Development of inhibition and switching

Citation for published version:

Digital Object Identifier (DOI):
10.1016/j.dcn.2018.03.002

Link:
Link to publication record in Edinburgh Research Explorer

Document Version:
Peer reviewed version

Published In:
Developmental Cognitive Neuroscience

General rights
Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy
The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.
Development of inhibition and switching: a longitudinal study of the maturation of interference suppression and reversal processes during childhood

Cassandra Richardson¹,², Mike Anderson¹,³,⁴, Corinne L. Reid⁵, & Allison M. Fox¹,³

¹ Neurocognitive Development Unit, School of Psychology, University of Western Australia, Western Australia; ² School of Psychology, University of Central Lancashire, UK; ³ School of Psychology, University of Western Australia, Western Australia; ⁴ School of Psychology and Exercise Science, Murdoch University, Western Australia; ⁵ School of Health in Social Science, University of Edinburgh, UK

Address for correspondence:

Dr Cassandra Richardson
School of Psychology
University of Central Lancashire
Preston, Lancashire PR1 2HE

T: +44 (01772) 893427   E: C.Richardson5@uclan.ac.uk

Running head: Development of Inhibition and Switching

Word Count: 6488

Tables: 1   Figures: 2
Abstract

Inhibition and switching are executive functions (EFs) that have different developmental trajectories across childhood. The development of specific processes unique to each EF may contribute to these trajectories. Interference suppression and reversal were examined in a large sample of children aged 7 and 9 years ($n = 120$) and followed-up after two-years to investigate developmental trajectories of inhibition and switching. The N2 and P3b components provided neural correlates of conflict monitoring and attentional processing of conflict involved in interference suppression and reversal. Interference suppression improved over time, however, switching performance did not significantly change between 7-11 years. Improvements in correct RT with age and time indicated increased efficiency of stimulus evaluation, response preparation and execution. N2 amplitude decreased with both age and time, indicating less reliance on conflict monitoring to signal cognitive control to manage stimulus and response conflict. P3b amplitude modulations indicated that different amounts of attention were allocated to updating mental representations of interference suppression and reversal task features. These data indicated different developmental trajectories of specific processes unique to inhibition and switching across the childhood period of 7-11 years, providing further empirical evidence that 7-11 years is a critical period for cognitive development.

Keywords: Inhibition; switching; conflict monitoring; N2; executive functions; development.
1. Introduction

The term executive functions (EFs) refers to a collection of higher order cognitive processes that provide top-down control during goal-directed behaviours (Diamond, 2013). These processes are, by necessity, highly adaptive and dynamic in order to facilitate optimal information processing and task performance (Miller & Cohen, 2001). The ability to monitor and update mental representations of goal requirements, inhibit prepotent responses and shift between tasks or mental sets are EFs that contribute to the performance of complex EFs, such as planning, abstract reasoning and problem solving (Miyake et al., 2000; Miyake & Friedman, 2012). When performance on executive tasks is modelled in children, working memory, inhibition and shifting are unitary and indistinguishable up to ~9 years (Brydges et al., 2012; Willoughby et al., 2012; however, see van der Ven et al., 2013). Longitudinal modelling replicated a unitary structure of EFs in children aged 8 years, but found that a two factor model was the best fit at age 10, with working memory being separable from an inhibition/shifting factor (Brydges et al., 2014a). This separation of working memory suggests that the processes specific to working memory may develop earlier than those involved in inhibition and shifting (Brydges et al., 2014a). Alternatively, it may be that there are processes specific to inhibition and shifting not shared with working memory. For example, control processes that provide a stop process are not a feature of working memory, but may explain the commonality between inhibition and shifting (Brydges et al., 2014a).

Investigating specific processes inherent in inhibition and shifting may contribute to further understanding development of these EFs in childhood. Inhibiting a prepotent response and switching between rules have different developmental trajectories; in particular, switching has a greater protracted development compared to inhibition in children aged 6-13 years (Davidson et al., 2006). The ability to withhold a prepotent response shows improvement from age 6, in contrast, the ability to unexpectedly stop and change rules begins
to become evident around 9-10 years. The paradigms used by Davidson et al. (2006) indicated that even children as young as 4 years old can successfully perform tasks that include experimental manipulations of conflict with unexpected rule changes. The current study employed a modified flanker task with a reversed condition (cf. van Veen & Carter, 2002). Reversal is a simple type of switching that involves focusing on the same dimension, but switching stimulus-response (S-R) mappings (Diamond, 2013). Most children aged 4.5-5 years are able to switch between colour or shape sorting dimensions (Diamond, 2002), and previous work using a variant of this paradigm found that children aged 7 and 9 were able to successfully perform the task (Richardson et al., 2011).

Conflict-monitoring is a process that provides a mechanism that triggers top-down cognitive control processes (Botvinick et al., 2001). Interference suppression and reversal can create conflict due to the task demands inherent in each condition. In the incongruent condition, conflict arises from competing mental representations of task relevant and irrelevant features of the stimuli. Successful performance requires suppressing attention to the irrelevant flankers. The reversed condition creates response conflict from competition between the prepotent congruent response and the required response in the opposite direction to the target and congruent flankers. The anterior cingulate cortex (ACC) is a brain region thought to be implicated in the detection and monitoring of conflict (Botvinick et al., 2004). When conflict is detected, it has been proposed that a feedback signal is sent from the ACC to the prefrontal cortex (PFC) to increase cognitive control in order to manage conflict in information processing (Botvinick et al., 2004).

