, 2 tailed; children: 0.10 mm, adults: 0.06 mm) or rotation (P = 0.2, 2 tailed; children: 0.00003 degrees, adults: 0.00001 degrees).

The general linear model of fMRI time series was applied to analyze the fMRI data (Friston and others 1995). All analyses were corrected to control for the number of independent comparisons made in the entire brain based on the theory of Gaussian random fields (Worsley and others

1995). The percent signal change refers to signal change with respect to a whole-brain mean activity of 100. Coordinates for localization of the activations were displayed in the Montreal Neurological Institute 152 space. For all statistical analyses of extracted voxel data, values that were more than 2 standard deviations from the mean were excluded.

The statistical analyses of brain activation data were performed in 2 steps: first single-subject fixed effect analyses and then group-level random effect analyses. For each subject, a fixed effect analysis was performed including all images from all events. In this analysis, contrast images were created by subtracting activity during the control task from activity during the WM task for each event (Friston and others 1998). Activity during distraction was additionally evaluated by subtracting WM delay activity from activity during distraction.

Therefore, each subtraction resulted in one contrast image per subject. To allow inferences to be made at the population level, random effects analyses were applied to the contrast images from the single-subject analyses. The main effect analyses of activity related to each WM event consisted of 1-sample *t*-tests applied to the linear combination of parameter estimates stored in the contrast images. Main effect analyses were performed for each group separately. Interactions between group and event-related activity were analyzed using a 2-sample *t*-test on the contrast images. Therefore, for each main effect analysis, one regressor was included, which consisted of one contrast image per subject and event. In the group interaction analyses, 2 regressors were included, corresponding to contrast images from adults and children. For the group analyses, we identified whether the interaction was a result of significantly increased activity in one group or the absence/attenuation of activity in the other group. Increased activity refers to brain regions that were found to have positive values after the subtraction of activity during control trials from WM trials. Negative values would be found in areas where activity during the control trials was stronger than activity during the WM trials. This could be related to an absence or attenuation of activity during the WM trials relative to the control trials. If the group difference showed that adults had stronger activity than children, then it was first tested whether this interaction was related to increased activity in adults. The interaction analysis was then performed within the areas that represented the main effect of increased activity for that event in adults. If the area was found in this additional analysis, it was concluded that the interaction represented increased activity in adults. Conversely, if the area did not appear in this second analysis, then the interaction could be related to an absence/attenuation of activity in children. The analysis was then performed in the areas that represented the main effect of absence/attenuation of activity in children for that event. If no interaction was found in the whole-brain analysis, group differences were tested using small volume correction.

Gender effects were analyzed for the areas in which interactions were found. BOLD-response values were extracted from the peak voxel in each cluster where an interaction was identified. These values were entered into a statistical package (JMP®, SAS Institute Inc., version 4.0.4), together with 2 additional covariates coding for group and gender. ANOVA analyses were performed comparing group differences in brain activity and controlling for gender. The effect of controlling for a factor is similar to that of removing the influence of that factor on the analysis, for example, covarying out or removing the variance due to this factor. Thus, when we control for gender, we remove the effect of gender on the interaction between brain activity in children and adults.

Similarly, the effect of performance was evaluated by extracting the BOLD-response values from the areas in which an interaction was found and controlling for accuracy on distracter trials in an analysis of group differences in the extracted values. When we control for performance, we remove the effect of performance in order to analyze whether there are any interactions that are unrelated to performance. Any such interaction may be better explained as originating from developmental factors than performance. Furthermore, correlation analyses were performed between accuracy on the distracter trials and activity in the regions identified by the interaction analyses to determine whether any of the significant developmental differences were also dependent on performance. Pearson's product-moment correlation coefficients were calculated by correlating the BOLD-response values from the regions in which group differences were found with distance scores, and the corresponding *P*-values were identified.

