

## Maturation of Cognitive Processes From Late Childhood to Adulthood

*Beatriz Luna, Krista E. Garver, Trinity A. Urban, Nicole A. Lazar, and John A. Sweeney*

To characterize cognitive maturation through adolescence, processing speed, voluntary response suppression, and spatial working memory were measured in 8- to 30-year-old ( $N = 245$ ) healthy participants using oculomotor tasks. Development progressed with a steep initial improvement in performance followed by stabilization in adolescence. Adult-level mature performance began at approximately 15, 14, and 19 years of age for processing speed, response inhibition, and working memory, respectively. Although processes developed independently, processing speed influenced the development of working memory whereas the development of response suppression and working memory were interdependent. These results indicate that processing speed, voluntary response suppression, and working memory mature through late childhood and into adolescence. How brain maturation specific to adolescence may support cognitive maturation is discussed.

Mental abilities, including problem solving and reasoning abilities, continue to develop during adolescence (Anderson, Anderson, & Gartner, 2001; Siegler, 1978). These improvements are supported by development in specific core cognitive processes that are still immature in late childhood, including processing speed (Hale, 1990), voluntary response suppression (Diamond & Goldman-Rakic, 1989; Fischer, Biscaldi, & Gezeck, 1997), and working memory (Zald & Iacono, 1998). It is unclear, however, (a) when these processes begin to reach mature adult levels of performance, (b) if the development of these processes is interdependent, or (c) how these improvements in cognition relate to brain maturation that occurs during this time. To address these issues, we studied age-related changes in performance in a cross-sectional study of 8- to 30-year-olds on tasks assessing processing speed, voluntary response inhibition, and working memory abilities. We used a systems neuroscience model of cognition to make inferences about the neural basis of cognitive development in these domains.

Processing speed, usually measured by simple reaction time, reflects the efficiency with which information is processed. Processing speed has been found to decrease exponentially through childhood and adolescence across cognitive domains (Adams & Lambos, 1986; Hale, 1990; Kail, 1993; Ruffer, Grapenthin, Huey, & Patterson, 1985). Voluntary response suppression (also referred to as inhibitory control), the ability to filter out distractors and retain a response set, is crucial for choosing a course of action based on a cognitive plan over alternative task-irrelevant behaviors (Bjorklund & Harnishfeger, 1995; Dempster, 1992). Inhibitory control, though sometimes viewed as simple attention (Demetriou, Christou, Spanoudis, & Platsidou, 2002), is one of the integrative executive functions, that is, a process used for goal-directed behavior (Fuster, 1997). Voluntary response suppression has been found to develop throughout childhood (Fischer et al., 1997; Levin, Culhane, Hartmann, Evankovich, & Mattson, 1991; Luciana & Nelson, 1998; Munoz, Broughton, Goldring, & Armstrong, 1998; Paus, Babenko, & Radil, 1990) and adolescence (Ridderinkhof, Band, & Logan, 1999; Ridderinkhof, van der Molen, Band, & Bashore, 1997). Working memory, the ability to maintain and manipulate information online, is essential for the voluntary control of behavior based on internal plans (Baddeley, 1986). Its development is believed to underlie the emergence of complex mental abilities (Case, 1992; Dempster, 1981; Nelson et al., 2000). Similar to voluntary response suppression and processing speed, there is evidence suggesting that working memory continues to improve through childhood as reflected by improvements in memory span (Dempster, 1981) and working

---

Beatriz Luna, Krista E. Garver, and Trinity A. Urban, Laboratory of Neurocognitive Development, Department of Psychiatry, University of Pittsburgh; Nicole A. Lazar, Department of Statistics, Carnegie Mellon University; John A. Sweeney, Center for Cognitive Medicine, Department of Psychiatry, University of Illinois at Chicago.

We give special thanks to Melanie Wilds and Steve Hegedus who tested participants and assisted in data scoring, to all participants of this study, and to support from the following grants: MH01727, NARSAD, MH62134, HD35469, MH01433.

Correspondence concerning this article should be addressed to Beatriz Luna, Laboratory of Neurocognitive Development, Western Psychiatric Institute & Clinic, University of Pittsburgh, 3501 Forbes Avenue, Oxford Building Room 738, Pittsburgh, PA 15213. Electronic mail may be sent to [lunab@upmc.edu](mailto:lunab@upmc.edu).

memory for spatial locations (Swanson, 1999; Zald & Iacono, 1998).

Although early cognitive development during infancy (Diamond & Goldman-Rakic, 1989) and childhood (Chelune & Baer, 1986; Levin et al., 1991; Luciana & Nelson, 1998; Welsh, Pennington, & Groisser, 1991) has been well characterized, relatively little is known about the period of maturation through late childhood and adolescence when adult levels of performance are fully established. Although individual variability limits the ability to pinpoint a precise age of full cognitive maturation, estimating an age range when adult-level behavior becomes evident is feasible using approaches similar to those used for the determination of cognitive milestones in infancy and childhood. Characterizing this transitional age range is important not only for societal issues related to defining expectations for mature responsible behavior but also for characterizing the course of development and its abnormality in neurodevelopmental disorders.

Processing speed, voluntary response inhibition, and working memory are all integral to the cognitive control of behavior, yet each has a distinct role. Increased processing speed provides a basis for more rapid and efficient cognitive control of behavior; voluntary response suppression allows for the filtering of distractors and focusing on goal-directed behavioral planning; and working memory permits response selection, preparation, and maintenance of plans until the optimal time for their use. These processes often interact to support optimally adaptive behavior, and they are supported by overlapping, but distinct, neuronal processes and make unique contributions to cognitive control. It is not clear whether these processes develop independently or concurrently. Although these processes work interactively in the cognitive control of behavior, they demonstrate independent developmental characteristics (Demetriou et al., 2002). Improvements in processing speed have been found to support healthy developmental changes in working memory, which in turn help support the transition from concrete to abstract thinking (Demetriou et al., 2002; Fry & Hale, 1996). It has been proposed that response inhibition and working memory modulate each other as susceptibility to interference influences the efficiency of working memory, and working memory allows the maintenance of anticipatory and preparatory states that can effectively support voluntary response suppression (Bjorklund & Harnishfeger, 1990; Dempster, 1981). Despite these initial efforts, relatively little is known about the degree of

independence of these cognitive systems in a developmental context.

Although environmental factors play a primary role, biological timetables also influence the range of developmental progression. Concurrent with the development of mental abilities from late childhood into adolescence are brain maturational processes such as synaptic pruning (Huttenlocher, 1990) and myelination (Yakovlev & Lecours, 1967) that enhance neuronal transmission during this period. Synaptic pruning, the selective elimination of unnecessary neuronal connections (Giedd et al., 1999; Huttenlocher, 1990; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999), can speed and enhance the precision of information processing. Increased myelination, the insulation of established axonal connections that optimizes the propagation of electrical signals throughout the central nervous system (Giedd et al., 1999; Yakovlev & Lecours, 1967), allows for the faster responses and superior integration of widely distributed circuitry necessary for the top-down modulation of behavior. Characterizing the neural basis of cognitive development is important to identify the parameters within which development can vary. Understanding the relationship between cognitive development and brain maturation, however, has been difficult in the absence of direct neurophysiological measures and, as such, has remained understudied. Initial behavioral studies suggest that adolescent development may be linked to the late maturation of prefrontal cortex (Diamond & Goldman-Rakic, 1989), which continues to develop through adolescence (Huttenlocher, 1990). The role of prefrontal cortex in supporting response suppression and working memory has been confirmed in humans in lesion (Pierrot-Deseilligny, 1991), pharmacological challenge (Luciana, Collins, & Depue, 1998), and neuroimaging studies (Sweeney et al., 1996). Developmental fMRI studies support these findings (Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002; Casey et al., 1995; Luna et al., 2001; Rubia et al., 2000; Tamm, Menon, & Reiss, 2002). By using neuroscience-based methods, including behavioral tasks whose neural substrate has been well characterized, we can take significant strides toward understanding the linkages between brain and cognitive maturation.

Neuroscience methods that use the eye movement system (oculomotor system) to understand cognition are particularly well suited for answering developmental questions. In oculomotor tasks, eye movement responses (saccades) are made in response to cognitive demands. The visually guided saccade (VGS) task, where participants are instructed to

fixate a suddenly appearing stimulus, can be used to assess processing speed (Leigh & Zee, 1999). The antisaccade task measures response inhibition by requiring participants to suppress a prepotent tendency to make a saccade to a suddenly appearing visual stimulus (Everling & Munoz, 2000; Hallett, 1978; Rivaud, Muri, Gaymard, Vermersch, & Pierrot-Deseilligny, 1994). The oculomotor delayed response (ODR) task (Hikosaka & Wurtz, 1983) is the prototypical test of spatial working memory that requires the execution of an eye movement guided only by the memory of a previously presented visual target location. The VGS task is an exogenous task requiring a response to external stimuli with only minimal cognitive processing. The antisaccade and ODR tasks are endogenous tasks requiring a voluntary cognitively driven response.