The N2 is an electrophysiological component generated in the vicinity of the ACC and is linked with conflict-monitoring processes (Ladouceur et al., 2007; Larson et al., 2014; van Veen & Carter, 2002). There are contradictory findings about the developmental trajectory of the N2. A decrease in N2 amplitude in adults was interpreted as indication that
adults were better able to manage conflict than children aged 4 (Rueda, Posner et al., 2004). However, Ladouceur and colleagues (Ladouceur et al., 2004; 2007) found that N2 amplitudes increased with age across adolescence. In contrast, consistent Nogo-N2 amplitude reductions are found with increasing age during childhood and adolescence, also interpreted to indicate age-related improvements in cognitive control (Hammerer et al., 2010; Johnstone et al., 2007; Jonkman, 2006; Lamm et al., 2006). The functional significance of the N2 depends on the paradigm eliciting the N2 component (Folstein & van Petten, 2008; Larson et al., 2014), and there is ongoing debate about the functional significance of the Nogo-N2. However, findings from a novel hybrid flanker-go/no-go paradigm have suggested that the N2 is better considered a marker of response conflict than response inhibition (Groom & Cragg, 2015).

There are also significant age-related changes within the PFC during development, which may influence the amplitude, latency and topography of event-related potentials (ERPs). For example, volume of activation is greater in children compared to adults (Casey et al., 1997), and reduced activity in the dorsolateral PFC (dlPFC) with concomitant increased focal activation in ventral regions of the PFC were found with increasing age in late childhood (Durston et al., 2006), during cognitive control paradigms. Importantly for the current study, the amplitude of the N2 can be sensitive to experimental manipulations of stimulus and response conflict in adults (van Veen & Carter, 2002) and children over the age of 10 (Liu et al., 2011; Pontifex et al., 2011). As such, the amplitude of the N2 can be used as a neural correlate of interference suppression and reversal, as N2 amplitude is associated with detection of conflict and can differentiate between the types of conflict involved in each of these specific processes.

Successful management of interference suppression and switching S-R mappings involves both detection and resolution of the conflict inherent in each process. Interference suppression requires top-down attentional control to resist interference from the irrelevant
features of the incongruent stimuli. Managing response conflict in switching requires
continuous evaluation of the relevant and irrelevant features of the stimuli in working
memory which, in turn, activates mental representations of S-R mappings in long term
memory (Melara & Algom, 2003). The P3b is an electrophysiological component that is
elicited during stimulus evaluation and indexes the timing and allocation of attentional
resources to updating mental representations of stimuli (Polich, 2007). There is some
evidence that the P3b is sensitive to conflict and the recruitment of cognitive control in adults
(Clayson & Larson, 2011; Groom & Cragg, 2015). There are inconsistent findings regarding
the developmental trajectory of the P3b in cognitive control paradigms. For example, Nogo-
P3 amplitude was larger in adults compared to children, with no significant differences in
Nogo-P3 and cue-P3 amplitudes between younger and older children (Jonkman, 2006).
However, P3 amplitude did not significantly differ between children and adults in a flanker
paradigm, and only differentiated between congruent and incongruent conditions in children
(Rueda, Posner et al., 2004). Experimental manipulations of conflict can influence allocation
of attention to updating mental representations of stimuli (e.g. Clayson & Larson, 2011;
Rueda, Posner et al., 2004), which indicates that the P3b can be used as a neural correlate of
attentional processing involved in managing stimulus and response conflict.

Development of cognitive processes during childhood is facilitated by an interaction
of experience and maturational changes in the brain. The current study employed a mixed
cross-sectional longitudinal design in order to examine the development of interference
suppression and reversal from 7 to 11 years, a critical period of childhood for the
development of EFs (e.g. Diamond, 2002; Brydges et al., 2014a). This mixed design allowed
for cross-sectional age-group comparisons between younger and older children, whilst the
follow-up provided an opportunity to examine development over time. Longitudinal designs
have greater power to detect developmental change as variability from individual differences
is statistically removed in analyses. Group comparisons at follow-up allowed for an examination of the effects of age and experience on interference suppression and reversal. There has been little longitudinal investigation of the developmental trajectories of specific processes unique to executive functions and their neural correlates during childhood. Examination of the differentiation of the neural correlates of specific executive functions across this period of childhood can also contribute to elucidating whether neural and behavioural development are parallel processes, or whether neural changes precede behavioural improvements in functioning.