Results

Behavioral Results

Accuracy on the WM task (Fig. 1) was defined as the distance from the location of the subject's response to the correct location, in millimeters. RT was defined as the time from the presentation of the cursor to the time at which the subject clicked. The behavioral analysis was based on data from 46 subjects (27 adults, 23.3 ± 2.4 years; 19 children, 12.7 ± 0.9 years), including behavioral data obtained during scanning (9 adults and 10 children). Due to mechanical problems with the optic trackball during scanning, behavioral data from 2 adults and 3 children could not be collected. The results showed a significant effect of condition (i.e., distracter vs. nondistracter conditions) ($F_{1,44} = 26.67$, $P < 0.0001$) and a significant effect of group (i.e., adults vs. children) ($F_{1,44} = 61.32$, $P < 0.0001$) (Fig. 2) on accuracy. In addition, children were significantly more distracted than adults (interaction group × condition; $F_{1,44} = 6.11$, $P = 0.017$), that is, children were less accurate than adults on trials that included distraction relative to trials that did not include distraction.

Analysis of the data from the scanned subjects alone showed a significant effect of condition (distracter vs. nondistracter) ($F_{1,17} = 19.90$, $P = 0.0003$) and a significant effect of group, with overall performance being worse for children compared with adults ($F_{1,17} = 23.17$, $P = 0.0002$). Furthermore, there was a trend indicating an interaction between group and condition ($F_{1,17} = 3.14$, $P = 0.094$). There were no significant group differences in RT, either for the whole group ($F_{1,44} = 2.45$, $P = 0.12$] or for the scanned subjects alone ($F_{1,17} = 0.12$; $P = 0.73$]. Mean RTs for the whole group on trials without and with distraction were, respectively, 2624 and 2456 ms for adults and 2735 and 2539 ms for children.

Imaging Results

Main Effect of Each Condition

The fMRI analyses were based on data collected from 11 adults and 13 children. The results from the main effect analysis for each condition are presented in Figure 3, Table 1 (adults), and Table 2 (children). The results that are presented for the distracter event are based on the subtraction of WM delay activity. These results were confirmed by the comparison of the 2 groups in distracter minus control delay activity.

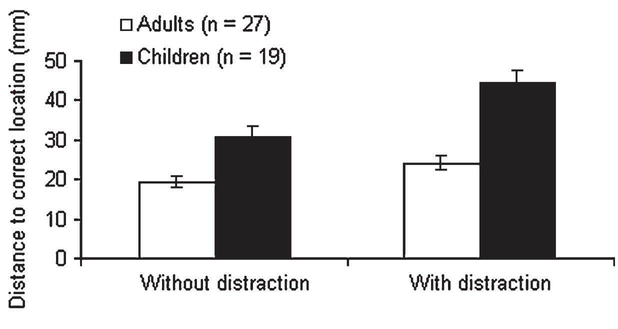

Figure 2. Performance on the WM task. The results were based on data from 46 subjects, including scan-performance data from 19 subjects and data from 27 subjects that did not participate in the scanning. Distance scores (i.e., the distance to the correct location) from long delay trials with and without distraction are presented separately. The columns show mean values together with the standard error of the mean.

