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Dissociable and Dynamic Components of Cognitive Control: A Developmental Electrophysiological Investigation

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Abstract

One standard task used to investigate the development of cognitive control is the Dimensional Change Card Sort (DCCS). Performance and patterns of brain activity associated with the DCCS show continued age-related advances into early adolescence. According to many theoretical accounts, the DCCS places demands on a single underlying executive control process. Three experiments examined the possibility that the DCCS places demands on multiple control processes that follow distinct developmental trajectories. In Experiment 1, rule switching and conflict processing made orthogonal contributions to DCCS performance. Rule switching was associated with a cue-locked late frontal negativity (LFN) event-related potential (ERP) and conflict processing was associated with stimulus-locked frontocentral N2. Moreover, rule switching and conflict processing followed distinct developmental trajectories. In Experiment 2, distributed cortical source models of the cue-locked LFN were associated with age-related differences in distributed network of regions associated with cognitive control. Source models of the stimulus-locked N2 were associated with conflict-related modulations in the anterior cingulate cortex (ACC) that varied as a function of age. In Experiment 3, dynamic modulations in conflict processing were associated with pronounced age-related behavioural and electrophysiological adaptations to prior conflict. Taken together the findings of the current set of studies suggest that multiple control processes underpin age-related advances in DCCS performance.

Keywords: cognitive control, Dimensional Change Card Sort, rule switching, conflict processing, event-related potentials, distributed cortical source modeling

Co-Authorship Statement

This thesis contains two manuscripts that are in press by Matthew Waxer and Dr. J. Bruce Morton. The original manuscripts, versions of which appear in Chapter 2 and Chapter 4 of this thesis were primarily written by Matthew Waxer.

Dedications

To my beautiful wife, Christine. Without her help, support, and never-ending love this thesis would have never been possible.

To my parents, Peter and Katherine. Their support, encouragement and devotion means the world to me.

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DISSOCIABLE AND DYNAMIC COMPONENTS OF COGNITIVE CONROL: A DEVELOPMENTAL ELECTROPHYSIOLOGICAL INVESTIGATION

Chapter 1: General Introduction

Everyday life requires flexible and ongoing adjustments in thought and behaviour to meet the challenges of a frequently changing environment. In some situations, a change in environmental context requires one to learn a new response. However, in other situations, the same response must be made but with slightly changed parameters. The ability to flexibly guide information processing and behaviour in the service of a goal is typically referred to as cognitive control. Cognitive control is a central aspect of many high-level cognitive functions including attention, working memory, and planning (Miller & Cohen, 2001). For example, consider the trade-off between speed and accuracy (Busemeyer & Townsend, 1993; Laming, 1979; Osman, Lou, Müller-Gethmann, Rinkenauer, Mattes, & Ulrich, 2000; Rabbit, 1966; Rinkenauer, Osman, Ulrich, Müller-Gethmann, & Mattes, 2004). If the likelihood of an error is low and speed is essential, then executing a given action as quickly as possible with less regard for accuracy would be adaptive. On the other hand, if the likelihood of an error is high and speed is less important, then increasing behavioural control, slowing down, and being more vigilant would be in one's vested interest. People are able to strategically trade off speed and accuracy. The ability to shift one's responses in favor of accuracy rather than speed may be considered an example of a basic form of cognitive control. More complex forms of cognitive control may involve modulating attention between pre-potent response tendencies and controlled, non-prepotent responses (e.g., Atkinson, Drysdale, & Fulham, 2003; Pardo, Pardo, Janer, & Raichle, 1990; West & Alain, 1999), or the ability to

flexibly switch between two cognitive tasks (e.g., De Jong, Berendsen, & Cools, 1999; Jersild, 1927; Rogers & Monsell, 1995; Wylie & Alport, 2000).

The development of cognitive control follows a protracted developmental trajectory that extends well into early adulthood (for review see Diamond, 2002; Morton, 2010). One of the classic examples of the development of cognitive control during the first year is seen in the progression of an infant's ability to perform the Piagetian A-not-B task (Piaget, 1954). Upon finding a hidden object in one of two locations (location A), the infant then has to override a competing response when the object is then hidden in the second location (location B). As originally described by Piaget (1954), infants (typically between 8 and 10 months of age) are able to successfully retrieve an object at one location (location A), but often continue to search for the object in the first location even after they have seen the object hidden at another location (location B). Although Piaget attributed the A-not-B error to an immature understanding of the object concept, a popularized contemporary interpretation of the A-not-B error is that infants have difficulty using a representation of the object's location to override a prepotent response (e.g., Diamond 1991). Young children's ability to perform this task gradually increases from 6 to 12 months of age.

During early childhood, one widely used measure of cognitive control is the Dimensional Change Card Sort (DCCS; Zelazo, Frye, & Rapus, 1996). In this task children are shown two target cards (e.g., a red flower and a blue rabbit) that vary along two dimensions (e.g., colour and shape), and are asked to sort a series of bivalent test cards (e.g., blue flowers and red rabbits). Children are initially instructed to sort the test cards according to one dimension and are subsequently instructed to switch and sort the

test cards according to the other dimension. Regardless of which dimension children are initially instructed to sort the test cards, 3- to 4-year-olds typically continue sorting test cards according to the first dimension when instructed to switch to the other dimension. While younger children typically perseverate on the initial sorting rule, by 5-years of age, children typically perform well on the DCCS.

Many theoretical accounts have linked age-related changes in DCCS performance to changes in a single executive process or structure. According to cognitive complexity and control (CCC) theory (Zelazo & Frye, 1997), age-related advances in DCCS performance are linked to age-related constraints on the representation and use of higher order rules. The representational re-description account downplays the importance of complexity and argues instead that age-related advances in DCCS performance reflect the ability to describe stimuli in a new way after having previously described them an old way (Kloo & Perner, 2005). Similar to the representational re-description account, the attentional inertia account downplays the importance of complexity, but instead argues that age-related advances in DCCS performance reflect inhibitory control of attention (Kirkham, Cruess, & Diamond, 2003). These aforementioned theoretical perspectives base inferences about the integrity and/or developmental status of these processes on performance in an entire trial (or group of trials). More specifically, in the standard DCCS children are administered 6 pre-switch and 6 post-switch trials, and are classified as passing if they sort at least 5 post-switch trials correctly (Zelazo, 2006). Passing or failing in this way is then considered a measure of higher-order rule use, the capacity for stimulus re-description, or the capacity for resisting attentional inertia. However, it is also conceivable that multiple cognitive control processes contribute to age-related advances

and performance on the DCCS. For example, trials always begin with a statement of the rule to be used, followed by the presentation of a test stimulus that embodies conflict. It is conceivable then that two processes, one related to the representation of the instruction cue and one related to the processing of conflict in the test stimulus, unfold in the timeframe of a single DCCS trial.

There is a growing consensus that the domain of cognitive control may include many different types of control effects and underlying mechanisms (e.g., Botvinick, Braver, Barch, Carter, & Cohen, 2001; Braver, Gray, & Burgess, 2007; Brown, Reynolds, Braver, 2007; Verguts & Notebaert, 2008). For example, MacDonald, Cohen, Stenger, and Carter (2000) investigated differential contributions of preparatory and response processes to cognitive control. Using a switching Stroop paradigm that had distinct preparatory and response-related trial periods, MacDonald et al. (2000) demonstrated that greater dorsolateral prefrontal cortex (DLPFC) activation was observed for colour naming relative to word reading during the preparatory period of the task. In contrast, during the response period of the task, greater anterior cingulate cortex (ACC) activation was observed for incongruent/conflict stimuli relative to congruent/non-conflict stimuli. These findings were interpreted as suggesting that the DLPFC and ACC are associated with dissociable cognitive control processes. More specifically, MacDonald et al. (2000) suggest that one of the functions of the DLPFC is to implement and maintain attention-guiding rules, whereas the ACC is involved in detecting instances of conflict.

The dissociation between control processes related to preparatory and response-related periods of a task has also received considerable attention in the event-related

potential (ERP) literature. A number of ERP studies of task switching have reported a late parietal positivity (LPP) for switch trials following an instruction cue, in anticipation of target/stimulus onset (e.g., Kieffaber & Hetrick, 2005; Karayanidis, Coltheart, Michie, & Murphy, 2003; Nicholson, Karayanidis, Poboka, Heathcote, & Michie, 2005; Rushworth, Passingham, & Nobre, 2002, 2005; Swainson, Jackson, & Jackson, 2006). Interestingly, the switch-related LPP is temporally modulated by the amount of time given for preparation (Karayanidis et al., 2003; Nicholson et al., 2005). When given little time to prepare for a task switch, the LPP is observed at the time of target/stimulus presentation; however, when given ample time to prepare for a task switch, the LPP is observed at the time of the presentation of the instruction cue. Moreover, when the LPP is observed at the time of the instruction cue, there are associated improvements in task switching, suggesting this component may be a marker of preparatory cognitive control (Swainson et al., 2006). Though it may seem reasonable to presume that the cortical generator of the LPP is located within the parietal lobes (e.g., Kimberg, Aguirre, & D'Esposito, 2000; Slagter, Weissman, Giesbrecht, Kenemans, Mangun, Kok, et al., 2006), source analyses have suggested a location within the ventromedial occipito-temporal cortex (Rushworth et al., 2002, 2005), which is a region associated with attentional selection (Nobre, Allison, & McCarthy, 1998).

A less common ERP component observed time locked to the presentation of an instruction cue is a late frontal negativity (LFN) for switch trials. The LFN has been observed in fewer studies than the LPP (Lorist, Klein, Nieuwenhuis, De Jong, Mulder, & Meijman, 2000; Tieges, Snel, Kok, Wijnen, Lorist, & Ridderinkhof, 2006), and it has been unclear whether this component reflects a distinct process or the same as the LPP. In

other words, the LFN and the LPP could be two ends of the same dipole. However, in a recent study, the amplitude of the LFN (but not the LPP) was shown to be mediated by caffeine intake (Tieges et al., 2006). Tieges and colleagues speculated that the cortical source of the LFN may be located within the frontal cortex, as caffeine is thought to increase activity within the dopaminergic pathways that connect the striatum with the frontal cortex; furthermore, this loop has been previously been implicated in task switching (Cools, Barker, Sahakian, & Robbins, 2003). Additionally, it has been recently shown that two separate preparatory cognitive control processes are indexed by the LPP and LFN respectively (Astle, Jackson, & Swainson, 2006, 2008). In a combined task-switching "go/no-go" paradigm, Astle et al. (2006) had participants prepared to change their behaviour (or to repeat it, depending on the trial type) following an instruction cue on every trial. On some ("no-go") trials, a subsequent target/stimulus did not appear, such that although participants prepared to perform the task, they never actually did so. Thus, switch trials following a "no-go" required a change in prepared, but not performed, task. Behavioural switch costs were not observed following "no-go" trials, and Astle et al. (2006) interpreted this finding as indicating changing one's intention to perform a task does not incur a cost relative to repeating one's intention. However, a change in which task was to be performed incurred a robust switch cost. In terms of ERPs, the LPP was associated with a change in intention, as it was observed following both "no-go" and "go" trials. The LFN, on the other hand, was only associated with a change in performance, as it was only observed after "go" trials. Although there is emerging evidence that the LFN and LPP are associated with dissociable cognitive control processes, the precise roles of these components in task switching remain unclear.

A number of electrophysiological investigations of conflict processing have reported a larger frontocentral N2 for incongruent trials relative to congruent trials (e.g., Donkers & van Boxtel, 2004; Ladouceur, Dahl, & Carter, 2007; Nieuwenhuis, Yeung, van den Wildenberg, & Riderinkhof, 2003; van Veen & Carter, 2002). The N2 is a negative deflection of the stimulus-locked ERP observed at medial-frontal sites 200-400 ms after stimulus onset. The N2 has traditionally been seen as a marker of response inhibition (e.g., Falkenstein, Hoormann, & Hohnsbein, 1999; Pfefferbaum, Ford, Weller, & Kopell, 1985; van Boxtel, van der Molen, Jennings, & Brunia, 2001). More recently however, a number of studies have demonstrated that the N2 is not elicited by the inhibition required to withhold an erroneous response, but by the detection of a conflict between simultaneously active but mutually incompatible responses (Donkers & van Boxtel, 2004; Nieuwenhuis et al., 2003; van Veen & Carter, 2002). For example, van Veen and Carter (2002) used a modified flanker task with four stimuli mapped to two responses, which produced three types of flanker-target combinations. One type of trial consisted of flankers identical to the target, another trial type consisted of flankers that differed from the target but were mapped on the same response (stimulus incongruent but not response incongruent), and the third type of trial consisted of flankers that differed from the target and were mapped to a different response (stimulus and response incongruent). In terms of the N2, van Veen and Carter (2002) found that the amplitude of the N2 was enhanced on response incongruent trials relative to stimulus incongruent trials and congruent trials. Similarly, using a Go/GO task in which participants were required to provide a normal response on Go trials and to press harder on GO trials, Donkers and van Boxtel (2004) observed larger N2 amplitudes on infrequent GO trials relative to Go

trials. Analogously, using a Go/No-Go task with infrequent Go trials, Nieuwenhuis et al. (2003) found increased N2 amplitudes on the infrequent Go trials relative to No-Go trials. Taken together the aforementioned evidence indicates that the frontocentral N2 may be used as a marker of conflict between response representations that occur prior to a response in situations that are characterized by high response conflict. Furthermore, source analysis of the N2 in adult samples has identified cortical source generators in the vicinity of the ACC (Nieuwenhuis et al., 2003; Ladouceur et al., 2007; van Veen & Carter, 2002). In summary, the switch-related LFN and LPP as well as the conflict-related N2 may index distinct cognitive control processes.

Taken together, the extent of functional neuroimaging studies have shown that distinct forms of cognitive control are associated with unique patterns of activation over a distributed network of regions, including the dorsolateral prefrontal cortex (DLPFC), ventrolateral prefrontal cortex (VLPFC), supplementary and pre-supplementary motor areas, the anterior cingulate cortex (ACC), superior and inferior aspects of the posterior parietal cortex, as well as subcortical structures including the thalamus and basal ganglia (e.g., Cole & Schneider, 2007; Corbetta & Shulman, 2002; Braver & Ruge, 2006). Moreover, the aforementioned regions follow protracted developmental timelines as indexed by measures of changes in synaptic density (Huttenlocher, 1978), cortical thickness (Giedd, Blumenthal, Jeffries, Castellanos, Liu, Zijdenbos, et al., 1999), myelination (Klingberg, Vaidya, Gabrieli, Moseley, & Hedehus, 1999, Yakovlev & Lecours, 1967), resting metabolic rate (Chugani, Phelps, & Mazziotta, 1987), and functional connectivity (Fair, Dosenbach, Church, Cohen, Brahmbhatt, Miezin et al, 2007; Kelly, Di Martino, Uddin, Shehzad, Gee, Reiss, et al., 2009). Taking the

aforementioned factors into consideration, the functional integrity of the network of regions involved in the implementation of cognitive control may be developmentally constrained.

At present there is a paucity of evidence that rule switching and conflict processing processes follow distinct developmental trajectories. To date, only three functional imaging studies have investigated age-related advances in dimensional switching (Casey, Davidson, Hara, Thomas, Martinez, et al., 2004; Moriguchi & Hiraki, 2009; Morton, Bosma, & Ansari, 2009). Moriguchi and Hiraki (2009) found that 3- and 5-year-old children who were able to successfully switch in the post-switch phase of the DCCS exhibited higher concentrations of oxygenated hemoglobin in the vicinity of the ventrolateral prefrontal cortex compared to children that perseverated. Age-related differences in patterns of brain activity associated with DCCS performance however also extend well into early adolescence. Morton et al. (2009) administered a modified DCCS to 14 children between 11- to 13-years of age and 13 young adults. All participants showed switch-related activity in the parietal cortex bilaterally, DLPFC bilaterally, right inferior frontal junction, pre-supplementary motor area, and the right superior frontal sulcus. Additionally, there were also are-related differences with children but not adults showing greater switch-related activity in the right superior frontal sulcus, and adults but not children showing greater switch-related activity in the left superior parietal cortex and right thalamus.

Developmental electrophysiology studies have provided preliminary evidence that conflict processes also follow a protracted developmental trajectory (Jonkman, Sniedt, Kemner, 2007; Ladouceur et al., 2007; Lamm, Zelazo, & Lewis, 2006). Ladouceur et al.

(2007) examined developmental differences in the error related negativity ERN and N2 in a sample of early adolescents, late adolescents, and adults. They found that both the development of the ERN and N2 did not develop until late adolescence, and that source localization analyses of the ERN and N2 indicated a cortical generator in the vicinity of the ACC for older adolescents and adults (Ladouceur et al., 2007). Similarly, Lamm et al. (2006) source localized the N2 to the ACC, and demonstrated that the source of the N2 in older children and children who performed better on tasks of executive function (regardless of age) was more anterior than that of younger children and children who performed poorly. Taken together, the available developmental neuroimaging evidence suggests that rule switching and conflict processing follow extended developmental trajectories that are supported by a distributed network of regions. However, it is presently unknown if the development of rule switching and conflict processing follow distinct developmental trajectories.

The present thesis presents three experiments that test a series of hypotheses that multiple cognitive control processes underpin age-related advances in successful DCCS task performance. The participants and data set for each of the three experiments was the same. The first experiment explored whether dissociable cognitive control processes are operative in the context of a single DCCS trial using converging behavioural and electrophysiological methods. The second experiment explored cortical generators of the ERP components associated with DCCS performance identified in Experiment 1. The third experiment explored the possibility that dynamic modulations in cognitive control follow distinct developmental trajectories.