Behavioural performance during versions of the flanker task changes with age; accuracy increases and correct reaction time (RT) becomes faster across childhood and adolescence (e.g. Checa et al., 2014; Ladouceur et al., 2004, 2007; Rueda et al., 2004). Accuracy indicates the ability to perform a cognitive task and improvements in accuracy can reflect cognitive development. Correct RT represents the time taken to evaluate a stimulus, prepare and execute a response, and faster correct RT is indicative of increasing efficiency and thus, development, of these processes. As such, it was expected that accuracy and correct RT would differ between the age groups and would improve with time. Whilst there is a paucity of research using response-incompatible conditions with children under the age of 10, we predicted that there would be amplitude reductions in the N2 with age and with time, as the majority of evidence has found N2 reductions with age (e.g. Hümmerer et al., 2010; Johnstone et al., 2007; Jonkman, 2006; Lamm et al., 2006; Rueda, Posner et al., 2004). The amplitude of the N2 and the P3 can also differentiate between experimental manipulations of conflict (e.g. Clayson & Larson, 2011; Pontifex et al., 2011; van Veen & Carter, 2002), and it was expected that the amplitude of the N2 and P3 would be increased with conflict.
2. Method

Project K.I.D.S. (Kids Intellectual Development Study) is a two-day holiday activity programme. During the two days, the children completed a range of neuropsychological tests, computer-based cognitive tasks, individual and group-based activities to investigate the cognitive, emotional, and social development of children. Approval for the study was provided by the Ethics Committee of the School of Psychology, University of Western Australia, Australia. Written informed consent was provided by each child and their parent or legal guardian. Brydges et al. (2014b) merged time 1 (T1) data from the sample reported here with a previously published dataset (Brydges et al., 2012) to create N2 and P3b latent variables for a structural equation model investigating the relationships between these ERP factors and an EF factor. The purpose of the Brydges et al. (2014b) analysis was to provide evidence that ERP factors were related to and predictive of an EF factor. The current study examined the development of specific EFs and measured ERP components as neural correlates of the specific processes inherent in inhibition and switching.

2.1. Participants

Children were recruited from local schools and were aged either 7 or 9 years at T1 and then followed-up two years later. We identified 121 children aged 7 and 9 years who had complete electroencephalography (EEG) recordings for the modified flanker task at T1 and time 2 (T2). Above chance performance on the flanker task was calculated using the binomial distribution, and one child aged 7 years was excluded on the basis of below chance performance on the congruent condition of the task at T1. The final sample consisted of 73 children aged 7 years (36 male; $M = 7.50$ years, SD .30) and 47 children aged 9 years (29 male; $M = 9.52$ years, SD .28) at T1. There were no significant differences between the 7 and
9 year-old samples on full-scale IQ as assessed using the WISC-IV at T1 \([M = 107.49, SD 13.56; M = 107.86, SD 11.33; 7 and 9 year-olds, respectively; F (1, 112) <1, p = .882, \eta^2 = .00]\). These IQ scores are comparable to the WISC-IV full-scale IQ scores \((M = 107.05, SD 12.63)\) reported in Brydges et al. (2014b). All participants were healthy at the time of testing, had no reported history of neurological or psychiatric conditions, and parental report of normal or corrected-to-normal vision and hearing. The Ishihara test was used to ensure that all participants were able to differentiate between red and green colours.

2.2. Experimental Paradigm

The experimental paradigm was a modified flanker task. Each trial commenced with a warning fixation cross which appeared 500 ms before the stimulus and remained on-screen until the presentation of the stimulus. Each stimulus consisted of an array of five fish presented on a blue background. An arrow on the body of the fish indicated direction and the target was the central fish. Participants were instructed to press a response button situated on a keyboard corresponding to the direction of the central fish. There were three conditions: in the congruent condition (.5 probability), the fish were green with the flankers pointing in the same direction; an incongruent condition (.25 probability), where the fish were also green, however, the flankers pointed in the opposite direction to the target; and a reversed condition (.25 probability), in which the flankers were congruent, but the fish were red, and required a response in the opposite direction to the central fish. Each fish subtended 0.9° horizontally and 0.6° vertically with 0.2° separating each fish and were presented for 300ms. Feedback was provided 300ms after each response, and the next trial commenced 500ms after the response. Speed and accuracy were equally emphasised. A practice block of eight trials was
administered to ensure the participants understood the task requirements. A total of 352 trials were randomly presented in two blocks separated by a 20 minute interval.

2.3. Electrophysiological Acquisition

The EEG was continuously recorded using an Easy-Cap™ fitted with 33 electrodes positioned according to the International 10-20 system (Fp1, Fp2, F8, F3, Fz, F4, F8, FT9, FC5, FC1, FCz, FC2, FC6, FT10, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO9, O1, O2, PO10, Iz). Eye movement and blink activity (electro-oculogram; EOG) were measured with bipolar leads placed above and below the left eye. The EEG was amplified with a NuAmps 40-channel amplifier, and digitized at a sampling rate of 250Hz, referenced to the right mastoid and a ground lead located at AFz. An average mastoid reference was calculated offline. Prior to recording, impedances were below 5kΩ. The ERP processing was conducted offline using NeuroScan software. Offline, the EEG recording was digitally filtered with a 0.1-30Hz zero phase shift band-pass filter (12dB down). The vertical ocular electrodes enabled offline blink reduction in the continuous EEG according to a standard regression algorithm (Semlitsch et al., 1986). This method calculates an average of blink EOG activity to obtain the regression weights. In this study, a minimum of \( n = 20 \) blinks was required for each individual blink average.