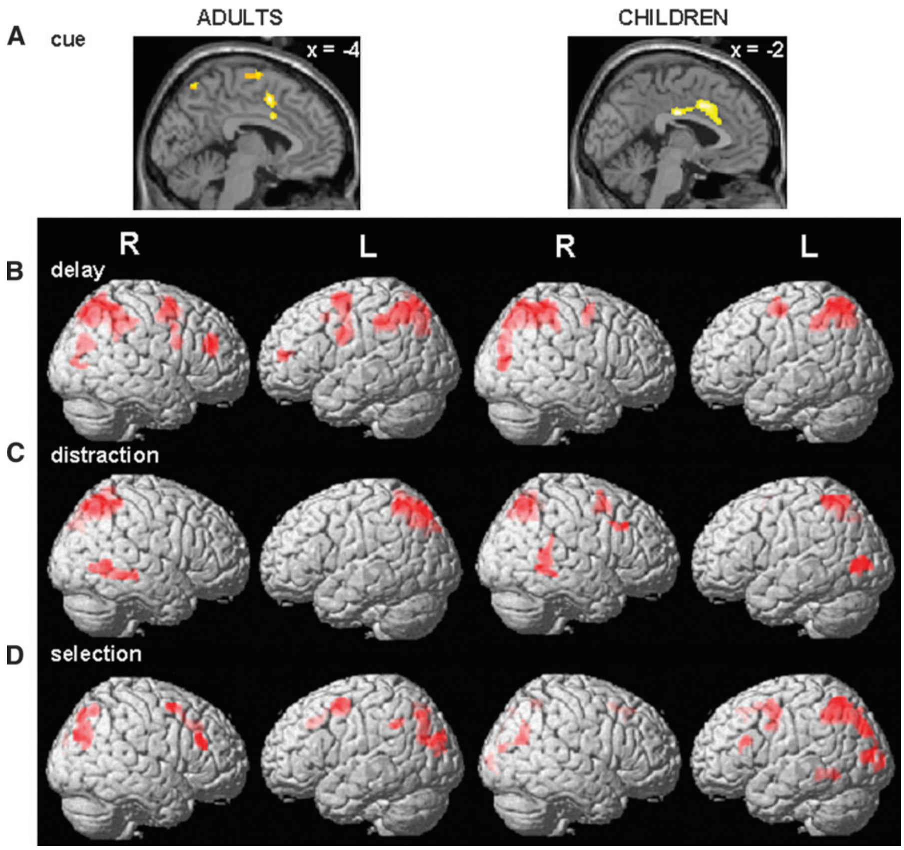

Figure 3. Brain activity related to each event for each group. Areas with significantly increased activity ($P < 0.05$, corrected) during cue (*A*), delay (*B*), distraction (*C*), and selection (*D*) are displayed separately for each group. Activity during cue presentation (*A*) is shown on a sagittal section of a single-subject T_1-weighted image. For the other events, the activations are rendered upon a canonical brain surface and are shown separately for the left (L) and the right (R) hemisphere. Red color coding reflects areas in which the activity was stronger during the WM trials compared with the control trials. For the distraction event, the red color reflects areas in which the activity was stronger during distraction compared with WM delay.

Group Differences in Brain Activity

Significant group differences in activity were found for all events. All the group differences were also significant after controlling for gender ($F_{1,22} > 15$, $P < 0.01$, for all analyses) and after controlling for interindividual differences in accuracy ($F_{1,22} > 7$, $P < 0.02$, for all analyses). The only event for which adults showed a significantly stronger increase in activity than children was the delay. A significant interaction is equivalent to

$$\text{Diff}(\text{interaction}) = [\text{WM}_{\text{adults}} - \text{control}_{\text{adults}}] - [\text{WM}_{\text{children}} - \text{control}_{\text{children}}].$$

A significant interaction can thus occur because of either a difference in activation or a difference in absence/attenuation of activity (i.e., when control activity > WM activity). Therefore, for each interaction it was determined whether the result was due to a difference in activation or in absence/attenuation of activity (Fig. 4 and Table 3). The group difference found during cue presentation was related to absence/attenuation of activity in adults (Fig. 4*A*). The areas in which group differences were found for the delay included 3 clusters located in the frontal and parietal cortices, which represented increased activity in adults (Fig. 4*B*). One cluster represented an absence/attenuation of activity in children in the anterior cingulate gyrus (Fig. 4*B*). For the areas in which group differences were found during distraction, a cluster in the superior frontal sulcus was related to significantly increased activity in children (Fig. 4*C*). Importantly, the location of this area was found to partially overlap the superior frontal region that was activated during the delay (Fig. 3*B*). The other group differences during distraction represented absence/attenuation of activity in adults (Fig. 4*C*). During selection, children showed stronger activation of the intraparietal sulcus compared with adults (Fig. 4*D*).