Compared with traditional psychological testing, oculomotor tasks are particularly well suited for evaluating the maturation of these cognitive processes across a wide age range. First, task instructions are straightforward so that they are understood throughout the age span and are less confounded by verbal or learning strategies that can complicate evaluation of developmental progression (Cohen & Ross, 1978; Ross, Radant, Young, & Hommer, 1994). Second, in eye movement tasks, the encoding and response processes use the same domain (visual), whereas in typical psychological tasks translation is required from the stimulus input modality (visual, auditory) to behavior measures (hand motor, speech), degrading the direct assessment of the cognitive process of interest. Third, independent cognitive processes can be accessed more directly with eye movement studies than with the multicognitive processes involved in typical testing. In the VGS task, there are minimal demands for response inhibition and working memory, providing a relatively direct assessment of processing speed. The antisaccade task requires inhibition of a suddenly appearing stimulus, requiring inhibition with minimal working memory demands. In the ODR task, there are no distractors interfering with the remembered eye movement response, providing a direct measurement of working memory. Finally, oculomotor tasks are especially well suited for informing us about the brain basis of development because these tasks have been used to characterize the neural basis of cognition in single-cell studies of nonhuman primates (Barbas, 2000; Funahashi, Chafee, & Goldman-Rakic, 1993; Funahashi & Takeda, 2002; Goldman-Rakic, 1988; Hikosaka & Wurtz, 1983;). The VGS task has been used to delineate the brain circuitry underlying oculomotor and attention systems (Cor-

beta et al., 1998; Luna et al., 1998; Petit, Clark, Ingeholm, & Haxby, 1997). Studies with the antisaccade task have revealed that a specific corticocortical circuitry supporting top-down modulation of behavior is necessary for response inhibition (Funahashi, Chafee, & Goldman-Rakic, 1993). The ODR task has been used to identify delay-dependent cells in prefrontal cortex believed to underlie working memory capacity (Funahashi & Takeda, 2002). These methods have given us a specific neural framework supporting eye movements that can provide insight into the neural basis of human cognitive development albeit in an indirect manner.

The purpose of this study was to characterize the maturation of cognition into adulthood and start understanding its link to brain maturation. We studied the development of three cognitive processes: processing speed, inhibitory control, and spatial working memory using oculomotor tasks in a cross-sectional design with a large population. We used this approach so we could make inferences about how maturation of specific brain circuitry might enhance each cognitive process. The following predictions were made. First, the transition to mature cognitive control of behavior will occur in adolescence for the endogenous tasks, whereas basic sensorimotor function involved in the ability to reflexively redirect gaze will be in place by the youngest ages of assessment. Second, although development will occur on a similar timeline for each cognitive process, maturation of these processes will be partially independent. Third, the age of maturation for these cognitive processes will be similar to the ages when anatomic brain maturation approaches adult levels.

## Method

### *Participants*

To characterize the transition to adult levels of cognitive control of behavior, we used participants from 8 to 30 years of age to include late childhood and early adulthood. This approach allowed us to establish developmental progressions through adolescence with comparable ranges before and after this milestone. Participants were 245 individuals (females = 93, males = 152); approximately 84% were Caucasian, 11% were African American, 3% were Asian, 1% were Hispanic, and 1% were other. The mean socioeconomic status (SES) considering parental SES for children and adolescents and individual SES for adults was 2.53 ( $SD = 1.06$ ). Participants were recruited through advertisements

in the local newspapers. All participants were medically healthy and free of medications known to affect eye movements and provided informed consent before participating in the study. They also had a negative family history in first-degree relatives for developmental cognitive disorders, learning disabilities, autism, affective disorders, and anxiety disorders. Participants were compensated for participation.

### Materials

Stimuli were densely packed, individually addressable red light emitting diodes (LEDs) subtending 0.2 degrees of visual angle that were embedded in a circular arc (1 m radius) at eye level in the horizontal plane and illuminated under computer control. Eye movement measurements were obtained with direct current electro-oculography (EOG) recordings of each eye (Grass Neurodata 12 Acquisition System). Data from the right eye were scored unless there were problems with this recording (i.e., signal clipping or high noise artifact). Electrodes placed above and below the left eye were used to detect blinks. All participants had at least 20/40 uncorrected or corrected visual acuity.

### Design and Procedure

Participants sat in a darkened room facing the stimulus arc with their chin on a chin rest and their head securely strapped to a head mount. The experimenter was in an adjacent room and used an intercom to provide instructions. Eye movement recordings were monitored throughout the testing to identify head movement and to determine whether participants needed to be realerted to task instructions. A brief tone originating behind the central fixation target sounded concurrently with the onset of a central fixation light to indicate the beginning of each trial. The fixation light was extinguished when peripheral stimuli were presented, except during the ODR task. The VGS task was the first task presented to avoid possible impact of previous performance of more complicated paradigms on this simple sensorimotor task. This task order also established a response tendency to look toward peripheral lights that needed to be suppressed in the antisaccade task that was presented next, followed by the ODR task. Figure 1 depicts each task.

**VGS task** Participants were required to fixate the central stimulus for 1.5 to 2.5 s, and then look immediately toward a peripheral light appearing at any of three angular displacements, 10, 20, or 30

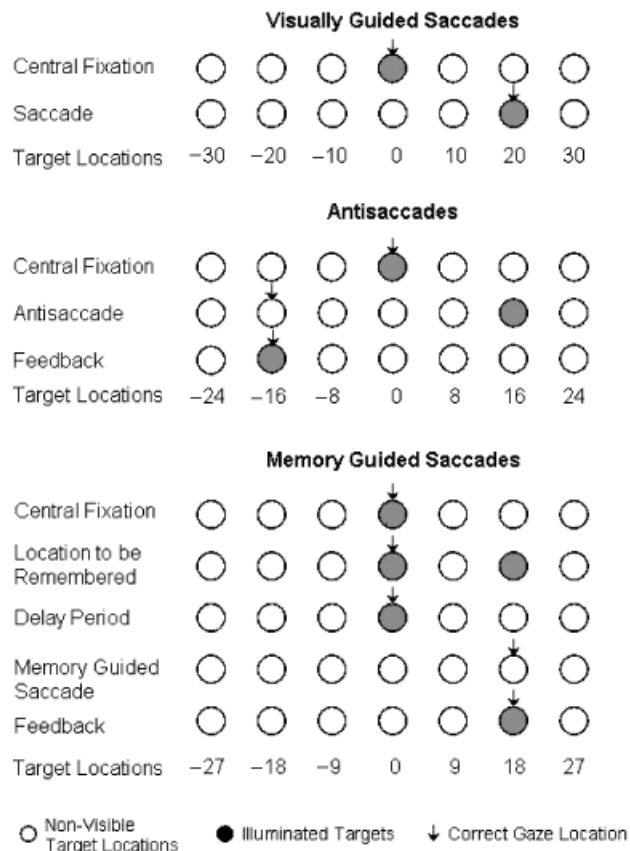


Figure 1. Description of tasks. Circles indicate possible target locations. Only the lighted cue noted by filled circles was visible during testing. Arrows indicate the correct location of gaze.

degrees of visual angle to the left or right of central fixation. Peripheral targets were presented for 1.5 s. The timing of presentation and location of the peripheral targets were unpredictable. The latency, accuracy (error in degrees of visual angle), and peak velocity of primary saccades to peripheral targets were measured. Fifty-four trials were presented.

**Antisaccade task** In this task, participants were required to fixate a central stimulus for 3 to 5 s, after which a peripheral stimulus appeared for 1.5 s at one of three locations, 8, 16, or 24 degrees, to the left or right of center fixation. Because suppressing saccades to targets presented close to the fovea is more difficult (performance is poorer; Smyrnis et al., 2002), varying target eccentricity is one way to vary task difficulty. Participants were not to look at the light but were to move their eyes immediately to the mirror location in the opposite direction; 1.5 s after the peripheral stimulus was presented, it was extinguished and feedback was provided by a light appearing at the location where participants should

have been fixating. Thirty-six trials were presented. The percentage of trials in which the participant looked toward the peripheral targets (response-suppression errors) and the latency, peak velocity, and accuracy of saccades toward the correct location were measured. Correct antisaccade trials were defined as those where the participant did not look at the peripheral target but looked at the opposite visual field. Incorrect trial response-suppression errors were defined as trials when participants made saccades toward the peripheral target. After making response-suppression errors, participants corrected their mistake on almost all trials by looking correctly into the opposite hemifield. The antisaccades that followed response-suppression errors were not included in analyses of saccade latency, velocity, or accuracy for antisaccade task performance. The primary variable of interest was the proportion of trials with response-suppression errors. This is appropriate because there was no evidence of age-related differences in speed-accuracy trade-off functions. Adults had shorter latencies than did children and a lower proportion of prosaccade errors. Additionally, when we performed a median split by latency and performed a *t* test to compare error rates across participants, this was not significant,  $t(75) = 0.04$ ,  $p = 0.97$ .

