Neural correlates of cognitive control in childhood and adolescence: Disentangling the contributions of age and executive function

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Abstract
Dense-array (128-channel) electroencephalography (EEG) was used to record event-related potentials (ERPs) from 33 participants between 7 and 16 years of age while they performed a Go/Nogo task. The frontal (Nogo) N2 component of the ERP was taken as an index of cognitive control, and examined in relation to both age and independent assessments of executive function (EF), including the Iowa Gambling Task (IGT), the Stroop task, a delay discounting task, and backward digit span. Better performance on the IGT and the Stroop task was associated with smaller N2 amplitudes, over and above effects of age. N2 latencies decreased with age but were not predicted by EF. Source modeling of the N2 revealed neural generators in areas suggestive of cingulate cortex and orbitofrontal cortex, and the locations of these generators varied systematically with EF (IGT and Stroop task): the cingulate generator was more anterior for good EF participants at all ages; the orbitofrontal generator was relatively left lateralized for younger and for poorer EF participants. Taken together, these findings suggest that age-related decreases in N2 amplitude, but not N2 latency, reflect the development of cognitive control and cannot be attributed solely to incidental changes that may affect assessments of the N2 (e.g., increases in skull thickness). Functionally relevant decreases in N2 amplitude may reflect changes in the regions of cortex giving rise to the N2.

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Cognitive control of one’s thoughts, actions, and emotions – studied under the rubric of executive function (EF) – emerges early in childhood and follows an extremely protracted developmental course that extends beyond adolescence (see Zelazo & Müller, 2002, for a review). In adults, EF depends importantly on the integrity of neural systems involving prefrontal cortex (PFC, e.g., Luria, 1962/1966; Stuss & Benson, 1986; Tranel, Anderson, & Benton, 1994), and lesions to PFC in childhood also produce impairments in EF (Anderson, Levin, & Jacobs, 2002). Relatively little is known, however, about the functional development of PFC. Although it is now well established that PFC continues to develop into adulthood (e.g., Giedd et al., 1999; Gogtay et al., 2004; O’Donnell, Noseworthy, Levine, & Dennis, 2005; Sowell et al., 2003), it remains unclear whether and to what extent the functions of PFC in general, and regions within PFC in particular, change as the brain develops.

Electroencephalography (EEG) provides a non-invasive method to measure brain activity in children, and recent technological advances, such as the introduction of high-density (e.g., 128-channel) arrays and refinements in programs for source analysis (Berg & Scherg, 1994), allow researchers to make well-supported inferences about the neural sources of scalp-recorded electrical activity (e.g., Fox, Schmidt, & Henderson, 2000; Nelson & Monk, 2001). Although this approach has considerable promise, developmental studies of neural function face a number of methodological challenges (cf. Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002; Segalowitz & Davies, 2004). Age differences in neural activity are often confounded with differences in performance on the task in which neural activity is measured (e.g., Johnstone, Pfeffer, Barry, Clarke, &
Developmental research on the N2, using both Go/Nogo paradigms and versions of the Eriksen flanker task (Eriksen & Eriksen, 1979), has generally shown a decrease in both amplitude and latency with age (Davis, Bruce, Snyder, & Nelson, 2003; Johnstone et al., 2005; Jonkman et al., 2003; Lewis, Lamm, Segalowitz, Stieben, & Zelazo, in press; Rueda, Posner, Rothbart, & Davis-Stober, 2004), although Ladouceur, Dahl, and Davis-Stober (2001) found larger N2 amplitudes with increasing age in a small sample of adolescents (five younger versus six older) tested with a flanker task. The more common finding of reduced amplitudes with age may be associated with cortical thinning (e.g., O’Donnell et al., 2005) and reductions in grey matter volume (e.g., Giedd et al., 1999; Gogtay et al., 2004), which may influence assessments of neural activity but be independent of the neurocognitive function in question.

One step towards addressing these challenges is to treat performance-related variables as a covariates when examining age differences in neural activity. Another step is to examine neural correlates of cognitive function and compare them to independent assessments of the function in question (Segalowitz & Davies, 2004). In this study, we did both. Dense-array (128-channel) electroencephalography was used to record event-related potentials (ERPs) from children and adolescents while they performed a Go/Nogo task. The frontal N2 component of the ERP, measured on successful Nogo trials, was taken as an index of cognitive control, and examined in relation to both age (from 7 to 16 years) and independent assessments of executive function, after controlling statistically for performance on the Go/Nogo task.