To exclude the possibility that group differences in brain activity were an effect of a generally lower signal-to-noise ratio in images acquired from children compared with adults, a control analysis was performed. This was done by comparing the amount of visual activation between the groups. If the signal-to-noise ratio was similar in children and adults, there would be no interaction in visually related activity. The analysis included subtraction of activity during the ITI from activity during the control cue, which was thought to result in activity related to visual stimulation. Significant activity was found in visual areas bilaterally in occipitotemporal cortex. Importantly, there was a lack of group differences in activity within these areas ($P = 0.25$ and 0.18, for the left and right region, respectively, using the same threshold as in the other group analyses). Thus, this analysis confirmed that the results of the group analyses were not an effect of a generally lower signal-to-noise ratio in children compared with adults.

Correlation between Brain Activity and Accuracy

Correlations were performed between distance scores and activity in each of the clusters in which interactions were

Table 1
Main effect of each event in adults

Event	Brain region		MNI coordinates x	y	z	*T*-score	Size (mm^3)
Cue							
	Frontal						
	Superior frontal gyrus	L	−-6	−16	74	5.65	936
	Pre-SMA	L	−4	6	48	7.76	1496
	Parietal						
	Superior parietal lobe	L	−6	−66	64	6.67	712
Delay							
	Frontal						
	Superior frontal sulcus	R	28	−8	50	12.46	4032
	Superior frontal sulcus	L	−14	12	46	8.99	872
	Superior frontal sulcus	L	−18	−4	62	8.9	4952
	Inferior frontal sulcus	R	40	38	20	11.11	2232
	Inferior precentral sulcus	R	46	8	24	9.15	976
	Inferior precentral sulcus	L	−42	−8	32	8.26	2232
	Inferior frontopolar gyrus	L	−34	50	12	7.08	968
	Parietal						
	Intraparietal sulcus/superior parietal lobe	R	40	−48	58	13.69	14896
	Intraparietal sulcus/superior parietal lobe	L	−36	−42	42	7.84	14800
	Occipital						
	Intraoccipital sulcus	R	34	−70	24	5.9	2248
Distraction							
	Parietal						
	Intraparietal sulcus/superior parietal lobe	R/L	−16	−78	52	6.24	24072
	Occipital						
	Middle occipital gyrus	R	52	−70	−2	5.28	3128
Selection							
	Frontal						
	Superior frontal sulcus	L	−20	6	54	10.52	2032
	Superior frontal sulcus	R	28	4	56	6.73	896
	Inferior frontal sulcus	R	42	30	24	9.55	1040
	Cingulate sulcus	R	6	26	38	10.37	1784
	Parietal						
	Intraparietal sulcus	R	14	−66	50	8.14	4032
	Intraparietal sulcus	L	−30	−46	38	6.46	888
	Intraparietal sulcus	L	−24	−72	26	6.16	3912

Note: All clusters were significant at $P < 0.05$, corrected for multiple comparisons. Activity during cue, delay, and selection was compared with control activity. Activity during distraction was compared with WM delay activity. MNI, Montreal Neurological Institute; Pre-SMA, presupplementary motor area; L, left; R, right.

