NeuroImage 56 (2011) 1648–1654

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

The development of future-oriented control: An electrophysiological investigation

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ARTICLE INFO

Article history:
Received 1 October 2010
Revised 27 December 2010
Accepted 1 February 2011
Available online 18 February 2011

ABSTRACT

Cognitive control, or the ability to focus attention and select task-appropriate responses, is not static but can be dynamically adjusted in the face of changing environmental circumstances. Several models suggest a role for conflict-monitoring in triggering these adjustments, whereby instances of response uncertainty are detected by the anterior cingulate cortex and strengthen attention-guiding rules actively maintained by lateral prefrontal cortex. Given the continued development of active maintenance mechanisms into adolescence, these models predict that the capacity to dynamically modulate control should be protracted in its development. The present study tested this prediction by examining age-related differences in behavioral and electrophysiological adaptations to prior conflict. Children, adolescents, and adults were administered the Dimensional Change Card Sort (DCCS; Zelazo, 2006) – a developmentally-appropriate task modified so that response conflict varied from trial to trial – as cortical activity was measured by means of event-related potentials (ERPs). Although all groups showed a robust conflict effect, there were pronounced age-related differences in behavioral and electrophysiological adaptations to prior conflict. First, responses to incongruent trials were faster following incongruent trials than following congruent trials, but only for adults and adolescents. Second, ERP components that indexed response conflict, and the cortical source of these components, were modulated by preceding conflict for adults and adolescents, but not children. Taken together, the findings suggest that adults and adolescents take advantage of prior conflict to prepare for the future, whereas children respond to cognitive challenges as they occur. Theoretical implications are discussed.

Introduction

Cognitive control is a higher-order cognitive process involved in the selection of task-relevant stimuli and responses (Miller and Cohen, 2001). Despite stable individual (Miyake et al., 2000) and developmental differences (Davidson et al., 2006), cognitive control is also subject to dynamic moment-to-moment changes in efficacy (for review, see Mansouri et al., 2009). For example, in stimulus–response compatibility tasks (Kornblum, 1994), participants adapt to the relative frequency of incompatible trials, such that interference costs decrease with increases in the frequency of stimulus–response incompatibility (Gratton et al., 1992; Botvinick et al., 2001). These adaptations occur rapidly, as illustrated by trial-to-trial variation in preparedness for conflict (Kerns et al., 2004), and vary continuously with parametric manipulations of prior congruency (Durston et al., 2003; Forster et al., 2011). Understanding the cognitive and neural basis of these effects is currently an important focus of cognitive neuroscience research.

According to several models (Botvinick et al., 2001; Braver et al., 2007), evaluative processes meditated by the anterior cingulate (ACC) monitor for the presence of conflict in competing response pathways. When instances of response conflict are detected, the ACC recruits additional control resources by strengthening attention-guiding rules maintained by lateral prefrontal cortex (PFC). When strengthened, rules can more effectively bias the processing of subsequent stimuli in favor of task-relevant features, leading to diminished conflict effects on subsequent incongruent trials. Consistent with these models, prior conflict is associated with attenuated activity in the ACC and increased activity in lateral PFC on subsequent incongruent trials (Liston et al., 2006; Kerns et al., 2004).

The focus of the current investigation was on possible age-related changes in such behavioral and neural adaptations to prior conflict. According to several accounts, (Botvinick et al., 2001; Braver et al., 2007; Forster et al., 2011), adaptations to prior conflict are made possible in part by the capacity of lateral PFC to form and maintain strong active representations of attention-guiding rules. However, by most anatomical and physiological measures, lateral PFC, and dorsal regions in particular, are among the latest developing cortical regions, showing continued changes in synaptic density (Huttenlocher and Dabholkar, 1997), cortical thickness (Giedd et al., 1999; Sowell et al., 2001; Shaw et al., 2008), myelination (Klingberg et al., 1999), and resting metabolic rate (Chugani et al., 1987) into late adolescence and early adulthood (for review, see Diamond, 2002). Computational models of development (Spencer et al.,

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1053-8119/$ – see front matter
doi:10.1016/j.neuroimage.2011.02.001

2009) suggest that one consequence of these protracted changes is that children have difficulty maintaining strong active representations of attention-guiding rules (Morton and Munakata, 2009; Munakata et al., 1997), and are therefore prone to dysfunctional control in object search (Munakata, 1998) and flexible rule-use tasks (Chevalier and Blaye, 2009; Morton and Munakata, 2002). One hypothesis that follows from these ideas is that there should be age-related differences in behavioral and neural adaptations to prior conflict, with these adaptations more pronounced in older participants (i.e., adults, adolescents) than in younger participants (i.e., children).

We tested this hypothesis through the use of converging behavioral and electrophysiological methods. Children, adolescents, and adults were administered a modified version of the Dimensional Change Card Sort (DCCS; Zelazo, 2006) as cortical activity was monitored by means of scalp-measured electrical potentials. Owing to its transparency and ease of administration, the DCCS is widely-used in developmental cognitive neuroscience studies of cognitive control (Moriguchi and Hiraki, 2009; Morton et al., 2009; Waxer and Morton, in press). In the version of the task used in this study, two bivalent target stimuli (i.e., a red rabbit and a blue truck) appeared at the top of the computer screen throughout the task, and on individual trials, participants sorted an imperative stimulus (centrally-presented) either by shape or by color (see Fig. 1). Half of the imperative stimuli embodied conflict insofar as they could legitimately be sorted either by color or by shape (i.e., they were bivalent stimuli that matched each target on a single dimension, as for example a blue rabbit), and half of the imperative stimuli did not (i.e., they were univalent stimuli that matched one target on one dimension, as for example a blue bar; henceforth univalent stimuli are referred to as "congruent"[1]). Because neither color nor shape is strongly prepotent in this task and to ensure bivalent stimuli (henceforth referred to as "incongruent"[1]) were a robust source of conflict, sorting criteria periodically changed (see also Liston et al., 2006).