2.4. Data Analysis

The EEG data were divided into epochs of -600 to 1000ms synchronised to the presentation of the stimulus in correct trials only. This interval included the warning fixation cross and T1 correction was applied from -600 to -500ms. Data from the midline sites (Fz, Cz and Pz) were analysed and epochs containing artefacts exceeding ±150µV were automatically
rejected. Epochs were averaged by stimulus type (congruent; incongruent; reversed). The mean amplitude for the N2 was calculated in a 304-480ms time window and the P3b in a 496-916ms window (see Figures 1 and 2). These time windows were calculated by creating difference waveforms at T1 and T2 (congruent-incongruent; congruent-reversed) for each participant. Difference waveforms were created to identify the amplitude specific to stimulus and response conflict as there is no conflict present in congruous trials. The difference waveforms were then averaged to create grand group averages and the latency windows were identified where the amplitude differed significantly from zero using one sample t-tests (see Guthrie & Buchwald, 1991). Multiple comparisons were not adjusted for as the number of data points would have compromised statistical power. A suggested way of dealing with this issue is to consider a large number of consecutive significant values to indicate the time windows for amplitude calculation (Guthrie & Buchwald, 1991). The P3b is typically maximal in a 250-500ms time window in adults, however, task demands and participant age influence P3 latency (Polich, 2007). Longer latency of ERP components is commonly found in children and others have found that the P3 occurs much later (after 500 ms) in children aged under 11 years (e.g. Lewis et al., 2006). The time windows identified in the current study are comparable to previous studies including children (300-550ms; 400-1100ms, N2 and P3, respectively; Rueda, Posner et al., 2004).

The distributions of the behavioural and electrophysiological data were analysed using Kolmogorov-Smirnov tests. The numbers of trials in the waveforms were not normally distributed, therefore, Mann Witney U tests with alpha values corrected for multiple comparisons (.05/6 = .008) were used to examine group differences. The numbers of trials within each waveform (congruent, incongruent, reversed at T1 and T2) did not significantly differ between younger and older children. The reliability of the ERP components was ensured by the numbers of trials in the waveforms (younger group median: 151, 71, 69;
congruent, incongruent, reversed at T1; 161, 77, 74; congruent, incongruent, reversed at T2;
older group median: 157, 76, 68; congruent, incongruent, reversed at T1; 159, 77, 73;
congruent, incongruent, reversed at T2). Recent investigation the reliability of ERP
components across the lifespan found that signal-to-noise ratio was asymptotic when 40+
trials were included in the average waveform (Hammerer et al., 2013). More specifically, 30
trials are sufficient for a conservative and reliable N2 waveform (Clayson & Larson, 2013).

The majority of the mean amplitudes of the N2 and P3b were normally distributed and
were analysed using mixed ANOVA models. The difference waveforms were not used in the
analyses because the congruency effect is identified by a significant difference between
congruent and incongruent conditions. Furthermore, previous studies have considered the
conditions separately and this was also done here to facilitate comparability between this and
previous studies. The location of maximal amplitude for the N2 was investigated using a 2
(time: time1; time 2) x 3 (condition: congruent; incongruent; reversed) x 3 (location: Fz, Cz, Pz) x 2 (group: Younger; Older) ANOVA model. A main effect of location \[ F (2, 236) = 237.47, p < .001, \eta^2 = .67 \] was explained by significantly greater N2 mean amplitudes at Fz than at Cz and Pz (both \( p < .001 \)). As the N2 was maximal at Fz, the mean amplitude of the
N2 at this location was analysed using a mixed design 2 (time: T1; T2) x 3 (condition: congruent; incongruent; reversed) x 2 (group: Younger; Older) ANOVA model. The location
of maximal amplitude of the P3b was also investigated using a 2 (time: T1; T2) x 3
(condition: congruent; incongruent; reversed) x 3 (location: Fz, Cz, Pz) x 2 (group: Younger; Older) ANOVA model. A main effect of location \[ F (2, 236) = 190.54, p < .001, \eta^2 = .62 \] was explained by a significantly greater P3b mean amplitude at Cz and Pz compared to Fz (both \( p < .001 \)). As there were no significant differences in the mean amplitude of the P3b at Cz and
Pz, the amplitude of the P3b was analysed with 2 (time: T1; T2) x 3 (condition: condition:
congruent; incongruent; reversed) x 2 (location: Cz, Pz) x 2 (group: Younger; Older)
ANOVA model. When the assumption of sphericity was violated, the Greenhouse-Geisser adjustment to the degrees of freedom was applied. Bonferroni correction was used to adjust for multiple comparisons.

The accuracy data were not normally distributed and were log transformed. However, the log transformations did not result in normal distributions. The accuracy data were negatively skewed as performance was >80% (see Table 1). As such, the accuracy data were analysed using non-parametric statistics. Group differences in accuracy in each condition at T1 and T2 were examined using Mann Witney U tests. Accuracy differences between the conditions were explored using Friedman tests separately for T1 and T2. The potential effects of time were examined using Wilcoxon tests. Alpha values were adjusted to correct for multiple comparisons. Behavioural responses made <100ms after stimulus presentation or >3 SD above the individual’s mean were excluded from the analysis. The correct RT data were also not normally distributed and were, therefore, also log transformed. The log transformations resulted in normal distributions and the transformed correct RT data were analysed using a mixed design 2 (time: T1; T2) x 3 (condition: congruent; incongruent; reversed) x 2 (group: Younger; Older) ANOVA model.

