

REPORT

Early development of subcortical regions involved in non-cued attention switching

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Abstract

This study examined the cognitive and neural development of attention switching using a simple forced-choice attention task and functional magnetic resonance imaging. Fourteen children and adults made discriminations among stimuli based on either shape or color. Performance on these trials was compared to performance during blocked trials requiring all color or all shape discriminations. Magnetic resonance echo planar images were acquired during performance of the task. Both children and adults showed robust bilateral activity of the caudate nucleus when switching attention between color and shape discriminations that correlated negatively with mean response latency on these trials. However, neither switching costs nor caudate activity correlated with age, suggesting early development of the underlying neural circuitry involved in switching between salient stimulus sets. Overall, children and adults differed in performance and patterns of brain activity on the task, with adults responding more accurately and faster than children, and recruiting more prefrontal and parietal regions. These results suggest an important role of subcortical regions (i.e. caudate nucleus) in non-cued attention switching, with increasing recruitment of cortical regions with age.

Introduction

The ability to switch or redirect our attention between competing inputs is a key component of cognitive functioning (Shallice, 1981, 1988; Kahneman, Treisman & Burkell, 1983; Baddeley, 1986; Cohen & Servan-Schreiber, 1992; Desimone & Duncan, 1995; Miller & Cohen, 2001) that becomes more efficient with age (Tipper, Bourque, Anderson & Brehaut, 1989; Diamond, 1990; Brainerd & Reyna, 1993; Dempster, 1993; Harnishfeger & Bjorkland, 1993; Zelazo, Burack, Benedetto & Frye, 1996; Casey, Durston & Fossella, 2001; Cepeda, Kramer & Gonzalez de Sather, 2001; Munakata & Yerys, 2001). Neural correlates of attention-switching behavior have been identified largely through neuro-imaging studies. In these studies, attention switching is accompanied by activity in the prefrontal cortex and the posterior parietal cortex, both connected to the dorsal striatum in

cortico-striatal loops (Alexander, DeLong & Strick, 1986; Alexander, Crutcher & DeLong, 1990; Dove *et al.*, 2000; Kimberg, Aguirre & D'Esposito, 2000; MacDonald, Cohen, Stenger & Carter, 2000; Sohn *et al.*, 2000; Cools, Barker, Sahakian & Robbins, 2001a, 2001b).

The importance of the striatum, particularly the caudate nucleus, in attention switching has been shown in a number of imaging, clinical and animal studies. Adult and developmental neuro-imaging studies show recruitment of this region in inhibiting competing stimulus or behavioral sets during saccade (Luna *et al.*, 2001), stimulus-response incompatibility (Casey *et al.*, 2002a) and attention-switching tasks (Sohn *et al.*, 2000). Individuals with Parkinson's disease, which primarily affects dopamine levels in the striatum, have been shown to be impaired in attention-switching tasks when stimuli prime the competing task set (Cools *et al.*, 2001b). Children with Attention Deficit Hyperactivity Disorder, a disorder

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with striatal structural and functional abnormalities (Castellanos *et al.*, 1996; Casey *et al.*, 1997; Vaidya *et al.*, 1998; Durston *et al.*, 2003), show switching deficits that are reduced with stimulants (e.g. Cepeda, Cepeda & Kramer, 2000) that alter dopamine-related striatal activity (Vaidya *et al.*, 1998; Volkow *et al.*, 2002). Learning studies have implicated the striatum in selection of novel events following repeating, structured sequences that require the individual to inhibit a learned response and shift attentional or behavioral set (Berns, Cohen & Mintun, 1997; Rauch *et al.*, 1998; Casey, Durston & Fossella, 2001; Casey *et al.*, 2002b; Durston *et al.*, 2003; McClure, Berns & Montague, 2003). These findings are consistent with the basal ganglia playing a critical role in inhibiting competing cognitive and motor responses proposed in models of basal ganglia function (Cools, 1980; Robbins & Sahakian, 1983; Mink, 1996; Redgrave, Prescott & Gurney, 1999a, 1999b; Casey, 2000; Casey, Durston & Fossella, 2001; Casey *et al.*, 2002b).