Importantly, the task generates robust behavioral and electrophysiological congruency effects for participants of all ages (Waxer and Morton, in press) that parallel congruency effects reported elsewhere in the literature. First, with respect to behavior, response times are slower to incongruent than congruent stimuli (see also Diamond and Kirkham, 2005), an effect that is more pronounced for younger than older participants and which is orthogonal to the effect of rule-switching (Waxer and Morton, in press). Second, with respect to electrophysiology, imperative stimuli elicit a fronto-central negativity that is greater in amplitude for incongruent than congruent stimuli (Waxer and Morton, in press). For adults and adolescents, this congruency effect is evident in the stimulus-locked N2; for children it appears slightly later, in the stimulus-locked N4. Importantly, individual differences in the amplitude of these fronto-central components are associated with individual differences in behavioral costs of stimulus congruency for participants of all ages. Specifically, larger (i.e., more negative) differences in the amplitude of these components on incongruent versus congruent trials are associated with larger behavioral congruency effects, but orthogonal to behavioral costs associated with rule switching. Modulation of the stimulus-locked N2 by response conflict is well-documented in the literature (van Veen and Carter, 2002a,b), is thought to index monitoring processes computed by the ACC (Yeung et al., 2004), and has been observed across a variety of tasks (Nieuwenhuis et al., 2003; van Veen and Carter, 2002a,b), including conflict adaptation paradigms (Forster et al., 2011; Freitas et al., 2009; but see Wendt et al., 2007). The behavioral and electrophysiological congruency effects elicited by the DCCS therefore converge with previously reported findings, and provide a sound methodological basis for the present investigation.

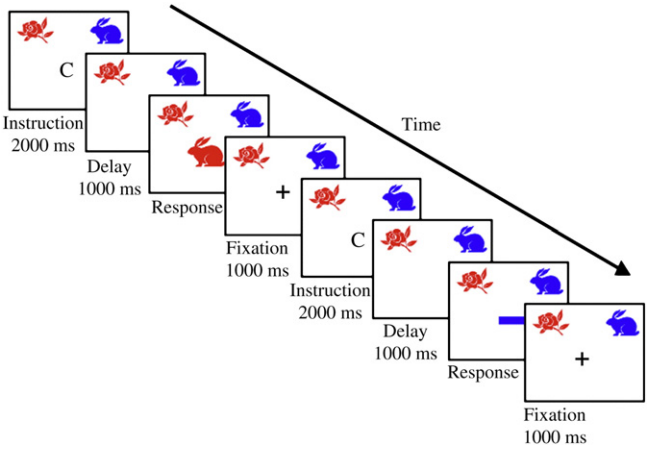

Fig. 1. An illustration of two trials from the version of the Dimensional Change Card Sort task used in the present study. Trials began with an instruction cue indicating the rule on that trial, followed by a delay period, followed by the presentation of a stimulus to which the participants responded, followed by a fixation point. Incongruent stimuli matched each target location on one feature; congruent stimuli matched only one target location on one feature.

To examine age-related differences in the dynamic modulation of cognitive control, we measured behavioral and electrophysiological adjustments to prior conflict in children, adolescents, and adults. Responses on incongruent trials are typically slower than responses on congruent trials. However, the degree of slowing is not static but varies as a function of the prior trial-type. For example, responses on incongruent trials that immediately follow incongruent trials (i.e., iI trials) are typically faster than responses on incongruent trials that immediately follow congruent trials (i.e., cI trials; Gratton et al., 1992; Kerns et al., 2004). Similarly, stimulus-locked N2 amplitudes on incongruent trials are smaller following prior incongruent trials than prior congruent trials (Forster et al., 2011). According to computational models of conflict monitoring (Botvinick et al., 2001; Braver et al., 2007), resolving prior incongruence strengthens attention-guiding rules (Kerns et al., 2004) and amplifies representations of task-relevant stimulus features (Egner and Hirsch, 2005), leading to greater preparedness for conflict and diminished N2 amplitudes on succeeding incongruent trials relative to trials preceded by congruence (Forster et al., 2011; Freitas et al., 2009).

We tested for age-related differences in these behavioral and electrophysiological effects with the following predictions. On the hypothesis that prior incongruence attenuates conflict-related activity in the ACC on subsequent incongruent trials, we predicted smaller N2 amplitudes on iI compared with cI trials, with the cortical source of the N2 in the vicinity of the ACC. Second, on the hypothesis that the development of active maintenance is protracted (Morton and Munakata, 2009; Munakata, 1998) and extends into adolescence, we predicted that behavioral and electrophysiological adaptations to prior conflict would be attenuated in children relative to adults and adolescents. Given greater latency in the modulation of fronto-central components by response conflict in children relative to adolescents and adults, we tested for sequential trial order effects in children both at the N2 and also at the N4. Finally, we predicted age-related differences in the association of behavioral (i.e., RT_cI – RT_iI) and electrophysiological adaptations (i.e., N2_cI – N2_iI) to prior conflict. Specifically, we predicted that for adults and adolescents, larger behavioral adaptation effects would be associated with larger (i.e., more negative) differences in N2 amplitudes across cI and iI trials, whereas for children, there would be no such association, either at the N2 or the N4.

[1] We refer to univalent stimuli as "congruent" and bivalent stimuli as "incongruent" in order to relate our methods more seamlessly with the literature, where use of "iI", "cI", "iC", and "cC" is quite conventional. To the extent that incongruent and our bivalent stimuli generate response conflict, and congruent and our univalent stimuli do not, use of these terms is not, in our view, misleading.

Materials and methods

Participants

Participants included 40 children (29 males), 20 adolescents (9 males), and 20 young adults (11 males). Children ranged in age from 9- to 11-years ($M = 10.2$), adolescents ranged in age from 14- to 15-years ($M = 15$), and adults ranged in age from 18- to 25-years ($M = 19.4$). Children and adolescents were recruited from a database of families who had expressed an interest in voluntary research participation; adults were students enrolled in introductory psychology courses who participated in exchange for course credit. Adults provided written consent to their participation. Parents provided written consent for their children's participation. All participants had normal, or corrected to normal visual acuity, normal color vision, no dental braces or metal implants, and all reported being right-handed.