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Chapter 2: Multiple Processes Underlying Dimensional Change Card Sort Performance: A Developmental Electrophysiological Investigation

The ability to flexibly attend to different dimensions of a stimulus is a core aspect of executive functioning (Miyake et al., 2000) that follows a protracted developmental trajectory (for a review, see Morton, 2010). One standard procedure for studying the development of cognitive flexibility is the Dimensional Change Card Sort (DCCS; Zelazo, 2006). In the task, children sort bivalent test cards (e.g., blue trucks and red flowers) into bins marked by bivalent target cards that each match the test cards on a single dimension (i.e., blue flowers and red trucks). On each of several pre-switch trials, children are instructed to sort the cards one way (e.g., by color). The sorting rules then change and children are instructed on each of several post-switch trials to sort the same cards a different way (i.e., by shape). Because test cards match each of the target cards on a single dimension, the test cards embody conflict insofar as rules based on colour and shape specify opposite responses to the same test stimulus. DCCS performance and associated patterns of brain activity change dramatically in the preschool years (Moriguchi & Hirake, 2009; Zelazo, 2006). Three-year-old children for example typically perseverate in the DCCS by showing persistent use of the pre-switch rules in the post-switch phase whereas 5-year-old children typically switch without error, and children who perseverate exhibit lower concentrations of oxygenated hemoglobin in ventrolateral prefrontal cortex during pre-switch and post-switch trials compared to children who correctly switch. Age-related differences in patterns of brain activity associated with the DCCS however extend well into early adolescence with 11- to 13-year-olds showing switch-related differences in superior prefrontal and superior parietal cortex activity compared to adults (Morton, Bosma, & Ansari, 2009).

Many theoretical accounts link age-related changes in DCCS performance to changes in a single executive process or structure, such as the capacity to represent and use higher-order rules (Zelazo et al., 2003) or the understanding that stimuli can be described in a new way even if they have been previously described in a different way (Kloo & Perner, 2005), and base inferences about the integrity or developmental status of these processes on performance in an entire trial (or group of trials). In the standard task, for example, children are administered 6 pre-switch and 6 post-switch trials, and are classified as passing if they sort correctly on at least 5 post-switch trials (Zelazo, 2006). Passing or failing in this way is then considered a measure of higher-order rule use or the capacity for stimulus re-description. It is possible however that multiple processes unfold within the timeframe of a single DCCS trial. Trials always begin with a statement of the rule followed by the presentation of a test stimulus that embodies conflict. It is conceivable then that two processes, one related to the representation of the instruction cue and one related to processing conflict in the test stimulus, unfold within the timeframe of a single trial (for discussion, see Kirkham, Cruess, & Diamond, 2003). Disambiguating these processes however is difficult using standard performance measures that treat individual trials as indivisible units of analysis.

In the present study therefore, event-related potentials (ERPs) were used to try and disambiguate distinct cue- and stimulus-related processes that were hypothesized to unfold within the timeframe of a single DCCS trial. ERPs are scalp-measured voltage fluctuations generated by the mass-firing of cortical pyramidal cells. Used in the context of studies of cognition, ERPs provide a direct, inexpensive, and non-invasive measure of information processing with exquisite temporal resolution. Children, adolescents, and

adults were administered a modified version of the DCCS, suitable for use with ERPs, in which rule switching was crossed with conflict processing. Trials began with an instruction-cue that indicated the sorting rule on that trial, followed by the presentation of a test stimulus. On switch trials, the rule differed from the previous trial, whereas on repeat trials, the rule remained the same. On half of these trials, the test stimulus was bivalent and could be legitimately sorted two ways. On the other half of these trials, the test stimulus was univalent and could be legitimately sorted only one way.

To examine whether distinct cue- and stimulus-related processes underlie DCCS performance, three general sources of evidence were considered. First, ERP components associated with instruction cue and test stimulus presentation were examined. Three components were of particular interest, a cue-related late frontal negativity (LFN), a cue-related late parietal positivity (LPP), and a test stimulus-related frontal N2, as the amplitude of these components have been shown in previous studies to be modulated by rule switching (Astle et al., 2008; Lorist et al., 2000; Tieges et al., 2006, Swainson et al., 2006) and conflict processing (Ladouceur et al., 2007; Nieuwenhuis et al., 2003) respectively. Evidence that the amplitude of these components is modulated in different ways by different processing demands would suggest distinct cue- and stimulus-related processes unfold within the timeframe of a single DCCS trial. Second, associations between cue- and stimulus-related components and behavioural performance measures were examined. If cue- and stimulus-related components reflect distinct underlying processes, then individual differences in these components should predict unique sources of variance in behavioural performance. Third, age-related differences in rule switching and conflict processing were examined. Evidence that ERP signatures and behavioural

effects associated with these processes exhibit differential patterns of developmental change would suggest that these processes are distinct.

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 and 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 colour 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; Morton et al., 2009; Zelazo, 2006) in which rule switching was orthogonally crossed with conflict processing (see Figure 1). Two bivalent target stimuli (e.g., a red flower and a blue rabbit) were present at the top of the screen throughout the task. 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 a bivalent or a univalent imperative stimulus was presented in the centre of the screen. Bivalent 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 colour or shape. Univalent 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 cancelled the response period. Individual trials were separated by a 1000ms response-cue-interval (RCI).

Trials were presented in a pseudorandom order that ensured the orthogonal crossing of rule switching and conflict processing. Thus, switch trials were followed by 3 repeat trials, and on 50% of these trials, the imperative stimulus was bivalent, whereas on the other 50%, it was univalent.

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. The total testing time for each participant was 90 minutes.

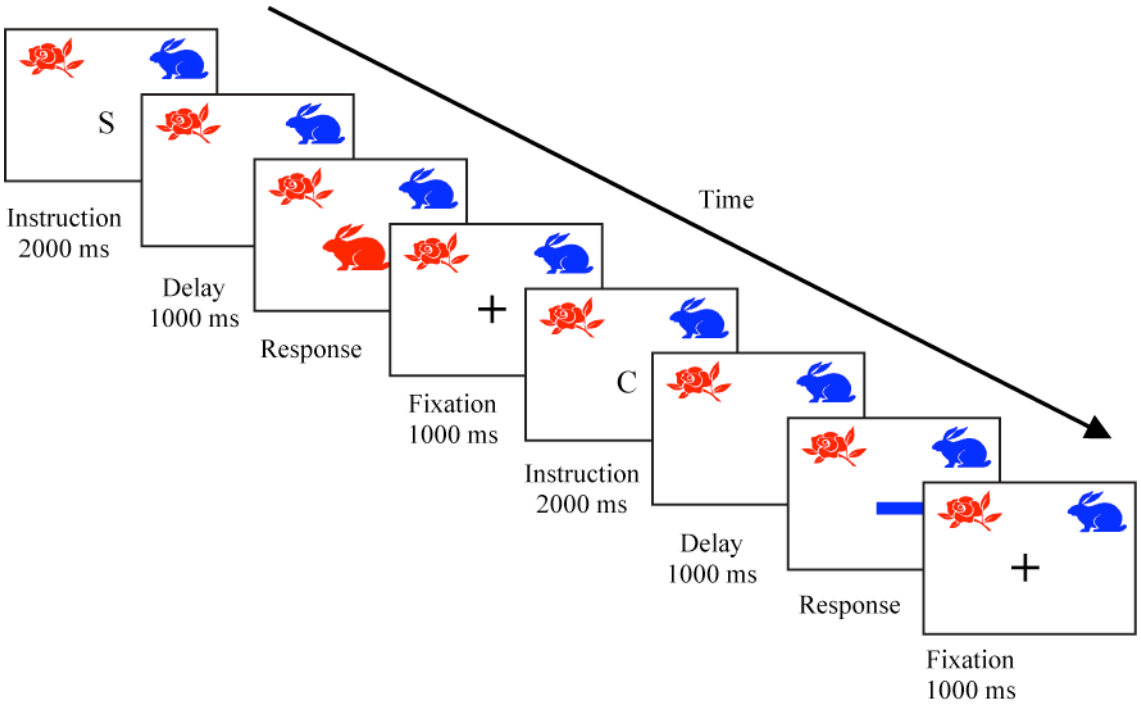

Figure 1. An illustration of two trials from the modified Dimensional Change Card Sort task used in the present study. Trials began with an instruction cue indicating the rule on that trial, followed by a delay period, followed by the presentation of a stimulus to which the participants responded, followed by a fixation point. On switch trials, the rule was different than the one on the previous trial; on repeat trials, the rule was the same as on the previous trial. Bivalent stimuli matched each target location on one dimension; univalent stimuli matched only one target location.

EEG data collection and processing

Electroencephalogram (EEG) recordings were made 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. Trials with either (1) premature (faster then 200ms) or incorrect responses; (2) responses slower than 3 standard deviations from the

participant's mean response time (RT) for each trial and stimulus type combination; (3) eye movement artifacts (70 μV threshold); (4) signals exceeding 200 μV; or (5) fast transits exceeding 100μV were rejected prior to averaging. Eye blinks were corrected using the algorithm developed by Gratton, Coles, and Donchin (1983). The EEG was then re-referenced to an average reference (Bertrand et al., 1985; Tucker et al., 1993). Segmentation was carried out in two ways: (1) instruction-locked data were segmented into epochs ranging from 200 ms before to 1000 ms after instruction cue onset; (2) stimulus-locked data were segmented into epochs ranging from 200 ms before to 600 ms after imperative stimulus onset. Instruction-locked data were offline filtered using a FIR 40 Hz lowpass filter, and stimulus-locked data were offline filtered using a FIR 1-30 Hz bandpass filter. Both instruction-locked and stimulus-locked epochs were baseline-corrected using data from the first 200 ms of the epoch. For the children a maximum of 54 segments per Trial Type contributed to an individual's ERP. For both adolescents and adults, a maximum of 102 segments per Trial Type contributed to an individual's ERP. Additionally, for the children a maximum of 108 segments per Stimulus Type contributed to an individual's ERP. For the adolescents and adults, a maximum of 204 segments per Stimulus Type contributed to an individual's ERP.

Results

Behavioural analyses

Trials with excessively short RTs (< 200 ms), error trials, and trials with RTs slower than 3 standard deviations from the participant's mean RT for each trial type and stimulus type combination were excluded from RT analysis (Ratcliff & Tuerlinckx, 2002). Additionally, the first 4 trials of each block were excluded from statistical

analysis. RTs and error rates were submitted to separate mixed ANOVAs with Age Group (adults, adolescents, and children) as a between-subjects variable, and Trial Type (switch, repeat 1, repeat 2, and repeat 3) and Stimulus Type (bivalent and univalent) as within-subjects variables. A Greenhouse-Geisser correction was applied when a significant violation of sphericity was indicated by Mauchly's test of sphericity.

Mean RTs for Trial Type, Stimulus Type, and Age Group are displayed in Figure 2. An Analysis of Variance (ANOVA) on RTs revealed effects of Age Group, F (2, 77) = 19.29, $p < .001$, Trial Type, F (3, 231) = 26.43, $p < .001$, and Stimulus Type, F (1, 77) = 92.08, $p < .001$. The only higher-order interaction was a two-way interaction between Stimulus Type and Age Group, F (2, 77) = 7.29, $p < .001$. Post-hoc contrasts, Bonferroni-corrected for multiple comparisons, indicated that conflict costs (i.e., bivalent RT – univalent RT) were larger for children than adults, t (58) = 3.23, $p < .005$, and adolescents, t (58) = 2.54, $p < .05$. Conflict costs for adolescents and adults did not differ. Post-hoc contrasts, Bonferroni-corrected for multiple comparisons, indicated that switch costs (i.e., switch RT – repeat RT) did not differ between any of the different age groups.

To ensure that the results of the aforementioned post-hoc contrasts were not the result of age-related differences in baseline RT, a second set of post-hoc contrasts, Bonferroni-corrected for multiple comparisons, were computed using scaled conflict costs (i.e., [(bivalent RT – univalent RT) / univalent RT]) and scaled switch costs (i.e., [(switch RT – repeat RT) / repeat RT]. These contrasts indicated that scaled conflict costs were larger for children than adults, t (58) = 5.12, $p < .001$, and adolescents, t (58) = 4.00, $p < .001$. Scaled conflict costs for adolescents and adults did not differ, t (38) = .94, *n.s.* Scaled switch costs did not differ between any of the different age groups. Thus, while

conflict costs varied as a function of age, switch costs did not differ between the three age groups.

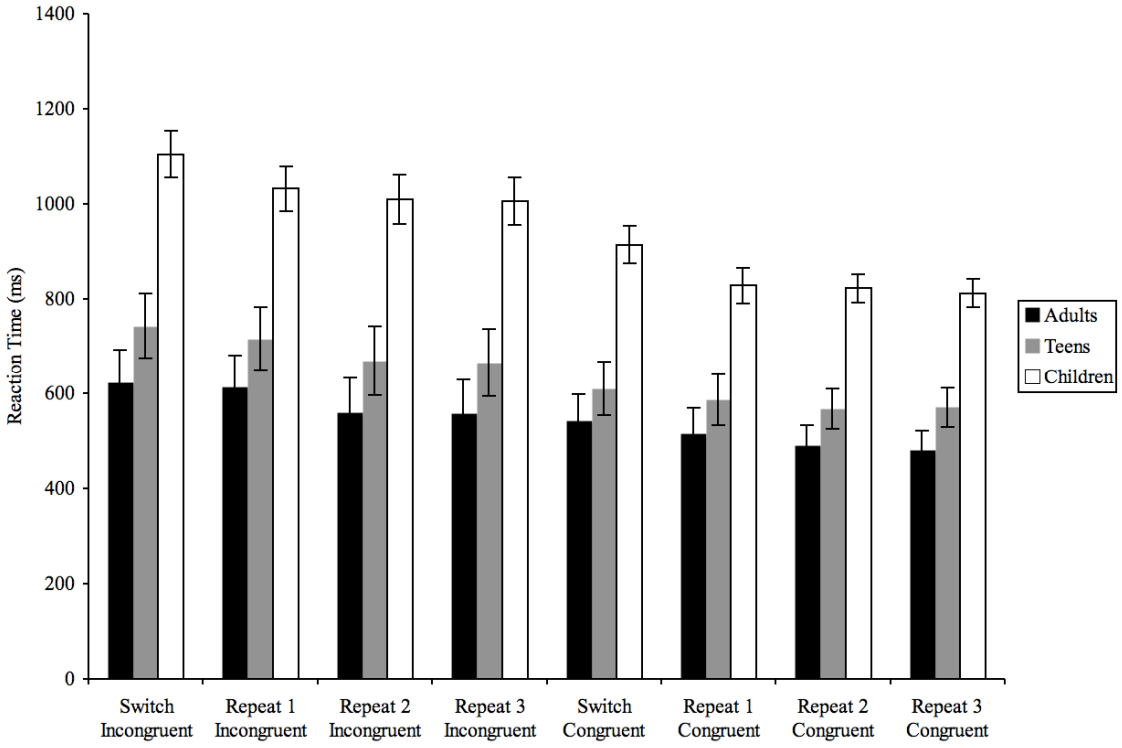

Figure 2. Reaction times as a function of Trial Type, Stimulus Type, and Age Group.

Mean error rates as a function of Trial Type, Stimulus Type, and Age Group are displayed in Figure 3. An ANOVA on error rates revealed main effects of Age Group, F (2, 77) = 4.68, $p < .01$, Trial Type, F (3, 231) = 51.53, $p < .001$, and Stimulus Type, F (1, 77) = 126.18, $p < .001$. There was also a three-way interaction between Trial Type, Stimulus Type, and Age Group, F (6, 231) = 6.07, $p < .001$. Follow-up ANOVAs indicated that the three age groups only varied in accuracy on switch bivalent trials, F (2,77) = 9.32, $p < .001$. Post-hoc contrasts indicated that children were less accurate than

adults, t (58) = -4.03, $p < .001$, and adolescents, t (58) = -2.80, $p < .05$, on switch bivalent trials.

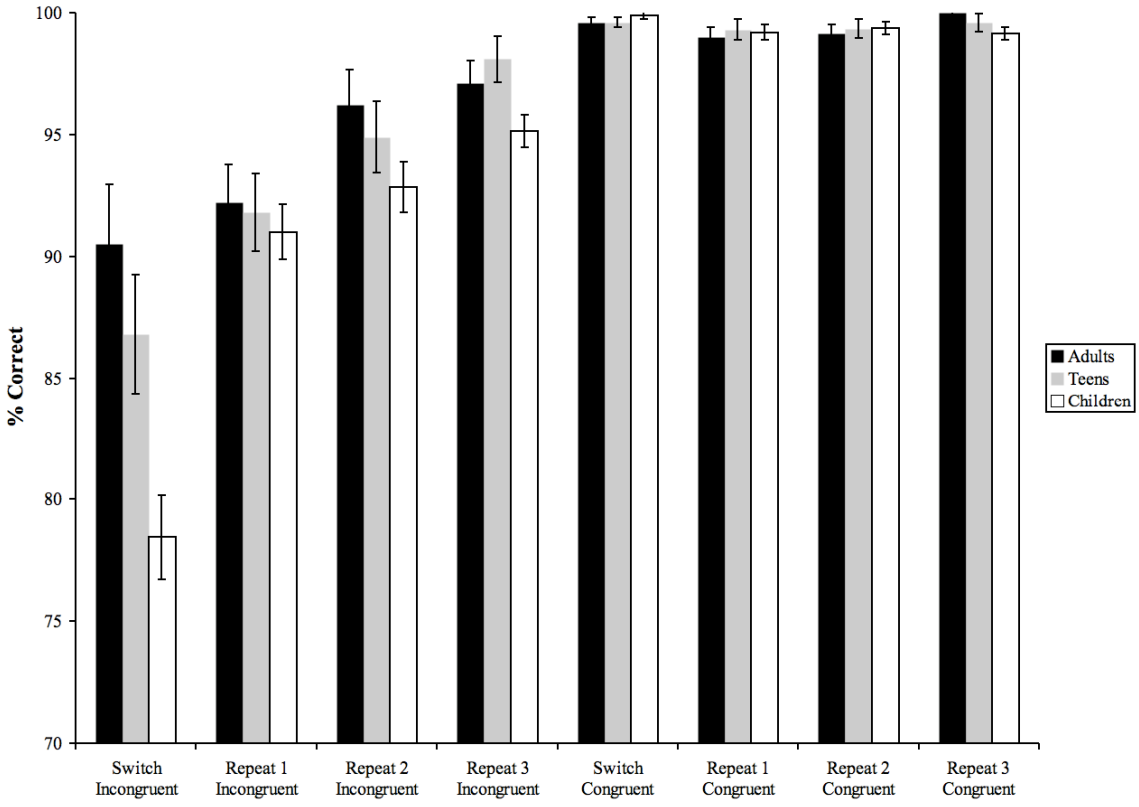

Figure 3. Error rates as a function of Trial Type, Stimulus Type, and Age Group.