The current study examined the neural correlates of attention switching in a simple forced-choice paradigm. The primary objective was to examine the cognitive and neural development of attention switching between salient stimulus features (color and shape). We hypothesized that frontostriatal and frontoparietal circuitry, previously implicated in attention-switching literature, would be activated during switches from one salient stimulus attribute to another. As developmental progressions have been shown in the ability to switch attention during childhood and in the underlying frontostriatal (Giedd *et al.*, 1996; Sowell *et al.*, 1999; Luna *et al.*, 2001; Casey *et al.*, 2002b) and frontoparietal (Sowell *et al.*, 2003) circuitry, we predicted poorer performance and less focal recruitment of this circuitry in children.

Materials and methods

Subjects

The sample included seven right-handed adults (two females, mean age 20.8, range 18–23 years) and seven right-handed children (three females, mean age 7.85, range 7–11 years). All subjects were screened for neurological and psychiatric illness and for any contraindication for a magnetic resonance imaging (MRI). Written informed consent was obtained from subjects before scanning.

Behavioral paradigm

The behavioral task was a simple, forced-choice discrimination task, previously described by Casey *et al.* (1994, 1997). Subjects selected which of three objects pre-

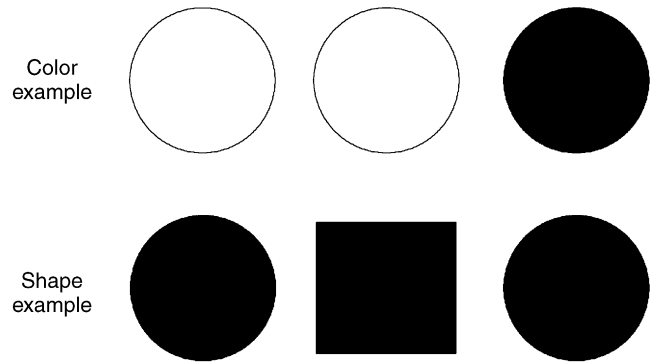


Figure 1 Illustration of example color and shape trials for the simple forced-choice attention-switching paradigm.

sented in the center of a screen was unique. The stimuli differed in either color or shape, but not both, such that the discrimination was easily apparent (see Figure 1). The unique attribute changed from trial to trial with the relevant attribute being color on one trial and shape on the subsequent trial, and alternated back and forth between color and shape. This switch was performed without cuing or instructing the subjects as to the relevant dimension in a simple forced-choice design. Performance on these trials was compared to performance during control conditions in which trials were blocked by stimulus attribute (either color or shape). The timing of the task was modified from the original rapid subject-paced design (Casey *et al.*, 1994, 1997), where a response to one trial initiated the onset of the subsequent trial, to an experimentally controlled design with stimulus duration of 500 ms and interstimulus interval of 1500 ms. Stimuli were presented on a rear projection screen in the bore of the magnet. Responses were collected using a fiber optic button box. Due to technical problems, behavioral data from two adult subjects were not included.

The three task conditions of (1) color discriminations, (2) shape discriminations and (3) switching between color and shape discriminations were presented in 30-second blocks of 15 2-second trials that were repeated in a 123321 order twice per 6-minute run. The conditions were brief 30-second blocks of 15 trials without instructions or delays between conditions.

Image acquisition

Subjects were first acclimated to the MRI environment in a simulator. Then T1-weighted images (spin echo, echo time [TE] minimum, repetition time [TR] 500, 256 × 256, 5 mm whole brain) were acquired in the same location as the echo planar images for localization purposes, using a GE 1.5 T scanner (General Electric, Wilmington,

MA) with a standard head coil. Next, echo planar images (echo planar gradient echo sequence, TE 40, TR 6000, flip 90 degrees, acquisition matrix 128 × 64) were acquired in 28 5-mm contiguous coronal slice locations with 60 images per slice across four runs of the experimental conditions. Each 6000 ms whole-brain image acquisition corresponded to three 2000 ms behavioral trials. Images were acquired for a total of four 6-minute runs.