Task and procedures

Participants performed a computer-administered variant of the Dimensional Change Card Sort (DCCS; Zelazo, 2006, Morton et al., 2009). On each trial, participants were presented with two bivalent target stimuli (e.g., a red flower and a blue rabbit) at the top of the screen (see Fig. 1). The location of the targets was counterbalanced across participants, but was fixed for each individual participant. Continuously presented trials began with a 2000 ms instruction period in which a centrally-presented instruction cue ("S" for shape; "C" for color) indicated the sorting rule for each trial, followed by a 1000 ms delay during which the sorting rule had to be maintained. Switch trials were trials in which the sorting rule changed from the previous trial; repeat trials were trials in which the sorting rule remained the same. Following the instruction period, either an incongruent or a congruent imperative stimulus was presented in the center of the screen. Incongruent stimuli matched each target on a single dimension (e.g., a red rabbit or a blue flower) and could therefore be legitimately sorted either by color or shape. Congruent stimuli matched one target on one dimension (e.g., a black rabbit, black flower, red bar, or blue bar) and could therefore be legitimately sorted in only one way. Participants sorted stimuli by depressing a button whose location corresponded with the location of one of the two target stimuli (e.g., pressing the right button sorted the red rabbit by color; pressing the left button sorted it by shape). Responses were registered on a PST button-box (Psychological Software Tools, Pittsburgh, PA) and canceled the response period. Individual trials were separated by a 1000 ms response–cue-interval (RCI).

Switch trials were followed by 3 repeat trials. On 50% of these trials, the imperative stimulus was incongruent, and on the other 50%, it was congruent. Because trial order was randomized, individual trials (congruent and incongruent alike) were preceded by congruent trials as often as they were by incongruent trials. Thus, by design, 25% of trials were congruent trials preceded by congruent trials (i.e., cC trials, where lower-case denotes the previous trial and upper-case denotes current trial), 25% were congruent trials preceded by incongruent trials (iC trials), 25% were incongruent trials preceded by congruent trials (cI trials) and 25% were incongruent trials preceded by incongruent trials (iI trials).

Participants were instructed about the basic nature of the task and the need to respond as quickly and accurately as possible. To ensure comprehension of the instructions, all participants completed 16 practice trials. Adolescent and adult participants then completed 6 blocks of 68 trials, and child participants completed 6 blocks of 36 trials. A brief rest was provided after each block.

EEG data collection and processing

Electroencephalogram (EEG) was recorded continuously with a 128-channel Electrical Geodesics system (EGI Inc, Eugene, OR; Tucker et al., 1993) at 200 Hz, with 0.1–80 Hz analog filtering referenced to the vertex (channel 129). Impedance of all channels was kept below 50 kΩ. Data were filtered offline using an FIR 1–30 Hz bandpass filter. Trials rejected prior to averaging included: (1) premature responses (faster than 200 ms); (2) errors and post-error events; (3) responses slower than 3 standard deviations from the participants' mean response time; (4) eye movement artifacts (70 μV threshold); (5) signals exceeding 200 μV; or (6) fast transits exceeding 100 μV. Eye blinks were corrected using the algorithm developed by Gratton et al., 1983. The EEG was then re-referenced to an average reference (Bertrand et al., 1985, Tucker et al., 1993). Continuous EEG was segmented into stimulus-locked condition-related epochs ranging from 200 ms before to 600 ms after stimuli onset. Epochs were baseline-corrected using data from the first 200 ms of the epoch.

Source-space analysis

Source localization was performed on baseline-corrected ERP data, using a 4-shell Sun-Stok model (Sun, 1997). Electrode position was recorded for each participant by means of a geodesic photogrammetry system (EGI Inc, Eugene, OR) and was used in the construction of each participant's forward model. The inverse matrix was calculated using the minimum norm least-squares (L2) method, subject to depth weighting, orientation weighting, truncated singular value decomposition regularization at 10^{-4} to stabilize the solution, and using the LORETA constraint (low resolution electromagnetic tomography; for review see Michel et al., 2004). Source space was restricted to 2447 cortical voxels ($7mm^3$) that each contained a source dipole and had assigned spatial coordinates based on the Montreal Neurological Institute (MNI) probabilistic atlas. All source modeling was performed using GeoSource software (EGI Inc, Eugene, OR; for a review of source modeling constraints see Michel et al., 2004).

To estimate the cortical generators of the N2 on cI and iI trials, one region of interest (ROI) centered on the anterior cingulate cortex (ACC) was generated using the MNI average adult MRI. Functional neuroimaging studies and computational models (Botvinick et al., 2001) of conflict adaptation implicate the ACC (Kerns et al., 2004; Kerns, 2006; Liston et al., 2006) in these effects. The ACC ROI was composed of a subset of dipoles from the source model. The latency range used for the cI and iI N2 was a 40 ms time window centered on the peak amplitude of the cI and iI N2 identified in the ERP analysis. Additionally, source waveform amplitudes for the average of all diploes within an ROI were Log_{10} transformed for the purpose of parametric statistical analysis (Thatcher et al., 2005).

Results

Behavioral analysis

Trials with excessively short RTs (<200 ms), error and post-error trials, and trials with RTs slower than 3 standard deviations from the participant's mean RT for each trial type were excluded from RT analysis (Ratcliff and Tuerlinckx, 2002). Response times and error rates were submitted to separate mixed analysis of variance (ANOVAs) with Age Group (adults, adolescents and children) as a between-subjects variable, and Previous Trial Type (congruent and incongruent), and Current Trial Type (congruent and incongruent) as within-subjects variables.