Table 2
Main effect of each event in children

Event	Brain region		MNI coordinates x	y	z	*T*-score	Size (mm^3)
Cue							
	Frontal						
	Pre-SMA/cingulate gyrus	L	−2	−16	32	4.2	4232
Delay							
	Frontal						
	Superior frontal sulcus	R	20	−4	54	6.82	2160
	Superior frontal sulcus	L	−20	−12	56	6.56	2912
	Parietal						
	Intraparietal sulcus/superior parietal lobe	L	−36	−60	58	9.59	11784
	Intraparietal sulcus/superior parietal lobe	R	26	−78	46	7.45	16712
Distraction							
	Frontal						
	Superior frontal sulcus	R	24	2	52	5.44	1888
	Inferior frontal sulcus	R	44	26	34	5.67	920
	Parietal						
	Intraparietal sulcus/superior parietal lobe	R	24	−68	52	10.93	4032
	Intraparietal sulcus/superior parietal lobe	L	−24	−52	64	6.53	4648
	Superior parietal lobe	R	12	−56	60	5.61	1960
	Temporal						
	Middle temporal gyrus	R	66	−46	−6	7.96	1992
	Occipital cortex						
	Occipital cortex	L	−38	−74	2	7.47	3088
Selection							
	Frontal						
	Superior frontal sulcus	L	−32	−2	46	9.25	4344
	Inferior frontal sulcus	L	−44	24	22	5.31	800
	Parietal						
	Intraparietal sulcus	L	−36	−56	58	10.11	14272
	Intraparietal sulcus	R	38	−68	24	8.87	1624
	Precuneus	L	−4	−56	54	6.03	920
	Temporal						
	Collateral sulcus	L	−32	−40	−8	7.33	1944

Note: All clusters were significant at $P < 0.05$, corrected for multiple comparisons. Activity during cue, delay, and selection was compared with control activity. Activity during distraction was compared with WM delay activity. MNI, Montreal Neurological Institute; Pre-SMA, presupplementary motor area; L, left; R, right.

found using whole-brain analyses. Negative correlations indicate that high performers (low distance scores i.e., high accuracy) have high brain activity and vice versa for positive correlations. Significant negative correlations were found in the prefrontal and bilateral parietal clusters in which adults showed stronger activation compared with children during the delay ($P < 0.05$, 2 tailed). For all other clusters that were identified by the interaction analyses, significant positive correlations were found ($P < 0.05$, 2 tailed). When each group was analyzed separately, there were no significant correlations between brain activity and performance. These correlations show that differences in activity between the groups were driven by age, rather than performance during scanning. A similar relationship was found in Durston and others (2002).

Discussion

We used an event-related fMRI design to isolate activity during separate WM events and analyzed differences in brain activity between adults and children. The main findings were that adults recruited the dorsolateral prefrontal cortex to maintain information online during the delay, and activity in this area was significantly stronger in adults than in children. Furthermore, the distracter had a stronger effect on activity in the superior frontal sulcus in children than in adults.

We suggest that during performance of a WM task with distraction during the delay, a distracter-resistant representation of the task-relevant information is created. Activity in the dorsolateral prefrontal cortex, including the superior frontal sulcus and in the intraparietal cortex, may underlie this representation. The distracter-resistant representation was most likely formed during the delay in all trials as the subjects were instructed that a distracter could appear in any trial. This is consistent with a previous study of WM and distraction (Sakai and others 2002). These findings are also in agreement with a study by Miller and others (1996), which showed that there is an area in the monkey prefrontal cortex that is important for resistance to distraction. The location of this area may be comparable with a region in the human brain that includes the location of the dorsolateral prefrontal activity found in the present study (Curtis and others 2004).

One advantage of the task used in the present study was that it enabled a continuous measure of accuracy to be used to indicate the level of performance. Thus, there was no distinction between false and correct trials, which could give rise to