Image processing and analysis

All scans were corrected for motion using three-dimensional motion correction automated image registration (Woods, Cherry & Mazziotta, 1992) and cross-registered to a representative female adult subject's anatomical scan. This representative brain was then brought into Talairach space using conventional landmarks within the AFNI analysis package (Cox, 1996). There were no significant differences in in-plane movement between age groups (children: $x = .03$ mm, $y = .59$ mm, $z = .17$ mm; adults: $x = .14$ mm, $y = .79$ mm, $z = .19$ mm). Mean magnetic resonance (MR) signal intensity was normalized across subjects and the images were spatially smoothed (8 mm full width half maximum, FWHM). As variance maps for MR signal did not differ between groups, voxel-wise ANOVAs were performed on the pooled data to examine the main effect with subject as the random variable (random effects model). A second ANOVA comparing the seven adults with the seven children tested the interaction of age group by task condition. Significant regions of MR signal change were identified by F ratios with $p < .01$ and a cluster size of 5 voxels minimum (estimated corrected $p < .00002$, Forman *et al.*, 1995) in the scanned plane (coronal).

Results

Behavioral results

The behavioral results showed a significant difference in overall response latency and accuracy of performance

for children and adults (830 versus 556 ms, $F_{(1,13)} = 18.4$, $p < .001$; 92% versus 99%, $F_{(1,13)} = 4.46$, $p < .05$), respectively. There were no significant differences in mean latency or accuracy among task conditions for either children (688, 708, 684 ms and 92%, 92%, 94%) or adults (552, 572, 545 ms and 100%, 99%, 100%) for the color, shape and switch conditions, respectively.

Imaging results

The ANOVA comparing all three conditions across all subjects showed robust activation of the caudate nucleus for the switching versus non-switching (shape, color) conditions (see top of Table 1 and Figure 2A). There were no significant differences in magnitude (per cent change in signal) or volume (number of voxels activated) between these two age groups, nor was there a significant correlation between activity in this region and age. The interaction of condition (3) × group (2) ANOVA showed adults activating superior frontal, superior parietal and middle temporal cortices more than children for the attention-switching condition (see Table 1 and Figure 2B). Adults also activated the fusiform gyrus more than children for the shape condition relative to the color and switching conditions (Figure 2C). In general, children activated all of these regions as much for the shape and color conditions as for the switching condition. The children did not reliably activate any regions more than adults for the switch versus non-switch conditions.

As the most robust activity associated with the switching condition across subjects was in the caudate nucleus, we examined the association between per cent change in MR signal in this region and behavioral performance (accuracy and reaction time), treating age as a covariate. The correlation with reaction time ($r = -.57$, $p < .05$) for the switching condition and per cent MR signal change in the caudate nucleus was significant (see Figure 3), but there was no association between activity in this region and performance for the non-switch conditions or with age.

Table 1 Regions of interest (ROI), Brodmans area (BA), Talairach coordinates (x , y , z), maximum and average F ratios, number of voxels and direction of MR signal change for main effects and interactions

ROI	BA	x	y	z	Max F	Voxels	F ratio	Effect/interaction
Main effect: condition ($n = 14$)								
R/l Caudate nucleus		-2	10	12	15.04	30	15.04	> for switch
Interaction: age group × condition ($n = 14$)								
R superior frontal gyrus	8	-44	15	32	21.44	7	9.14	> switch for adults
L superior parietal poble	7	19	-53	52	11.08	8	8.58	> switch for adults
R fusiform gyrus	19, 37	-34	-53	-9	10.64	10	8.16	> shape for adults
L/r precuneus	7	19	-58	30	9.96	6	8.98	> switch for adults
R middle temporal gyrus	21, 20	-37	-58	-10	13.03	8	8.20	> switch for adults