The frontal N2 is usually observed at medial–frontal sites 200–400 ms following stimulus presentation, and it is larger on successful Nogo trials than on Go trials (e.g., Eimer, 1993; Falkenstein, Hoormann, & Hohnsbein, 1999; Jodo & Kayama, 1992; Jonkman et al., 2003). Although there is some debate regarding how to interpret the frontal N2 – for example, whether it reflects response inhibition (e.g., Jodo & Kayama, 1992; Jonkman et al., 2003) or conflict monitoring (e.g., Botvinick, Braver, Barch, Carter, & Cohen, 2001; Nieuwenhuis, Yeung, Van Den Wildenberg, & Ridderinkhof, 2003) – there is a general consensus that it is associated with aspects of cognitive control. Source analysis of the N2 in adult samples has identified cortical generators in both cingulate cortex (e.g., Nieuwenhuis et al., 2000; van Veen & Carter, 2002) and right orbitofrontal cortex (Bokura, Yamaguchi, & Kobayashi, 2001).

Developmental research on the N2, using both Go/Nogo paradigms and versions of the Eriksen flanker task (Eriksen & Eriksen, 1979), has generally shown a decrease in both amplitude and latency with age (Davis, Bruce, Snyder, & Nelson, 2003; Johnstone et al., 2005; Jonkman et al., 2003; Lewis, Lamm, Segalowitz, Stieben, & Zelazo, in press; Rueda, Posner, Rothbart, & Davis-Stober, 2004), although Ladouceur, Dahl, and Davis-Stober (2004) found larger N2 amplitudes with increasing age in a small sample of adolescents (five younger versus six older) tested with a flanker task. The more common finding of reduced amplitudes with age may be associated with cortical thinning (e.g., O’Donnell et al., 2005) and reductions in grey matter volume (e.g., Giedd et al., 1999; Gogtay et al., 2004), which in turn may be brought about by synaptic pruning. A related possibility is that amplitude reductions reflect increasingly efficient or focal activation of relevant areas of PPC (cf. Casey et al., 1997). However, reductions in N2 amplitude could also reflect a variety of other age-related changes that may be only incidentally associated with neurocognitive function (Pfefferbaum, 1990). These changes include increases in skull density and thickness, increases in the thickness of the superficial layer of cerebrospinal fluid (CSF), and increases in cortical folding. Thus, it is not yet known to what extent changes in N2 amplitude reflect developmental processes that are closely tied to executive function.

In the current study, we compared N2 amplitudes and latencies to performance on four independent measures of EF. EF is a heterogeneous construct, and different aspects of EF are associated with different regions of PFC (Zelazo & Müller, 2002). To determine which aspects of EF may be associated with N2 activation, we developed a relatively comprehensive battery of age-appropriate measures of EF that included not only traditional measures associated with lateral PFC, but also measures associated with more ventral and medial regions of PFC. The former measures included backward digit span, a measure of working memory taken from the Wechsler Intelligence Scales for Children (WISC-III; Wechsler, 1991), and the Stroop Color–Word Task (Stroop, 1935), a measure of selective attention and response inhibition. The latter measures included the Iowa Gambling Task (Bechara, Damasio, Damasio, & Anderson, 1994) and a delay discounting task (Green, Fry, & Myerson, 1994; Richards, Zhang, Mitchell, & de Wit, 1999), both of which tap aspects of affective decision making (Monterosso, Ehrman, Napier, O’Brien, & Childress, 2001).

ERPs were recorded during three blocks of a Go/Nogo task, including one block (the second block) that was more difficult and during which children received negative feedback about their performance. The manipulation of difficulty and feedback allowed us to assess the neural correlates of cognitive control across a range of motivational states. This manipulation also served to increase participants’ concentration and minimize their boredom, allowing us to gather data from a larger number of successful Nogo trials and hence, to obtain more reliable estimates of the N2 (which was especially important for the youngest participants). In an effort to equate task difficulty across the age range, stimulus durations (and inter-trial intervals) were adjusted dynamically in response to participants’ accuracy. This allowed us to maintain a Nogo error rate of approximately 50% for all children (see Garavan, Ross, & Stein, 1999).