3. Results

3.1. Behavioural Data: Accuracy and Correct RT

The only significant difference between the groups with regard to accuracy was at T1 for the incongruent condition ($p = .022$; see Table 1). However, after correcting for multiple comparisons ($0.05/6 = .008$), this difference was no longer significant. As accuracy did not differ between the groups, the age groups were combined to examine the effects of time and condition. The Friedman tests for accuracy at T1 and T2 were both significant (both $p < .001$).
There was a decrease in accuracy with conflict at both time points (congruent > incongruent > reversed; all \( p < .001 \)). The Wilcoxon tests indicated that there were significant improvements in accuracy in the congruent and incongruent conditions with time (\( p < .001 \); \( p = .001 \), respectively). In contrast, accuracy in the reversed condition did not significantly differ between T1 and T2. Therefore, the expected performance improvements with time were only found for congruent and incongruent conditions. In contrast to our expectations, performance did not significantly differ between the age groups.

As can be seen in Table 1, significant main effects of time, condition and group were found with correct RT [\( F(1, 118) = 327.93, p < .001, \eta^2 = .74; F(2, 236) = 303.15, p < .001, \eta^2 = .72; F(1, 118) = 42.05, p < .001, \eta^2 = .26 \), respectively]. The main effects of time and group indicated that correct RT differed between the age groups, in that younger children had longer correct RT, and that correct RT was shorter over time, in line with expectations. Bonferroni corrected post-hoc examination of the condition effect revealed an increase in correct RT with conflict (congruent < incongruent < reversed; all \( p < .001 \)).

A significant interaction between time and condition was also found [\( F(2, 236) = 13.81, p < .001, \eta^2 = .11 \)]. This interaction was explained by different patterns of condition effects at T1 and at T2. At T1, there were significant differences in correct RT between congruent and incongruent conditions, and congruent and reversed conditions (both \( p < .001 \)), with increased correct RT in the conflict conditions. However, there were no significant differences between the incongruent and reversed conditions, indicating that correct RT did not differ between these conditions at T1. At T2, there were significant differences between each of the conditions; bonferroni corrected post-hoc examination of the condition effect revealed an increase in correct RT with conflict (congruent < incongruent < reversed; all \( p < .001 \)).
Table 1.
Accuracy and response times for the experimental conditions within the modified flanker task for each group at T1 and T2.

<table>
<thead>
<tr>
<th></th>
<th>Younger (n = 73)</th>
<th>Older (n = 47)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Time 1</td>
<td>Time 2</td>
</tr>
<tr>
<td>Correct (%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Congruent</td>
<td>90.3 (9.0)</td>
<td>93.7 (6.6)</td>
</tr>
<tr>
<td>Incongruent</td>
<td>86.4 (13.8)</td>
<td>89.7 (9.6)</td>
</tr>
<tr>
<td>Reversed</td>
<td>83.0 (15.9)</td>
<td>86.4 (12.5)</td>
</tr>
<tr>
<td>Correct RT (ms)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Congruent</td>
<td>943.3 (302.0)</td>
<td>650.1 (159.7)</td>
</tr>
<tr>
<td>Incongruent</td>
<td>1090.5 (364.0)</td>
<td>735.9 (197.2)</td>
</tr>
<tr>
<td>Reversed</td>
<td>1056.2 (383.0)</td>
<td>784.7 (137.2)</td>
</tr>
</tbody>
</table>

Note. Median (IQR).

3.2. N2 Component

As shown in figure 1, there were main effects of time \(F(1, 118) = 53.55, p < .001, \eta^2 = .31\], group \(F(1, 118) = 3.98, p = .048, \eta^2 = .03\] and condition \(F(2, 236) = 101.52, p < .001, \eta^2 = .46\]. The main effect of time on the N2 indicated that amplitude decreased during the two-year T2 period. The main effect of group indicated that the younger group had
significantly greater negative N2 amplitude than the older groups at both time points. Bonferroni corrected post-hoc examination of the condition effect revealed an increase in the negativity of the N2 with conflict (congruent < incongruent < reversed). These significant main effects are in line with predictions.

An interaction between time and condition \([F(2, 236) = 3.33, p = .038, \eta^2 = .03]\) indicated different patterns of N2 amplitude between the conditions at T1 and at T2. At T1, post-hoc examination of the condition effect \([F(2, 236) = 61.11, p < .001, \eta^2 = .34]\) revealed that the reversed condition elicited a significantly more negative N2 amplitude than the congruent and incongruent conditions (both \(p < .001\)), whilst there were no significant differences between the congruent and incongruent conditions. At T2, the main effect of condition \([F(2, 236) = 60.78, p < .001, \eta^2 = .34]\) revealed an increase in amplitude with conflict (congruent < incongruent < reversed; all \(p < .001\)) reported in the main effect.
Figure 1. Grand group averages for the congruent, incongruent and reversed waveforms in each group of children at T1 at T2 at Fz. The shaded area indicates the time window used to calculate the mean amplitude of the N2 component.
3.3. P3b Component

Main effects of time, condition and group were found on the mean amplitude of the P3b \([F (1, 118) = 6.31, p = .013, \eta^2 = .05; F (2, 236) = 113.44, p < .001, \eta^2 = .49; F (1, 118) = 4.57, p = .035, \eta^2 = .04\), respectively; see Figure 2]. Bonferroni corrected examination of the main effect of condition indicated an increase in mean P3b amplitude with conflict (congruent < incongruent < reversed; all \(p < .001\)), as expected.