Mean RTs for the four different trial types are displayed in Fig. 2. An ANOVA on RTs revealed main effects of Age Group, $F(2, 77) = 19.99$, $p < .001$, Previous Trial Type, $F(1, 77) = 5.94$, $p < .017$, and Current Trial Type, $F(1, 77) = 79.54$, $p < .001$. This analysis also revealed 2-way interactions between Previous Trial Type and Age Group, $F(2, 77) = 20.84$, $p < .001$, as well as between Current Trial Type and Age Group, $F(2, 77) = 4.77$, $p < .01$. Additionally, there was a 3-way interaction between Previous Trial Type, Current Trial Type, and Age Group, F (2,

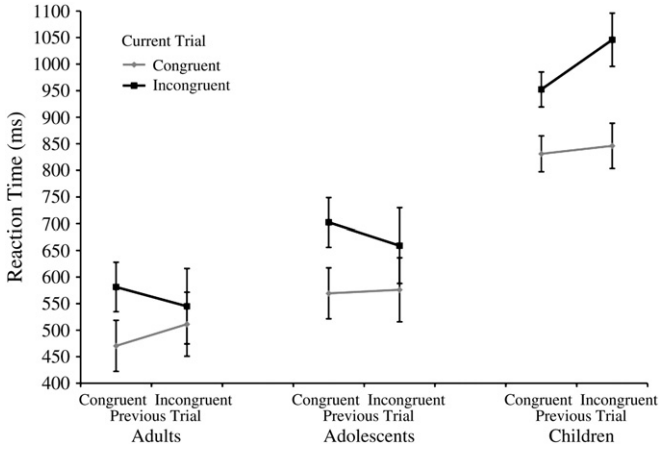

Fig. 2. Reaction times as a function of trial type and age group.

77) = 10.03, p<.001. Post-hoc contrasts, Bonferroni corrected for multiple comparisons, indicated that adults, t (19) = −4.13, p<.005, and adolescents, t (19) = −4.20, p<.001, were faster on iI trials than cI trials, whereas children were slower on iI trials than cI trials, t (39) = 4.75, p<.001. Additionally, adults were faster on cC trials than iC trials, t (19) = −4.60, p<.001, whereas cC trials and iC trials did not differ for the adolescents, t (58) = −1.13, *n.s.*, and children, t (39) = −0.97, *n.s.* These differences were not the result of basic age-differences in baseline response speed, as adaptation effects expressed as a percent facilitation on iI relative to cI trials (i.e., (cI-iI/cI)*100) indicated that adults, t (59) = 6.44, p<.001, and adolescents, t (59) = 6.42, p<.001, showed larger adaptation effects compared to children, but did not differ from each other, t (39) = .01, *n.s.*

To ensure that the aforementioned results were not the result of associative priming (e.g., Mayr et al., 2003), we re-analyzed the RT data excluding exact stimulus repetition trials. The pattern of results for the Age Group × Previous Trial Type × Current Trial Type ANOVA excluding stimulus repetitions was consistent with the analysis present above (see Table 1). The main effects of Age Group, F (2, 77) = 19.88, p<.001, and Current Trial Type, F (1, 77) = 69.65, p<.001, remained significant. Additionally, this analysis revealed 2-way interactions between Age Group and Previous Trial Type, F (2, 77) = 23.66, p<.001, as well as between Age Group and Current Trial Type, F (2, 77) = 6.62, p<.01. Furthermore, the 3-way interaction between Age Group, Previous Trial Type, and Current Trial Type, F (2, 77) = 11.08, p<.001, remained significant. Thus, the conflict adaptation effects persisted even after accounting for the potential contribution of associative priming. Since the pattern of behavioral results did not meaningfully change when trials that would lead to associative priming were removed, ERP analyses and subsequent source modeling of the ERP data were conducted on all trials to maximize signal-to-noise ratio.

Mean error rates as a function of Current Trial Type (congruent versus incongruent), Preceding Trial Type (congruent versus incongruent), and Age Group (children, adolescents, and adults) are displayed in Fig. 3. An ANOVA on accuracy revealed a main effect of Current Trial Type, F (1, 77) = 96.06, p<.001, with greater accuracy on congruent than incongruent trials. Additionally, there were 2-way interactions between Current Trial Type and Age Group, F (2, 77) = 3.39, p<.05, and between Previous Trial Type and Current Trial Type, F (1, 77) = 6.85, p<.01. Post-hoc contrasts, Bonferroni corrected for multiple comparisons, indicated that accuracy was greater on cC than on cI, t (79) = 10.01, p<.001, and iI, t (79) = 10.00, p<.001, trials. Additionally, accuracy was greater on iC trials than cI, t (79) = 6.21, p<.001, and iI trials, t (79) = 9.30, p<.001.

ERP analysis

Fig. 4 shows the stimulus-locked ERP components at FCz for cC, iC, cI, and iI trials. As is clearly visible, adolescent and adult waveforms showed a pronounced negativity approximately 200 ms post-stimulus (i.e., N2) whose amplitude was modulated by the interaction of previous and current trial congruency. To explore these differences further, adaptive mean N2 amplitudes for previous and current trial type were examined at 3 frontocentral electrode sites (Cz, FCz/6, and Fz/11). The N2 adaptive mean was defined as the average electrical activity within a 50 ms time window surrounding the peak of the N2. Adaptive mean N2 amplitudes were submitted to a 4-way mixed ANOVA with Age Group (children, adolescents and adults) as a between-subjects variable, Previous Trial Type (congruent and incongruent), Current Trial Type (congruent and incongruent), and Electrode Site (Cz, FCz, and Fz) as within-subjects variables. This analysis revealed main effects of Age Group, F (2, 77) = 21.39, p<.001, Electrode Site, F (2, 156) = 40.31, p<.001, and Current Trial Type, F (1, 78) = 6.77, p<.01. There was also a 2-way interaction between Age Group and Electrode Site, F (4, 156) = 3.93, p<.01. Additionally there was a 3-way interaction between Previous Trial Type, Current Trial Type and Age Group, F (2, 78) = 3.79, p<.05. Post-hoc contrasts, Bonferroni corrected for multiple comparisons, indicated that the amplitude of the N2 was larger on cI trials relative to iI trials for adults, t (19) = −3.16, p<.05, and adolescents, t (19) = −6.84, p<.001, but not for children, t (39) = −0.13, *n.s.* The amplitude of the N2 did not differ between cC trials relative to iC trials for all age groups.

As congruency effects for children appear later in time, at the N4, we also tested whether conflict adaptation would be evident on this later component. Thus, children's mean N4 amplitudes were submitted to a

Table 1
Correlation of behavioral and electrophysiological measures of conflict adaptation. Greater behavioral adaptation (RT_cI – RT_iI) was associated with larger (i.e., more negative) differences in N2 amplitude across cI and iI trials in adults and adolescents, but not children, either at the N2 or the N4.