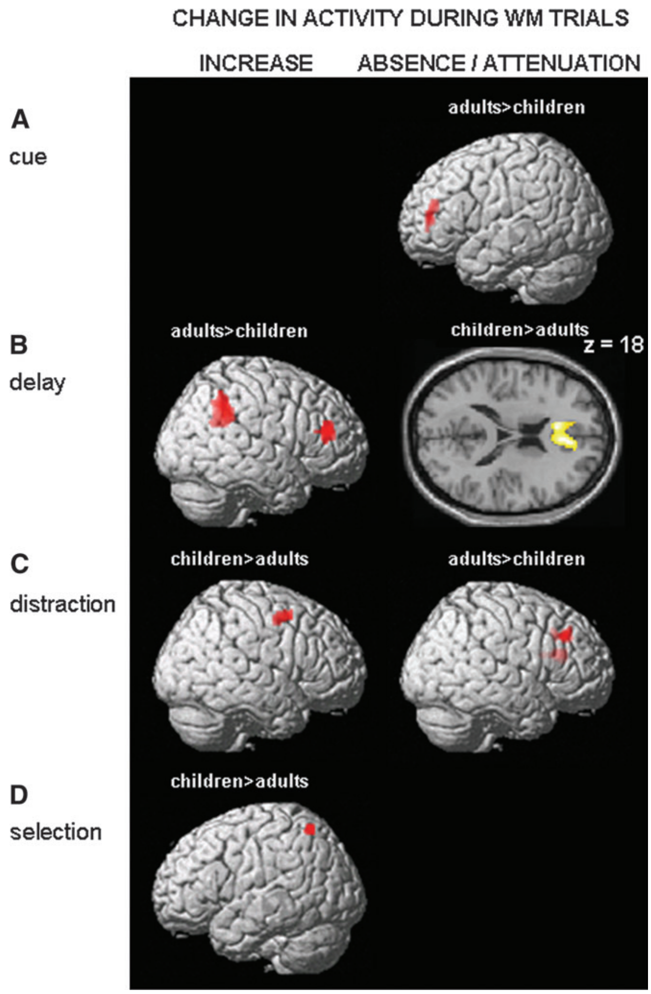

Figure 4. Group differences in brain activity. Significant group differences in brain activity were found for all events and were identified as representing either significantly increased activity in one group or an absence/attenuation of activity in the other group (Table 3). The group that showed the strongest effect is indicated for each of the events cue (*A*), delay (*B*), distraction (*C*), and selection (*D*). Absence/attenuation of activity during the delay (*B*) is shown on an axial section of a single-subject T_1-weighted image. The other group differences are rendered upon a canonical brain surface. The red color coding used for the figures in the left column, that is, those listed under "Increase", is the same as that used in Figure 3. The red color on the figures in the right column reflects areas in which brain activity was stronger during control trials compared with WM trials. For the distraction event, the red color in this column indicates areas in which the activity during the WM delay was stronger than during distraction. Thus, absence/attenuation of activity refers to either a lack of change in activity or attenuation of activity relative to the control event.

group differences in error-related activity. Furthermore, the results could not be related to differences in RT. Children were significantly more distracted than adults, which replicates previous findings of higher WM capacity in adults and higher distractibility in children (Dempster and Cooney 1982; Lavie and others 2004). Regarding the validity of the group comparisons, previous studies have shown that it is feasible to use the same stereotactic space for normalization in children and adults (Burgund and others 2002) and to compare brain activity between the groups (Kang and others 2003). The lack of a group difference in visual areas indicates that the group differences in WM-related activity were specific for the cognitive components rather than reflecting nonspecific differences in signal to noise or hemodynamics.

Maintenance, Selection, and Distraction of Information in Visuospatial WM

Delay-related activity was found bilaterally in the superior frontal sulcus and intraparietal cortex, which is consistent with Rowe and others (2000). In contrast to Rowe and others (2000), the present study showed significant delay-related activity in an additional area of the dorsolateral prefrontal cortex. It is unlikely that any activity related to response selection could have been misinterpreted as delay-related activity in the present study as trials in which no response was required were included to increase the ability to separate activity related to delay and selection. Also, differences in delay-related activity between the studies may reflect a contextual effect related to the presence or lack of distraction in the task.

Two areas in the dorsolateral prefrontal cortex were significantly activated during the delay in adults, whereas children only activated one area in this part of the cortex. The extra activity in adults could represent additional recruitment of neuronal mechanisms that may be necessary to ignore distraction. It is possible that this area in the middle frontal gyrus is recruited during all trials, as the distracters could have appeared in any trial. Consistent with this, the dorsolateral prefrontal cortex has previously been found to be crucial for correct performance on distracter trials in a visuospatial WM task (Sakai and others 2002). Also, distractibility, measured with an oddball paradigm, was related to increased activity in this area (Bledowski and others 2004).