**ODR task** While participants held central fixation, a target was presented for 100 ms at 9, 18, or 27 degrees of visual angle to the right or left of center. Participants were not to look at the peripheral target when it appeared but to remember its location while holding central fixation. After a varying delay period of 1, 2, 4, or 8 s during which participants had to remember the peripheral location, the central light was extinguished, which was the participants' cue to look at the place where the peripheral target had been presented. After 2 s, a target appeared at the to-be-remembered location and participants were to fixate that target. This cue provided feedback about performance on each trial. Twenty-four trials were presented. Measurements obtained included the number of failures to suppress saccades to peripheral targets shortly after their brief presentation (response-suppression failures), peak velocity, latency and accuracy of primary saccades, and the accuracy of fixation after participants made as many saccades as required to fixate the remembered location. We measured the accuracy of the initial and final saccades to the remembered location. The initial saccade is primarily driven by processes supporting a voluntary response in the absence of a visual stimulus, planned during the delay period and initiated when participants drive their gaze to the remembered lo-

cation. The last saccade is driven primarily by spatial information in working memory and reflects a participant's effort to correct for any disparity between eye position and remembered target location that persists after prior saccades. The initial attempt to direct the eyes to a remembered location reflects how accurately participants could voluntarily shift their eyes to a remembered location, and the final resting eye position (after as many saccades as needed were made to achieve the desired target location) primarily reflects the accuracy of the remembered spatial location information maintained in working memory.

Before each task, careful standardized instructions were provided until participants demonstrated understanding of the procedure. In the antisaccade and ODR tasks, participants were trained using slow presentations of the task during which the tester pointed locations where the participants were to look and explained verbally why this was the correct location. Participants were then asked to explain the task to the tester. These procedures, together with the fact that all participants made some correct responses on all tasks, ensured that lack of comprehension of task instructions was not the basis for performance failure.

#### *Data Processing*

Eye movement recordings were analyzed off-line using customized software developed in this laboratory. Data were smoothed with a finite impulse response filter designed to pass through a signal between 16 and 70 Hz to reduce high-frequency noise with a minimum of signal distortion. The passband frequencies were chosen empirically with custom filter design software. Only latencies greater than 70 ms were included to eliminate premature responses that were not guided by task stimuli. Eye position recordings were converted from raw voltages to degrees of visual angle for each trial independently using data acquired while participants fixated the central fixation cue and the peripheral location toward which participants were to move their eyes. Saccade onset was identified using velocity information, with the duration of saccades computed as the time between the rise and fall of eye velocity beyond a 30 deg/s criterion. Performance on each trial was reviewed to identify blink artifacts and occasional failures of the software to identify primary saccades. Quantitative assessment of oculomotor function was performed without knowledge of participant characteristics.

### Data Analysis

We performed several analyses to answer the following questions.

*What is the shape of the curve characterizing improvements in cognition with age?* Different curve-fitting regression analyses (linear, exponential, inverse, logarithmic, quadratic, and cubic) were applied for each of the response measures with age as a continuous predictor variable. This allowed us to identify the variables that changed significantly with age and to characterize the nature of developmental changes. We also applied the three-parameter exponential function described by Kail (1991a), which has been used successfully to characterize developmental improvements in reaction time. We used the last age bin (in the 2-year binning) as the reference on which to calculate the slope of the change, denoted  $mi$  in Kail's equation:  $mi = 1 + b * \exp(-c * age)$ , where we need to estimate  $b$  and  $d$ . This model considers age as a categorical variable that is compared with the goal state of adulthood.

*What is the approximate age when adult-level performance becomes evident?* Changepoint analyses were performed to estimate the age of transition to adult-level performance on variables that the regression analyses indicated had significant age-related performance change. Changepoint analyses, which can only be applied to a cross-sectional design because they require independent samples, indicate the time point where performance changes. For this study, we were interested in when performance stops improving, after which adult-level performance is achieved. A piecewise linear regression was fit to the data, with the split point (i.e., changepoint) being placed at each age in turn, where age was the independent variable. The changepoint was determined as the age that minimized the residual sum of squares of all of the piecewise linear models. Given that the changepoint analyses have not been used extensively in the child development literature, we also performed  $t$  tests comparing performance at different age bins to confirm the transition age.

*Are the cognitive processes investigated interdependent?* To explore the interdependence of the three cognitive systems, we calculated correlations and explored the relationship among performance parameters on different tasks using multiple regressions. Multiple regression analyses allowed us to enter all possible task measures into one equation as opposed to multiple partial correlation analyses. We standardized all task measures using  $z$  scores, enabling us to investigate more accurately the relationships among different task measures. To portray the

relationship between age and performance with one value, we used the residuals of the inverse regression, which was found to have the best fit with the data. A stepwise multiple regression analysis was performed to estimate how much of the variability in each cognitive system was predicted by development in the other cognitive systems. This procedure allowed us to obtain a measure of the interdependence of the three cognitive systems of interest within a developmental context.

*Were age effects present for laterality, sex difference, or task difficulty?* Repeated measures analyses of variance (ANOVAs) were performed with age as a categorical variable to test for effects of laterality (visual field of stimulus presentation), sex differences, and task difficulty (delay duration for the ODR task and target eccentricity for the other tasks). Age was divided into categorical ranges for these analyses (8 to 9 years old,  $N = 26$ ; 10 to 11 years old,  $N = 29$ ; 12 to 13 years old,  $N = 22$ ; 14 to 15 years old,  $N = 26$ ; 16 to 17 years old,  $N = 19$ ; 18 to 19 years old,  $N = 29$ ; 20 to 25 years old,  $N = 62$ ).

## Results

### Curve-Fitting Analyses: Shape of Developmental Progression

Compared with linear, exponential, quadratic, and cubic models, inverse regression models [ $Y = b_0 + (b_1/t)$ ] provided the highest level of significance and  $r^2$  between age and response variables. Inverse models demonstrated fits of age with latencies of VGS,  $F(1, 243) = 101.32$ ,  $p < .0001$ ,  $r^2 = 0.29$ ; antisaccade,  $F(1, 243) = 26.12$ ,  $p < .0001$ ,  $r^2 = 0.10$ ; and ODR,  $F(1, 243) = 91.31$ ,  $p < .0001$ ,  $r^2 = 0.27$ , to remembered locations (see Figure 2 and Table 1). Significant age-related change was also shown for the proportion of response-suppression errors in the antisaccade task,  $F(1, 243) = 116.92$ ,  $p < .0001$ ,  $r^2 = 0.33$  (see Figure 3), but not in the ODR task. In the ODR task, age was significantly related to accuracy of the initial saccades,  $F(1, 243) = 109.93$ ,  $p < .0001$ ,  $r^2 = 0.31$ , and accuracy of the final resting eye positions,  $F(1, 243) = 99.62$ ,  $p < .0001$ ,  $r^2 = 0.29$  (see Figure 4). The accuracy of visually guided and antisaccades did not change significantly with age. Similar results were obtained when applying the Kail (1991b) model to the latency to respond from each task (see Table 2).

### Transition to Mature Performance

The changepoint occurred at age 15 for the latency to initiate a saccade regardless of the cognitive

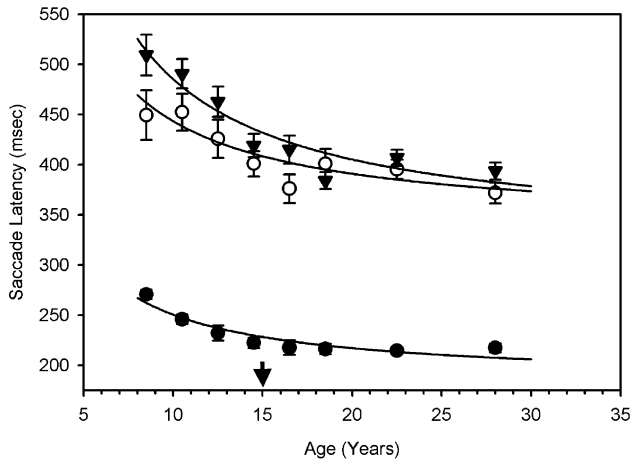


Figure 2. Mean  $\pm 1$  standard error of the mean (SEM) of the latency to initiate a saccade in each task for each age group. Solid circles depict the latency to initiate a saccade to a visual stimulus during the visually guided saccade (VGS) task. Open circles depict the latency to initiate an eye movement to the opposite location of a visual target in the antisaccade (AS) task. Solid triangles depict the latency to initiate an eye movement to a remembered location in the oculomotor delayed response (ODR) task. Thick lines indicate the inverse curve fit on the mean latency to initiate an eye movement response in milliseconds by age in years. Arrows depict the ages at which changepoint analyses indicate adult levels of performance were reached.

aspects of the task (see Figure 2). Results indicated a changepoint at age 14 for the maturation of response-suppression errors (see Figure 3) and for the accuracy of the initial memory-guided saccade (see Figure 4). The final changepoint for the accuracy of the final resting position in the ODR task was age 19 (see Figure 4).