If age differences in N2 amplitude and latency reflect changes in cognitive control, then N2 amplitudes and latencies should be associated with EF over and above any association with age. Specifically, reductions in N2 amplitude and latency should be associated with better EF, parallelizing previously reported associations with age. Cortical generators of the N2 were estimated using Brain Electrical Source Analysis (BESA; Berg & Scherg, 1994). The estimated generators were expected to overlap with those identified in adults (i.e., generators in cingulate cortex and right orbitofrontal cortex), and possibly to show increasing anteroposteriorization as a function of increasing EF proficiency (cf. Rubia et al., 2003).
1. Methods

1.1. Participants

Participants were 33 English-speaking children and adolescents (15 boys) between the ages of 7.17 and 16.75 years (mean = 11.87 years; S.D. = 2.76). All participants had normal or corrected-to-normal vision, and were free of any psychiatric diagnoses or medication. Participants were recruited through a local newspaper and paid $60.00 CDN plus a toy or gift certificate for their participation. An additional six participants were tested but eliminated from further analyses because they had fewer than six correct Nogo trials (see below). The ages of these children were 7.08, 8.33, 9.00, 10.42, 10.08, and 11.92 years.

1.2. Procedure

Participants were tested during two sessions separated by about 4 months (mean = 116.67 days; S.D. = 49). EEG was recorded during the second test session, which took place in the laboratory and lasted about 45 min. EF was measured during the second test session, which took place in children's homes and lasted approximately 30 min. The procedures used in this study were approved by the appropriate ethics committee and have therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

1.2.1. EEG testing

Upon arrival at the laboratory, participants were given a brief introduction to the testing environment and the EEG system, and then parental consent and participant assent were obtained. Participants were informed that they would receive a prize for playing a computer game and were shown two toy bins. One of the bins contained small, undesirable toys such as small plastic cars, while the second bin contained more desirable, age-appropriate toys such as large action figures, games, and $10.00 gift certificates from a local music store. Participants were informed that they would perform a test with well- and accumulated points, they would have their choices of rewards, but that otherwise their choices would be limited to the less desirable toy bin. They were then asked to choose a reward they would like to earn. An electrode sensor net was then applied and participants were seated in front of a computer monitor, with the distance and alignment to the monitor controlled by use of a chin rest. Participants were instructed to make responses in the game by clicking a button on a response pad using the index finger of their dominant hand (writing hand).

The Go/Nogo task was adapted from a task used by Garzon et al. (1999) and presented using E-Prime Version 1.1 (Psychological Software Tools, Pittsburgh, PA). On each trial, a letter stimulus was presented at a central location on the computer monitor. Participants were instructed to respond quickly and accurately to each letter (Go stimulus) except when the same letter appeared on consecutive trials (Nogo stimulus), in which case they were to withhold responding. Participants were given 30 practice trials, followed by 3 blocks of test trials: the first and third blocks each consisted of 200 trials (including 66 Nogo trials in a pseudorandom sequence). The second block consisted of 150 trials (40 Nogo trials). Different pairs of similarly shaped letters were used for each block (block 1: x and y; block 2: o and p; block 3: u and d) to enhance novelty. The Nogo error rate on all three blocks was maintained at an intertrial level by adjusting the stimulus duration (and thus the inter-trial intervals) dynamically. When participants correctly withheld their responses on Nogo trials and these trials were preceded by correct Go trials, the stimulus duration was decreased by 50 ms (80 ms on block 2). When they responded incorrectly on Nogo trials, the stimulus duration was increased by 50 ms on Blocks 1 and 3, and by 30 ms on block 2. The adjustment of stimulus duration was intended to provide participants with all ages with the same level of challenge, and to allow us to obtain a sufficient number of correct and incorrect trials for ERP analysis. The feedback was provided by a red bar in the middle of the screen following incorrect responses, omitted responses, and late responses (i.e., responses that occurred following the stimulus window). No feedback was provided after correct responses.

Children were reminded at the beginning of the task that a high number of points was needed to win the "big prize" they had chosen. After every 20 trials, the number of points they had accumulated was displayed in red on a window on the screen. Points were added for correct Nogo trials and subtracted for errors on both Go and Nogo trials. In block 1, children saw their points steadily increase, usually to over 1000. However, changes to the stimulus-duration-adjustment algorithm (see above) together with changes to the point-adjustment algorithm caused them to lose all their points by the end of block 2. With a return to the more generous algorithms, children then regained their points in block 3 to win the desirable prize. Earning points, losing them in block 2, and then regaining them was intended to motivate and engage participants.