ERP analyses

Figure 4 shows the proportion of trials lost due to signal artifacts for each stimulus and trial-type combination. A 3-way mixed ANOVA was used to test for effects of Age Group (children, adolescents, and adults), Trial Type (switch, repeat 1, repeat 2, and repeat 3), and Stimulus Type (bivalent and univalent) on the proportion of trials lost due to artifacts. A Greenhouse-Geisser correction was applied when a significant violation of sphericity was indicated by Mauchly's test of sphericity. This analysis revealed main effects of Trial Type, F (3, 200) = 56.38, $p < .001$ (more rejections on

switch than on repeat trials), and Stimulus Type, F (1, 77) = 129.97, $p < .001$ (more rejections on bivalent than univalent trials), and an interaction between Trial Type and Stimulus Type, F (3, 184) = 56.14, $p < .001$. Importantly though, there were no effects of age, and no interactions with age, meaning that the artifact rejection procedure did not differentially influence the data from the different age groups.

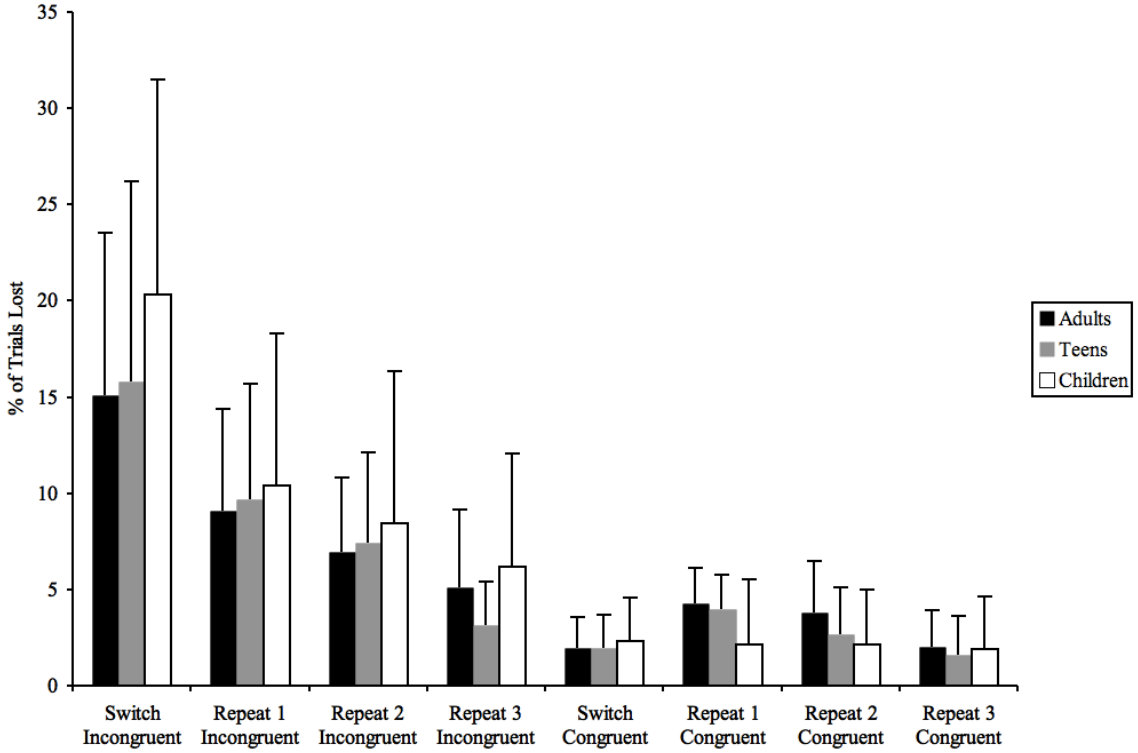

Figure 4. Proportion of trials lost due to ERP artifacts as a function of Trial Type, Stimulus Type and Age Group.

Figure 5 shows the instruction cue-locked ERPs at electrode F3, Fz, and F4 (left, middle, and right columns respectively) for the three age groups. As clearly shown, each age group showed a late negativity whose amplitude was greater on switch trials than repeat trials. To explore this difference further, and to distinguish whether the cue-locked component was an LFN or an LPP, mean instruction cue-locked LFN/LPP amplitudes

were examined at 3 frontal sites (F3/24, Fz/11, and F4/124), 3 central sites (C3/36, Cz/VREF, and C4/104), and 3 posterior electrode sites (P3/52, Pz/62, and P4/92). Mean LFN/LPP amplitude was defined as the mean electrical activity from 300ms to 1000ms post instruction cue onset. Mean LFN/LPP amplitudes were submitted to a 4-way mixed ANOVA with Age Group (children, adolescents, and adults) as a between-subjects variable, Trial Type (switch, repeat 1, repeat 2, and repeat 3), Electrode Site (anterior, central, and posterior), and Electrode Side (left, midline, and right) as within-subjects variables.

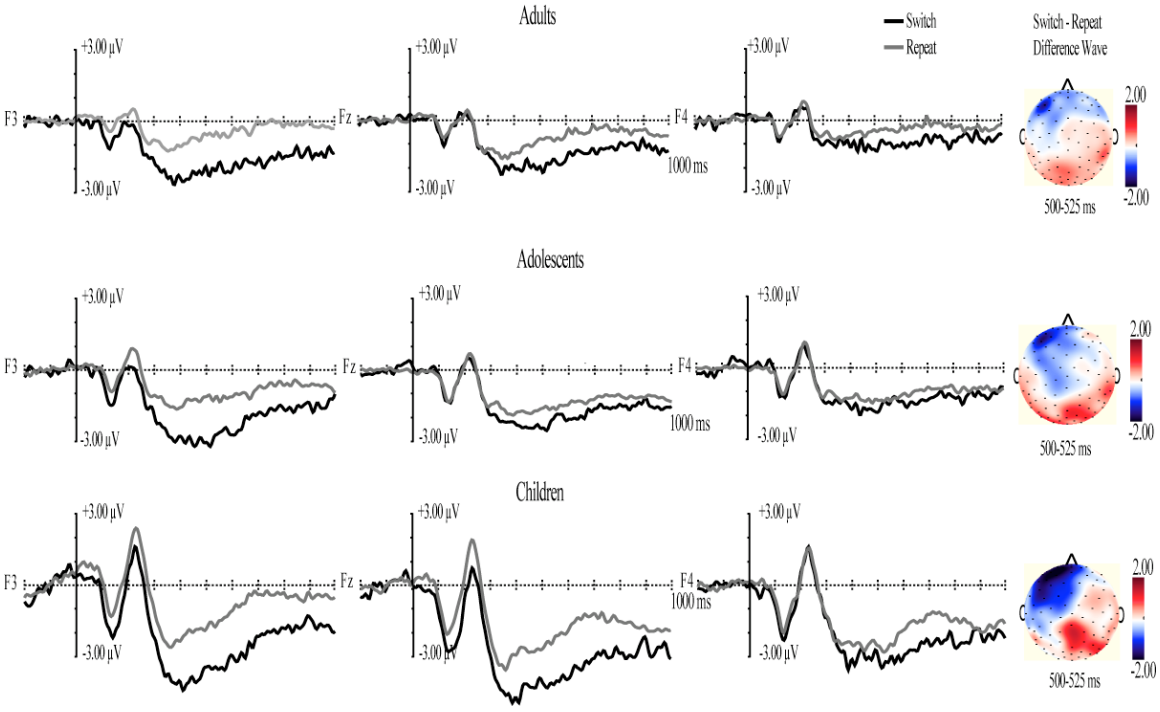

Figure 5. Grand averaged instruction cue-locked waveforms and LFN difference wave topographical maps for adults, adolescents, and children. Each wave board plots a 200 ms baseline and 1000 ms post instruction cue onset. Each topographical map plots anterior electrodes on the top of the topo map.

A Greenhouse-Geisser correction was applied when a significant violation of sphericity was indicated by Mauchly's test of sphericity. This analysis revealed main effects of Trial Type, F (3, 211) = 5.22, $p < .01$, and Electrode Site, F (1, 94) = 39.56, $p < .001$. Additionally there were two-way interactions between Trial Type and Electrode Side, F (5, 342) = 2.32, $p < .05$, between Trial Type and Electrode Site, F (3, 231) = 7.04, $p < .001$, and between Electrode Site and Electrode Side, F (3, 241) = 4.47, $p < .01$. Furthermore, there was a three-way interaction between Trial Type, Electrode Site and Electrode Side, F (6, 621) = 1.97, $p < .05$.

To decompose the three-way interaction, mean LFN/LPP amplitudes were examined separately at frontal, central, and posterior electrode sites. For each Electrode Site, mean amplitudes were submitted to a two-way repeated measures ANOVA with Trial Type (switch, repeat 1, repeat 2, and repeat 3), and Electrode Side (left, midline, and right) as within-subjects variables. Mean amplitudes did not differ as a function of Trial Type, or Electrode Side at either the posterior or central electrodes, suggesting the late-negativity was not an LPP, but an LFN (therefore, hereafter, this component is referred to as an LFN). The ANOVA for the frontal electrode sites revealed a main effect of Trial Type, F (3, 188) = 9.47, $p < .001$. Post-hoc contrasts, Bonferroni-corrected for multiple comparisons, indicated that mean LFN amplitudes were greater for switch trials than repeat 1 trials, t (79) = -4.35, $p < .001$, repeat 2 trials, t (79) = -4.48, $p < .001$, and repeat 3 trials, t (79) = -3.86, $p < .001$. Mean LFN amplitudes did not differ between the 3 repeat trials. In addition to a main effect of Trial Type, there was a two-way interaction between Trial Type and Electrode Side, F (5, 363) = 3.39, $p < .01$. Bonferroni-corrected post-hoc contrasts indicated that the LFN difference (i.e., switch LFN – repeat LFN) was

larger at electrode F3 than electrode Fz, t (79) = -2.22, $p < .05$, and electrode F4, t (79) = -4.68, $p < .001$. Additionally, the LFN difference was larger at electrode Fz than electrode F4, t (79) = -2.75, $p < .01$.

Figure 6 shows the stimulus-locked ERP components at Fcz for switch bivalent, switch univalent, repeat bivalent, and repeat univalent trials for the three age groups. As is clearly visible, adolescent and adult waveforms showed a pronounced negativity approximately 200ms post-stimulus (hereafter referred to as an N2) whose amplitude was more negative following bivalent than univalent stimuli, and regardless of whether the trial was a switch trial or a repeat trial. To explore these differences further, adaptive mean N2 amplitudes for each trial and stimulus type combination were examined at 3 frontocentral electrode sites (Cz, FCz/6, and Fz/11), where the adaptive mean measured the average voltage within a 50 ms time window surrounding the peak of the N2 for each individual (for review, see Luck 2005). Adaptive mean N2 amplitudes were submitted to a 4-way mixed ANOVA with Age Group (children, adolescents, and adults) as a between-subjects variable, Trial Type (switch, repeat 1, repeat 2, and repeat 3), Stimulus Type (univalent and bivalent) and Electrode Site (Cz, FCz, and Fz) as within-subjects variables. This analysis revealed main effects of Stimulus Type, F (1, 77) = 5.88, $p < .05$, Electrode Site, F (2, 154) = 42.87, $p < .001$, and Age Group, F (2, 77) = 13.23, $p < .001$. There was also a 2-way interaction between Stimulus Type and Age Group, F (2, 77) = 3.47, $p < .05$. Post-hoc contrasts indicated that the amplitude of the N2 was larger on bivalent stimuli relative to univalent stimuli for the adults, t (19) = -4.92, $p < .001$, and adolescents, t (19) = -4.47, $p < .001$, but not for the children, t (39) = .68, *n.s*. The

amplitude of the N2 was not modulated by Trial Type, F (3, 201) = 1.38, *n.s.*, and did not interact with any other factors.

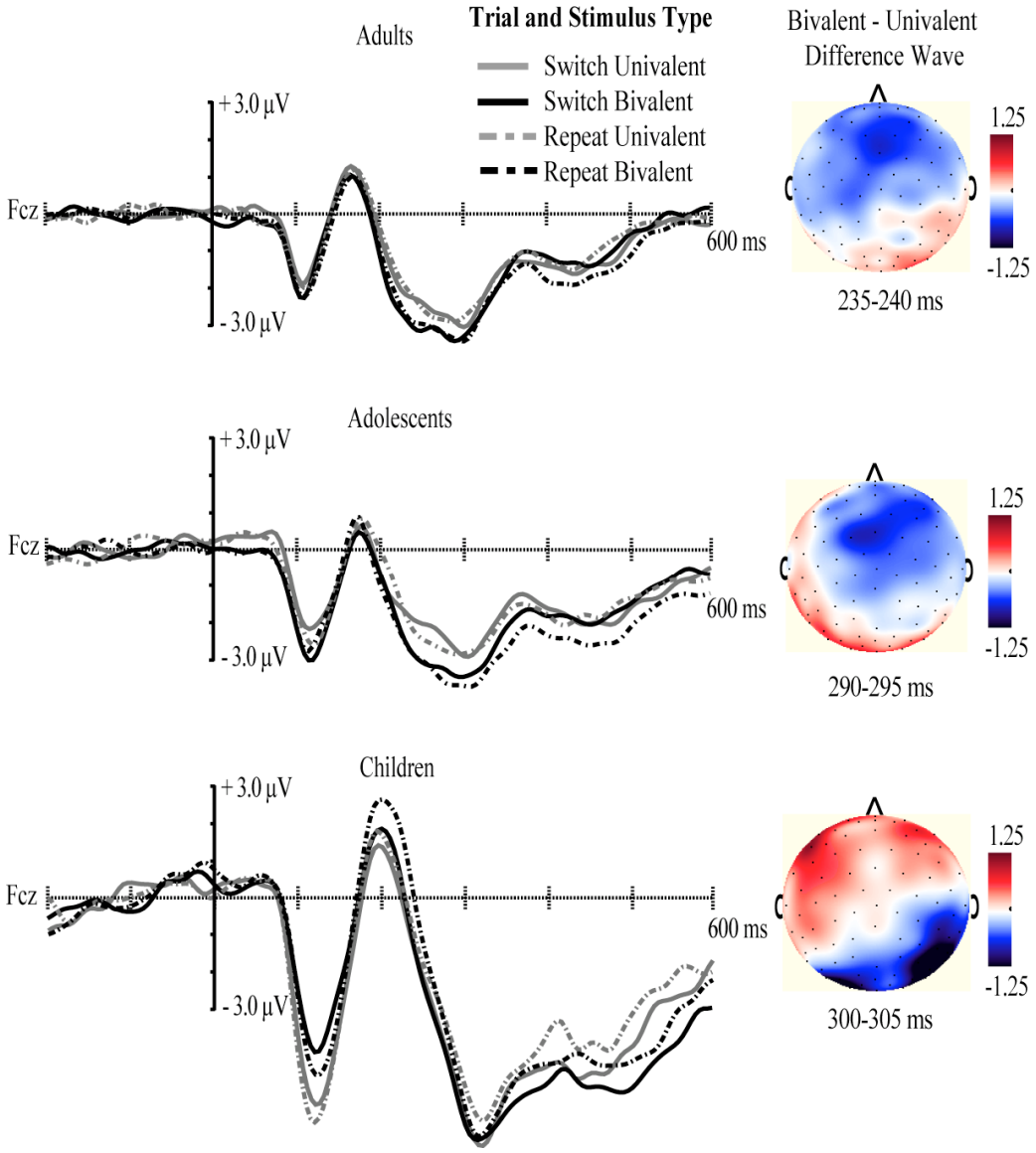

Figure 6. Grand averaged stimulus-locked waveforms and N2 difference wave topographical maps for adults, adolescents, and children. Each wave board plots a 200 ms baseline and 600 ms post stimulus onset. Each topographical map plots anterior electrodes on the top of the topo map.

Differences in N2 latencies were examined using a 4-way mixed ANOVA with Age Group (children, adolescents, and adults) as a between-subjects variable, Trial Type (switch, repeat 1, repeat 2, and repeat 3), Stimulus Type (univalent and bivalent) and Electrode Site (Cz, Fcz, and Fz) as within-subjects variables. A Greenhouse-Geisser correction was applied when a significant violation of sphericity was indicated by Mauchly's test of sphericity. This analysis revealed a main effect of Age Group, F (2, 77) = 58.02, $p < .001$. Post-hoc contrasts, Bonferroni-corrected for multiple comparisons, indicated that the peak latency of the N2 was delayed for the children relative to the adults, t (58) = 8.48, $p < .001$, and relative to the adolescents, t (58) = 9.09, $p < .001$. Peak N2 latencies did not differ between the adults and adolescents, t (38) = .53, *n.s*.

Although the children did not exhibit a conflict-related N2, inspection of their stimulus-locked grand average showed a greater negativity following bivalent than univalent stimuli between 400-450 ms post stimulus onset, which was labeled as the N4. To investigate this difference further, a Stimulus Type (univalent and bivalent) by Electrode Site (Cz, FCz, and Fz) repeated measures ANOVA was conducted on mean N4 amplitudes. Mean N4 amplitude was defined as the average electrical activity from 400-450 ms post stimulus onset. This analysis revealed a main effect of Stimulus Type, F (1, 39) = 4.53, $p < .05$, that indicated that the amplitude of the N4 was greater for bivalent stimuli relative to univalent stimuli. Additionally, there was a main effect of Electrode Site, F (1, 39) = 15.42, $p < .001$. Post-hoc contrasts, Bonferroni-corrected for multiple comparisons, indicated that the mean N4 amplitude was greater at Fcz, t (39) = -5.83, $p < .001$, and Fz, t (39) = -4.51, $p < .001$, relative to Cz.