*T* tests comparing performance in the different age bins confirm the results of the changepoint

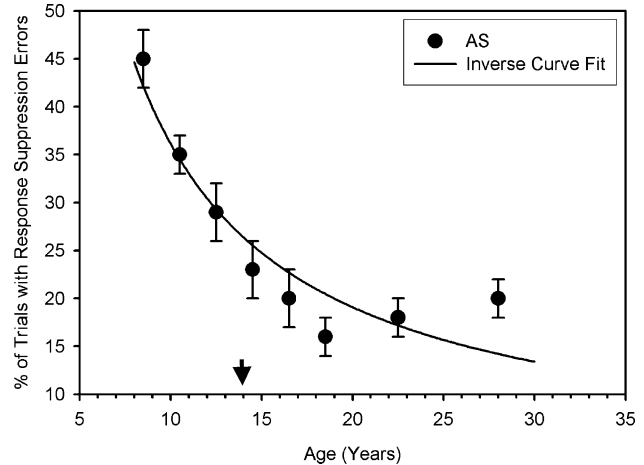


Figure 3. Solid circles depict the mean  $\pm 1$  standard error of the mean (SEM) for the percentage of trials with a response-suppression failure in the antisaccade (AS) task. Thick lines depict the inverse curve fit on the response-suppression failures by age in years. The arrow depicts the age at which changepoint analyses indicate adult level of performance were reached.

analyses. *T* tests (see Figures 2–4) corrected for multiple comparisons (six tasks on independent 2-year age groups, corrected  $p < .008$ ) indicated that by 14 to 15 years of age, performance was equivalent to that of adults for most variables except the latency to initiate an antisaccade and the accuracy of the final memory-guided saccade. The latency to initiate a visually guided saccade was longer in the 8- to 9-year-olds,  $t(86) = 10.82, p < .0001$ ; 10- to 11-year-olds,  $t(89) = 6.01, p < .0001$ ; and 12- to 13-year-olds,  $t(82) = 2.74, p < .001$ , compared with 20- to 25-year-olds. The latency to initiate an antisaccade was longer in the 8- to 9-year-olds,  $t(86) = 2.47, p = .015$

Table 1

Parameters From the Inverse Regression Function With Age for Each Variable

	Significance of the inverse fit			Constant (intercept)			Age (slope)		
	$R^2$	SE	$F(1, 243)$	$b_0$	SE	$t$ value	$b_1$	SE	$t$ value
VGS latency	.29	26.69	101.32**	183.45	4.68	39.19**	669.32	66.49	10.07**
AS latency	.10	82.47	26.12**	338.37	14.46	23.40**	1049.96	205.45	5.11**
ODR latency	.27	67.37	91.31**	324.98	11.82	27.50**	1604.00	167.86	9.56**
AS <i>P</i> error	.32	0.13	116.92**	0.02	0.02	0.95	3.40	0.31	10.81**
ODR <i>P</i> error	.01	0.07	3.50	0.03	0.01	2.80*	0.32	0.17	1.87
ODR accuracy of 1 <sup>st</sup> saccade	.31	1.17	109.92**	1.79	0.21	8.66**	30.71	2.93	10.49**
ODR accuracy of last saccade	.29	0.88	99.62**	1.45	0.15	9.42**	21.87	2.19	10.00**
VGS accuracy	.01	0.55	1.81	1.68	0.10	17.29**	1.85	1.37	1.35
AS accuracy	.01	1.64	1.28	6.19	0.29	21.53**	4.62	4.09	1.13

Note. VGS = visually guided saccade; AS = antisaccade; ODR = oculomotor delayed response.

\* $p < .05$ . \*\* $p < .01$ .

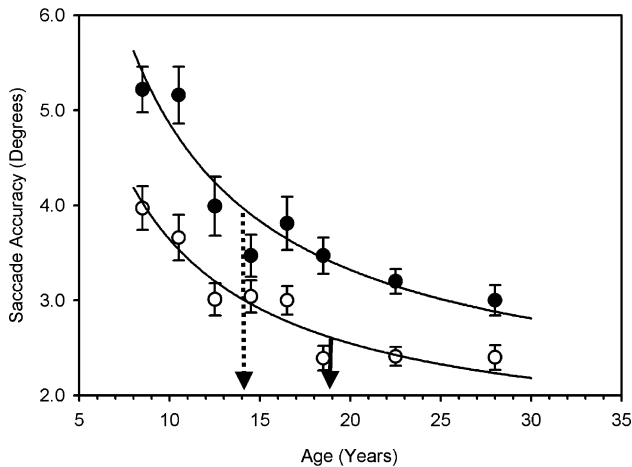


Figure 4. Mean  $\pm$  1 standard error of the mean (SEM) of the accuracy to initiate a memory-guided saccade (solid circles) and the accuracy of the final gaze location (open circles) in the oculomotor delayed response task for each age group. Thick lines indicate the inverse curve fit for these data across the age range studied. Arrows depict the age at which changepoint analyses indicate adult levels of performance were reached.

(not significant with correction for multiple comparison), and 10- to 11-year-olds,  $t(89) = 3.01$ ,  $p < .001$ , compared with the adult group. The latency to initiate a memory-guided saccade was longer in the 8- to 9-year-olds,  $t(86) = 33.31$ ,  $p < .0001$ ; 10- to 11-year-olds,  $t(89) = 5.38$ ,  $p < .0001$ ; and 12- to 13-year-olds,  $t(82) = 3.45$ ,  $p < .001$ , compared with the 20- to 25-year-olds. The proportion of antisaccade errors was higher in the 8- to 9-year-olds,  $t(86) = 9.23$ ,  $p < .0001$ ; 10- to 11-year-olds,  $t(89) = 6.06$ ,  $p < .0001$ ; and 12- to 13-year-olds,  $t(82) = 3.59$ ,  $p < .001$ , compared with the 20- to 25-year-olds. The accuracy of the initial memory-guided saccade was better in the 20- to 25-year-olds than in the 9- to 10-year-olds,

$t(86) = 8.13$ ,  $p < .0001$ ; 11- to 12-year-olds,  $t(89) = 7.07$ ,  $p < .0001$ ; and 12- to 13-year-olds,  $t(82) = 2.83$ ,  $p < .01$ . The accuracy of the final resting eye position in the ODR task was better in the 20- to 25-year-olds than in the 8- to 9-year-olds,  $t(86) = 7.33$ ,  $p < .0001$ ; 10- to 11-year-olds,  $t(89) = 5.75$ ,  $p < .0001$ ; 12- to 13-year-olds,  $t(82) = 3.09$ ,  $p < .01$ ; 14- to 15-year-olds,  $t(86) = 3.38$ ,  $p < .001$ ; and 16- to 17-year-olds,  $t(79) = 3.00$ ,  $p < .01$ .

#### Correlation and Multiple Regression Analyses: Interdependence of Cognitive Processes

In Table 3 we present the results of correlations between each of the variables. Response latency for all tasks was significantly correlated. Latency of visually and memory-guided responses correlated with prosaccade error rates in the antisaccade task. Prosaccade error rates were correlated with both measures of response accuracy in the ODR task, which were correlated with each other. Neither prosaccade error rate in the antisaccade task nor accuracy in the ODR task was associated with variability in the latency to initiate a saccade to a visual target in the VGS task, suggesting that the development of processing speed proceeds relatively independently from the development of response inhibition or working memory abilities. Accuracy of the final resting eye position in the ODR task (the accuracy measure most representative of maintenance capacity of working memory) accounted for 2% of the variability in prosaccade error rate in the antisaccade task (adjusted  $r^2 = .02$ ,  $F = 6.25$ ,  $p < .05$ ), and adding latency of saccade initiation in the VGS task did not significantly increase  $r^2$ . This result suggests that although development of response inhibition is primarily independent of the develop-

Table 2  
Parameters for Kail's (1991b) Exponential Model

	<i>b</i>	<i>t</i> value ( <i>df</i> = 7)	<i>c</i>	<i>t</i> value ( <i>df</i> = 7)	Residual standard error
VGS latency	3.92 (0.68)	5.79	0.32 (0.02)	17.32*	.008**
AS latency	0.76 (0.31)	2.56	0.15 (0.04)	4.10*	.063**
ODR latency	1.69 (0.70)	2.41	0.20 (0.04)	4.90*	.043**
AS <i>P</i> error	22.37 (16.04)	1.40	0.33 (0.08)	4.35*	.162
ODR <i>P</i> error					
ODR accuracy of 1st saccade	3.36 (1.09)	3.10	0.17 (0.03)	5.59*	.099*
ODR accuracy of last saccade	3.74 (1.61)	2.33	0.20 (0.04)	4.88*	.088
VGS accuracy	0.18 (0.21)	0.88	0.06 (0.08)	0.80	.077
AS accuracy	7.26 (208.17)	0.03	0.66 (3.30)	0.20	.053

Note. *b* = intercept; *c* = decay parameter; VGS = visually guided saccade; AS = antisaccade; ODR = oculomotor delayed response.  
\* $p < .05$ . \*\* $p < .01$ .