The time by group interaction \([F (1, 118) = 11.89, p = .001, \eta^2 = .09\] superseded the main effects of time and group; there was a significant increase in the P3b amplitude in the younger group over time \([F (1, 72) = 19.69, p < .001, \eta^2 = .22]\), however, the P3b amplitude did not significantly differ in the older group between T1 and T2. Interactions between condition and time, and between condition and location were also found \([F (2, 236) = 7.06, p = .002, \eta^2 = .06; F (2, 236) = 28.37, p < .001, \eta^2 = .19\], respectively]. In order to examine these interactions, each condition was considered separately. There were no significant differences over time or between Cz and Pz in the amplitude of the P3b in the congruent condition. For the incongruent condition, the P3b amplitude did not differ significantly between Cz and Pz, however, there was a trend suggestive of an increase over time \([F (1, 118) = 3.75, p = .055, \eta^2 = .03]\). The mean amplitude of the P3b in the reversed condition was maximal at Pz \([F (1, 118) = 4.96, p = .028, \eta^2 = .04]\) and also significantly increased over time \([F (1, 118) = 11.39, p = .001, \eta^2 = .09]\).
Figure 2. Grand group averages for the congruent, incongruent and reversed waveforms in each group of children at T1 at T2 at Pz. The shaded area indicates the time window used to calculate the mean amplitude of the P3b component.
4. Discussion

The current study investigated developmental trajectories of interference suppression and reversal in order to contribute to further understanding the development of inhibition and switching during the period of 7-11 years in childhood. We predicted that interference suppression and reversal abilities would be improved by age and with time. However, there were no significant age-group differences in accuracy, and whilst interference suppression improved over time, switching accuracy did not significantly change between 7-11 years. We also predicted that behavioural performance would become more efficient, as indexed by correct RT, with age and over time, and this was indeed found for all experimental conditions. As expected, the amplitude of the N2 was reduced with age and with time, suggesting less reliance on conflict monitoring to signal cognitive control to manage stimulus and response conflict from 7-11 years. Additionally, and in line with predictions, both N2 and P3b amplitudes were sensitive to different types of conflict. However, N2 amplitude only differentiated between each condition at T2. At T1, there were no significant N2 amplitude differences between congruent and incongruent conditions. Taken together, these data indicated different developmental trajectories of specific processes unique to inhibition and switching across the childhood period of 7-11 years. Furthermore, the patterns of results for these specific cognitive processes and neural correlates indicate a complex relationship between cognitive and neural development.

There was a significant decrease in accuracy with conflict at both T1 and T2 indicating that children found interference suppression and reversal more challenging than the congruent condition. The high degree of accuracy indicated that even children as young as 7 years had developed specific processes unique to inhibition and switching. Interference
suppression improved over time, indicating that inhibition continues to develop between 7-11 years (cf. Cragg, 2016). In contrast, switching did not significantly change over time, indicating that maturation and experience did not improve the ability to manage an unexpected rule change involving stop and switch processes. However, it is not known whether these specific abilities were at adult levels. There were numerical similarities in accuracy in the reversed condition between the current study (82.8-86.4%) and van Veen and Carter (2002) who reported accuracy of 81.5% in the comparable response-incongruent condition in adults. However, trial timings and stimuli differed between the studies; it is not known whether the letter stimuli in van Veen and Carter (2002) had an impact on performance due to the different processing demands of orthographic stimuli. The current study also included feedback which may have influenced performance and motivation. Nonetheless, this study is consistent with previous findings of different developmental trajectories of inhibition and switching during this period of childhood (Davidson et al., 2006).

Correct RT represents the time taken to evaluate a stimulus, prepare and execute a response. A significant difference in correct RT between congruent and incongruent conditions is a consistent finding in adults (Correa et al., 2009; Kopp et al., 1996; Clayson & Larson, 2011; van Veen & Carter, 2002), adolescents and children (Checa et al., 2014; Ladouceur et al., 2004, 2007; Pontifex et al., 2011; Rueda et al., 2004; Rueda, Posner et al., 2004). The increase in RT in the incongruent condition indicates that suppressing attention to irrelevant flankers increases stimulus evaluation time (cf. van Veen & Carter, 2002). There was a further significant increase in RT with reversal, consistent with previous studies with adults (van Veen & Carter, 2002) and children over 10 years (Pontifex et al., 2011). The increase in RT indicates that there are additional cognitive demands inherent in the reversed condition, namely, inhibiting a prepotent response and switching the S-R mapping. Of most
interest, were the findings that correct RT reduced with both age and time, indicating that performance became more efficient across this period of childhood. The improvements in RT could be explained by the increasing acquisition and implementation of rules, skills and strategies to support behavioural performance, such as the ability to inhibit task irrelevant processing (Dempster, 1993). The decrease in RT could also be influenced by age-related improvements in fine motor skills and neural maturation. White matter integrity in frontal and frontal-parietal regions was linked with improvements in processing speed in children and adolescents (Mabbott et al., 2006). Furthermore, maturation of the cortico-spinal tract in the left hemisphere and inferior fronto-occipital fasciculus in the right hemisphere were found to uniquely contribute to reaction time in right-handed children aged 4-13 years (Scantlebury et al., 2014).