Brain-behaviour correlation analyses

To examine possible links between instruction cue-locked ERPs and behavioural performance, two-tailed Pearson correlations were conducted between the LFN amplitude difference (i.e., switch LFN – repeat LFN), switch cost (i.e., switch RT – repeat RT), and conflict costs (i.e., bivalent RT – univalent RT) at 3 electrode sites (F3, Fz, and F4). These correlations were Bonferroni-corrected for multiple comparisons and were conducted separately for each age group (see Table 1). For the adults, greater switch costs were associated with a larger LFN difference at electrode site F3, $r = -.58$, $p < .05$, and at electrode site Fz, $r = -.54$, $p < .05$. For the adolescents, greater switch costs were associated with a larger LFN difference at electrode sites F3, $r = -.62$, $p < .01$, and Fz, $r = -.50$, $p < .05$. For the children, greater switch costs were associated with a larger LFN difference at electrode sites F3, $r = -.46$, $p < .001$, Fz, $r = -.33$, $p < .05$, and F4, $r = -.39$, $p < .05$. For all groups, LFN amplitude differences were unrelated to conflict costs.

Table 1. Brain-behaviour correlations between switch costs, conflict costs, and LFN difference wave amplitudes at electrode sites F3, Fz and F4.

Age Group		Conflict Cost RT	Switch Cost RT	LFN Diff F3	LFN Diff Fz	LFN Diff F4
Adults	Conflict Cost RT	-	.03	-.30	.07	.25
	Switch Cost RT	.03	-	-.58**	-.54*	-.39
Adolescents	Conflict Cost RT	-	.03	.27	.06	-.16
	Switch Cost RT	.03	-	-.62**	-.50*	-.13
Children	Conflict Cost RT	-	.17	.04	-.07	.15
	Switch Cost RT	.17	-	-.46**	-.33*	-.39*

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

To examine possible links between stimulus-locked ERPs and behavioural performance, two-tailed Pearson correlations were conducted between the N2 amplitude differences (i.e., bivalent N2 – univalent N2), conflict cost (bivalent RT – univalent RT), and switch cost (switch RT – repeat RT) at 3 frontocentral electrode sites (Cz, Fcz, and Fz). An additional set of correlations was conducted between the N4 amplitude difference (i.e., bivalent N4 – univalent N4), conflict cost, and switch cost for the children. These correlations were conducted separately for each age group and are displayed in Table 2. For the adults, greater conflict costs were associated with a larger N2 difference at electrode sites Fcz, $r = -.59$, $p < .01$, and Fz, $r = -.48$, $p < .05$. For the adolescents, greater conflict costs were associated with a larger N2 difference at electrode sites Fcz, $r = -.59$, $p < .01$, and Fz, $r = -.48$, $p < .05$. For both the adults and adolescents, N2 amplitude differences were unrelated to switch costs. Conflict costs and switch costs were not associated with N2 amplitude differences for the children. Additionally, switch costs were unrelated to N2 amplitudes for bivalent only and univalent only trials for all three age groups (see Table 3A and B). However, conflict costs were associated with a larger N4 difference at electrode site Fcz, $r = -.49$, $p < .05$, and electrode site Fz, $r = -.64$, $p < .01$ for the children. N4 amplitude differences were unrelated to switch costs. Additionally, switch costs were unrelated to N4 amplitudes for bivalent only and univalent only trials (see Table 3C and D).

Table 2. Brain-behavior correlations between switch costs, conflict costs, and stimulus-locked ERP components. (A) Correlations between switch costs, conflict costs and N2 difference wave amplitudes at electrode sites Cz, Fcz, and Fz. (B) Correlations between switch costs, conflict costs, and N4 difference wave amplitudes at electrode sites Cz, Fcz, and Fz for the children.

(A)

Age Group		Conflict Cost RT	Switch Cost RT	N2 Diff Cz	N2 Diff Fcz	N2 Diff Fz
Adults	Conflict Cost RT	-	-.29	-.00	-.56**	-.48*
	Switch Cost RT	-.29	-	-.08	.14	-.17
Adolescents	Conflict Cost RT	-	-.25	-.25	-.59**	-.48*
	Switch Cost RT	-.25	-	.10	.20	-.01
Children	Conflict Cost RT	-	.20	-.25	-.27	-.29
	Switch Cost RT	.20	-	-.08	-.08	-.09

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

(B)

Age Group		Conflict Cost RT	Switch Cost RT	N4 Diff Cz	N4 Diff Fcz	N4 Diff Fz
Children	Conflict Cost RT	-	.20	-.19	-.49*	-.64**
	Switch Cost RT	.20	-	-.13	-.23	-.20

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

Table 3. Brain-behavior correlations between switch costs, and stimulus-locked ERP components. (A) Correlations between switch costs and N2 amplitudes for bivalent stimuli only at electrode sites Cz, Fcz, and Fz. (B) Correlations between switch costs and N2 amplitudes for Univalent stimuli only at electrode sites Cz, Fcz, and Fz. (C) Correlations between switch costs and N4 amplitudes for bivalent stimuli only at electrode sites Cz, Fcz, and Fz. (D) Correlations between switch costs and N4 amplitudes for univalent stimuli only at electrode sites Cz, Fcz, and Fz.

(A)

Age Group		N2 Bivalent Cz	N2 Bivalent Fcz	N2 Bivalent Fz
Adults	Switch Cost RT	-.07	-.06	.12
Adolescents	Switch Cost RT	-.17	-.14	.01
Children	Switch Cost RT	-.17	-.14	.01

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

(B)

Age Group		N2 Univalent Cz	N2 Univalent Fcz	N2 Univalent Fz
Adults	Switch Cost RT	-.04	.02	.09
Adolescents	Switch Cost RT	-.01	.08	.00
Children	Switch Cost RT	-.01	.08	.00

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

(C)

Age Group		N4 Bivalent Cz	N4 Bivalent Fcz	N4 Bivalent Fz
Children	Switch Cost RT	-.04	-.11	.07

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

(D)

Age Group		N4 Univalent Cz	N4 Univalent Fcz	N4 Univalent Fz
Children	Switch Cost RT	-.16	.03	.01

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

Discussion

Many theoretical accounts characterize executive demands associated with the DCCS in terms of a single process that operates over an entire trial. The present findings are consistent with the hypothesis that multiple executive processes unfold within the timeframe of a single trial. First, presentation of an instruction cue at the outset of a trial was associated with a late frontal negativity (LFN) that reached maximal amplitude over electrodes F3, Fz and F4, whereas presentation of an imperative stimulus later in the trial was associated with a frontal-central N2 that reached maximal amplitude over electrodes Cz, Fcz, and Fz. Second, LFN and N2 components were modulated by different processing demands. LFN amplitude was greater following instruction cues that denoted a rule switch compared to cues that denoted a rule repetition. By contrast, N2 amplitude was not modulated by rule switching, but was modulated by conflict, with greater amplitude to bivalent stimuli than univalent stimuli. Third, LFN and N2 components were associated in unique ways with variance in RT. Larger differences between the LFN

on switch versus repeat trials were associated with larger switch costs, but were unrelated to differences in conflict costs. By contrast, larger differences between the N2 on bivalent versus univalent trials were associated with larger conflict costs, but were unrelated to switch costs. Fourth and finally, switch and conflict-related processes showed distinct developmental trajectories. Participants of all ages took longer to respond on switch trials than on repeat trials, but the magnitude of this switch cost showed no age-related change. As well, all participants showed greater left-lateralized LFN amplitudes on switch trials compared to repeat trials, but the magnitude of this difference showed no age-related change. By contrast, participants of all ages took longer to respond to bivalent than univalent stimuli, but the magnitude of this effect was greater for children than for adolescents and adults. As well, stimulus conflict modulated an earlier component in adolescents and adults (the N2) than in children (N4), suggesting protracted changes in conflict processing. Taken together, the findings are consistent with the idea that two executive processes, one related to the representation of an instruction cue and one related to the processing of an imperative stimulus, unfold within the timeframe of a single DCCS trial. One important question concerns the nature of the processes indexed by these components.

Switch-related LFNs have been observed in a number of cued task switching paradigms (Astle et al., 2008; Lorist et al., 2000; Mueller et al., 2009; Tieges et al., 2006), particularly paradigms in which different tasks compete for the same motor responses. When different tasks are associated with different responses, the switch-related LFN is either diminished (Astle et al., 2008) or absent (Mueller et al., 2007). One possibility then is that the LFN reflects the inhibition of task-sets that have been

established by prior motor responses. Consistent with this view, asymmetrical LFN patterns have been observed in cued oculomotor switching tasks in which participants switch between pro- and antisaccade tasks (Mueller et al., 2009). Because prosaccadic eye movements (i.e., eye movements toward peripherally-presented visual stimuli) are strongly prepotent, they need to be suppressed in order for antisaccades (i.e., eye movements away from peripherally-presented visual stimuli) to be generated. To then switch from generating antisaccades to generating prosaccades, the inhibition of a prosaccadic task set must be overcome. By contrast, generating prepotent prosaccades does not require the suppression of antisaccades. Consequently, switching from a pro- to an antisaccade task does not require overcoming the inhibition of an antisaccade task set. Consistent with the view that the LFN indexes the overcoming of task-set inhibition, larger cue-related LFNs are observed when participants switch from an antisaccade to a prosaccade task compared to when they switch from a prosaccade to an antisaccade task. It is worth noting that in the present study, the LFN was left-lateralized. The significance of this however is unclear. This effect could be related to participant handedness, although it seems unlikely given that participants responded to test stimuli using both hands and the LFN was observed well before participants responded (i.e., during the cue period). Regrettably, it is not possible to directly clarify these issues with the current data set, given that all participants were right-handed. These issues therefore await clarification in future studies.

Traditionally, the frontal N2 has been considered an index of response inhibition (Falkenstein et al., 1999; Garavan et al., 2002; Pfefferbaum et al., 1985). However, an alternative view is that the frontal N2 indexes conflict monitoring processes subserved by

the anterior cingulate cortex (ACC; Botvinick et al., 2001; Nieuwenhuis et al., 2003; van Veen & Carter, 2002). On this view, the ACC monitors and detects instances in which two or more incompatible response tendencies are simultaneously active. Having detected such instances of conflict, the ACC engages brain areas (e.g., lateral prefrontal cortex) capable of resolving conflict (Kerns et al., 2004; Liston et al., 2006). Previous developmental studies have shown that while the overall amplitude and latency of the N2 decrease with age (Davis et al., 2003; Lamm et al., 2006; Rueda et al., 2004), conflict-related modulations of the N2 follow a protracted developmental trajectory. For example, Lamm et al. (2006) found that the amplitude of the N2 decreased with increasing age, and that within age, smaller N2 amplitudes were associated with better performance on executive function tasks. With respect to conflict processing and the N2, Ladouceur et al. (2007) found that response conflict modulated N2 amplitude in older adolescents and adults, but not in younger adolescents. Consistent with these prior findings: (1) within-age variability in the amplitude of the N2 in the present study was associated with within-age variability in the magnitude of the conflict-related interference effect, with larger amplitudes associated with larger conflict-related interference effects; and (2) conflict-related modulation of N2 amplitude was evident for older (adults and adolescents) but not younger participants. The present results also extend these findings by identifying a later component, the N4, in the youngest participants that was modulated by response conflict and that was associated with individual differences in the conflict-related behavioural interference effect. Whether this component reflects conflict processing that is similar to that observed in older participants but simply delayed in time is currently unclear. A more focused examination of these components and their association with age-related

changes in conflict processing certainly seems warranted. For now, one can only say that there are protracted changes in conflict processing that may be related to age-related changes in the function of medial PFC.

It may be tempting to draw parallels between the cue-related effects found in the present study and processes highlighted in various accounts of DCCS performance. According to Cognitive Complexity and Control theory (CCC-r; Zelazo et al., 2003), for example, switching between pairs of lower-order rules requires the representation and use of higher-order rules, especially in instances in which lower-order rules specify opposite responses to the same stimulus. It is possible then that greater LFN amplitudes on switch relative to repeat trials reflect the representation of higher-order rules required for switching. Another alternative is that the switch-related LFN indexes working memory processes. According to the attentional inertia account (Kirkham et al., 2003), the DCCS involves working memory and the inhibitory control of attention, in so far as participants need to keep two sets of rules in mind and inhibit attention to previously relevant stimulus features. Repeatedly sorting cards in one way is thought to establish a mind-set for a particular dimension of the test cards. When instructed to switch sorting criteria, participants need to keep the new sorting rules in mind and suppress attention to the previously relevant stimulus dimension. Switch-related LFN differences may therefore reflect working memory processes related to keeping new sorting rules in mind. Yet another alternative is that the switch-related LFN indexes the active representation of task rules on switch trials. According to the active-latent model (Morton & Munakata, 2001), repeated experience sorting cards one way (e.g., by shape) strengthens latent representations of these features and leads to a bias to continue sorting cards in this way.

When the sorting rule changes (i.e., to color), there is a need to overcome the bias to sort the old way. This is made possible by an active representation of the new task rules. Active representations, then, need to be stronger on switch trials than repeat trials in order to overcome bias unique to switch trials. The accounts differ slightly in that the active-latent model links age-related performance changes in the DCCS to changes in the strength with which task rules can be actively held in mind, whereas the attentional inertia account does not claim that working memory is an important locus of developmental change in the DCCS. If the LFN does index processes like working or active-memory, the present findings may be more consistent with the attentional inertia than the active-latent account, as these cue-related components showed little age-related variability.

Any firm parallels between processes indexed by the LFN and those described in the CCC-r, attentional inertia, and active-latent accounts should however be drawn with caution. First, these theories are directed at characterizing changes in cognitive flexibility that occur early in development rather than the later-occurring changes that were the focus of this study. Indeed, age-related differences in switch costs were not apparent in the present data set, and thus the possibility that between-group and/or age-related differences in switch-costs are associated with differences in the LFN has yet to be explored. Even if group differences in the LFN had been observed in the present study though, it is unclear whether these differences would best be characterized as indexing differences in higher-order rule use, active memory, or working memory processes. If they did, one would presumably predict larger LFN differences to be associated with smaller switch costs. There is evidence, for example, that actively representing attention-

guiding rules is associated with activity in dorsolateral prefrontal cortex (DLPFC), and that greater DLPFC activity is associated with smaller behavioural costs (MacDonald et al., 2000). However, in the present study, larger LFN differences were associated with larger not smaller behavioural (i.e., switch) costs. Thus, while it remains conceivable that higher-order rule use, working and or active memory are important for DCCS performance, it is not clear that these processes are indexed by the LFN.

Additional parallels may be drawn between processes highlighted in several accounts of DCCS performance and the stimulus-related N2 modulation found in the present study. CCC-r theory for example, (Zelazo et al., 2003) proposes a close association between conflict detection and higher-order rule use, such that reflection and the subsequent representation of a higher-order rule causally follows from the detection of conflict between lower-order rules. Given that N2 amplitudes were greater for bivalent than univalent stimuli, and larger N2 valence effects were associated with larger conflict costs, there appears to be a close correspondence between stimulus-related N2 modulation observed in the present study and the notion of conflict detection specified in CCC-r. What is unclear from this account however is why the stimulus-locked N2 was not associated in any way with rule switching or the LFN, given the close association between conflict processing and rule representation laid out in CCC-r. An alternative possibility is that stimulus-locked N2 reflects stimulus re-description (Kloo & Perner, 2005). According to the re-description account, successful DCCS performance is predicated on an understanding that bivalent test cards can be described in two different ways. Given their age, this conceptual understanding was likely not an issue for participants in this study, suggesting perhaps that the conflict-related N2 indexes the

process of re-describing a stimulus. What is unclear from this account however is why the conflict-related modulation of N2 amplitude was not amplified on switch trials, given the close association of re-description and rule switching. Yet another possibility is that the stimulus-locked N2 reflects conflict between latent representations of colour and shape that compete for representation in responses (Morton & Munakata, 2002). While this may be true, the active-latent account also predicts a close association between switching and response conflict, such that response conflict should be amplified on switch trials relative to repeat trials. However, this was not the case—switch and conflict costs did not interact. One final possibility is that the stimulus-locked N2 observed in the present study reflects the inhibition of attention. According to the attentional-inertia account (Kirkham et al., 2003), attention gets "stuck" on previously relevant features and needs to be inhibited. It is possible then that greater N2 amplitudes on bivalent than on univalent trials reflect the inhibition of attention to previously relevant stimulus features, a process that presumably is more pronounced in the face of bivalent than univalent stimuli. What is not clear from this perspective however is why larger differences in the amplitude of the N2 across bivalent and univalent trials were associated with larger conflict costs. If differences in the amplitude of the N2 index the inhibition of attention, then larger N2 differences ought to reflect more inhibition. By extension, larger N2 differences should have been associated with smaller not larger conflict costs.

Models that are directed at fractionating executive processes involved in task-switching are perhaps best positioned to accommodate the present findings. One such model (Brown et al., 2007) proposes that switch costs and conflict costs reflect different tradeoffs between exploration (i.e., consideration of alternative means) and exploitation

(i.e., focusing on relevant features of the environment). On this account, switch costs, or the slowing of responses following a rule switch, represent an emphasis on exploration over exploitation. Given an unstable environment with frequent rule shifts, it is difficult to predict where to allocate attention for optimal performance. One means of addressing this uncertainty is to slow the speed of response, and more fully process available stimuli. By contrast, given a stable environment in which a consistent set of cues remains relevant, it makes sense to emphasize exploitation and focus attention on specific features of the environment. In this context, responses to incongruent stimuli become faster with each repeated instance, as in the Gratton effect, where responses to incongruent stimuli are faster when preceded by incongruent as compared to congruent trials (Gratton et al., 1992; Kerns et al., 2004). In this formulation then, switch costs and conflict costs are additive, and reflect two distinct processes that work in tandem in the context of tasks such as the DCCS: a general slowing process, operative on switch trials, that adapts performance to unanticipated changes in task demands, but is insufficient for selecting task-relevant stimulus features; and an attentional focusing process, driven by stimulus incongruence, that attenuates interference from task irrelevant stimulus features but is insufficient for adapting to unexpected changes in task demands. This model arguably provides the most plausible and comprehensive framework for interpreting the cue-locked LFN and stimulus-locked N2 respectively. In particular, it is possible that the LFN reflects a general slowing process that occurs in response to switch cues, given that larger differences predicted greater slowing on switch trials but not conflict trials. By extension, the N2 may reflect an attentional focusing process driven by stimulus incongruence, given that larger differences predicted greater conflict costs, but not greater switch costs.