EEG was recorded during all three blocks using a 128-channel Geodesic Sensor Net (Tucker, 1993). Data were sampled at 250 Hz, using EGI software (EID, Eugene, OR), and impedances for all EEG channels were kept below 50 kΩ. All channels were referenced to Cz (channel 129 during recording). EEG epochs ranging from 400 ms before to 1000 ms after stimulus onset were collected in block 1, and ERP data were filtered using an FIR 1–30 Hz bandpass filter. Stimulus-locked averages were calculated with epochs ranging from 400 ms before to 1000 ms after stimulus onset.

Correct Nogo trials that were not preceded and followed by correct Go trials were removed because they most likely reflected attentional lapses or chronic non-responding. Data from all three blocks were averaged together to increase the ERP trial counts. As noted, children with fewer than six correct Nogo trials were eliminated from further analysis. The mean number (S.D.) of trials contributing to the N2 was 21 (13.79). ERP data from correct Nogo trials were adjusted using the 400 ms preceding stimulus onset as a baseline. The N2 was then coded as the largest negative deflection following the N1 that had a mediofrontal topography and a latency between 200 and 450 ms post-stimulus. Rating was carried out by a coder blind to any characteristics of the participants. N2 latency was recorded as the latency from stimulus onset to the peak identified in the amplitude analysis.

In order to estimate the cortical generators of the Nogo N2 waveforms, temporal–spatial regional source modeling (from 200 ms before stimulus onset to 600 ms after stimulus onset) was performed on non-baseline-corrected, grand-averaged data using BESA (Berg & Scherg, 1994). We examined Nogo N2 waveforms rather than Nogo minus Go difference waveforms because we were interested not only in these aspects of cognitive control indicated exclusively by the Nogo N2 but also in those aspects that are shared with the Go-N2. Source models were derived using a spherical head model with an isotropic realistic head approximation factor of 20. Regional sources were fitted using a Principal Components Analysis (PCA) algorithm on residual data. Thus, each regional source was placed to explain the greatest amount of residual variance within a specific time range. Improvements to the model, either through additional regional sources or changes in locations, were evaluated primarily on the basis of reductions in the residual variance. A final model was considered adequate when the residual variance was less than 5% (Berg & Scherg, 1994).

1.2.2. EF testing

All testing during the second session was conducted in a quiet area of children's homes, with no distracting elements (other family members, telephones, televisions, pets, etc.). Tasks were presented in the following fixed order: IGT, the first part of the Stroop Color-Word task (the component and incongruent color word conditions), delay discounting, the second part of the Stroop Color-Word task (negative, neutral, and positive word conditions), and digit span (both forward digit span and backward digit span). For each task, the participant and experimenter were seated side by side at a table.

The procedure for the IGT was identical to that used by Bechara et al. (1994), except that the task was administered on a laptop computer, using E-prime software. In this task, participants were shown four decks of cards. They could select cards from a deck by clicking on the deck with the mouse. When turned, each card revealed a combination of gains and losses (measured in play money). Participants were given a stake of $2000 and asked to win as much money as possible by choosing cards from any of the four decks (one card per trial), as possible by choosing cards from any of the four decks (one card per trial), as otherwise (the advantageous decks) would result in a net loss. Each card from the disadvantageous decks provided a higher reward than each card from the advantageous decks ($100 versus $50), but the variable (and unpredictable) losses associated with cards from disadvantageous decks...
were much larger on average than the losses associated with the advantageous decks. In keeping with evidence that data from later trials on the IGT provide a more reliable index of performance (Montepare et al., 2001), the dependent variable was the net score on these trials, negatively scored (i.e., the number of disadvantageous choices minus the number of advantageous choices made in the last 20 trials). Lower scores indicated better performance.