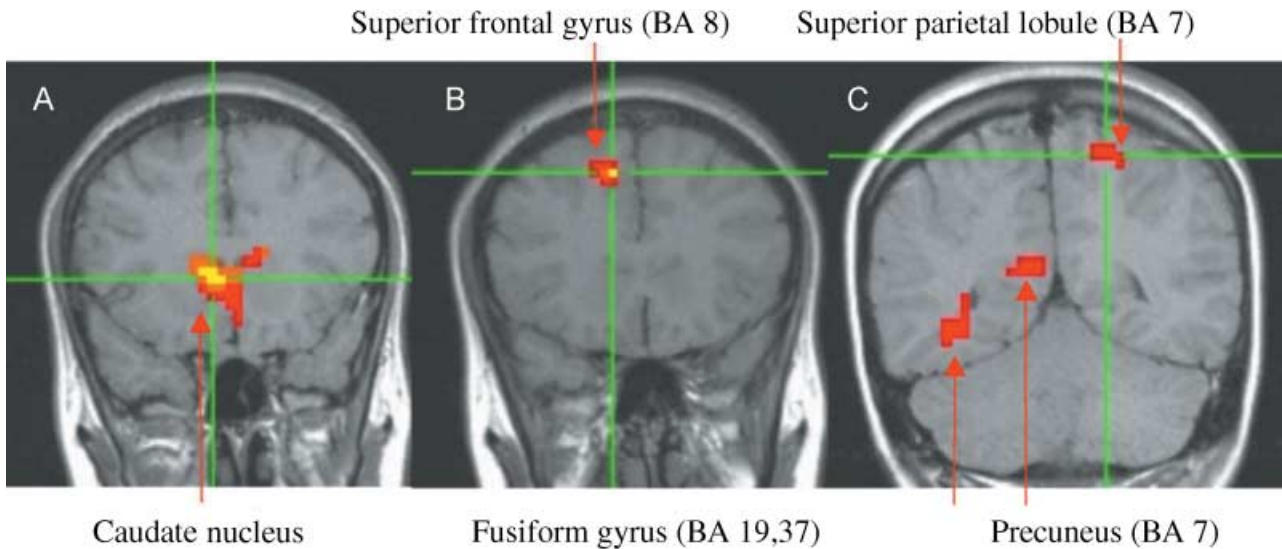


Figure 2 Localization of caudate nucleus activation (A) for the main effect of condition across all ages and of superior frontal (B) and superior parietal (C) activation in the coronal plane for the interaction of age group by condition.

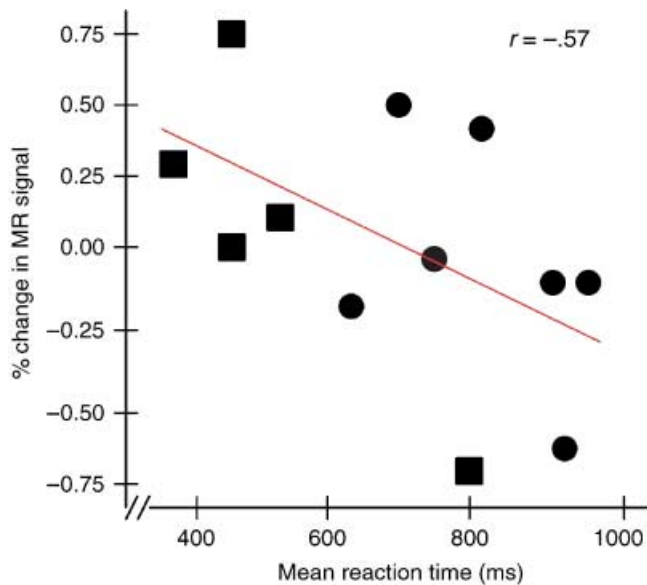


Figure 3 Plot of correlation between per cent MR signal change in the caudate nucleus and reaction time during the switching condition for all subjects.

Note: Adults are denoted by filled squares and children by filled circles.

Discussion

The results suggest an important role of the caudate nucleus in simple non-cued attention switching, with increasing recruitment of cortical regions with maturity.