Although consistent in principle, further research clearly is warranted to test the cogency of these speculations.

Whatever the underlying nature of the processes indexed by the LFN and the N2, at a minimum, the current findings suggest that distinct cue- and stimulus-related processes unfold within the timeframe of a single DCCS trial. As such, these findings help to shed light on the nature of cognitive control processes underlying successful DCCS task performance, and suggest means of characterizing these processes more precisely in the future.

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Chapter 3: Source Localization of Processes Underlying Dimensional Change Card Sort Performance: A Developmental Study

Cognitive control, or the ability to flexibly adapt thoughts and actions in accordance with internal goals, is an essential aspect of higher-cognition that develops gradually through childhood and early adolescence (Diamond, 2002; Morton, 2010). Two fundamental components of cognitive control are the ability to flexibly switch between mental operations (Monsell, 2003) and the ability to identify and process conflict (Botvinick et al., 2001). Age-related advances in switching have been associated with changes in the function of the dorsolateral prefrontal cortex (DLPFC), inferior frontal cortex, medial prefrontal cortex (MPFC), and the superior parietal cortex (Casey et al., 2004; Crone et al., 2006; Morton et al., 2009). Additionally, evidence from functional neuroimaging studies have consistently implicated the involvement of the anterior cingulate cortex (ACC) and DLPFC in conflict processing (Kerns et al., 2004; MacDonald et al., 2000; Nieuwenhuis et al., 2003), and age-related advances in conflict processing have been associated with maturational changes in the ACC and DLPFC. (Jonkman et al., 2007; Ladouceur et al., 2007; Lamm et al., 2006). Taken together, these findings are consistent with the idea that cognitive control is supported by a distributed network of regions, including lateral prefrontal, medial prefrontal, posterior parietal, and anterior cingulate cortices (Barber & Carter, 2005; Cole & Schneider, 2007). Moreover, the maturation of this network follows a protracted developmental timeline as indexed by changes in synaptic density (Huttenlocher, 1978), cortical thickness (Giedd et al., 1999), myelination (Klingberg et al., 1999, Yakovlev & Lecours, 1967), resting metabolic rate (Chugani et al., 1987), and functional connectivity (Fair et al., 2007; Kelly et al., 2009).

One standard task used for studying the development of cognitive control is the Dimensional Change Card Sort (DCCS; Zelazo, 2006). In the task, children sort bivalent test cards (e.g., blue rabbits and red boats) into bins marked by bivalent target cards that each match the test cards on a single dimension (i.e., blue boats and red rabbits). On each of several pre-switch trials, children are instructed to sort the cards one way (e.g., by shape). The sorting rules then change and children are instructed on each of several post-switch trials to sort the same cards a different way (i.e., by colour). Because test cards match each of the target cards on a single dimension, the test cards embody conflict insofar as rules based on colour and shape specify opposite responses to the same test stimulus. DCCS performance changes dramatically in the preschool years. For example, three-year-old children typically perseverate in the DCCS by continuing to use the pre-switch rules in the post-switch phase, whereas five-year-old children typically switch without error (for review, see Zelazo, 2006). Despite a sizable cognitive-behavioural literature (e.g., Jordan & Morton, 2008; Kirkham et al., 2003; Perner & Lang, 2002; Zelazo et al., 2003), relatively little is known about the neural correlates of age-related advances in DCCS performance.

To date, only two studies have examined developmental changes in neural activity associated with DCCS performance (Moriguchi & Hiraki, 2009; Morton et al., 2009). Using near-infrared spectroscopy (NIRS), Moriguchi and Hiraki (2009) found that 3- and 5-year-old children who were able to successfully switch in the post-switch phase of the DCCS exhibited higher concentrations of oxygenated hemoglobin in the vicinity of the ventrolateral prefrontal cortex compared to children that perseverated. However, given that the NIRS array of channels only covered the participant's forehead, it is unclear whether the pattern of activity observed was confined to the ventrolateral prefrontal cortex. In a developmental fMRI study, Morton et al.

(2009) administered a modified DCCS to 14 children between 11- to 13-years of age and 13 young adults. All participants showed switch-related activity in the parietal cortex bilaterally, DLPFC bilaterally, right inferior frontal junction, pre-supplementary motor area, and the right superior frontal sulcus. Additionally, there were also age-related differences with children but not adults showing greater switch-related activity in the right superior frontal sulcus, and adults but not children showing greater switch-related activity in the left superior parietal cortex and right thalamus. Taken together, these findings suggest that a distributed network of prefrontal, parietal and subcortical regions supports the development of dimensional switching in the DCCS.

What is unclear from these findings however is whether dimensional switching is the only top-down executive process that contributes to age-related advances in DCCS performance. The experimental designs used by both Morigichi and Hiraki (2009) and Morton et al. (2009) are limited in this respect as both used block designs. More specifically, Morigichi and Hiraki (2009) only compared pre-switch versus post-switch activity. The block design implemented by Morton et al. (2009) also only compared differences in activity on switch blocks relative to repeat blocks. Switch blocks contained 4 switch trials and 4 repeat trials, whereas repeat blocks only contained repeat trials. The use of block designs by these studies did not allow the possibility to explore whether multiple executive control processes are operative within a single DCCS trial. To do so would require the use of event-related designs.

Experiment 1 (see Chapter 2) tested the contribution that rule switching and conflict processing made to DCCS performance. Children, adolescents, and adults performed a modified version of the DCCS, suitable for use with event-related potentials (ERPs), in which rule switching was orthogonally crosses with conflict processing. Throughout the task, two bivalent

target stimuli (i.e., a red rabbit and a blue truck) appeared at the top of the computer screen, and on individual trials, participants sorted an imperative stimulus either by shape or by colour. Half of the imperative stimuli embodied conflict insofar as they could legitimately be sorted either by colour or by shape (i.e., they 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). When administered in this way, the task generates a switch-related late frontal negativity (LFN) that is orthogonal to a conflict-related frontocentral N2. Additionally, there were age-related differences in the amplitude of the conflict-related N2, with adolescents and adults showing a robust conflict-related N2 but not children. The amplitude of the switch-related LFN did not vary as a function of age. Taken together, the findings of Experiment 1 suggest that distinct cue- and stimulus-related processes unfold within the timeframe of a single DCCS trial. However, drawing comparisons between the ERP effects observed in Experiment 1 and the existing functional neuroimaging literature is somewhat problematic given that ERP data lacks the spatial resolution of NIRS and fMRI. One solution to this issue is to use distributed cortical source modeling. Source modeling of ERP data adds a spatial dimension to the ERP time series recordings, which allows for a more direct comparison and integration with fMRI findings.

In the present study therefore, distributed cortical source modeling was used to try to elucidate the neural sources that underlie the switch-related LFN and the development of the conflict-related N2. Predictions were as follows. On the hypothesis that dimensional switching is associated with activation of a distributed network of regions (Casey et al., 2004; Morton et al., 2009), it was predicted that the switch-related LFN would be generated by cortical sources in the DLPFC, the superior parietal cortex, and ACC. Second, on the hypothesis that conflict

processing is associated with activation of the ACC (Jonkman et al., 2007; Ladouceur et al., 2007; MacDonald et al., 2000), it was predicted that the conflict-related N2 would be driven by a cortical generator in the vicinity of the ACC. Third, on the hypothesis that age-related changes in cognitive control are quite protracted and extend into adolescence, it was predicted that there would be age-related differences in the strength of cortical source activity for both the switch-related LFN (Morigichi & Hiraki, 2009; Morton et al., 2009) and conflict-related N2 (Ladouceur et al., 2007; Lamm et al., 2006).

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 colour 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; Morton et al., 2009; Zelazo, 2006) in which rule switching was orthogonally crossed with conflict processing (see Chapter 2 Figure 1). Two bivalent

target stimuli (e.g., a red flower and a blue rabbit) were present at the top of the screen throughout the task. 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 colour) 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 a bivalent or a univalent imperative stimulus was presented in the centre of the screen. Bivalent 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 colour or shape. Univalent 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 colour; pressing the left button sorted it by shape). Responses were registered on a PST button-box (Psychological Software Tools, Pittsburgh, PA) and cancelled the response period. Individual trials were separated by a 1000ms response-cue-interval (RCI).

Trials were presented in a pseudorandom order that ensured the orthogonal crossing of rule switching and conflict processing. Switch trials were followed by 3 repeat trials, and on 50% of these trials, the imperative stimulus was bivalent, whereas on the other 50%, it was univalent.

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. The total testing time for each participant was 90 minutes.

Source-space analysis

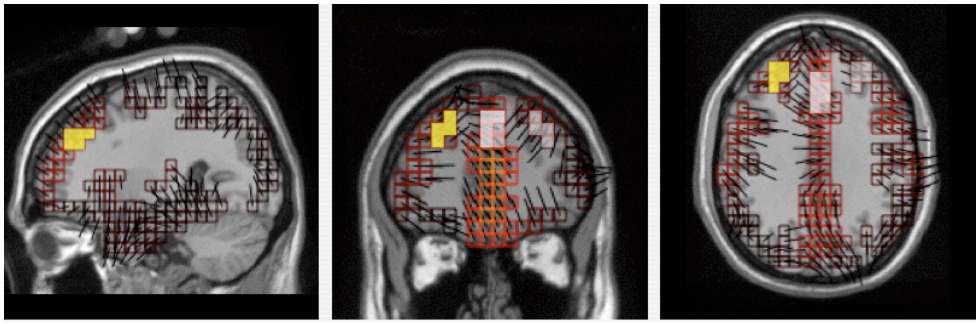
Source localization was performed on baseline-corrected ERP data, using a 4-shell Sun-Stok model (Sun, 1997). Electrode position was recorded for each participant by means of a geodesic photogrammetry system (EGI Inc, Eugene, OR) and was used in the construction of each participant's forward model. The 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 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 for the LFN, six regions of interest (ROIs) were generated using the MNI-average adult MRI. The six regions of interest approximate activation in the dorsolateral prefrontal cortex (DLPFC) bilaterally, the parietal cortex bilaterally, and the anterior cingulate cortex (ACC) bilaterally (See Figure

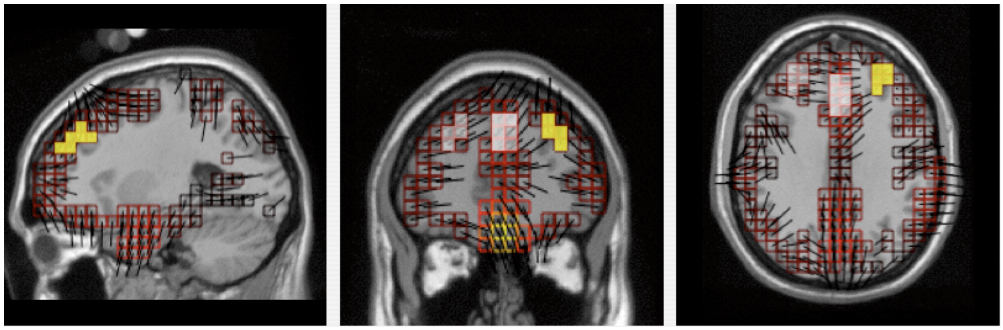
2). Previous functional neuroimaging studies of the DCCS, and task switching more generally, have observed greater activity in the aforementioned regions during task-switch trials relative to task-repeat trials (Dove et al., 2000; Kimberg et al., 2000; Morton et al., 2009; Rushworth et al., 2002; for review see Barber & Carter, 2005). Each ROI was composed of a subset of dipoles (or voxels) from the source model. Source waveform amplitudes (nA) for the average of all dipoles within an ROI were Log_{10} transformed for the purpose of parametric statistical analysis (Thatcher, North, & Biver, 2005). Furthermore the latency range for the LFN was subdivided into seven time bins that were 100 ms long, beginning 300 ms post instruction cue onset.

To estimate the cortical generators for the N2, one ROI was generated using the MNI average adult MRI. This ROI approximates activation in the ACC (See Figure 3). Functional neuroimaging studies of conflict monitoring have consistently implicated the involvement of the ACC (Braver et al., 2001; Kerns et al., 2004; MacDonald et al., 2000; van Veen & Carter 2005). The ACC ROI was composed of a subset of dipoles (or voxels) from the source model. The latency range used for the N2 and N4 was a 50ms time bin centred on the peak amplitude of the 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).

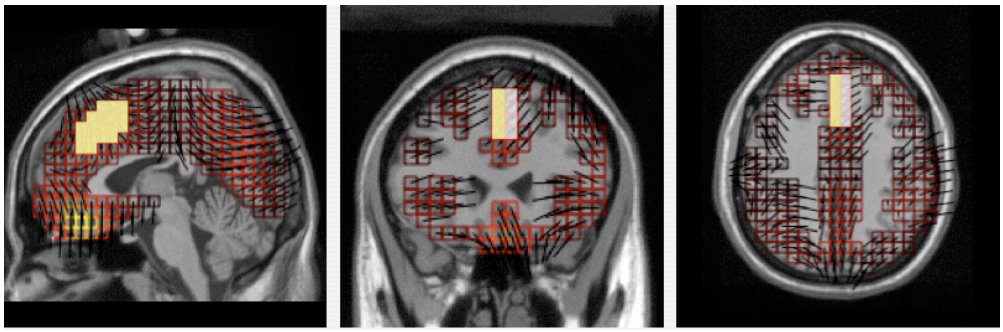
Left DLPFC ROI



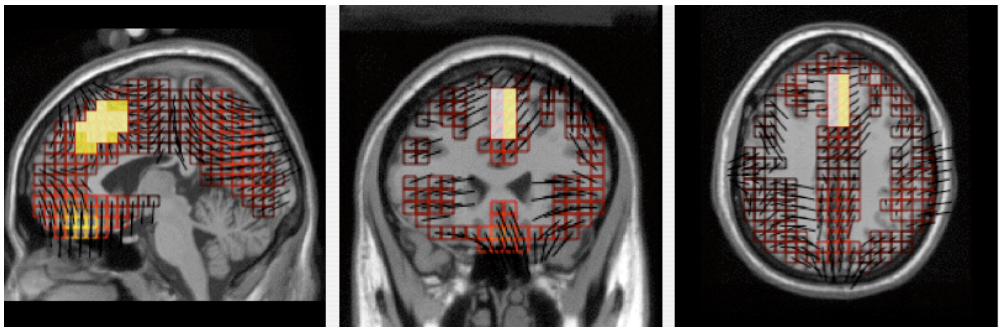
Right DLPFC ROI



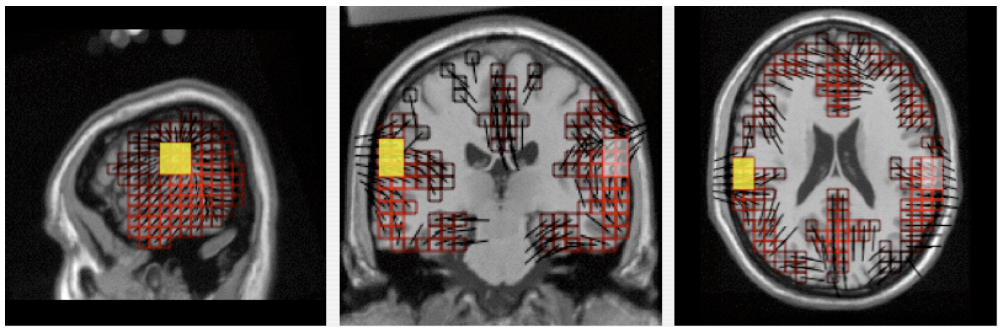
Left ACC ROI



Right ACC ROI



Left Parietal ROI



Right Parietal ROI

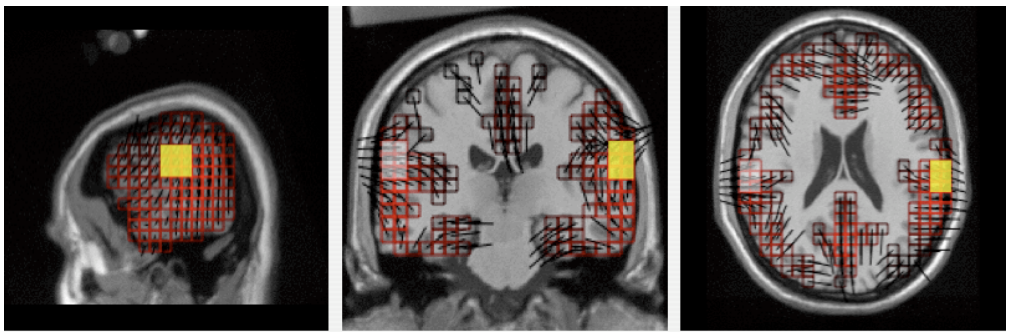


Figure 2. Regions of Interest (ROI's) used to source model the switch-related LFN. ROI's are highlighted in yellow.