Age group		N2 Diff Cz	N2 Diff Fcz	N2 Diff Fz
Children	Adaptation Rt	−.09	−.03	−.08
Adolescents	Adaptation Rt	.004	−.67**	−.08
Adults	Adaptation Rt	−.23	−.59**	−.53*
Age group		N4 Diff Cz	N4 Diff Fcz	N4 Diff Fz
Children	Adaptation Rt	.03	−.19	−.25

** p<.01, two-tailed.
* p<.05, two-tailed.

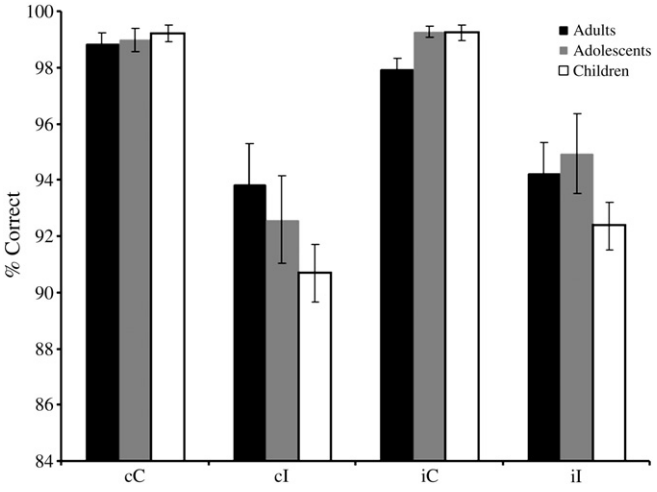

Fig. 3. Error rates as a function of trial type and age group.

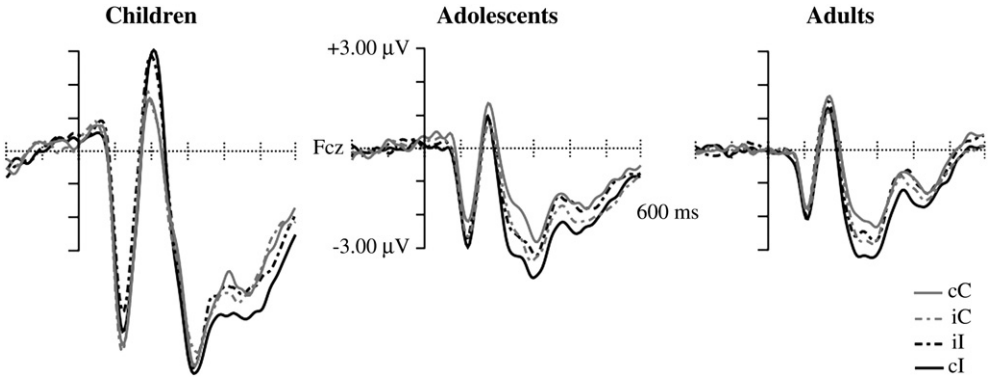

Fig. 4. Grand averaged stimulus-locked waveforms at electrode Fcz for children, adolescents, and adults. Each wave board plots a 200 ms baseline and 600 ms post stimulus onset.

3-way repeated measures ANOVA with Previous Trial Type (congruent and incongruent), Current Trial Type (congruent and incongruent), and Electrode Site (Cz, FCz, and Fz) as within-subjects variables. This analysis confirmed that the amplitude of the N4 was modulated by Current Trial congruency, F, $(1, 39) = 5.02$, $p < .05$, but not by preceding trial congruency, $F\,(1, 39) < 1$, *n.s.*

To ensure that the aforementioned ERP findings were not contaminated by differences in earlier components, we also examined conflict modulations at the P1. Adaptive mean P1 amplitudes for each previous and current trial type were examined at 3 frontocentral electrode sites (Cz, Fcz, and Fz), where the P1 adaptive mean was defined as the average electrical activity within a 50 ms time window surrounding the peak of the P1. Adaptive mean P1 amplitudes were submitted to a 4-way mixed ANOVA with Age Group (children, adolescents, and adults) as a between-subjects variable, Previous Trial Type (congruent and incongruent), Current Trial Type (congruent and incongruent), and Electrode Site (Cz, FCz, and Fz) as within-subjects variables. This analysis revealed a main effect of age group, $F\,(2, 77) = 4.78$, $p < .001$. Post-hoc contrasts, Bonferroni corrected for multiple contrasts revealed that the overall amplitude of the P1 was greater for children than adolescents $t\,(59) = 3.09$, $p < .01$. There were no other effects or interactions.

Brain behavior correlation analysis

To examine the relationship between individual differences in the behavioral conflict adaptation effect (i.e., RT cI – RT iI) and individual differences in the magnitude of N2 and N4 amplitude modulation (i.e., N2 cI – N2 iI), two-tailed Pearson correlations were conducted at 3 frontocentral electrode sites (Cz, FCz, and Fz). These correlations were Bonferroni corrected for multiple comparisons and were conducted separately for each age group (see Table 1). For the adults, greater reaction time differences were associated with larger N2 amplitude differences at electrode site FCz, $r = -.59$, $p < .005$, and electrode site Fz, $r = -.53$, $p < .01$. For the adolescents, greater reaction time differences were associated with larger N2 differences at electrode site FCz, $r = -.67$, $p < .001$. However, for children, individual differences in behavioral adaptation were not associated with individual differences in N2 or N4 modulation by prior conflict.