Table 3

*Intercorrelations ( $r^2$ ) for Performance Parameters for the Visually Guided Saccade, Antisaccade, and Oculomotor Delayed Response Tasks*

	Visually guided saccade		Antisaccade		Oculomotor delayed response			
	Accuracy	Latency	Accuracy	<i>P</i> errors	Latency	Accuracy	Rest accuracy	<i>P</i> errors
Visually guided saccade								
Saccade latency	-.13*	.46***	.06	.29***	.50***	.39***	.38***	.01
Saccade accuracy		-.11**	.10	.15*	-.04	.25***	.12	.01
Antisaccade								
Saccade latency			-.14*	.11	.30***	.15*	.25***	-.09
Saccade accuracy				.15*	.13*	.18**	.14*	.07
<i>P</i> errors					.44***	.41***	.42***	.39***
Oculomotor delayed response								
Saccade latency						.36***	.43***	.16*
Saccade accuracy							.67***	.13*
Rest accuracy								.15*

\* $p < .05$ , two-tailed. \*\* $p < .01$ , two-tailed. \*\*\* $p < .001$ , two-tailed.

ment of processing speed, working memory does modestly contribute to its maturation. Prosaccade error in the antisaccade task accounted for 2% of the variability in the accuracy of primary memory-guided saccades (adjusted  $r^2 = .02$ ,  $F = 6.25$ ,  $p < .05$ ), and adding latency to initiate a saccade to a visual target modestly increased the fit (adjusted  $r^2 = .03$ ,  $F = 5.27$ ,  $p < .05$ ). This result suggests that the development of working memory is primarily independent of development of other cognitive systems, though development of response inhibition and processing speed contribute to the maturation of this process.

#### ANOVAs: Differences in Development

Overall results are presented separately for each age group in Table 4. Confirming the preceding curve-fitting analyses, the latency to initiate an eye movement response, the percentage of response-suppression errors, and the accuracy to make a response to a remembered visual target improved with age.

**Laterality** Responses to stimuli presented in the right visual field were significantly better than those presented in the left visual field for all measures of antisaccades and for saccade velocity and accuracy in the VGS task, but there was no Age  $\times$  Visual Field interaction. There was no main effect for visual field in relation to response accuracy in the ODR task.

**Task difficulty** There was a Visual Field  $\times$  Target Eccentricity (task difficulty)  $\times$  Age effect,  $F(7, 237) = 2.20$ ,  $p < .05$ , for prosaccade errors in the antisaccade task. Participants younger than 18 had a

more pronounced visual field effect; that is, more errors were committed in response to stimuli presented in the right than left visual field, and this occurred for trials with the closest target eccentricity, which has the highest demand for response inhibition. As expected, there was a main effect for delay,  $F(1, 237) = 273.37$ ,  $p < .0001$ , in the ODR task, where response latencies were longer when delay periods were briefer, probably because response preparation is not yet complete before the cue to initiate the remembered saccades is presented. There was a Delay Period Duration  $\times$  Age interaction,  $F(7, 237) = 2.84$ ,  $p < .01$ , in the latency to initiate a saccade in the ODR task, where the shortest delay period had the smallest age effect: main effect of age with 1-s delay,  $F(7, 244) = 2.37$ ,  $p < .05$ ; 2-s delay,  $F(7, 244) = 5.01$ ,  $p < .0001$ ; 4-s delay,  $F(7, 244) = 11.72$ ,  $p < .0001$ ; and 8-s delay,  $F(7, 244) = 13.63$ ,  $p < .0001$ . There was no Delay  $\times$  Age interaction in the accuracy of saccades in the ODR task.

The VGS task inherently imposes fewer cognitive demands than do the antisaccade and ODR tasks. This was evident in the differences in the latency to initiate an eye movement in the different tasks,  $F(1, 242) = 14775.68$ ,  $p < .0001$  (see Table 4 and Figure 2), where the mean latency to initiate a response to a visual target ( $M = 227$  ms,  $SD = 32$ ) was considerably shorter than the cognitively driven responses (antisaccade  $M = 407$ ,  $SD = 87$ ; ODR  $M = 430$ ,  $SD = 79$ ). There was an Age  $\times$  Task latency effect,  $F(7, 237) = 5.81$ ,  $p < .0001$ , where the age effect was more significant for the VGS task,  $F(7, 237) = 15.96$ ,  $p < .0001$ , or ODR task,  $F(7, 237) = 13.77$ ,  $p < .0001$ , than for the antisaccade task,  $F(7, 237) = 3.74$ ,  $p < .01$ .

Table 4

*Means and Standard Deviations by Age Groups for Each Key Performance Parameter for Each Task*

Age group	Latency			Accuracy of initial saccade			Accuracy of final saccade	Proportion of trials with response suppression errors	
	VGS <i>M (SD)</i>	AS <i>M (SD)</i>	ODR <i>M (SD)</i>	VGS <i>M (SD)</i>	AS <i>M (SD)</i>	ODR <i>M (SD)</i>	ODR <i>M (SD)</i>	AS <i>M (SD)</i>	ODR <i>M (SD)</i>
8–9 ( <i>N</i> = 26)	271 (24)	449 (126)	509 (104)	1.73 (0.43)	6.71 (2.09)	5.22 (1.21)	3.97 (1.19)	.45 (.14)	.11 (.11)
10–11 ( <i>N</i> = 29)	246 (26)	452 (100)	491 (79)	2.00 (0.70)	6.97 (1.91)	5.16 (1.64)	3.66 (1.28)	.35 (.13)	.04 (.05)
12–13 ( <i>N</i> = 22)	232 (35)	426 (90)	463 (70)	1.90 (0.49)	5.96 (1.14)	3.99 (1.45)	3.01 (0.78)	.29 (.13)	.03 (.04)
14–15 ( <i>N</i> = 26)	222 (27)	401 (64)	419 (59)	1.79 (0.50)	6.61 (1.81)	3.47 (1.10)	3.04 (0.85)	.23 (.15)	.05 (.06)
16–17 ( <i>N</i> = 19)	218 (32)	376 (62)	415 (60)	1.99 (0.59)	6.56 (1.24)	3.81 (1.24)	3.00 (0.67)	.20 (.12)	.03 (.04)
18–19 ( <i>N</i> = 29)	216 (28)	401 (78)	384 (45)	1.68 (0.49)	6.43 (1.27)	3.47 (1.04)	2.39 (0.70)	.16 (.11)	.05 (.06)
20–25 ( <i>N</i> = 62)	214 (22)	395 (76)	407 (64)	1.74 (0.55)	6.23 (1.54)	3.20 (1.00)	2.41 (0.77)	.18 (.12)	.06 (.08)
26–30 ( <i>N</i> = 32)	217 (25)	372 (58)	394 (49)	1.71 (0.56)	6.70 (1.79)	3.00 (0.92)	2.40 (0.74)	.20 (.12)	.05 (.05)
Total ( <i>N</i> = 245)	227 (32)	407 (87)	430 (79)	1.80 (0.55)	6.50 (1.64)	3.80 (1.41)	2.89 (1.04)	.24 (.15)	.05 (.07)

Note. VGS = visually guided saccade; AS = antisaccade; ODR = oculomotor delayed response.

Response accuracy also differed with the cognitive demands of each task,  $F(1, 242) = 692.30$ ,  $p < .0001$ , where the accuracy of a response to a visual target (VGS  $ME = 1.8$  degrees,  $SD = .55$ ) was better than the cognitively driven responses (antisaccade  $M = 6.5$  degrees,  $SD = 1.6$ ; ODR  $M = 3.8$  degrees,  $SD = 1.4$ ). The proportion of response-suppression errors was greater in the antisaccade task than in the ODR task,  $F(1, 237) = 657.13$ ,  $p < .0001$ , with the antisaccade task ( $M = .24$ ,  $SD = .15$ ) generating a higher rate of errors than the ODR task ( $M = .05$ ,  $SD = .07$ ).

*Sex differences* In the VGS task, females had shorter saccade latencies,  $F(1, 229) = 4.12$ ,  $p < .05$ , and higher accuracy,  $F(1, 229) = 14.27$ ,  $p < .01$ , than did males. There were no other main effects of sex or Sex  $\times$  Age interactions.

### Discussion

We characterized the transition to mature cognitive control of behavior by measuring age-related changes in processing speed, voluntary response suppression, and working memory. Results demonstrate that voluntary/cognitive control of behavior continues to develop through adolescence. These cognitive processes developed in mostly independent streams, though there was a modest, yet significant, interrelationship among them.

#### *Profile of Development*

Regression analyses demonstrated that developmental change in performance on our oculomotor

tasks was best represented by an inverse curve function rather than linear, exponential, logarithmic, or quadratic functions. Similar to Kail and Park (1992), we found that an exponential fit significantly represented developmental changes, including those depicting improvements in reaction time; however, the inverse fit yielded higher levels of association between response variables and age. The inverse curve allows for steep changes and asymptotes to occur in one function, indicating that from childhood to adolescence there is a large improvement in performance followed by a plateau between late adolescence and early adulthood. The three-parameter exponential curve yielded a developmental shape similar to the function depicted for synaptic pruning and age in prefrontal cortex (Huttenlocher, 1990), underscoring the contribution of brain-maturation factors to cognitive development. These results provide strong evidence that processing speed, voluntary response suppression, and spatial working memory mature in middle to late adolescence.

As expected, peak saccade velocity across tasks and accuracy in the VGS task did not change over the age range investigated (Abel, Troost, & Dell'Osso, 1983; Cohen & Ross, 1978). These findings confirm that the basic motor mechanisms for saccade control are mature by our youngest age of 8 years.

Our results indicate that hemispheric specialization for cognitive processing of visuospatial information is mature by the youngest ages, suggesting that important aspects of cortical organization become established before synaptic pruning and

myelination are complete. Hemispheric specialization may be an earlier component of brain maturation that is a substrate on which later neocortical specialization and organization take place.