ACC ROI

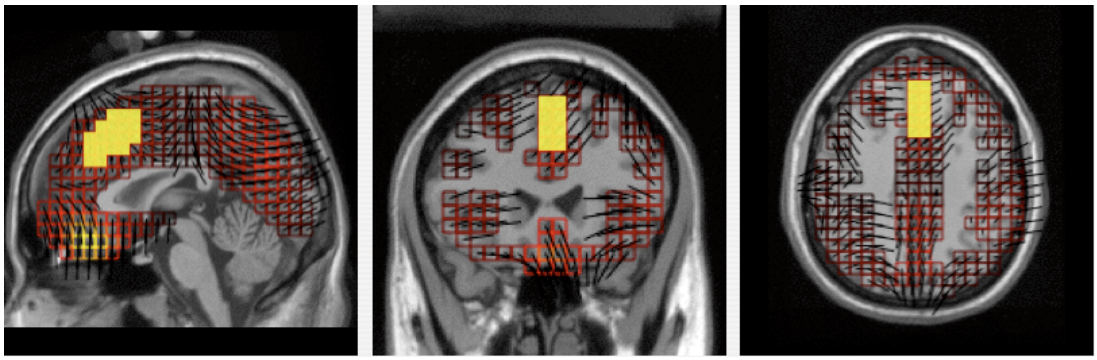


Figure 3. Region of Interest (ROI) used to source model the conflict-related N2. ROI is highlighted in yellow.

Results

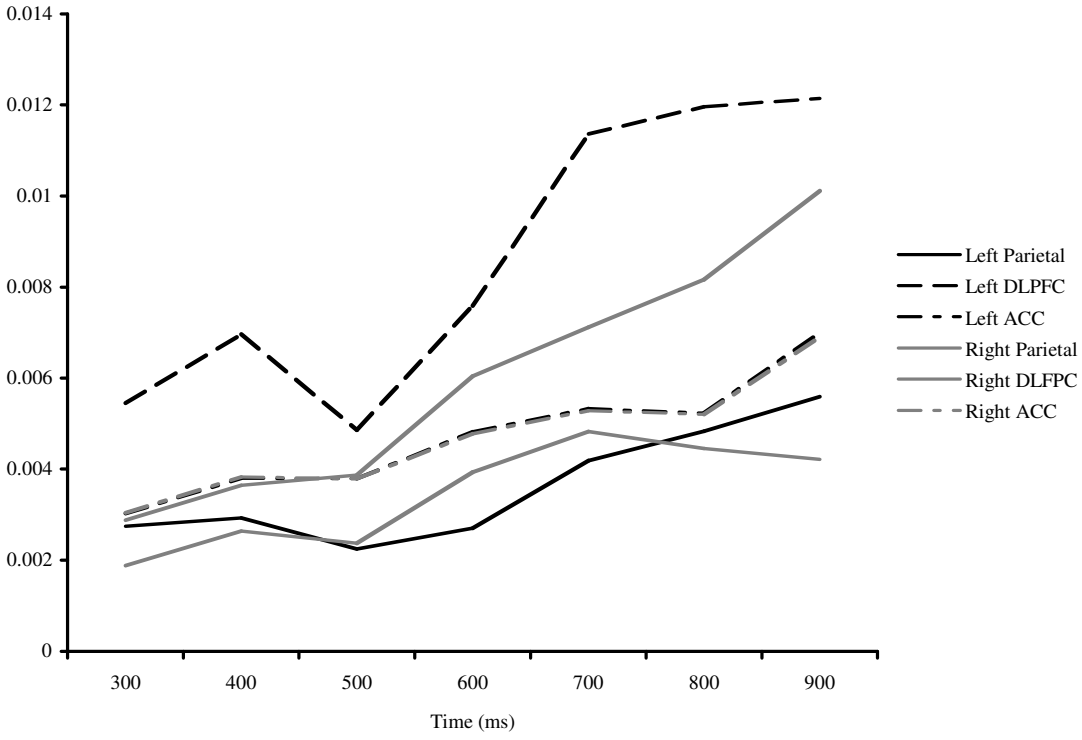
To investigate differences in the cortical generators of the LFN, distributed cortical source models were generated for each age group using the LFN difference wave (switch LFN - repeat LFN). Means source waveform amplitudes (nA) were extracted for three regions of interest bilaterally (DLPFC, superior parietal cortex, and the ACC). Furthermore the latency range of the LFN was subdivided into seven time bins that were 100 ms long, beginning 300 ms post instruction cue onset. LFN source waveforms for each ROI are displayed in Figure 4. Mean LFN source waveform amplitudes were then submitted to a 4-way mixed ANOVA with Age Group (children, adolescents, and adults) as a between-subjects variable, Region of Interest (DLPFC, superior parietal cortex, and the ACC), Hemisphere (right, left), and Time Bin (300-400 ms, 400-500 ms, 500-600 ms, 600-700 ms, 700-800 ms, 800-900 ms, 900-1000 ms) as within-subjects variables. This analysis revealed main effects of Hemisphere, F (1, 77) = 61.77, $p < .001$, Time Bin, F (6, 462) = 28.87, $p < .001$, and Age Group, F (2, 77) = 26.39, $p < .001$. Additionally, this analysis revealed a 2-way interaction between ROI and Hemisphere, F (2, 154) = 24.15, $p < .001$, and a 3-way interaction between ROI, Hemisphere, and Age Group, F (4, 154) = 3.19, $p < .05$.

To decompose the three-way interaction between ROI, Hemisphere, and Age Group, 3 separate 2-way mixed ANOVAs were conducted at each ROI using Hemisphere as a within-subjects factor and Age Group as a between-subjects factor. The post-hoc ANOVA for the superior parietal cortex revealed a main effect of Hemisphere, F (1, 77) = 8.97, $p < .01$. Post-hoc contrasts, Bonferroni-corrected for multiple comparisons, indicated that for all age groups the left superior parietal cortex was modulated by

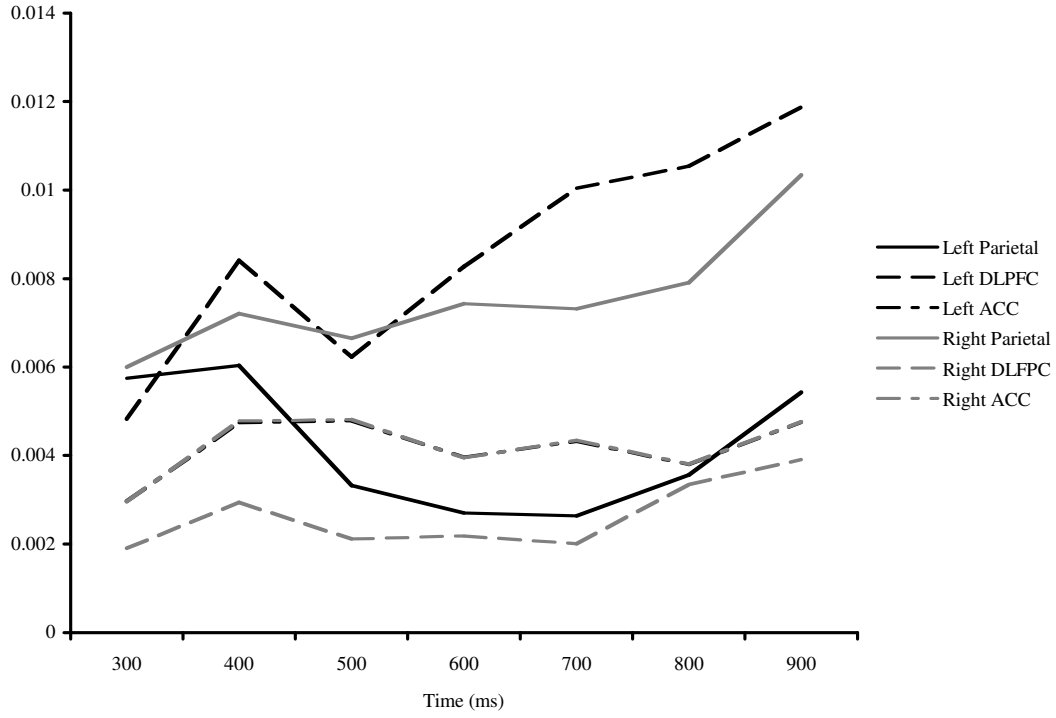
switching more than the right superior parietal cortex, t (79) = 3.04, $p < .01$. Additionally, this analysis revealed a main effect of Age Group, F (2, 77) = 24.05, $p < .001$. Bonferroni-corrected post-hoc contrasts indicated that children showed greater Switch-related modulations in the superior parietal cortex relative to both adolescents, t (58) = 4.76, $p < .001$, and adults, t (58) = 6.33, $p < .001$.

Switch-related modulations in the superior parietal cortex did not differ between adolescents and adults, t (38) = 1.35, *n.s*. The post-hoc ANOVA for the ACC revealed a main effect of Age Group, F (2, 77) = 19.56, $p < .01$. Post-hoc contrasts, Bonferroni-corrected for multiple comparisons, indicated that children showed greater Switch-related ACC modulations relative to both adolescents, t (58) = 4.9, $p < .001$, and adults, t (58) = 5.31, $p < .001$. Switch-related ACC modulations did not differ between adolescents and adults, t (38) = .36, *n.s*. The post-hoc ANOVA for the DLPFC revealed main effects of Hemisphere, F (1, 77) = 71.62, $p < .001$, and Age Group, F (2, 77) = 24.02, $p < .001$. Additionally, this analysis revealed an interaction between Hemisphere and Age Group, F (2, 77) = 3.82, $p < .05$. Planned post-hoc contrasts, Bonferroni-corrected for multiple comparisons, indicated that adults showed a greater Switch-related modulation the left than the right DLPFC, t (19) = 5.98, $p < .01$. Adolescents showed a greater Switch-related modulation in the left than the right DLPFC as well, t (19) = 4.60, $p < .01$. Children did not show a hemispheric difference in Switch-related DLPFC modulations, t (39) = 1.92, *n.s*. However, children did exhibit greater overall Switch-related modulations of the DLPFC than both adolescents, t (58) = 5.03, $p < .01$, and adults, t (58) = 6.21, $p < .01$. Switch-related DLPFC modulations did not differ between adolescents and adults, t (38) = 1.03, *n.s*.

Adults



Adolescents



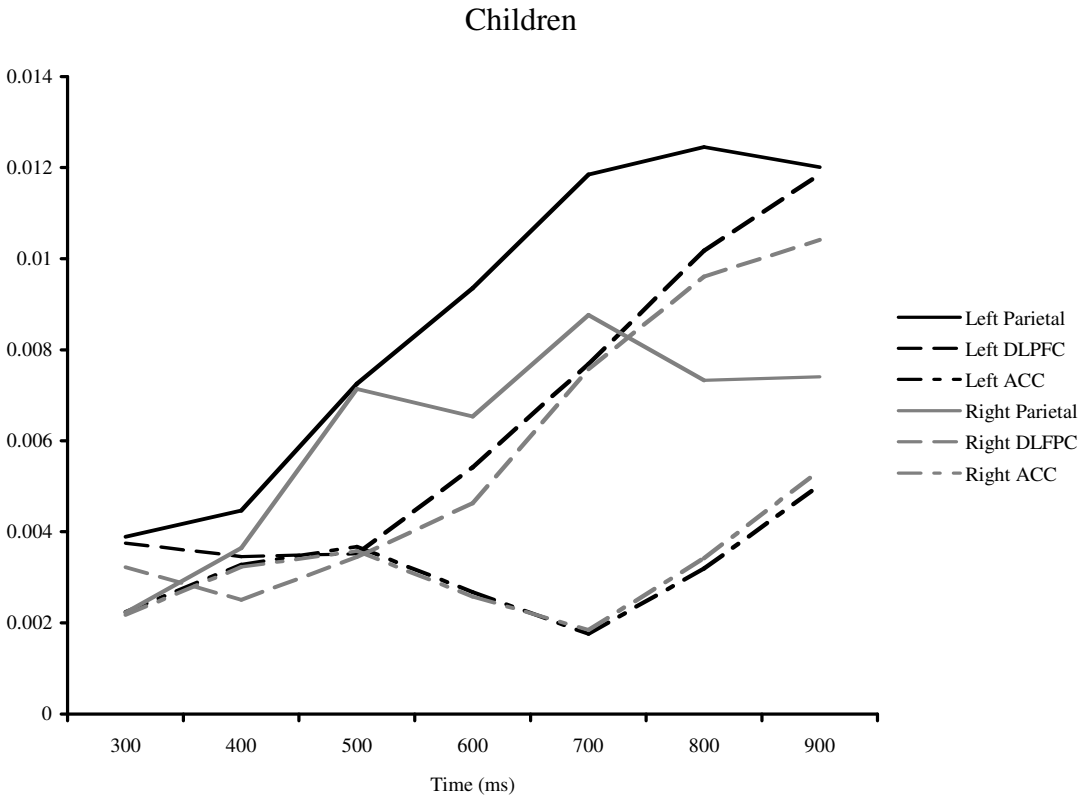


Figure 4. LFN source waveforms as a function of ROI, Hemisphere and Age Group.

To investigate differences in the cortical generators of the N2, distributed cortical source models of the N2 difference wave (i.e., bivalent N2 – univalent N2) were generated. Mean source waveform amplitudes were extracted for a region corresponding to the ACC. A univariate ANOVA revealed that mean ACC source amplitudes differed across the three age groups, F (2, 79) = 9.98, $p < .001$. As seen in Figure 5, greater conflict-related ACC modulations were observed for the adults, t (59) = 2.90, $p < .01$, and adolescents, t (59) = 4.17, $p < .001$, relative to the children.

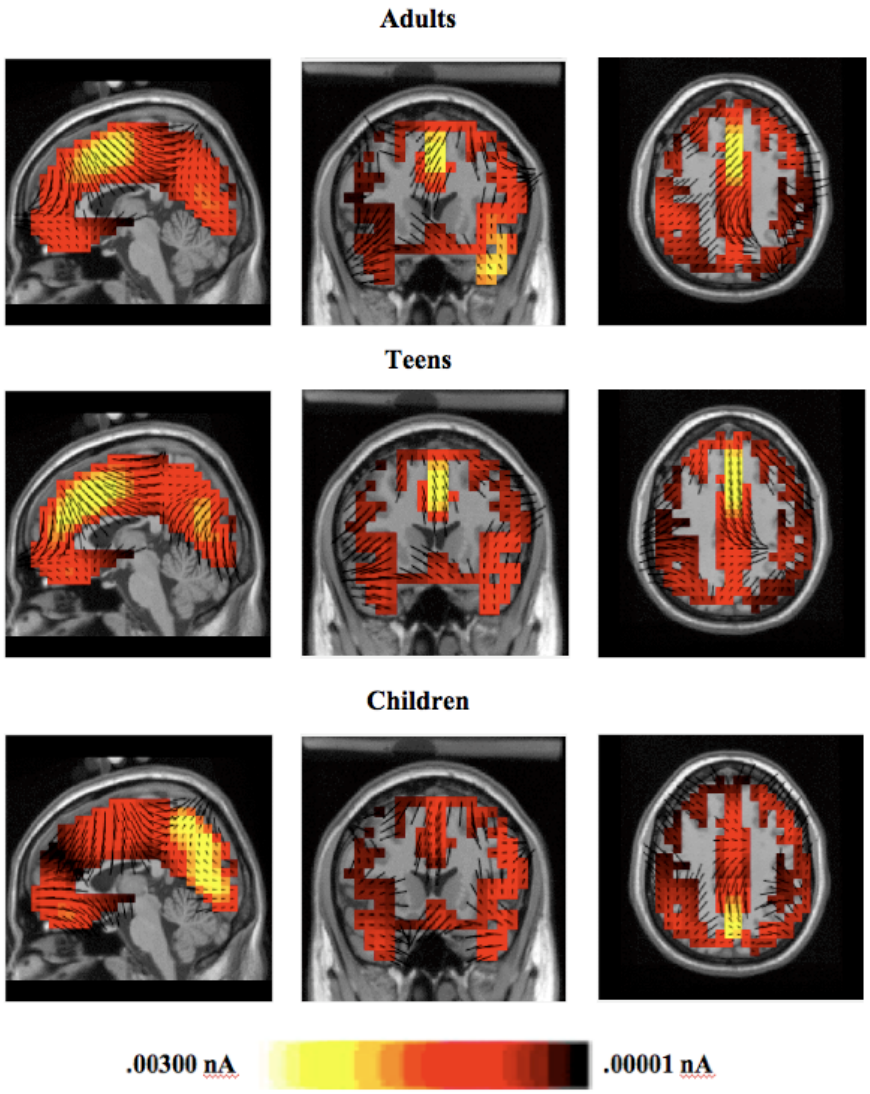


Figure 5. Source models of the conflict-related N2 difference wave as a function of Age Group.

Discussion

Age-related advances in executive control, as observed in tasks such as the DCCS, follow a protracted developmental trajectory. Although these age-related advances have been attributed to the development of the prefrontal cortex (Bunge & Zelazo, 2006; Diamond, 2002; Morton & Munakata, 2002), there is a paucity of direct

evidence for this proposed association. To date, the two studies that have examined neural correlates associated with age-related advances in DCCS performance have focused exclusively on rule switching, and have done so using block designs. The findings of Experiment 1 (see Chapter 2) however, indicated that through the use of an event-related design at least two executive processes contribute to successful DCCS performance (i.e., rule switching and conflict processing). More specifically, rule switching was associated with a cue-locked LFN and conflict processing was associated with a stimulus-locked N2. However, drawing any direct parallels between the findings of Experiment 1 and existing functional imaging literature is problematic as ERP data lack the requisite spatial resolution. To address this issue, the present study used distributed cortical source modeling to examine age-related differences in cortical sources associated with rule switching and conflict processing. Distributed cortical source models were generated using developmental ERP data reported in Experiment 1. Source models of the switch-related LFN indicated that a distributed network of regions including the DLPFC, superior parietal cortex and ACC were modulated by rule switching. Source models of the stimulus-locked N2 revealed the ACC was modulated by conflict processing. Additionally, source models of both the cue-locked LFN and stimulus-locked N2 were associated with pronounced age-related differences. More specifically, children showed greater Switch-related modulations in the left superior parietal cortex, bilateral ACC, and bilateral DLPFC relative to adolescents and adults. Although children exhibited greater overall Switch-related DLPFC modulations relative to adolescents and adults, this modulation was bilaterally distributed, whereas adolescents and adults exhibited Switch-related modulations confined to the left DLPFC. Additionally, greater

conflict-related ACC modulations were observed for adolescents and adults relative to children. In sum, these findings point towards important age-related differences in cortical sources involved in successful DCCS performance.