Source space analyses

Fig. 5 shows the source model activations (in nA) for cI and iI trials. As is clearly visible, adolescent and adult source model activations in

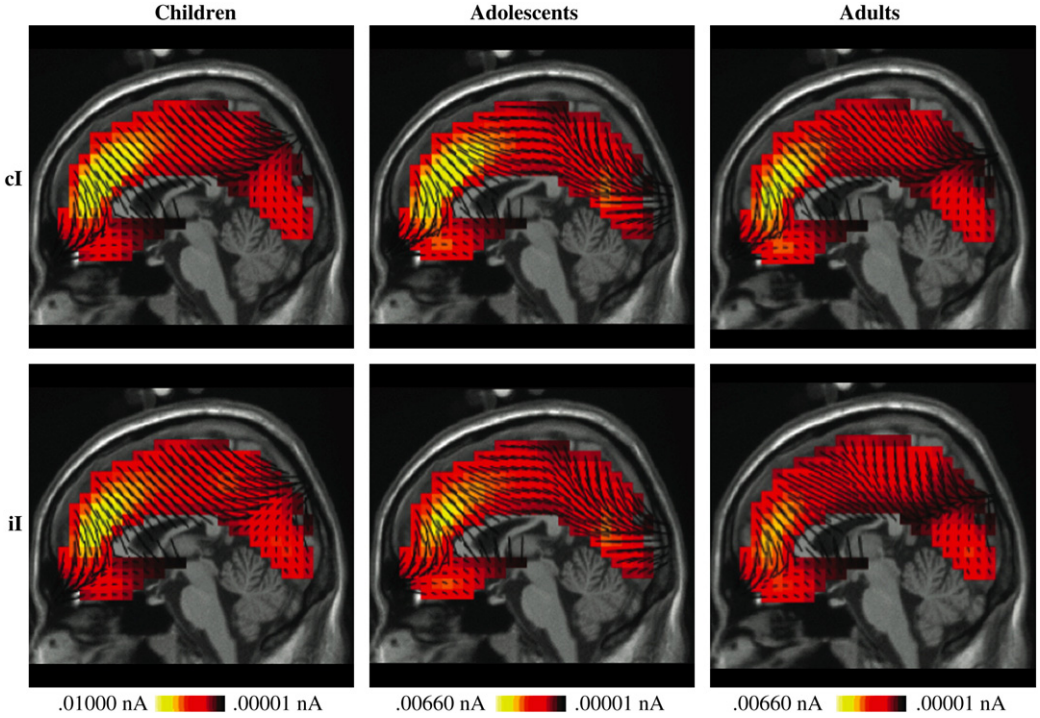

Fig. 5. Modeled source activations (in nA) displayed using the Montreal Neurological Institute (MNI) average adult MRI scan for peak N2 amplitude on cI and iI trials for each age group.

the vicinity of the ACC were greater for cI trials than iI trials. To explore these differences further, mean source model activity from the ACC ROI were submitted to a 2-way mixed ANOVA with Age Group (children, adolescents and adults) as a between-subjects variable and Trial Type (cI and iI) as a within-subjects variable. This analysis revealed main effects Age Group, F (2, 78) = 35.12, p<.001, and Trial Type, F (1, 78) = 25.08, p<.001. Additionally there was a 2-way interaction between Age Group and Trial Type, F (2, 78) = 8.68, p<.001. Post-hoc contrasts, Bonferroni corrected for multiple comparisons, indicated that ACC source activity was greater for cI than iI trials for the adults, t (19) = 4.13, p<.001, and adolescents, t (19) = 4.09, p<.001, but not the children, t (39) = 0.05, *n.s.*

Discussion

The present study examined age-related differences in brain and behavioral adaptations to prior conflict. Children, adolescents, and adults were administered a modified version of the DCCS (Zelazo, 2006) in which stimulus congruency varied from trial to trial while cortical activity was monitored by means of EEG. Adults showed reliable behavioral and electrophysiological effects of prior congruency. Specifically, responses to iI trials were faster and more accurate compared with cI trials, and the amplitude of a fronto-central N2, source-localized to the ACC, was smaller on iI compared with cI trials. Finally, individual differences in N2 amplitude modulation were associated with individual differences in the magnitude of sequential trial order effects, with larger (i.e., more negative) differences between the N2 on cI versus iI trials associated with larger post-conflict behavioral adjustments. These effects parallel findings of prior adult studies (Forster et al., 2011; Freitas et al., 2009; but see Wendt et al., 2007). In one, prior conflict modulated stimulus-locked N2-amplitudes on subsequent trials, but not response-locked LRPs (Freitas et al., 2009). In the other, parametric variation in prior conflict magnitude was associated with parametric modulation in stimulus-locked N2 amplitudes and behavioral response times on subsequent incongruent trials (Forster et al., 2011), with greater prior conflict associated with greater electrophysiological and behavioral adaptation on subsequent trials. And as in the current data, individual differences in N2 modulation by prior conflict were negatively associated with subsequent behavioral adjustment, with greater (more negative) differences in N2 amplitude across iI and cI trials associated with greater differences in RT across iI and cI trials. Thus, while this is the first study to examine behavioral and electrophysiological adaptations to prior response conflict using the DCCS, the results (at least for adults) parallel effects reported in two prior independent studies.

The present study extends these findings by showing age-related differences in this overall pattern. Specifically, adolescents showed effects of previous trial congruency reminiscent of those observed in adults (in response times, N2 amplitudes, and ACC source activity), but children showed no evidence of behavioral or electrophysiological adaptation to prior conflict. This was true despite the fact that children showed robust effects of congruency in response time and N4 amplitude (Waxer and Morton, in press). In sum, the findings suggest age-related differences in brain and behavioral adaptations to prior conflict.

Whether these data unequivocally implicate differences in higher-order processes is of course unclear. There is evidence, for example, that conflict adaptation effects can be explained, at least in part, by associative priming (Mayr et al., 2003) and feature integration (Hommel et al., 2004). On these accounts, responses on iI trials are faster than responses on cI trials because of exact stimulus and response repetitions specific to iI trials. It seems unlikely however that stimulus-specific processes of this kind could entirely account for the present findings, as the magnitude of post-conflict behavioral adjustments did not change when the effects of stimulus repetition were controlled. Similar findings have been reported elsewhere (Egner and Hirsch, 2005; Freitas et al., 2009; Kerns et al., 2004; Ullsperger et al., 2005).