For the most part, there were no Sex  $\times$  Age effects, suggesting that the cognitive development measured in this study is not gender biased. This result agrees with studies indicating few sex differences in brain morphology once relative brain size is controlled (Giedd, Castellanos, Rajapakse, Vaituzis, & Rapoport, 1997; Sowell, Trauner, Gamst, & Jernigan, 2002). Our results did show, however, that females had shorter latencies and higher accuracy in VGS tasks than did males. Accuracy and latency in the VGS task reflects processes underlying basic sensorimotor control, in contrast to these measures in the antisaccade and ODR tasks, which reflect a higher level of cognitive control of behavior. The basis for these gender differences is unclear. One possible factor is that the caudate nucleus is larger in females than in males after relative brain size has been controlled (Giedd et al., 1997; Sowell et al., 2002). The caudate contributes to oculomotor control via its pathway to substantia nigra and superior colliculus (Leigh & Zee, 1999). Another factor that may influence the age range of maturation is pubertal development. Pubertal changes are significant in adolescence and have been shown to have an effect on cortical maturation and sex differentiation in cognitive development (Clark & Goldman-Rakic, 1989; McEwen, 2001). In the present study we did not assess pubertal status, but future studies should examine the relationship between this factor and the rate of emergence of cognitive abilities in the type of cognitive domains evaluated in this study.

#### *Transition to Mature Performance*

Changepoint analysis, which indicates the time point when performance stops improving, is a useful strategy for estimating the age at which performance plateaus and differences across tasks in the age at which full maturation are achieved. Changepoint analyses indicated that processing speed, voluntary response suppression, and spatial working memory mature during adolescence.

*Development of processing speed* Typically, processing speed is measured as the reaction time to initiate responses in neuropsychological or problem-solving tasks that require multilevel cognitive processing (Kail, 1993; Kail & Park, 1992). We were interested in obtaining information processing speed by measuring the reaction time to initiate an eye movement, which is a basic, yet cognitive, task. This approach is

distinguished from typical studies that emphasize the speed of higher cognitive processing because we are interested in characterizing the core capability of basic voluntary control of behavior. Results indicated that processing speed continues to decrease throughout childhood, even on exogenous tasks, maturing in middle adolescence. This maturation age agrees with results from previous developmental oculomotor studies (Fischer et al., 1997; Fukushima, Hatta, & Fukushima, 2000; Klein & Foerster, 2001; Ross, Radant, Young, & Hommer, 1994) and developmental studies of simple manual reaction time (Elliott, 1970; Fry & Hale, 1996; Guttentag, 1985; Kail, 1991b).

Our results showed that the latency to initiate a response to a visual target, regardless of cognitive demands, matures at approximately age 15. Maturation of the latency to initiate an eye movement to a visual target showed a developmental trend similar to what is seen with the antisaccade and ODR tasks, where participants generate a cognitively driven eye movement to a location that is computed without a target at the location to which the saccade shifts gaze. These results support the hypothesis that developmental differences in information processing are based on increasing quantity of processing resources with age across a wide range of cognitive domains (Kail, 1991b).

*Development of voluntary response suppression.* Changepoint analyses indicate that mature levels of response suppression begin at approximately age 14, which supports results from other developmental studies of antisaccades (Fischer et al., 1997; Munoz et al., 1998). There was a twofold decrease in the number of response-suppression errors in both the antisaccade and ODR tasks from childhood to adulthood (see Table 4). The rate of errors was approximately 5 times larger in the antisaccade task than in the ODR task, probably because of the release of fixation in the antisaccade task that increases the likelihood of prosaccade errors compared with the maintenance of fixation during the presentation of the peripheral target in the ODR task that reduces the likelihood of initiating saccades to suddenly appearing targets.

Results suggest that the capacity to suppress a response is present early (all children could perform a correct antisaccade on at least one trial), as has been seen in infancy (Johnson, 1995), but efficiency (the ability to perform correct antisaccades consistently) continues to improve into adolescence. First, developmental improvements in the antisaccade task were demonstrated in the proportion of trials where saccade suppression occurred. Moreover, there was a

lack of age effects regarding response-suppression errors in the ODR task (low inhibitory load) in contrast to the significant age-related improvements in the antisaccade task (high inhibitory load), indicating that sufficient inhibitory control are present at an earlier age to suppress context-inappropriate responses when inhibitory load demands are low. These results suggest that the transition into mature levels of response inhibition involve improvements in using an existing ability rather than the acquisition of fundamentally new processing capacities.

*Development of spatial working memory.* Change-points occurred at approximately age 14 for the accuracy of the initial memory-guided saccade and age 19 for the ability to accurately fixate remembered locations when given the opportunity to make as many saccades as desired to achieve that resting fixation. Both initial and final saccades in the ODR task are guided by spatial working memory; however, the initial saccade reflects the maintenance of a spatial location in working memory, the ability to develop and maintain a motor plan, and the ability to initiate a voluntary eye movement without sensory guidance. Accuracy of the final resting eye position reflects spatial working memory capacity more directly because it is the participant's best final judgment of where the visual target was presented. Both processes changed with age, although cognitive control of voluntary motor responses appeared to mature earlier than responses guided primarily by spatial working memory. The maturation of the working memory component at age 19 indicates relatively late development of working memory capacity. These results suggest a different pattern of early development than is evident in the gradual loss of this ability in elderly individuals. We have previously reported, using these exact tasks, that healthy elderly adults generate inaccurate initial saccades but accurate final saccades, suggesting that their working memory is intact but their ability to initiate voluntary saccades without sensory guidance declines somewhat with age (Sweeney, Rosano, Berman, & Luna, 2001).

The ODR task used in this study tested the capacity to encode and maintain information in working memory without concurrent processing or internal manipulation of remembered information and is therefore different from many working memory tasks that test for processing load effects and resistance to interference, which emphasize manipulation rather than maintenance (Swanson, 1999). Our findings indicate that a significant component of developmental progression in working memory is due to improvement in the fundamental

ability to maintain information over time for intended use. It is interesting that the lack of a significant age-related decrease in performance with increasing working memory delays suggests that the developmental effect in working memory observed in the present study did not involve an improved ability to maintain information over longer periods of time. Rather, because similar age-related changes in performance were evident with delay periods as short as 1 s, it seems more likely that the age-related change in our maintenance task reflects improvement in the ability to encode information in working memory. Prefrontal cortex has been associated with the ability of 12-month-old infants to maintain information for relatively long periods (more than 10 s; Diamond & Goldman-Rakic, 1989). Taken together, these results suggest that the contributions of prefrontal cortex to the maintenance of information may be mature early, and what is evident in later development is the ability to accurately encode information. This interpretation indicates that one aspect of what characterizes the maturation of working memory is an increase in the spatial resolution of the information encoded, which fits well with brain structural changes known to occur at this age that would also improve spatial resolution. That is, the mature circuitry with refined networks of connections afforded by synaptic pruning could allow more precise information to be represented in working memory.

#### *Interdependence of Developmental Processes*

Processing speed, voluntary response suppression, and working memory are essential for cognitive control of behavior. Complex behavior is rarely dependent on only one of these processes. Our results indicate that these three processes develop, for the most part, independently though concurrently. The development of processing speed was not affected by the development of working memory or response inhibition, indicating that developmental increases in the speed of information processing reflect a distinct process. The development of working memory, however, was modestly influenced by developmental improvements in both processing speed and response inhibition. Faster processing of information may allow information to be more rapidly and effectively encoded in working memory, whereas improvements in response inhibition may decrease working memory demands as only relevant information is processed. These results agree with those who have found that processing speed predicts development of working memory (Demetriou et al.,

2002; Kail, 1997). On the other hand, developmental improvements in the ability to voluntarily suppress a prepotent response were assisted by developmental improvements in working memory. Working memory may support the preparation to inhibit a response, which is known to be crucial in the ability to perform an antisaccade (Everling, Dorris, & Munoz, 1998). Processing speed did not assist in the development of voluntary response suppression, supporting theories of inhibitory control of behavior as an independent ability (Ridderinkhof & van der Molen, 1997; Williams, Ponesse, Schachar, Logan, & Tannock, 1999). The results demonstrating interdependence among these processes were significant, yet modest, accounting for only 2% to 3% of the variance, indicating that their development is primarily independent. We found similar independent trajectories of these cognitive processes in our previous aging studies that indicated a much greater decline in voluntary response suppression than working memory with age (Sweeney et al., 2001). Standard neuropsychological and problem-solving tasks could indicate a larger interdependence between these domains because of the interrelated processes often required for complex task performance. Our procedures, perhaps more selective in their probing of working memory and response-inhibition systems, may enable a more independent measurement of these cognitive processes, providing a more precise assessment of their true interrelatedness. Taken together, these results suggest that although cognitive maturation in these domains develops for the most part independently, each process modestly facilitates the maturation in the other domains.