There was no switch cost *per se* for children or adults during this forced-choice task as indexed by mean response latency and accuracy in contrast to the attention-switching literature (Sudevan & Taylor, 1987; Allport, Styles & Hsieh, 1994; Rogers & Monsell, 1995; Meiran, 1996; Hayes, Davidson, Keele & Rafal, 1998; Allport & Wylie, 2000; Sohn *et al.*, 2000; DiGirolamo *et al.*, 2001; Rushworth *et al.*, 2002; Sylvester *et al.*, 2003). This finding may reflect the implicit detection of a switch without requiring significant involvement of cortical regions to redirect attention. Consistent with this explanation is that the most reliable activity across all subjects was in the caudate nucleus, a region that has been implicated in implicit learning (Berns *et al.*, 1997; Rauch *et al.*, 1998). In these imaging studies, following repeating events or sequences, a novel or random event results in recruitment of the striatum (Berns *et al.*, 1997; Casey *et al.*, 2001; 2002a; McClure *et al.*, 2003; Rauch *et al.*, 1998). Accordingly, rapid learning of the regularity of the task resulted in detection of changes in expected stimulus attributes during the switch condition. This interpretation is consistent with the notion that the basal ganglia are involved in attentional shifts to an unexpected event requiring inhibition of competing attentional or behavioral sets as proposed by Redgrave *et al.* (1999a) and others (Cools, 1980; Robbins & Sahakian, 1993; Mink, 1996), even when these shifts require minimal recruitment of higher level control systems.

Detection of a switch in this simple forced-choice task appears to require minimal cognitive conflict or control given the lack of cost in response latencies and lack of

significant activity in regions implicated in conflict monitoring and resolution (e.g. anterior cingulate cortex, Carter *et al.*, 1998; Botvinick *et al.*, 1999). It is true that detection of elementary features of objects such as color and shape require little to no attentional resources (e.g. 'pop out' effect, Treisman & Gelade, 1980; Treisman, 1988). Yet, some mechanism must support the ease with which we switch between salient events in our environment. The caudate nucleus has been proposed to reflect such a mechanism (Cools, 1980; Redgrave *et al.*, 1999a) by inhibiting competing representations. This interpretation is consistent with our previous theoretical work on the role of the basal ganglia in selective attention (Casey, 2000; Casey *et al.*, 2001, 2002b) and with prior work by Corbetta *et al.* (1991) using a similar paradigm. They showed that when subjects had to make a judgment about a unique feature of a stimulus display that was different on one of three dimensions (color, shape, movement) robust basal ganglia activity was observed. An interpretation of those data is that when the subjects attended to a single dimension they simultaneously suppressed attention to the other two dimensions. The interpretation of caudate activity reflecting greater suppression of competing stimulus attributes for switching trials is further supported by the negative correlation between activity in this region and mean reaction time during the switch trials. In other words, faster reaction times during switch trials could be related to greater suppression of competing information paralleled by greater caudate activity.

The lack of differences among task conditions for children or adults contradicts our previous reports using a similar forced-choice task (Casey *et al.*, 1994, 2000). In those studies, the timing of stimulus presentation was subject-driven, with a response to the current trial leading to the rapid onset of the subsequent trial. In the current study, the stimulus presentation was much slower, occurring once every 2 seconds. This lengthening in delay between stimuli may have reduced interference from the preceding trial. As such, the relatively long interstimulus interval may have provided sufficient time for the representations of the previous trial or attractor state to dissipate, requiring less top-down attentional control in suppressing competing representations. Dopamine-related changes in the striatum provide a possible gating mechanism for coding new inputs and updating old ones (Cohen, Braver & Brown, 2002) over this time-frame, which is consistent with greater striatal activity being correlated with successful, rapid shifting to a new attentional set. Alternatively, the small sample size may have provided insufficient power to detect switch costs or striatal differences during switching. Examination of individual subjects' imaging and behav-

oral data showed reliable and consistent findings with the group averages, thus this alternative explanation seems less likely.