One possibility is that the findings point to developmental changes in proactive control. As outlined in the Dual Mechanisms of Control theory (Braver et al., 2007), proactive – or future-oriented – control involves an anticipatory representation of attention-guiding rules through sustained activity in lateral PFC. Attention-guiding rules in turn bias the processing of imperative stimuli in favor of task-relevant features and help to mitigate conflict before it arises. Reactive – or moment-to-moment – control is a late-correction process, mediated by transient ACC and lateral PFC activity, that manages conflict after it occurs. On the assumption that the effects of prior incongruency carry forward into the succeeding trial by virtue of the proactive maintenance of attention-guiding rules, and that the capacity to form and maintain strong representations of attention-guiding rules follows a protracted developmental trajectory (Morton and Munakata, 2009; Munakata, 1998), the DMC model provides a useful framework for understanding the present findings. On this account, faster responses, smaller N2 amplitudes, and smaller ACC source model activity on iI compared with cI trials by adults and adolescents reflect the impact of proactive control. Prior incongruency establishes a strong representation of attention-guiding rules that is proactively maintained into the succeeding trial and partially mitigates conflict before it arises. Because active maintenance mechanisms are underdeveloped early in life (Marcovitch et al., 2007; Morton and Munakata, 2009; Munakata, 1998), these effects are attenuated in children. Viewed in this way, the current findings converge with previous evidence (Chatham et al., 2009) that early in development, children rely predominantly on reactive control, whereas only later in development do they utilize both reactive and proactive control processes.

One caveat of the present study though is that the results bear most heavily on changes in future-oriented – or proactive – control processes, but don't examine potential differences in spontaneous – or reactive – control processes. A second caveat is that the current findings offer only indirect evidence (i.e., attenuated response conflict effects following conflict trials) of hypothesized changes in future-oriented control processes. One important goal of future investigations therefore would be to examine age-related differences in adaptive control but to focus on processes that temporally-precede the response conflict effects observed in this study.

The emergence of future-oriented cognition in development has been the focus of considerable theoretical discussion (Haith et al., 1994) and is certainly an important hallmark of cognitive developmental change. Limitations notwithstanding, the current study points to important developmental changes in dynamic future-oriented control processes and suggests that conflict adaptation effects may be a useful means of probing these changes.

References

Bertrand, O., Perrin, F., Perier, J., 1985. A theoretical justification of the average-reference in topographic evoked potential studies. Electroencephalogr. Clin. Neurophysiol. 62, 462–464.
Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. Psychol. Rev. 108, 624–652.
Braver, T.S., Gray, J.R., Burgess, G.C., 2007. In: Conway, A.R.A., Jarrold, C., Kane, M.J., Miyake, A., Towse, J. (Eds.), Variation in Working Memory. Oxford University Press, Oxford, pp. 76–106.
Chatham, C.H., Frank, M.J., Munakata, Y., 2009. Pupillometric and behavioral markers of a developmental shift in the temporal dynamics of cognitive control. Proc. Natl Acad. Sci. USA 106, 5529–5533.
Chevalier, N., Blaye, A., 2009. Setting goals to switch between tasks: effect of cue transparency on children's cognitive flexibility. Dev. Sci. 45, 782–797.
Chugani, H.T., Phelps, M.E., Mazziotta, J.C., 1987. Positron emission tomography study of human brain functional development. Ann. Neurol. 4, 487–497.
Davidson, M.C., Amso, D., Anderson, L.C., Diamond, A., 2006. Development of cognitive control and executive functions from 4 to 13 years: evidence from manipulations of memory, inhibition, and task switching. Neuropsychologia 44, 2037–2078.