The amplitude of the N2 was modulated by conflict at both T1 and T2, with switching eliciting the most negative conflict-monitoring signal, indicating that conflict detection was greatest for unexpected response conflict. At T1, the N2 did not differentiate between congruent and incongruent conditions, indicating that the conflict inherent in interference suppression did not elicit a significantly increased N2 compared to the N2 in the congruent condition. Whilst the lack of a N2 congruency effect is not unprecedented (Ladouceur et al., 2004; Rueda et al., 2004; van Veen & Carter, 2002), the inclusion of a reversed condition may have influenced the processing of incongruent stimuli due to the additional demands of switching in comparison to interference suppression. The N2 congruency effect may also be influenced by modifications of the flanker task, probability of the incongruent condition, trial sequences and inclusion of cues (Clayson & Larson, 2011; Correa et al., 2009; Kopp et al., 1996). In contrast to T1, the N2 differentiated between each of the conditions at T2 indicating that the N2 became more sensitive to types of conflict with experience and maturation. However, these condition effects occurred with age-related amplitude reductions, which
indicated less reliance on conflict monitoring to signal cognitive control from 7-11 years. These amplitude reductions may indicate a shift in the contribution of the conflict-monitoring signal from the ACC to trigger cognitive control processes to more task-related activation of regions linked with formulation of task relevant mental representations and goal-directed motor processes.

The reduction in N2 amplitude with age is consistent with the Nogo-N2 amplitude reductions found with increasing age during childhood and adolescence (Hämmerer et al., 2010; Johnstone et al., 2007; Jonkman, 2006; Lamm et al., 2006). Whilst there are similarities in the findings between these studies, they cannot be directly compared due to the use of different paradigms to elicit the N2 components (Larson et al., 2014), different preprocessing methods and different time windows for identifying the N2s. A range of time windows have been employed (e.g. 200-350ms: Hämmerer et al., 2010; 320–360ms: Jonkman, 2006; 200-450ms: Lamm et al., 2006). These different latency ranges may reflect the different cognitive demands inherent in each paradigm and emphasises the longer latency of ERP components in children compared to adults.

The amplitude of the P3b was sensitive to conflict at both T1 and T2 indicating that interference suppression and reversal elicited different degrees of attentional resources to updating mental representations of stimuli in children aged 7-11 years. Interference suppression requires top-down attentional control to resist interference from irrelevant features of the incongruent stimuli. This type of attentional processing is more analogous to the P3a than the P3b, as the P3a is associated with focused attention during stimulus evaluation, whereas the P3b is linked with allocation of attention and subsequent memory processing (Polich, 2007). However, the P3a is typically differentiated from the P3b with an oddball paradigm, in which non-task-related high frequency stimuli are interspersed with low frequency target stimuli. The P3a also differs from the P3b in topography and timing (Picton,
Modulation of the P3b with interference suppression and reversal indicated that there was evaluation of stimulus features in working memory in both conditions, regardless of whether top-down attentional control was necessary for interference suppression. Previous work has also found a significant increase in P3b amplitude with response incompatible conditions (Frühholz et al., 2011; Pontifex et al., 2011) and reduced stimulus probability (Melara et al., 2008). The increase of P3b amplitude with response conflict suggests that switching elicits greater evaluation of stimulus features in working memory, which may be held active longer in order to activate the correct response in long term memory (Frühholz et al., 2011).

There are inconsistent findings about the development of the P3b when children and adults are compared (e.g. Jonkman, 2006; Rueda, Posner et al., 2004) and there is a paucity of data about the P3b elicited during flanker tasks in children. We found an increase in P3b amplitude in the younger group. However, P3b amplitude did not significantly change in the older group with time. These results indicated that the greatest age-related change in P3b amplitude was between 7-9 years, suggesting that, regardless of experimental condition, greater attention was allocated to processing stimuli with experience and maturation. There was also a trend that the P3b amplitude increased in the incongruent condition, and was significantly increased in the reversed condition with time. These amplitude increases indicated a developmental change in that more attention was allocated to updating mental representations of conflict-related stimuli with experience and maturation.

There has been little longitudinal investigation of the specific processes unique to inhibition and switching using a modified flanker paradigm incorporating stimulus and response conflict manipulations in children aged 7-11 years. The current study found a differentiation between interference suppression and switching S-R mappings, specific processes unique to inhibition and switching, respectively, in children aged 7-11 years.
Previous structural equation modelling of Project K.I.D.S. data found that inhibition and shifting were indistinguishable at 10 years (Brydges et al., 2014a), which indicated that these latent variables did not differentiate at this age, possibly due to the age groups being amalgamated at T2 and/or specific processes had not developed sufficiently to differentiate the inhibition and shifting latent variables. The current study only investigated development of two specific processes rather than all of the specific processes subsumed under inhibition and shifting. Previous work has identified the anti-saccade task as an optimal measure of inhibition (Friedman & Miyake, 2004; Michel & Anderson, 2009), and it is possible that different specific processes unique to inhibition and switching may have different developmental trajectories to the ones reported here. It is also problematic to directly compare results from this study with structural equation models (e.g. Brydges et al., 2014a; Brydges et al., 2014b). The modified flanker task in this study was designed to specifically manipulate interference and switching within a single task and statistical analyses focused on age and time differences. In contrast, modelling requires specification of relationships between variables, tests those relationships and allows for measurement of latent variables, which are free of measurement error and are ‘pure’ rather than observed measures of constructs.