Consistent with our hypotheses, developmental differences were shown in faster responses and greater accuracy for the adults across all conditions, and in greater activation of frontoparietal regions for the switch relative to non-switch conditions. These findings may suggest a less mature endogenous frontoparietal attention system (Sohn *et al.*, 2000; Sowell *et al.*, 2003) in children or may reflect less explicit awareness of the switch between stimulus attributes in the attention-switching condition for children relative to adults. Although we did not assess the extent to which individuals were aware of the switch, developmental studies have suggested an increase in explicit awareness for underlying task structures with age (e.g. Karmiloff-Smith, 1986; Thomas & Nelson, 2001). For example, behavioral data from Thomas and Nelson (2001) show increases in explicit awareness for repetitive stimulus-response sequences in a serial reaction time task. Older children and adults demonstrate significantly more awareness than younger children, and are able to use this awareness to improve performance beyond the level attained through implicit learning alone.

The pattern of activity in caudate and frontoparietal cortical regions is interesting in light of recent findings by Sohn *et al.* (2000). They reported caudate, prefrontal and parietal activity in a more complex switching paradigm with adults. In that study, they showed greater caudate activity when there was no cue of a switch and greater frontoparietal activity when subjects were cued of a switch. In the current study, subjects were given no foreknowledge or instructions that a switch would occur, consistent with the increased activity of the caudate in the Sohn *et al.* study when there was no cue. This aspect of the task differs from traditional switching paradigms that explicitly cue the subject and may explain the lack of switching costs. Developmentally, our results suggest greater reliance on subcortical implicit systems (caudate) than cortical explicit systems (frontoparietal) in the performance of this task.

A secondary finding that distinguished adults from children was related to the pattern of activity in the fusiform gyrus, a region the adults activated more than the children. This region was activated during the shape discrimination condition relative to the color or switching condition for the adults and has been implicated in other studies of shape and object recognition (Sugio *et al.*, 1999; Ishai, Ungerleider, Martin & Haxby, 2000; Joseph & Gathers, 2002). Greater activity in this region for adults is consistent with the view that adults appreciate the configural properties of objects more

(Gauthier & Tarr, 2002). Children may use this strategy less and have a tendency to rely on more featural information when making discriminations (Savitsky & Izard, 1970; Carey & Diamond, 1977; Diamond & Carey, 1977).

In sum, the findings suggest that simple forced-choice switches of attention between stimulus attributes (e.g. color, shape) require minimal cognitive control and appear to be supported more by subcortical (e.g. caudate nucleus) than cortical regions (e.g. frontoparietal regions). This pattern of results suggests that the current attention-switching task differs from the traditional task-switching literature. The most striking difference is that the switching and non-switching conditions do not require that explicit cues and instructions be held on-line in order to attend the relevant task information. The two conditions are identical in terms of task instructions. Thus, the lack of cortical activity in the children and minimal recruitment of these regions in adults is consistent with minimal on-line representation of task demands. As such, children and adults show similar patterns of activity (in subcortical regions) and similar costs in reaction time between simple switching and non-switching conditions. Similar findings have been reported by our group (e.g. Casey *et al.*, 2002a) on tasks that require the subject to switch between blocks of one behavioral set in favor of another. In that study, costs as measured by per cent differences in reaction time between compatible and incompatible stimulus–response conditions did not show developmental differences, although overall reaction times and accuracy differed between children and adults. These findings may be relevant to the developmental literature on probabilistic learning showing early development in the ability to anticipate a stimulus and detect unexpected changes even in infancy (Johnson, Posner & Rothbart, 1991; Saffran, Aslin & Newport, 1996; Kirkham, Slemmer & Johnson, 2002). As such, our findings suggest early development of a neural mechanism for simple attention and learning behavior. Finally, the findings of robust activity in the caudate nucleus in this paradigm across development suggest that it may be a sensitive probe for detecting subtle caudate abnormalities in both developmental and adult clinical populations that have attention and learning deficits.

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