In the Stroop task, participants were presented with a series of words and asked to name the color in which each word appeared (Stroop, 1933). The following five conditions were administered: (1) congruent color word, (2) incongruent color word, (3) incongruent color word, (4) neutral word, and (5) positive word. For the current analyses, however, we were interested in the incongruent color word condition (i.e., the canonical interference condition) and the neutral word condition (a baseline measure of color naming that allowed us to control for any age-related differences in the automatism of reading). In each condition, participants were shown a laminated card with 21 words arranged in two columns and instructed to name the colors, starting with column one, as quickly and accurately as possible, without skipping any. Words were presented in three colors: red, blue, and green. In the incongruent color word condition, color words were presented in colors that were incongruent with the word (e.g., the word RED shown in blue). In the neutral word condition, stimuli were a variety of simple, affectively neutral, non-color words (e.g., apple, book, cake, and grass). Performance was timed using a stop watch and the number and types of errors (corrected or uncorrected) were recorded. Response times (RTs) for each condition were adjusted to account for the number of corrected errors. Following the procedure outlined by Stroop (1933), we subtracted twice the average time per word for each corrected error. The total RT for the neutral word condition was then subtracted from the total RT for the incongruent color word condition to yield a measure of interference. To adjust for baseline differences in RT, this difference score was then divided by the total RT for the neutral word condition, yielding a proportion dubbed the Stroop interference score. This variable was used for all analyses. Lower scores indicated better performance.

A computerized delay discounting task was adapted from Richards et al. (1999). Participants were given a series of choices between $10, which would be delayed by 1, 2, 30, 180, or 365 days, and a smaller amount of money available immediately. For each delay, an adjusting-amount algorithm adjusted the magnitude of the immediate reinforcer until it was subjectively equivalent in value to the delayed reward—this value of the immediate reinforcer was referred to as the indifference point (ID). Participants’ data were fitted to the hyperbolic function, \( kD^k \), described in Mazur (1987), in order to calculate values for \( k \) and \( D \), which provides a measure of the rate at which each participant discounted reinforcers as a function of delay. In the hyperbolic function, \( A \) is the nominal amount of the delayed reward ($10) and \( D \) is the length of the delay. The distribution of \( k \) values was skewed, which is typical for this type of data (e.g., Johnson & Bickel, 2002), so all values were log-transformed for the purposes of analysis (Alessi & Petry, 2003). This variable was used for all statistical analyses. Lower scores indicated better performance.

To ensure that participants were appropriately engaged by the task, they were told that after the task one of their choices would be granted at random. Regardless of their choices, however, participants received $10 at the end of the task.

<table>
<thead>
<tr>
<th>Measures</th>
<th>N</th>
<th>Mean</th>
<th>S.D</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>IGT</td>
<td>30</td>
<td>47</td>
<td>7.02</td>
<td>−16.00 to 16.00</td>
</tr>
<tr>
<td>Stroop interference</td>
<td>32</td>
<td>33</td>
<td>20</td>
<td>−15 to 63</td>
</tr>
<tr>
<td>Stroop errors (incongruent)</td>
<td>32</td>
<td>1.19</td>
<td>1.57</td>
<td>0-7</td>
</tr>
<tr>
<td>Delay discounting</td>
<td>29</td>
<td>−1.90</td>
<td>1.96</td>
<td>−4.18 to −28</td>
</tr>
<tr>
<td>Backward digit span</td>
<td>33</td>
<td>36</td>
<td>22</td>
<td>−20 to 80</td>
</tr>
<tr>
<td>Go RT (ms)</td>
<td>33</td>
<td>377.87</td>
<td>63.84</td>
<td>307.36-575.35</td>
</tr>
<tr>
<td>Go/Nogo stimulus duration (ms)</td>
<td>33</td>
<td>567.83</td>
<td>118.58</td>
<td>400.71-777.91</td>
</tr>
<tr>
<td>Nogo errors</td>
<td>33</td>
<td>86.25</td>
<td>12.65</td>
<td>60.02-110.44</td>
</tr>
</tbody>
</table>

Note: IGT = Iowa Gambling Task; RT = reaction time; Stroop errors (incongruent) = number of errors on the incongruent color word condition of the Stroop task. Lower scores indicate better performance for all measures of EF.