Consistent with the notion that cognitive control is supported by a distributed network of regions (e.g., Corbetta & Shulman, 2002; Braver & Ruge, 2006), many functional neuroimaging studies have reported Switch-related activations in the DLPFC, ventrolateral PFC, supplementary and pre-supplementary motor areas, ACC, and superior and inferior aspects of the posterior parietal cortex. Evidence from developmental functional imaging studies have indicated that the functional maturation of these regions follows a protracted developmental trajectory (Casey et al., 2004; Morton et al., 2009), with adults typically showing greater switch-related activation than children. Although the present findings are broadly consistent with the notion that the development of dimensional switching is supported by age-related differences in the efficacy of a distributed control network, there are several interesting points of contrast. Similar to the findings reported by Morton et al. (2009), there was evidence of an age-related decrease in the magnitude of prefrontal switch-related activity. Rubia et al. (2006) also found evidence of an age-related decrease in switch-related activity in the dorsolateral and medial prefrontal cortex. However, in contrast to the findings of Morton et al. (2009), age-related hemispheric differences in DLPFC Switch-related modulations were observed in the current study. While children exhibited greater Switch-related modulations in the right DLPFC than adolescents and adults, they also exhibited lower Switch-related modulations in the left DLPFC than adolescents and adults. At present, the reason for this difference is unknown and warrants further investigation. However, one possibility is that

this pattern of findings may reflect a developmental shift from a diffuse to focal pattern of activity. Durston et al. (2006) report evidence of an age-related attenuation of activation in DLPFC regions, paralleled by increased focal activation in ventral PFC regions during performance of a cognitive control task. The DLPFC is thought to be important for higher-order contextual representations (Miller & Cohen, 2001) and a number of computational models have linked performance in tasks such as the DCCS (Morton & Munakata, 2002) to the efficacy of active representations of contextually appropriate information by lateral regions of the prefrontal cortex. The present findings are consistent with the notion that dimensional switching in the DCCS is associated with DLPFC function.

Another important point of contrast concerns the nature of developmental changes in Switch-related parietal cortex modulations. Parallel to existing findings from developmental neuroimaging studies (Casey et al., 2004; Morton et al., 2009; Rubia et al., 2006) reporting developmental changes in the switch-related modulations of the left parietal cortex, the present study also found evidence of this association. However, while the existing developmental neuroimaging studies found evidence of an age-related increase in switch-related activity in the left parietal cortex, this current research of an age-related decrease in Switch-related modulations of the left superior parietal cortex. Several explanations may be given for this discrepancy. One possibility is that this discrepancy is related to differences in the tasks used to examine dimensional switching. For example, Casey et al. (2004) used a forced-choice discrimination task, which can be driven by bottom-up processes, whereas dimensional switching in tasks such as the DCCS are driven by endogenous top-down control processes. It is more challenging to

reconcile the different patterns of left superior parietal cortex modulations found by Morton et al. (2009) with that found in the present study. One possible explanation of the difference is that Morton et al. (2009) used a block design to analyze their imaging data, while the present study used an event-related design. Yet another possibility is that these differences arise out of using fundamentally different neuroimaging techniques (i.e., fMRI vs. source modeling of ERPs). However, despite these differences, the available evidence points towards the superior parietal cortex playing an important role in dimensional switching.

Yet another point of contrast concerns the nature of age-related changes in switch-related ACC modulations. While the ACC has been consistently implicated as being involved in the distributed network of regions involved in implementation of cognitive control (e.g., Barber & Carter, 2005; Cole & Schneider, 2007; Corbetta & Shulman, 2002; Braver & Ruge, 2006), age-related differences in switch-related ACC modulations have not been observed. The present findings observed an age-related decrease in switch-related ACC modulations. This pattern of ACC activity may reflect age-related changes in the amount of conflict (Botvinick et al., 2001) experienced on switch trials, or it may reflect differences in error-likelihood estimations (Brown and Braver, 2005).

The present findings from the source models of the conflict-related N2 are consistent in many respects with a large corpus of neuroimaging studies indicating the involvement of the ACC in conflict processing (e.g., MacDonald et al., 2000; Nieuwenhuis et al., 2003; for review see Carter & van Veen, 2007). Moreover, the findings of the present study are consistent with existing developmental source modeling studies of the conflict-related N2 (e.g., Jonkman et al., 2006; Ladouceur et al., 2007). In

one source localization study Niewenhuis et al. (2003) found that the ACC was the plausible generator of the conflict-related N2. In a developmental source localization study, Ladouceur et al. (2007) found that the conflict-related N2 and corresponding ACC dipole source activity matured late in adolescence and early adulthood. Consistent with this finding, this current study suggests that there are age-related differences in the magnitude of conflict-related ACC source modulations, with adolescents and adults exhibiting greater conflict-related ACC modulations relative to children. Taken together, these findings point towards the ACC playing a pivotal role in conflict processing, and that age-related advances in conflict processing follows a protracted developmental trajectory.

There are certain methodological issues arising from this current investigation that merit discussion. First, although electrode placement was taken into consideration for the generation of each participant's source model, the present version of Geosource software only contains an adult forward model. Second, source localization analyses are based on the computation of inverse solutions and at best provide only an estimate for the location of neural generators. Therefore, it is not entirely clear if changes in the LFN and N2 are due to structural or functional changes. Future research co-registering ERP and fMRI measures related to rule switching and conflict processing contributions to successful DCCS performance, along with structural and diffusion tensor imaging techniques would allow this question to be addressed more fully.

In summary, taken together with the present findings, evidence from developmental neuroimaging studies of switching (Casey et al., 2004; Crone et al., 2006; Morton et al., 2009; Rubia et al., 2006) and conflict processing (Jonkman et al., 2006;

Ladouceur et al., 2007) add important information to an already complex body of evidence investigating developmental changes in cognitive control and their associated neural correlates. The results of the present study also provide novel findings showing are-related differences in the pattern of Switch-related cortical source modulations associated with the generation of the Switch-related LFN. The results of the present study also parallel that of Ladouceur et al. (2007) in showing that the conflict-related N2 develops in parallel with the functional maturation of the ACC. Although the present study makes an important contribution to the understanding of how a distributed network of regions contribute to DCCS performance and cognitive control more generally, further research is still required to more precisely reconcile differences between neuroimaging studies of cognitive control.

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Chapter 4: The Development of Future-Oriented Control: An Electrophysiological Investigation

Cognitive control is a higher-order cognitive process involved in the selection of task-relevant stimuli and responses (Miller & Cohen, 2001). Despite stable individual (Miyake, Friedman, Emerson, Witzki, Howerter, & Wager, 2000) and developmental differences (Davidson, Amso, Anderson, & Diamond, 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, Braver, Barch, Carter, & Cohen, 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, Gray, & Burgess, 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 favour 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 behavioural and neural adaptations to prior conflict. According to several accounts, (Botvinink 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 protracted changes in synaptic density (Huttenlocher et al., 1979), cortical thickness (Giedd et al., 1999; Sowell, Thompson, Tessner, & Toga, 2001), 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, Thomas, & McClelland, 2009) suggest that one consequence of these protracted changes is that children have difficulty maintaining strong active representations of attention-guiding rules (Morton & Munakata, 2009; Munakata, McClelland, Johnston, & Siegler, 1997), and are therefore prone to dysfunctional control in object search (Munakata, 1998) and flexible rule-use tasks (Chevalier & Blaye, 2009; Morton & Munakata, 2002). One hypothesis that follows from these ideas is that there should be age-related differences in behavioural 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).

This hypothesis was tested through the use of converging behavioural 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 & Hirake, 2009; Morton, Bosma, & Ansari, 2009; Experiment 1). 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 colour (see Chapter 2 Figure 1). Half of the imperative stimuli embodied conflict insofar as they could legitimately be sorted either by colour 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). Because neither colour nor shape is strongly prepotent in this task and to ensure bivalent stimuli (henceforth referred to as ―incongruent) were a robust source of conflict, sorting criteria periodically changed (see also Liston et al., 2006).

Importantly, the task generates robust behavioural and electrophysiological congruency effects for participants of all ages (Experiment 1) that parallel congruency effects reported elsewhere in the literature. First, with respect to behaviour, response times are slower to incongruent than congruent stimuli (see also Diamond &

Kirkham, 2005), an effect that is more pronounced for younger than older participants and which is orthogonal to the effect of rule switching (Experiment 1). Second, with respect to electrophysiology, imperative stimuli elicit a frontocentral negativity that is greater in amplitude for incongruent than congruent stimuli (Experiment 1). 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 frontocentral components are associated with individual differences in behavioural 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 behavioural congruency effects, but orthogonal to behavioural costs associated with rule switching. Modulation of the stimulus-locked N2 by response conflict is well-documented in the literature (vanVeen & Carter, 2002a, 2002b), is thought to index monitoring processes computed by the ACC (Yeung, Botvinick, & Cohen, 2004), and has been observed across a variety of tasks (Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003; vanVeen & Carter, 2002a, 2002b), including conflict adaptation paradigms (Forster et al., 2011; Freitas, Banai, & Clark, 2009; but see Wendt, Heldmann, Munte, & Kluwe, 2007). The behavioural and electrophysiological congruency effects elicited by the DCCS therefore converge with previously reported findings, and provide a sound methodological basis for the present investigation.

To examine age-related differences in the dynamic modulation of cognitive control, behavioural and electrophysiological adjustments to prior conflict were measured 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 & 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).

Age-related differences in these behavioural and electrophysiological effects were examined with the following predictions. On the hypothesis that prior incongruence attenuates conflict-related activity in the ACC on subsequent incongruent trials, smaller N2 amplitudes on iI compared with cI trials were predicted, as was a cortical source of the N2 in the vicinity of the ACC. Second, on the hypothesis that the development of active maintenance is protracted (Morton & Munakata, 2009; Munakata, 1998) and extends into adolescence, it was predicted that behavioural and electrophysiological adaptations to prior conflict would be attenuated in children relative to adults and adolescents. Given greater latency in the modulation of frontocentral components by response conflict in children relative to adolescents and adults, sequential trial order effects in children were tested both at the N2 and also at the N4. Finally, it was predicted

that there would be age-related differences in the association of behavioural (i.e., RT_cI – RT_iI) and electrophysiological adaptations (i.e., N2_cI – N2_iI) to prior conflict. Specifically, it was predicted that for adults and adolescents, larger behavioural 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.

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 colour 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; Morton et al., 2009; Zelazo, 2006,). 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 Chapter 2 Figure 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 centre 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 colour 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 cancelled the response period. Individual trials were separated by a 1000ms 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. The total testing time for each participant was 90 minutes.

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 then 200ms); (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 100μV. 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) centred 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 centred 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

Behavioural 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 & 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 Figure 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, 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.*

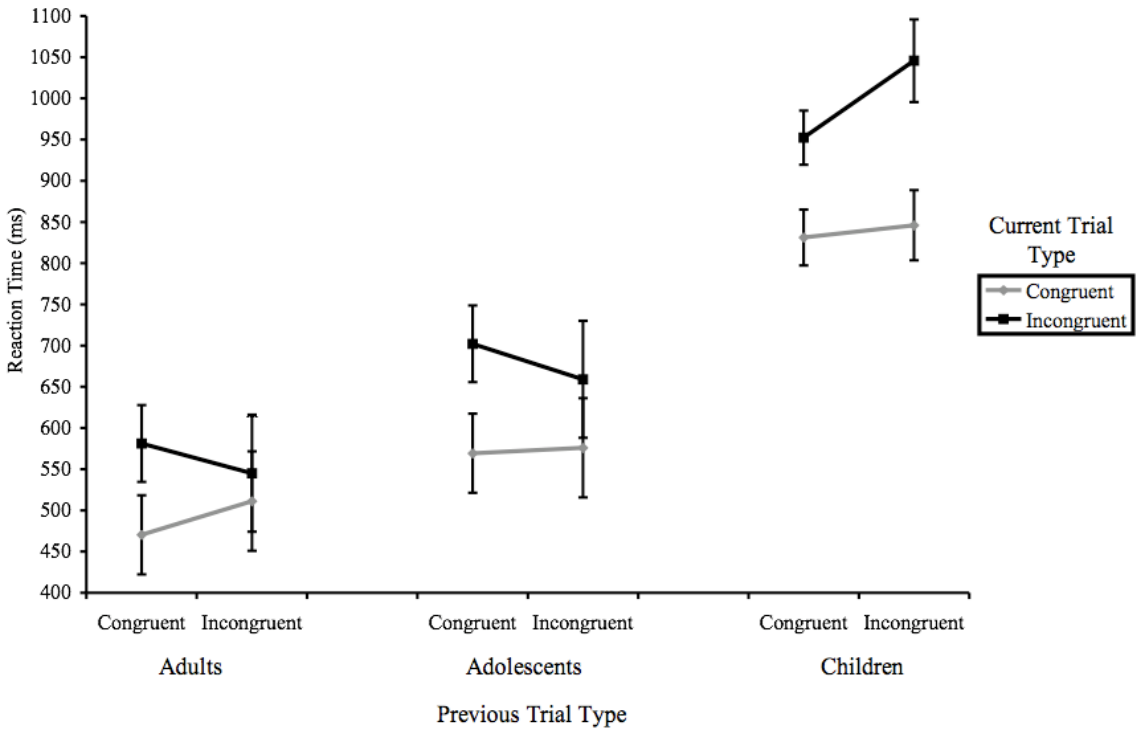

Figure 2. Reaction times as a function of trial type and age group.

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 a 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), the RT data was re-analyzed excluding exact stimulus repetition trials. The pattern of results for the Age Group x Previous Trial Type x Current Trial Type ANOVA excluding stimulus repetitions was consistent with the analysis present above (see Figure 2). 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 behavioural 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 vs. incongruent), Preceding Trial Type (congruent vs. incongruent), and Age Group (children, adolescents, and adults) are displayed in Figure 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, $p < .001$.

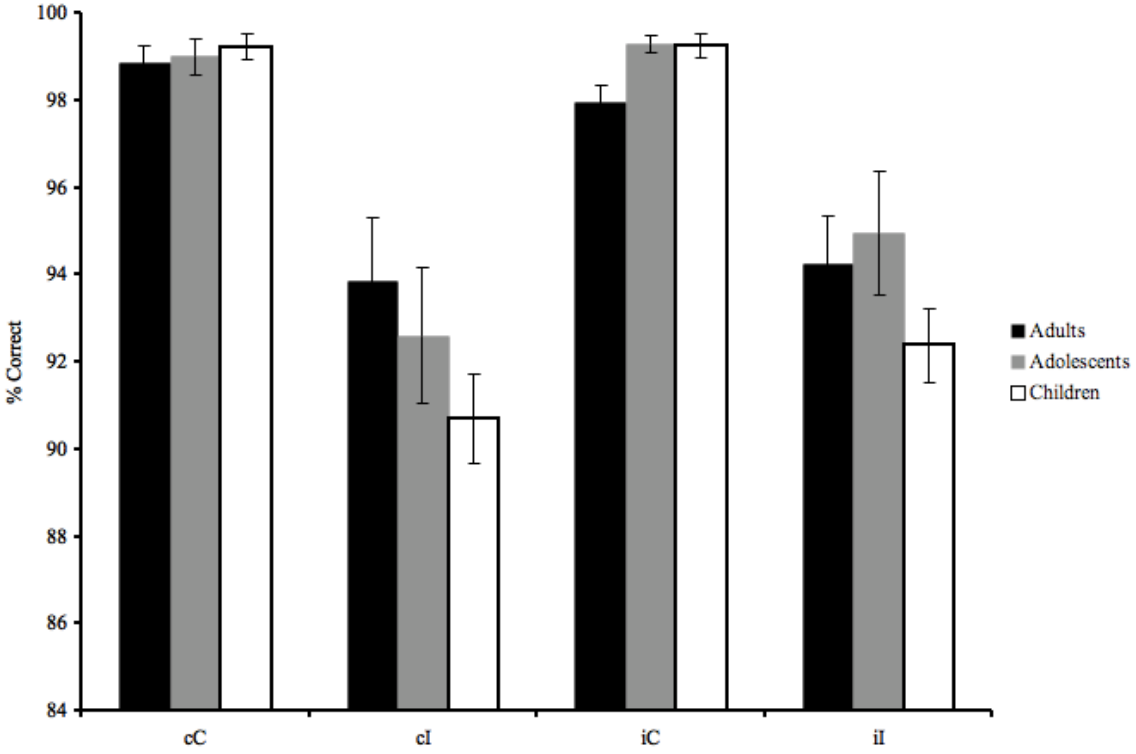

Figure 3. Error rates as a function of Trial Type and Age Group.

ERP analysis

Figure 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 200ms 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.

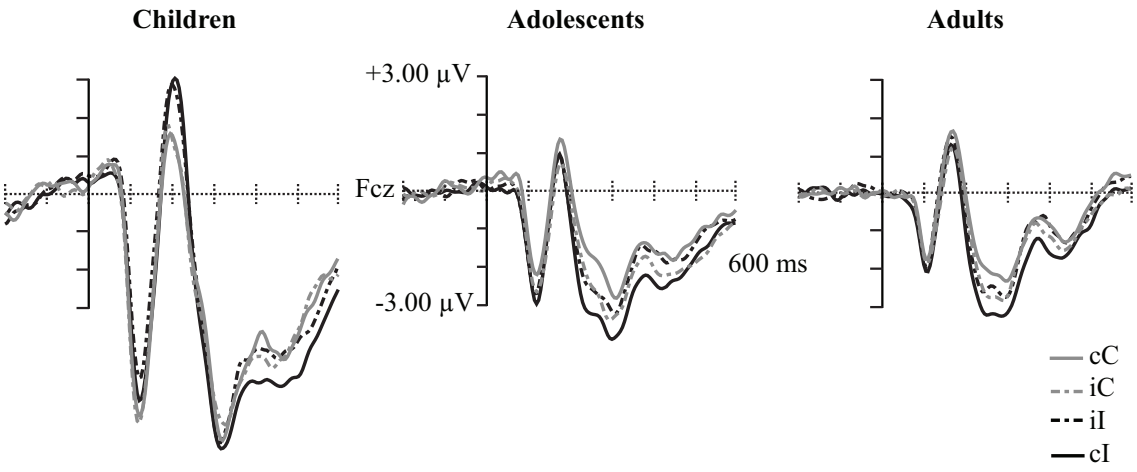

Figure 4. Grand averaged stimulus-locked waveforms at electrode Fcz for children, adolescents, and adults. Each wave board plots a 200 ms baseline and 600 ms post stimulus onset.