Diamond, A., 2002. Normal Development of Prefrontal Cortex from Birth to Young Adulthood: Cognitive Functions, Anatomy, and Biochemistry. In: Stuss, D.T., Knight, R.T. (Eds.), Principles of Frontal Lobe Function. Oxford University Press, London, pp. 466–503.
Diamond, A., Kirkham, N.Z., 2005. Not so grown up as we like to think: parallels between cognition in childhood and adulthood. Psychol. Sci. 16, 291–297.
Durston, S., Davidson, M.C., Thomas, K.M., Worden, M.S., Tottenham, N., Martinez, A., Watts, R., Ulug, A.M., Casey, B.J., 2003. Parametric manipulation of conflict and response competition using rapid mixed-trial event-related fMRI. Neuroimage 20, 2135–2141.
Egner, T., Hirsch, J., 2005. Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. Nat. Neurosci. 8, 1784–1790.
Forster, S.E., Carter, C.S., Cohen, J.D., Cho, R.Y., 2011. Parametric manipulation of the conflict signal and control-state adaptation. J. Cogn. Neurosci. 23, 923–935.
Freitas, A.L., Banai, R., Clark, S.L., 2009. When cognitive control is calibrated: event-related potential correlates of adapting to information-processing conflict despite erroneous response preparation. Psychophysiology 46, 1226–1233.
Giedd, J.N., Blumenthal, J., Jeffries, N.O., Castellanos, F.X., Lui, H., Zijdenbos, A., Paus, T., Evans, A.C., Rapoport, J.L., 1999. Brain development during childhood and adolescence: a longitudinal MRI study. Nat. Neurosci. 2 (10), 861–863.
Gratton, G., Coles, M.G.H., Donchin, E., 1983. A new method for off-line removal of ocular artifact. Electroencephalogr. Clin. Neurophysiol. 55, 468–484.
Gratton, G., Coles, M.G.H., Donchin, E., 1992. Optimizing the use of information: strategic control of activation of responses. J. Exp. Psychol. Gen. 121, 480–506.
Haith, M.M., Benson, J.B., Roberts Jr., R.J., 1994. The Development of Future-Oriented Processes. University of Chicago Press, Chicago.
Hommel, B., Proctor, R.W., Vu, K.P.L., 2004. A feature-integration account of sequential effects in the Simon task. Psychol. Res. 68, 1–17.
Huttenlocher, P.R., Dabholkar, A.S., 1997. Regional differences in synaptogenesis in human cerebral cortex. J. Comp. Neurol. 387, 167–178.
Kerns, J.G., 2006. Anterior cingulate and prefrontal cortex activity in an fMRI study of trial-to-trial adjustments on the Simon task. Neuroimage 33, 399–405.
Kerns, J.G., Cohen, J.D., MacDonald, A.W., Cho, R.Y., Stenger, A., Carter, C.S., 2004. Anterior cingulate conflict monitoring and adjustments in control. Science 303, 480–506.
Klingberg, T., Vaidya, C.J., Gabrieli, J.D.E., Moseley, M.E., Heduhux, M., 1999. Myelination and organization of frontal white matter in children: a diffusion tensor MRI study. NeuroReport 10, 2817–2821.
Kornblum, S., 1994. The way irrelevant dimensions are processed depends on what they overlap with: the case of Stroop- and Simon-like stimuli. Psychol. Res. 56, 130–135.
Liston, C., Matalon, S., Hare, T.A., Davidson, M.C., Casey, B.J., 2006. Anterior cingulate and posterior parietal cortices are sensitive to dissociable forms of conflict in a task-switching paradigm. Neuron 50, 643–653.
Mansouri, F.A., Tanaka, K., Buckley, M.J., 2009. Conflict-induced behavioural adjustment: a clue to the executive functions of the prefrontal cortex. Nat. Rev. Neurosci. 10, 141–152.
Marcovitch, S., Boseovski, J., Knapp, R.J., 2007. Use it or lose it: examining preschoolers' difficulty in maintaining and executing a goal. Dev. Sci. 10, 559–564.
Mayr, U., Awh, E., Laurey, P., 2003. Conflict adaptation effects in the absence of executive control. Nat. Neurosci. 6, 450–452.
Michel, C.M., Murry, M.M., Lantz, G., Gonzalez, S., Spinelli, L., de Peralta, R.G., 2004. EEG source imaging. Clin. Neurophysiol. 115, 2195–2222.
Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci. 24, 193–222.
Miyake, A., Friedman, N.P., Emerson, M.J., Witzki, A.H., Wager, T.D., 2000. The university and diversity of executive functions and their contributions to complex "Frontal Lobe" tasks; a latent variable analysis. Cogn. Psychol. 41, 49–100.
Moriguchi, Y., Hiraki, K., 2009. Neural origin of cognitive shifting in young children. Proc. Nat. Acad. Sci. U.S.A. 106, 6017–6021.
Morton, J.B., Munakata, Y., 2009. Connectionist Approaches to Perseveration: Understanding Universal and Task-Specific Aspects of Children's Behavior. In: Spencer, J.P., Thomas, M., McClelland, J.L. (Eds.), Toward a Unified Theory of Development: Connectionism and Dynamic Systems Theory Re-Considered. Oxford University Press, pp. 141–164.
Morton, J.B., Munakata, Y., 2002. Active versus latent representations: a neural network model of perseveration, dissociation, and decalage. Dev. Psychobiol. 40, 255–265.
Morton, J.B., Bosma, R., Ansari, D., 2009. Age-related changes in brain activation associated with dimensional shifts of attention: an fMRI study. Neuroimage 46, 249–256.
Munakata, Y., 1998. Infant perseveration and implications for object permanence theories: a PDP model of the A-not-B task. Dev. Sci. 2, 161–184.
Munakata, Y., McClelland, J.L., Johnson, M.H., Siegler, R.S., 1997. Rethinking infant knowledge: toward an adaptive process account of successes and failures in object permanence tasks. Psychol. Rev. 104, 686–713.
Nieuwenhuis, S., Yeung, N., Wildenberg, W.V.D., Ridderinkhof, K.R., 2003. Electrophysiological correlates of anterior cingulate function in a go/no-go task: effects of response conflict and trial type frequency. Cogn. Affect. Behav. Neurosci 3, 17–26.
Ratcliff, R., Tuerlinckx, F., 2002. Estimating parameters of the diffusion model: approach to dealing with contaminant reaction times and parameter variability. Psychon. Bull. Rev. 9, 438–481.
Shaw, P., Kabani, N.J., Lerch, J.P., Eckstrand, K., Lenroot, R., Gogtay, N., Greenstein, D., Clasen, L., Evans, A., Rapaport, J.L., Giedd, J.N., Wise, S.P., 2008. Neurodevelopmental trajectories of the human cerebral cortex. J. Neurosci. 28, 3586–3594.
Sowell, E.R., Thompson, P.M., Tessner, K.D., Toga, A.W., 2001. Mapping continued brain growth and gray matter density reduction in dorsal frontal cortex: Inverse relationships during postadolescent brain maturation. J. Neurosci. 15, 8819–8829.
Spencer, J.P., Thomas, M.S.C., McClelland, J.L., 2009. Toward a Unified Theory of Development: Connectionism and Dynamic Systems Theory re-Considered. New York, Oxford.
Sun, M., 1997. An efficient algorithm for computing multishell spherical volume conductor models in EEG dipole source localization. IEEE T. Biomed. Eng. 44, 1243–1252.
Thatcher, R.W., North, D., Biver, C., 2005. Parametric vs. non-parametric statistics of low resolution electromagnetic tomography (LORETA). Clin. EEG Neurosci. 36, 1–8.
Tucker, D.M., Liotti, M., Pots, G.F., Russell, G.S., Posner, M.I., 1993. Spatiotemporal analysis of brain electrical fields. Hum. Brain Mapp. 1, 134–152.
Ullsperger, M., Bylsma, L.M., Botvinick, M.M., 2005. The conflict adaptation effect: it's not just priming. Cogn. Affect. Behav. Neurosci. 5, 467–472.
van Veen, V., Carter, C.S., 2002a. Anterior cingulate as a conflict monitor: fMRI and ERP studies. Physiol. Behav. 77, 477–482.
van Veen, V., Carter, C.S., 2002b. The timing of action-monitoring processes in the anterior cingulate cortex. J. Cogn. Neurosci. 14, 593–602.
Waxer, M., Morton, J.B., in press. Multiple processes underlying Dimensional Change Card Sort performance: A developmental electrophysiological investigation. J. Cog. Neurosci.
Wendt, M., Heldmann, M., Munte, T.F., Kluwe, R.H., 2007. Disentangling sequential effects of stimulus- and response-related conflict and stimulus–response repetition using brain potentials. J. Cogn. Neurosci. 19, 1104–1112.
Yeung, N., Botvinick, M.M., Cohen, J.D., 2004. The neural basis of error detection: conflict monitoring and the error-related negativity. Psychol. Rev. 111, 931–959.
Zelazo, P.D., 2006. The dimensional change card sort (DCCS): a method for assessing executive function in children. Nat. Protoc. 1, 297–302.