2. Results

2.1. Behavioral analyses

Errors on the Go/Nogo task were controlled through the dynamic adjustment of stimulus duration, with better performance leading to shorter stimulus durations, so performance on the Go/Nogo task was measured by RTs on correct Go trials and also by stimulus duration. Go RTs below 200 ms or above 1000 ms were excluded from analysis because they were assumed to reflect non-deliberate behavior. Behavioral data from the Go/Nogo task and from the four measures of EF are summarized in Table 1. Simple and age-partialled Pearson correlations were conducted to examine relations among the key behavioral measures. As indicated in Table 2, age (in months) was significantly related to all measures of performance except Stroop interference and delay discounting. Older children had shorter Go RTs and shorter stimulus durations, and they performed better on the IGT and backward digit span. Performance on the Go/Nogo task was also related to performance on the IGT, although these relations were not significant after partialling age. The failure to find significant correlations among measures of EF (using both simple and age-partialled correlations) is consistent with our expectation that these measures assess different aspects of EF. The finding that neither Stroop interference nor delay discounting was related to age suggests either that these measures were not sensitive to developmental changes in this age range or that they measure differences in EF (including developmental differences) that are not related to age.

2.2. ERP analyses

Because the N2 is likely produced by multiple cortical generators (e.g., Bokura et al., 2001), and different electrode sites...
might prove more or less sensitive to these generators, N2 amplitudes were first examined at three medial–frontocentral sites (Fz, FCz, and Cz) and then considered in relation to the four measures of EF (IGT, Stroop interference, delay discounting, and backward digit span; see Table 3). For each measure of EF, the site yielding the highest correlation was selected for inclusion in analyses involving that measure. In addition to maximizing relations between N2 amplitudes and each measure of EF, this strategy reduced the overall number of analyses to be conducted. Analyses for IGT were conducted at site Fz. Analyses for Stroop interference and delay discounting were conducted at site Cz. Backward digit span analyses were conducted at site FCz.

To assess the separate contributions of age and EF to N2 amplitudes and latencies, we conducted a series of multiple regression analyses that controlled for two variables that have the potential to affect ERP amplitudes and latencies: the number of trials contributing to the ERP (trial count) and stimulus duration. For each of the four measures of EF, we conducted two regression analyses with trial count, stimulus duration, and gender entered in the first step in order to remove their influence. For the first analysis for each measure, we entered age in the second step followed by EF. For the second analysis for each measure, we entered EF in the second step followed by age. The first analysis allowed us to determine whether each measure of EF predicted N2 amplitudes and latencies over and above trial count, stimulus duration, gender, and age. The second analysis allowed us to determine whether age predicted N2 amplitudes and latencies over and above trial count, stimulus duration, gender, and each measure of EF. The results of these analyses are presented in Table 4.

Table 3. Correlations between EF and N2 amplitudes at sites Fz, FCz, and Cz

<table>
<thead>
<tr>
<th>Measure</th>
<th>Fz</th>
<th>FCz</th>
<th>Cz</th>
</tr>
</thead>
<tbody>
<tr>
<td>IGT</td>
<td>.47</td>
<td>-.34</td>
<td>-.25</td>
</tr>
<tr>
<td>Stroop interference</td>
<td>-.15</td>
<td>-.30</td>
<td>-.49*</td>
</tr>
<tr>
<td>Delay discounting</td>
<td>-.10</td>
<td>-.29</td>
<td>-.30</td>
</tr>
<tr>
<td>Backward digit span</td>
<td>-.16</td>
<td>-.17</td>
<td>-.12</td>
</tr>
</tbody>
</table>

Notes: IGT: Iowa Gambling Task. Lower scores indicate better performance for all measures. *p < .05. **p < .01 (two-tailed).

As can be seen in Table 4, N2 amplitudes were predicted by performance on the IGT and Stroop task (over and above age), but not by age (over and above any measure of EF). Neither delay discounting nor backward digit span predicted N2 amplitudes. In contrast, N2 latencies were predicted by age (over and above all measures of EF), but not by any of the measures of EF.

For the purpose of displaying grand-averaged waveforms, participants were divided into two age groups, children (7.00–10.99 years) and adolescents (11.00–16.75 years). Within each age group, and separately for each measure of EF, participants were divided into poor and good EF groups based on median splits. Fig. 1 displays waveforms for each measure of EF entered third.
EF and each age × EF group. As can be seen in the waveforms for the IGT and the Stroop task, N2 amplitudes are larger for participants with poor EF (regardless of age). Also, for all measures of EF, peak N2 latencies occur later for younger participants.