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, whether conflict adaptation would be evident on this later component was also tested. Thus, children's mean N4 amplitudes were submitted to a 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, conflict modulations at the P1were also examined. 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-behaviour correlation analysis

To examine the relationship between individual differences in the behavioural 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 behavioural adaptation were not associated with individual differences in N2 or N4 modulation by prior conflict.

Table 1. Correlation of behavioural and electrophysiological measures of conflict adaptation. Greater behavioural 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

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

Source space analyses

Figure 5 shows the source model activations (in nA) for cI and iI trials. As is clearly visible, adolescent and adult source model activations in the vicinity of the ACC were greater for cI trials than iI trials.

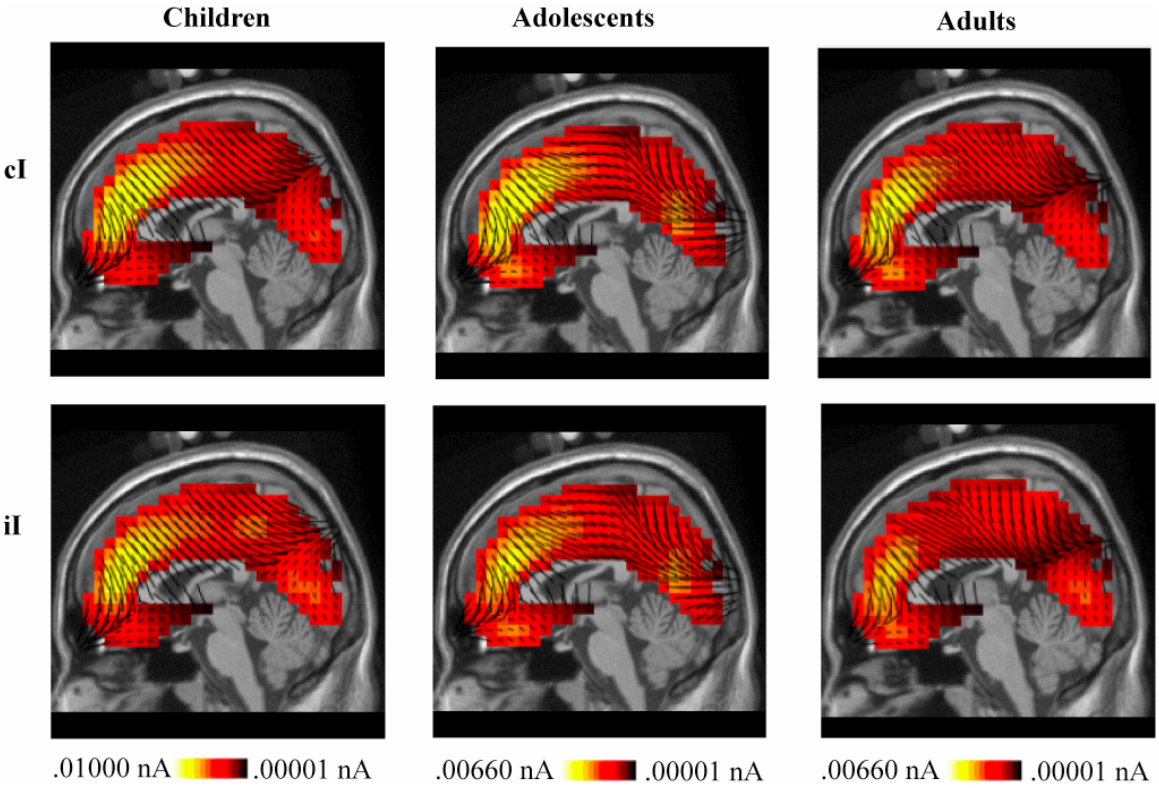

Figure 5. Modeled source activations (in nA) displayed using the Montreal Neurological Institute (MNI) average adult MRI scan for peak N2 amplitude on cI and iI trials for each age group.

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 behavioural 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 behavioural 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 frontocentral 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 behavioural 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 (Frietas et al., 2009). In the other, parametric variation in prior conflict magnitude was associated with parametric modulation in stimulus-locked N2 amplitudes and behavioural response times on subsequent incongruent trials (Forster et al., 2011), with greater prior conflict associated with greater

electrophysiological and behavioural adaptation on subsequent trials. And as in the current data, individual differences in N2 modulation by prior conflict were negatively associated with subsequent behavioural 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 behavioural 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 behavioural 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 (Experiment 1). In sum, the findings suggest age-related differences in brain and behavioural 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 behavioural adjustments did not change when the effects of stimulus repetition were controlled.

Similar findings have been reported elsewhere (Egner & 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 favour 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 & Munakata, 2007; 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, Boseovski, & Knapp, 2007; Morton & 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, Benson, & Roberts, 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.

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Chapter 5: General Discussion

The ability to make flexible adjustments in thought and behaviour to meet the challenges of a frequently changing environment is an essential aspect of human cognition. The development of cognitive control follows a protracted timeline with improvements being seen into early adulthood (for review see Diamond, 2002; Morton, 2010). Yet, a comprehensive understanding of the processes and mechanisms that bring about this developmental change remains elusive. The current set of studies aimed to investigate whether age-related advances in DCCS performance are supported by multiple cognitive control processes that follow distinct developmental trajectories. The results of Experiment 1 suggest that multiple control processes unfold within the timeframe of a single DCCS trial. Rule switching and conflict processing made additive contributions to variability in reaction time, and were associated with distinct electrophysiological components (i.e., a cue-locked Switch-related LFN and a stimulus-locked conflict-related N2). Moreover, rule switching and conflict-related processes showed distinct developmental trajectories. Using distributed cortical source modeling, the results of Experiment 2 suggest that the Switch-related LFN is associated with a distributed network of regions that includes the DLPFC, superior parietal cortex, and the ACC. Additionally, the results of Experiment 2 also indicate that age-related advances in conflict processing are associated with the maturation of the ACC. The findings of Experiment 3 suggest that the development of conflict processing is dynamically modulated by contextual demands.

The current research has a number of implications for our knowledge of the development of cognitive control. First, it helps to elucidate our understanding of the

cognitive control processes involved in DCCS task performance. While many theoretical accounts of characterize executive demands associated with the DCCS in terms of a single process that operates over an entire trial (Kirkham et al., 2003; Kloo and Perner, 2005; Zelazo et al., 2003), the findings of Experiment 1 suggest that multiple control processes underpin DCCS performance. More specifically, the results of Experiment 1 suggest that rule switching and conflict processing follow distinct developmental trajectories, with the development of conflict processing emerging later than rule switching.

The current set of studies also represents one of the first attempts to examine dynamic moment-to-moment modulations of cognitive control processes from a developmental perspective. To large extent, research has focused on examining the development of cognitive control from a coarser level of analysis. For example, there is a substantial corpus of literature indicating that the development of conflict processing follows a protracted developmental trajectory (e.g., Davidson et al., 2006; Jonkman et al., 2007; Ladouceur et al., 2007; Lamm et al., 2006). Consistent with this notion, the results of Experiment 1 showed that the development of conflict processing is late maturing, with children being more susceptible to the effects of conflict. However, additional insight into the processes and underlying mechanisms of cognitive control can be gleaned from examining sequential trial order effects. The results of Experiment 3 showed that although children, adolescents and adults showed a robust conflict effect, there were pronounced age-related differences in behavioural and electrophysiological adaptations to prior conflict. Taken together, the findings of Experiment 1 and 3 suggest that adults and

adolescents take advantage of prior conflict to prepare for the future, whereas children respond to the cognitive challenges of conflict as they occur.

Second, this research helps to further elucidate the relationship between the development of cognitive control and the prefrontal cortex. One of the prevailing hypotheses in developmental cognitive neuroscience is that age-related advances in cognitive control can be localized in the lateral PFC (Dempster, 1992; Diamond, 2002; Kirkham et al., 2003). However, one critical challenge to this hypothesis is that there is a growing body of evidence that complex cognitive operations that support cognitive control are not localized in the lateral PFC, but are distributed over a network of regions, including lateral PFC, medial PFC, superior parietal cortex, ACC, and subcortical structures such as that basal ganglia and thalamus (Casey et al., 2007; Cole & Schneider, 2007; Morton et al., 2009). Moreover, the organization of this distributed network undergoes dramatic change over the course of development (Fair et al., 2007; Kelly et al., 2009; Stevens et al., 2007). The results of Experiment 2 and 3 are broadly consistent with the notion that cognitive control is supported by a distributed network of regions. Distributed cortical source models of the cue-locked LFN revealed Switch-related modulations in the DLPFC, ACC, and superior parietal cortex. Moreover, these Switch-related modulations showed considerable age-related variability. This is pattern of findings is somewhat puzzling given that the switch-related LFN difference wave was not associated with any developmental variability. Distributed cortical source models of the stimulus-locked N2 revealed age-related differences in conflict-related ACC modulations. Finally, the results of the distributed cortical source models from Experiment 3 revealed that exposure to prior conflict was associated with a decrease in

conflict-related ACC source activity for adults and adolescents, but not children. It is of interest to note that the conflict-related ACC modulations observed in Experiment 2 are more dorsal and posterior to the ACC conflict adaptation effects observed in Experiment 3. At present the precise reason for this discrepancy is unclear and warrants further investigation.

Although the aforementioned experiments have shown promise in elucidating cognitive control processes underlying DCCS task performance, a number of shortcomings limit the confidence with which the results can be interpreted. First, the experimental paradigm that was used was a predictable switching task, and as such may have inadvertently affected the pattern of results observed. Previous investigations of task switching in adults have indicated that performance on predictable switching paradigms can vary markedly from that of unpredictable switching paradigms (e.g., Swainson et al., 2006). For example, behaviour on distinct repeat trials either plateaus to significantly faster performance (i.e., predictable task switching) or shows increasing benefits from one repeat trial to the next (i.e., unpredictable task switching). It is then possible that adults in the current study relied on and benefited from sequence predictability, whereas adolescents and children did not. Although the present set of experiments cannot directly address this limitation, future research investigating developmental differences in performance on predictable and unpredictable task switching paradigms is warranted.

A second limitation of this set of experiments, and of ERP source analysis in general, is related to the estimation of source space activity. More specifically, voltage differences between scalp electrodes were used to estimate the most likely cortical

generator(s) of a particular ERP component of interest. In recent years, methods for modeling source-space activation, and the questions that can be asked of these data have improved. However, the calculation of source-space activation is still based on an inverse model, and as the number of possible solutions is far greater than the number of preset constraints, the problem is considered "ill posed." Therefore, additional model constraints have to be specified. Some of the frequently used logical source model constraints are incorporated in the LORETA and LAURA algorithms (for a review see Michel et al., 2004). However, each modeling constraint of the inverse solution may produce slightly different results. Therefore it is important to evaluate the "fit" between the inverse model and scalp topography. Moreover, it is important to apply a number of constraints to determine which inverse solution has the best "fit" before extracting data and doing statistical analyses. This method of comparing inverse solutions to the topography was applied a number of times before source-space data were extracted using LORETA constraints. However, because of limitations inherent in all source-space analyses, replication of the source space results obtained in Experiment 2 and Experiment 3 are required before these results can be considered reliable.

Despite the inherent limitations of the paradigm and source modeling methods used, the findings of the current set of experiments provide initial and important insight into how distinct cognitive control processes contribute to successful DCCS performance. Taken together with the present findings, evidence from developmental neuroimaging studies of switching (Casey et al., 2004; Morton et al., 2009, Rubia et al., 2006) and conflict processing (Jonkman et al., 2006; Ladouceur et al., 2007) add to a complex body

of evidence regarding developmental changes in cognitive control and their associated neural correlates.

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Appendix A

Consent Form:

Western

Consent Form

A Developmental Investigation of the Dynamics of Cognitive Control Using ERP

I have read the Information Letter, have had the nature of Dr. Morton's study explained to me and I agree that ____________________ may participate in the study.
Your child's name

All questions have been answered to my satisfaction.

____
Parent/Guardian's Name (Please Print)

______________________ ____________________
Parent/Guardian's Signature Date

____
Name of Person Obtaining Informed Consent (Please Print)

_____________________________________ ______________
Signature of Person Obtaining Informed Consent Date

>>

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Appendix B

Ethics approval:

Office of Research Ethics

The University of Western Ontario
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Use of Human Subjects - Ethics Approval Notice

Principal Investigator: Dr. J.B. Morton
Review Number: 13497S **Revision Number:** 2
Review Date: April 17, 2009 **Review Level:** Expedited
Protocol Title: A Developmental Investigation of the Dynamics of Cognitive Control Using ERP
Department and Institution: Psychology, University of Western Ontario
Sponsor: NSERC-NATURAL SCIENCES ENGINEERING RSRCH COU
Ethics Approval Date: April 17, 2009 **Expiry Date:** December 31, 2009
Documents Reviewed and Approved: Revised Study End Date
Documents Received for Information:

This is to notify you that The University of Western Ontario Research Ethics Board for Non-Medical Research Involving Human Subjects (NMREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the applicable laws and regulations of Ontario has granted approval to the above referenced revision(s) or amendment(s) on the approval date noted above.

This approval shall remain valid until the expiry date noted above assuming timely and acceptable responses to the NMREB's periodic requests for surveillance and monitoring information. If you require an updated approval notice prior to that time you must request it using the UWO Updated Approval Request Form.

During the course of the research, no deviations from, or changes to, the study or consent form may be initiated without prior written approval from the NMREB except when necessary to eliminate immediate hazards to the subject or when the change(s) involve only logistical or administrative aspects of the study (e.g. change of monitor, telephone number). Expedited review of minor change(s) in ongoing studies will be considered. Subjects must receive a copy of the signed information/consent documentation.

Investigators must promptly also report to the NMREB:

a) changes increasing the risk to the participant(s) and/or affecting significantly the conduct of the study;
b) all adverse and unexpected experiences or events that are both serious and unexpected;
c) new information that may adversely affect the safety of the subjects or the conduct of the study.

If these changes/adverse events require a change to the information/consent documentation, and/or recruitment advertisement, the newly revised information/consent documentation, and/or advertisement, must be submitted to this office for approval.

Members of the NMREB who are named as investigators in research studies, or declare a conflict of interest, do not participate in discussion related to, nor vote on, such studies when they are presented to the NMREB.

Chair of NMREB: Dr. Jerry Paquette

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cc: ORE File

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Thesis Supervisor: Dr. Mary Desrocher

HONORS AND ACADEMIC AWARDS

The University of Western Ontario: Western Graduate Research Scholarship

The University of Western Ontario: Special University Scholarship

York University: Entrance Scholarship

York University: Continuing Student Scholarship

York University: Member of the Deans List

York University: Graduate cum Laude

RELATED WORK EXPERIENCE

Teaching Assistant
The University of Western Ontario
2003-2009

ARTICLES PUBLISHED IN REFEREED JOURNALS

Waxer, M., & Morton, J. B. (in press). Dissociable processes underlying task switching: An electrophysiological investigation. *Journal of Cognitive Neuroscience*.

Waxer, M., & Morton, J. B. (in press). The Development of Future-Oriented Control: An Electrophysiological Investigation. *NeuroImage*.

Waxer, M., & Morton, J. B. (in press). Children's Judgments of Emotion From Conflicting Cues in Speech: Why 6-Year-Olds are so Inflexible. *Child Development.*

Waxer, M., & Morton, J. B**.** (in press). Cognitive Conflict and Learning. In R. M. Seel (Ed.), *Encyclopedia of the Sciences of Learning*. New Jersey: Springer.

CONFERENCE PRESENTATIONS

Waxer, M., & Morton, J. B. (2010). Examining the neural time course of conflict adaptation effects during rule-switching. Poster presented at the annual conference of the Cognitive Neuroscience Society, Montreal, Canada.

Waxer, M., & Morton, J. B. (2009). Dissociable components of cognitive control: An electrophysiological investigation of rule-switching. Poster presented at the annual conference of the Cognitive Neuroscience Society, San Francisco, CA.

Wong, A.H.C., **Waxer, M.,** & J. B. Morton (2009). An investigation of cognitive flexibility using event-related potentials. Poster presented at the annual meeting of the Canadian Psychological Association, Montreal, Canada.

A.S. Love, E. Sejdic, M.E. Markowski, **M. Waxer,** J.B. Morton, R. Sobot, **A Brain-Controlled 3D Sonar Scanner**, IEEE Canadian Conference on Electrical and Computer Engineering, (2008), CCECE 2008, Niagara Falls, Ontario, Canada, May 4-7, 2008.

Waxer, M., & Morton, J. B**.** (2008). Age-related differences in dissociable components of cognitive control. Poster presented at the annual conference of the Cognitive Neuroscience Society, San Francisco, CA.

Waxer, M, & Morton, J. B. (2007). Children attention to emotional and nonemotional information in speech. Poster presented at the biennial meeting of the Society for Research in Child Development, Boston, MA.

Morton, J. B., & **Waxer, M.** (2005). Working memory span and the anti-saccade task: an ERP investigation of preparatory processes. Poster presented at the annual conference of the Cognitive Neuroscience Society, New York, NY.