One function of the dorsolateral prefrontal cortex may be to maintain task-relevant information in mind. A large part of the evidence for the contribution of the dorsolateral prefrontal cortex to maintenance of spatial information in WM comes from studies of nonhuman primates. However, it has been suggested that the human homologue to the area that is responsible for this function in monkeys is located in a more posterior and dorsal region within the human prefrontal cortex (Courtney and others 1998). This area, in the superior frontal sulcus, specifically activates during the delay of spatial WM tasks (Courtney and others 1998; Smith and Jonides 1999), whereas more anterior parts of the dorsolateral prefrontal cortex have been shown to be important for spatial as well as object WM (McCarthy and others 1994; Owen and others 1998; Smith and Jonides 1999; Curtis and others 2004). In the present study, the adults may have used a strategy to maintain the information as a single object consisting of 3 spatially separate entities, thus activating areas related to both spatial and object information. It is possible that this creates a more stable representation of the information. This strategy may not be developed in children, forcing them to rely on only the spatial information maintained primarily in the superior frontal sulcus. Children may also maintain some of the irrelevant information that is related to the distracter. Vogel and others (2005) suggested that low WM–capacity individuals maintain irrelevant information in WM, whereas high-capacity individuals only maintain task-related information. It is possible that this maintenance of irrelevant information is reflected by the activity in the superior frontal sulcus during distraction in children. This explanation is emphasized by the overlap in the superior frontal sulcus between distracter- and delay-related activity in children.

The parietal cortex was activated bilaterally during the delay, distraction, and selection. The functions of the parietal cortex that are relevant to visuospatial WM include maintenance of

Table 3

Group differences in brain activity related to each WM event

Interaction	Brain region		MNI coordinates			*T*-score	Size (mm^3)
			x	*y*	*z*		
Group differences related to increased activity							
Delay							
Adults > children	Frontal						
	Inferior frontal sulcus/middle frontal gyrus	R	38	36	16	5.32	1800
	Parietal						
	Intraparietal cortex	R	42	−48	32	4.62	3696
	Intraparietal cortex	L	−42	−46	36	3.92	4024
Distraction							
Children > adults	Frontal						
	Superior frontal sulcus	R	18	6	50	4.39	232
Selection	Parietal						
Children > adults	Intraparietal sulcus	L	−30	−62	60	4.7	384
Group differences related to absence/attenuation of activity							
Cue							
Adults > children	Frontal						
	Inferior frontal gyrus	L	−50	22	12	5.89	688
	Anterior cingulate sulcus	L	−14	46	10	5.08	736
Delay							
Children > adults	Frontal						
	Anterior cingulate gyrus	R/L	6	34	18	4.35	3584
Distraction							
Adults > children	Frontal						
	Superior frontal sulcus	R	22	30	36	4.44	712
	Inferior frontal sulcus	L	−18	22	24	3.95	496
	Anterior cingulate gyrus	R	10	26	20	6.65	896
	Frontal cortex	R	24	36	4	5.28	520
	Temporal						
	Insula	L	−32	−14	−16	4.42	536

Note: All voxel values were significant at $P < 0.05$, corrected for multiple comparisons. MNI, Montreal Neurological Institute; L, left; R, right.

information (Jonides and others 1993; Jha and McCarthy 2000; Pollmann and von Cramon 2000; Corbetta and others 2002), top–down attention (Corbetta and others 2002; de Fockert and others 2004; Mayer and others 2004), and direction of attention to a peripheral location (Corbetta and others 2002, 2000). The presence of activity in the presupplementary motor area during cue presentation may reflect spatial attention and memory (Simon and others 2002).

Conclusion

This study confirms previous findings in showing that the ability to ignore distraction is not fully mature in children. Importantly, the present study adds possible neural explanations to the development of this ability. Stronger activity in the frontal and parietal cortices in adults compared with children during the WM delay may indicate a more stable representation of the maintained information. Furthermore, stronger activity in the superior frontal sulcus in children during distraction may reflect maintenance of irrelevant information instead of relevant information.

Notes

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