2.3. Source analysis
Source analyses were conducted to determine how the neural generators underlying participants’ N2s varied with age and with the two measures of EF that predicted N2 amplitude (IGT and Stroop interference). For both children (7.00–10.99 years) and adolescents (11.00–16.75 years), participants were divided into poor and good EF groups based on median splits for both the IGT and the Stroop task. Participants who were classified as poor performers for either measure of EF were included in the poor EF group for this analysis. The composition of the resulting age × EF groups is shown in Table 5. Poor EF groups did not differ in age from good EF groups, either for children (t(16) = −.46, p = .66) or adolescents (t(13) = −.93, p = .37). Stimulus-locked grand averages (for all electrode sites) were generated for each group and used in source analyses.

As can be seen in Fig. 2, peak N2 activity was characterized by a strong ventral source for all groups. The estimated location of this source was right orbitofrontal cortex for the good EF adoles-

![Fig. 1. Stimulus-locked, grand-averaged waveforms (for Nogo trials) at sites Cz, FCz, and Fz, presented separately younger and older children and as a function of performance on the IGT, Stroop interference, k values on the delay discounting task, and backward digit span.](image-url)
Fig. 2. BESA temporal–spatial regional source models (from 200 ms before stimulus onset to 600 ms after stimulus onset) presented separately as a function of age (younger vs. older) and EF (poor vs. good). Models depict regional sources based on stimulus-locked, grand-averaged, correct Nogo waveforms, shown here at peak N2 amplitudes. The sizes of the regional sources are proportional to activation strength using the same scale across all groups.

3. Discussion

The frontal Nogo N2 is generally considered to be an index of cognitive control (e.g., Botvinick et al., 2001; Jodo & Kayama,
is also reflected in the correlations with electrode sites shown in Table 3. In contrast, measures of working memory, such as backward digit span, are typically associated with lateral PFC but not orbitofrontal cortex or cingulate cortex (D’Esposito & Postle, 2002). Although the psychological functions of the IGT are difficult to specify, it is clear that this task taps processes required for affective decision-making (e.g., Bechara, 2004). The Stroop task, on the other hand, provides a measure of selective attention and response inhibition (MacLeod, 1991). The pattern of results obtained here provides some information about which aspects of cognitive control (e.g., conflict detection in cingulate cortex versus rule use in orbitofrontal cortex) might be indexed by N2 amplitudes in children and adolescents, although further research is required to characterize these aspects more precisely.

Whereas N2 amplitudes were associated with aspects of EF, N2 latencies were associated with age but not EF. N2 latencies, therefore, may be associated with age-related changes that are relatively independent of the development of EF—for example, enhanced conductivity due to the myelination of axons. Cortical and subcortical myelination has been found to continue to develop into adulthood (e.g., Sowell et al., 2003).

Although source modeling of the N2 suggested orbitofrontal and cingulate generators in both children and adolescents, the location of the cingulate generator was more anterior for participants who performed better on the IGT and Stroop task, so this study provides some evidence that frontolization of cingulate activity may be associated with the development of cognitive control, and indeed, may be instrumental to this development (cf. Rubia et al., 2000).

Interestingly, the estimated location of the orbitofrontal generator for the good EF adolescents was right orbitofrontal cortex, consistent with previous findings from adults (e.g., Bokura et al., 2004). In contrast, the location of this source was relatively left lateralized for children (versus adolescents), especially those who performed poorly on the measures of EF. This pattern of results suggests that both EF and age may be related to a migration of the ventral source from left to right orbitofrontal cortex. Although the causes of this putative migration are unclear, one possibility is that children, especially poor EF children, may be more likely to rely on verbal strategies in this task (cf. Bunge et al., 2002).

4. Conclusion

This study attempted to disentangle the contributions of age and the development of EF to the frontal Nogo N2, an index of cognitive control in adults. Better performance on the IGT and the Stroop task was associated with higher N2 amplitudes, over and above effects of age, and N2 latencies decreased with age but were not predicted by EF. These findings suggest that age-related decreases in N2 amplitude, but not N2 latency, do indeed reflect the development of cognitive control and cannot be attributed solely to incidental changes that may affect assessments of the N2. Changes in the locations of the neural generators of the N2, including frontolization of the cingulate source, and right lateralization of the ventral source, also appear to be related to EF. The patterns of relations obtained in this study shed light on the complex interplay between age, development, and cognitive control.
on the aspects of cognitive control indexed by N2 amplitude in children and adolescents, but further research is required to characterize these aspects more precisely.

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