#### *Brain Processes Underlying Cognitive Development*

Brain maturation processes that speed neuronal transmission and support integrated brain function may underlie the improvements in processing speed, response inhibition, and working memory that occur throughout adolescence. Concurrent with cognitive development are important brain maturation processes including synaptic pruning and myelination that increase efficiency in information processing (Changeux & Danchin, 1976; Huttenlocher, 1990; Yakovlev & Lecours, 1967). Synaptic pruning, the loss of unnecessary neuronal connections throughout the association cortex and striatum (Giedd et al., 1999; Huttenlocher, 1990; Sowell et al., 1999), can speed and enhance the precision of information processing. Increased myelination, the insulation of established connections that optimizes the propaga-

tion of electrical signals throughout the central nervous system (Giedd et al., 1999; Yakovlev & Lecours, 1967), allows for faster responses and for superior integration of widely distributed circuitry necessary for the top-down modulation of behavior. Widely distributed circuitry allows prefrontal executive regions to influence subcortical and other cortical regions to control adaptive behavior. This view suggests that developmental improvements are supported by changes in the efficiency with which brain mechanisms can collaborate and access resources. Our developmental fMRI studies using the antisaccade task support this view (Luna et al., 2001). Our neuroimaging results indicated that, although the basic brain circuitry subserving voluntary response inhibition was functional by childhood and adolescence, adults demonstrated increased activation of distant brain regions known to underlie preparation of correct antisaccades and cognitive processes related to timing and learning, indicating that functional integration of brain circuitry supports mature voluntary control of behavior. Taken together, behavioral and neuroimaging results suggest that the period of development when we reach adult levels of performance is characterized by improvements in existing processes via progressively more efficient use of brain circuitry.

Though the parallels between the developmental profiles of cognitive abilities observed in the present study with those in brain maturation are clear, it is less clear how brain maturation explains the independent developmental course of these cognitive abilities. We suggest that, as brain maturation allows for more efficient and integrated brain function, a qualitative change occurs in cognition that may differ with the neural circuitry underlying each cognitive process. Developmental improvements in processing speed may reflect the overall benefit of increased efficiency of neuronal communication associated with increased myelination, whereas development of response inhibition and working memory may reflect the increased efficiency of particular brain regions associated with local refinements in brain circuitry, reflecting changes in synaptic organization.

#### *Oculomotor Tasks for Assessing Cognition*

Given the similar developmental timelines of our results and those previously reported using neuropsychological tests, our results provide evidence that eye movement paradigms measure similar cognitive development processes as do more traditional approaches. This is important because eye movement

studies offer several advantages for extrapolating from behavioral measurements back to the brain mechanisms underlying cognitive development. Because eye movement responses require fewer intermodal translations, are less susceptible to practice effects and the use of varying strategies for dealing with cognitive problems, and are useful in identical form across much of the age span, they can provide an important window into the development of the maturing capacities of brain mechanisms supporting cognition. Oculomotor methodologies are particularly useful for investigating the neurobiological basis of impaired development in the clinical setting (Everling & Fischer, 1998; Luna & Sweeney, 1999, 2001) because they allow the probing of the integrity of specific well-characterized brain circuitry in relation to impaired cognitive abilities.

### Summary

Processing speed, voluntary response suppression, and working memory mature at different points during adolescence. These processes, for the most part, mature independently but work cooperatively in assisting development in the other cognitive abilities. Oculomotor tasks are sensitive to late development of cognitive abilities and provide a neurophysiological window into the parallel changes in brain maturation that provide an important basis for the development of higher cognitive abilities.

### References

- Abel, L. A., Troost, B. T., & Dell'Osso, L. F. (1983). The effects of age on normal saccadic characteristics and their variability. *Vision Research*, 23, 33–37.
- Adams, R. J., & Lambos, W. A. (1986). Developmental changes in response preparation to visual stimuli. *Perceptual & Motor Skills*, 62, 519–522.
- Anderson, P., Anderson, V., & Gartner, A. F. (2001). Assessment and development of organizational ability: The Rey Complex Figure Organizational Strategy Score (RCF-OSS). *Clinical Neuropsychologist*, 15, 81–94.
- Baddeley, A. (1986). *Working memory*. New York: Oxford University Press.
- Barbas, H. (2000). Connections underlying the synthesis of cognition, memory, and emotion in primate prefrontal cortices. *Brain Research Bulletin*, 52, 319–330.
- Bjorklund, D. F., & Harnishfeger, K. K. (1990). The resources construct in cognitive development: Diverse sources of evidence and a theory of inefficient inhibition. *Developmental Review*, 10, 48–71.
- Bjorklund, D. F., & Harnishfeger, K. K. (1995). The evolution of inhibition mechanisms and their role in human cognition and behavior. In F. N. Dempster & C. J. Brainerd (Eds.), *Interference and inhibition in cognition* (pp. 141–173). San Diego, CA: Academic Press.
- Bunge, S. A., Dudukovic, N. M., Thomason, M. E., Vaidya, C. J., & Gabrieli, J. D. (2002). Immature frontal lobe contributions to cognitive control in children: Evidence from fMRI. *Neuron*, 33, 301–311.
- Case, R. (1992). The role of the frontal lobes in the regulation of cognitive development. *Brain and Cognition*, 20, 51–73.
- Casey, B. J., Cohen, J. D., Jezzard, P., Turner, R., Noll, D. C., Trainor, R. J., et al. (1995). Activation of prefrontal cortex in children during a nonspatial working memory task with functional MRI. *NeuroImage*, 2, 221–229.
- Changeux, J. P., & Danchin, A. (1976). Selective stabilisation of developing synapses as a mechanism for the specification of neuronal networks. *Nature*, 264(5588), 705–712.
- Chelune, G. J., & Baer, R. A. (1986). Developmental norms for the Wisconsin Card Sorting test. *Journal of Clinical & Experimental Neuropsychology*, 8, 219–228.
- Clark, A. S., & Goldman-Rakic, P. S. (1989). Gonadal hormones influence the emergence of cortical function in nonhuman primates. *Behavioral Neuroscience*, 103, 1287–1295.
- Cohen, M. E., & Ross, L. E. (1978). Latency and accuracy characteristics of saccades and corrective saccades in children and adults. *Journal of Experimental Child Psychology*, 26, 517–527.
- Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., et al. (1998). A common network of functional areas for attention and eye movements. *Neuron*, 21, 761–773.
- Demetriou, A., Christou, C., Spanoudis, G., & Platsidou, M. (2002). The development of mental processing: Efficiency, working memory, and thinking. *Monographs of the Society for Research in Child Development*, 67(1, Serial No. 156).
- Dempster, F. N. (1981). Memory span: Sources of individual and developmental differences. *Psychological Bulletin*, 89, 63–100.
- Dempster, F. N. (1992). The rise and fall of the inhibitory mechanism: Toward a unified theory of cognitive development and aging. *Developmental Review*, 12, 45–75.
- Diamond, A., & Goldman-Rakic, P. S. (1989). Comparison of human infants and rhesus monkeys on Piaget's AB task: Evidence for dependence on dorsolateral prefrontal cortex. *Experimental Brain Research*, 74, 24–40.
- Elliott, R. (1970). Simple reaction time: Effects associated with age, preparatory interval, incentive-shift and mode of presentation. *Journal of Experimental Child Psychology*, 9, 86–107.
- Everling, S., Dorris, M. C., & Munoz, D. P. (1998). Reflex suppression in the anti-saccade task is dependent on prestimulus neural processes. *Journal of Neurophysiology*, 80, 1584–1589.

- Everling, S., & Fischer, B. (1998). The antisaccade: A review of basic research and clinical studies. *Neuropsychologia*, 36, 885–899.
- Everling, S., & Munoz, D. P. (2000). Neuronal correlates for preparatory set associated with pro-saccades and anti-saccades in the primate frontal eye field. *Journal of Neuroscience*, 20, 387–400.
- Fischer, B., Biscaldi, M., & Gezeck, S. (1997). On the development of voluntary and reflexive components in human saccade generation. *Brain Research*, 754, 285–297.
- Fry, A. F., & Hale, S. (1996). Processing speed, working memory, and fluid intelligence: evidence for a developmental cascade. *Psychological Science*, 7, 237–241.
- Fukushima, J., Hatta, T., & Fukushima, K. (2000). Development of voluntary control of saccadic eye movements. I. Age-related changes in normal children. *Brain and Development*, 22, 173–180.
- Funahashi, S., Chafee, M. V., & Goldman-Rakic, P. S. (1993). Prefrontal neuronal activity in rhesus monkeys performing a delayed anti-saccade task. *Nature*, 365(6448), 753–756.
- Funahashi, S., & Takeda, K. (2002). Information processes in the primate prefrontal cortex in relation to working memory processes. *Reviews in the Neurosciences*, 13, 313–345.
- Fuster, J. M. (1997). *The prefrontal cortex* (3rd ed.), New York: Raven Press.
- Giedd, J. N., Blumenthal, J., Jeffries, N. O., Castellanos, F. X., Liu, H., Zijdenbos, A., et al. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neuroscience*, 2, 861–863.
- Giedd, J. N., Castellanos, F. X., Rajapakse, J. C., Vaituzis, A. C., & Rapoport, J. L. (1997). Sexual dimorphism of the developing human brain. *Progress in Neuro-Psychopharmacology & Biological Psychiatry*, 21, 1185–1201.
- Goldman-Rakic, P. S. (1988). Topography of cognition: Parallel distributed networks in primate association cortex. *Annual Review of Neuroscience*, 11, 137–156.
- Guttentag, R. E. (1985). A developmental study of attention to auditory and visual signals. *Journal of Experimental Child Psychology*, 39, 546–561.
- Hale, S. (1990). A global developmental trend in cognitive processing speed. *Child Development*, 61, 653–663.
- Hallett, P. E. (1978). Primary and secondary saccades to goals defined by instructions. *Vision Research*, 18, 1279–1296.
- Hikosaka, O., & Wurtz, R. H. (1983). Visual and oculomotor functions of monkey substantia nigra pars reticulata. II. Visual responses related to fixation of gaze. *Journal of Neurophysiology*, 49, 1254–1267.
- Huttenlocher, P. R. (1990). Morphometric study of human cerebral cortex development. *Neuropsychologia*, 28, 517–527.
- Johnson, M. H. (1995). The inhibition of automatic saccades in early infancy. *Developmental Psychobiology*, 28, 281–291.
- Kail, R. (1991a). Development of processing speed in childhood and adolescence. In H. W. Reese (Ed.), *Advances in child development and behavior* (pp. 151–185). San Diego, CA: Academic Press.
- Kail, R. (1991b). Developmental change in speed of processing during childhood and adolescence. *Psychological Bulletin*, 109, 490–501.
- Kail, R. (1993). Processing time decreases globally at an exponential rate during childhood and adolescence. *Journal of Experimental Child Psychology*, 56, 254–265.
- Kail, R. (1997). Processing time, imagery, and spatial memory. *Journal of Experimental Child Psychology*, 64, 67–78.
- Kail, R., & Park, Y. (1992). Global developmental change in processing time. *Merrill-Palmer Quarterly*, 38, 525–541.
- Klein, C., & Foerster, F. (2001). Development of prosaccade and antisaccade task performance in participants aged 6 to 26 years. *Psychophysiology*, 38, 179–189.
- Leigh, R. J., & Zee, D. S. (1999). *The neurology of eye movements* (3rd ed.), New York: Oxford University Press.
- Levin, H. S., Culhane, K. A., Hartmann, J., Evankovich, K., & Mattson, A. J. (1991). Developmental changes in performance on tests of purported frontal lobe functioning. *Developmental Neuropsychology*, 7, 377–395.
- Luciana, M., Collins, P. F., & Depue, R. A. (1998). Opposing roles for dopamine and serotonin in the modulation of human spatial working memory functions. *Cerebral Cortex*, 8, 218–226.
- Luciana, M., & Nelson, C. (1998). The functional emergence of prefrontally-guided working memory systems in four- to eight-year-old children. *Neuropsychologia*, 36, 273–293.
- Luna, B., & Sweeney, J. A. (1999). Cognitive functional magnetic resonance imaging at very-high-field: Eye movement control. *Topics in Magnetic Resonance Imaging*, 10, 3–15.
- Luna, B., & Sweeney, J. A. (2001). Studies of brain and cognitive maturation through childhood and adolescence: A strategy for testing neurodevelopmental hypotheses. *Schizophrenia Bulletin*, 27, 443–455.
- Luna, B., Thulborn, K. R., Munoz, D. P., Merriam, E. P., Garver, K. E., Minshew, N. J., et al. (2001). Maturation of widely distributed brain function subserves cognitive development. *NeuroImage*, 13, 786–793.
- Luna, B., Thulborn, K. R., Strojwas, M. H., McCurtain, B. J., Berman, R. A., Genovese, C. R., et al. (1998). Dorsal cortical regions subserving visually-guided saccades in humans: An fMRI study. *Cerebral Cortex*, 8, 40–47.
- McEwen, B. S. (2001). Invited review: Estrogens effects on the brain: Multiple sites and molecular mechanisms. *Journal of Applied Psychology*, 91, 2785–2801.
- Munoz, D. P., Broughton, J. R., Goldring, J. E., & Armstrong, I. T. (1998). Age-related performance of human subjects on saccadic eye movement tasks. *Experimental Brain Research*, 121, 391–400.
- Nelson, C. A., Monk, C. S., Lin, J., Carver, L. J., Thomas, K. M., & Truwitt, C. L. (2000). Functional neuroanatomy of spatial working memory in children. *Developmental Psychology*, 36, 109–116.

- Paus, T., Babenko, V., & Radil, T. (1990). Development of an ability to maintain verbally instructed central gaze fixation studied in 8- to 10-year-old children. *International Journal of Psychophysiology*, 10, 53–61.
- Petit, L., Clark, V. P., Ingeholm, J., & Haxby, J. V. (1997). Dissociation of saccade-related and pursuit-related activation in human frontal eye fields as revealed by fMRI. *Journal of Neurophysiology*, 77, 3386–3390.
- Pierrot-Deseilligny, C. (1991). Cortical control of saccades in man. *Acta Neurologica Belgica*, 91, 63–79.
- Ridderinkhof, K. R., Band, G. P. H., & Logan, G. D. (1999). A study of adaptive behavior: Effects of age and irrelevant information on the ability to inhibit one's actions. *Acta Psychologica*, 101, 315–337.
- Ridderinkhof, K. R., & van der Molen, M. W. (1997). Mental resources, processing speed, and inhibitory control: A developmental perspective. *Biological Psychology*, 45, 241–261.
- Ridderinkhof, K. R., van der Molen, M. W., Band, G. P., & Bashore, T. R. (1997). Sources of interference from irrelevant information: A developmental study. *Journal of Experimental Child Psychology*, 65, 315–341.
- Rivaud, S., Muri, R. M., Gaymard, B., Vermersch, A. I., & Pierrot-Deseilligny, C. (1994). Eye movement disorders after frontal eye field lesions in humans. *Experimental Brain Research*, 102, 110–120.
- Ross, R. G., Radant, A. D., Young, D. A., & Hommer, D. W. (1994). Saccadic eye movements in normal children from 8 to 15 years of age: A developmental study of visuo-spatial attention. *Journal of Autism and Developmental Disorders*, 24, 413–431.
- Rubia, K., Overmeyer, S., Taylor, E., Brammer, M., Williams, S. C., Simmons, A., et al. (2000). Functional frontalisation with age: Mapping neurodevelopmental trajectories with fMRI. *Neuroscience and Biobehavioral Reviews*, 24, 13–19.
- Ruffer, W. A., Grapenthin, R. R., Huey, L. A., & Patterson, B. J. (1985). Comparisons for psychomotor tasks: Grade and sex of secondary school youths. *Perceptual & Motor Skills*, 60, 27–30.
- Siegler, R. S. (1978). The origins of scientific reasoning. In R. S. Siegler (Ed.), *Children's thinking: What develops?* (pp. 104–149). Hillsdale, NJ: Erlbaum.
- Smyrnis, N., Evdokimidis, I., Stefanis, N. C., Constantindis, T. S., Avramopoulos, D., Theleritis, C., et al. (2002). The antisaccade task in a sample of 2,006 young males. II. Effects of task parameters. *Experimental Brain Research*, 147(7), 53–63.
- Sowell, E. R., Thompson, P. M., Holmes, C. J., Jernigan, T. L., & Toga, A. W. (1999). *In vivo* evidence for post-adolescent brain maturation in frontal and striatal regions. *Nature Neuroscience*, 2, 859–861.
- Sowell, E. R., Trauner, D. A., Gamst, A., & Jernigan, T. L. (2002). Development of cortical and subcortical brain structures in childhood and adolescence: A structural MRI study. *Developmental Medicine & Child Neurology*, 44, 4–16.
- Swanson, H. L. (1999). What develops in working memory? A life span perspective. *Developmental Psychology*, 35, 986–1000.
- Sweeney, J. A., Mintun, M. A., Kwee, S., Wiseman, M. B., Brown, D. L., Rosenberg, D. R., et al. (1996). Positron emission tomography study of voluntary saccadic eye movements and spatial working memory. *Journal of Neurophysiology*, 75, 454–468.
- Sweeney, J. A., Rosano, C., Berman, R. A., & Luna, B. (2001). Inhibitory control of attention declines more than working memory during normal aging. *Neurobiology of Aging*, 22, 39–47.
- Tamm, L., Menon, V., & Reiss, A. L. (2002). Maturation of brain function associated with response inhibition. *Journal of the American Academy of Child and Adolescent Psychiatry*, 41, 1231–1238.
- Welsh, M. C., Pennington, B. F., & Groisser, D. B. (1991). A normative-developmental study of executive function: A window on prefrontal function in children. *Developmental Neuropsychology*, 7, 131–149.
- Williams, B. R., Ponesse, J. S., Schachar, R. J., Logan, G. D., & Tannock, R. (1999). Development of inhibitory control across the life span. *Developmental Psychology*, 35, 205–213.
- Yakovlev, P. I., & Lecours, A. R. (1967). The myelogenetic cycles of regional maturation of the brain. In A. Minkowski (Ed.), *Regional development of the brain in early life* (pp. 3–70). Oxford, England: Blackwell Scientific.
- Zald, D. H., & Iacono, W. G. (1998). The development of spatial working memory abilities. *Developmental Neuropsychology*, 14, 563–578.