This study provided an opportunity to examine relationships between neural and cognitive development between 7-11 years. The current study found different patterns of change over time for behavioural and neural measures which argue against the view that neural and cognitive development occur in parallel. There was some evidence suggesting that neural development may precede cognitive development, in that the N2 amplitude reduction with age and maturation has been interpreted as indicating cognitive development (e.g. Jonkman, 2006; Lamm et al., 2006). The reduction in the N2 could also indicate maturation of the ventrolateral PFC (vIPFC) and dIPFC, thus providing the neural architecture to support
development of cognitive control processes. The P3b showed some amplitude increases over time, which argued against a global reduction in ERP component amplitudes with experience and maturation across this period of childhood. In addition, improvements in correct RT with age and time may be facilitated and preceded by white matter maturation. However, electrophysiological activity cannot inform on grey and white matter structure or function. Furthermore, as there were only two measurements points in the study, it is not possible to distinguish if neural development preceded cognitive development, rather the study indicated that there were some changes in neural and cognitive measures between T1 and T2. There are also methodological issues in the current study that have the potential to influence the amplitude and morphology of the ERP components, such as a lack of jittering of the inter-stimulus interval and jittering of the inter-trial interval. It is also possible that processing of the feedback could carry-over into the next trial, due to the short interval between feedback presentation and the commencement of the next trial.

Understanding the development of EFs during childhood is not only of theoretical importance, but has practical application. Executive functioning in childhood has been linked with school readiness and academic achievement (Duncan et al., 2007; Gathercole et al., 2004). Importantly, cognitive training can lead to improvements in executive functioning and early intervention in childhood may help reduce achievement gaps within cohorts (Diamond & Lee, 2011). The current study has provided evidence of differential developmental trajectories of inhibition and switching and some separation of cognitive and neural development across this period of childhood. This study has provided a unique longitudinal investigation of interference suppression and switching, providing further empirical evidence that 7-11 years is a critical period for cognitive development.
A supplementary analysis using the time window 250-350ms for the N2 component was conducted (see supplementary analysis). This analysis found that N2 amplitude was significantly reduced at T2 in the older group only, suggesting less reliance on conflict monitoring to signal cognitive control to manage stimulus and response conflict from 9 years. A main effect of condition supported the finding reported above that the reversed condition elicited the most negative N2 amplitude. In addition, a three-way interaction was found and indicated a differentiation between the experimental conditions at T2, but differed between the groups; significant N2 amplitude differences were found between the congruent and reversed conditions in both groups. However, N2 amplitude only differed between congruent and incongruent conditions in the older group at T2. This interaction supported the conclusions detailed above that the N2 became more sensitive to types of conflict with experience and maturation.

Acknowledgements

This research was supported by an Australian Research Council discovery grant DP0665616 awarded to M.A., A.M.F., C.L.R, and Professor Dorothy V. M. Bishop. We wish to thank Aoibheann O’Brien and Catherine Campbell for their help with coordination of Project K.I.D.S.

References


doi:10.1016/j.tics.2004.10.003


doi:10.1016/j.intell.2012.05.006


doi:10.3389/fpsyg.2014.00326


Diamond, A. (2002). Normal Development of Prefrontal Cortex from Birth to Young


Development of inhibition and switching: a longitudinal study of the maturation of interference suppression and reversal processes during childhood

Supplementary Analysis

An analysis using a time window of 250-350 ms for the N2 (cf. Groom & Cragg, 2015) was conducted to address the potential concern that the identification of the time windows for the N2 ERP component was confounded by unequal group sizes. Despite unequal group sizes, there were no significant differences between the groups in the number of trials contributing to the grand group averages for each condition at each time point. A main effect of condition was found \[ F(2, 236) = 3.54, p = .031, \eta^2 = .03 \]. Bonferroni corrected post-hoc examination of the condition effect revealed an increase in the negativity of the N2 with response conflict (reversed > congruent). A time by group interaction \[ F(1, 118) = 9.70, p = .002, \eta^2 = .08 \] indicated different patterns of change in N2 amplitude over time between the groups. In the younger group, N2 amplitude did not significantly differ between T1 and T2 \[ F(1, 72) = 3.30, p = .073, \eta^2 = .04 \]. In contrast, there was a significant reduction in N2 amplitude with time in the older group \[ F(1, 46) = 8.65, p = .005, \eta^2 = .16 \]. A three-way interaction was also found \[ F(2, 236) = 5.80, p = .003, \eta^2 = .05 \]. In order to investigate the three-way interaction, the groups were considered separately. Time by condition interactions were found for each group \[ F(2, 144) = 8.80, p < .001, \eta^2 = .11; F(2, 92) = 8.33, p < .001, \eta^2 = .15; \] younger and older groups, respectively]. Post hoc analyses found that the N2 amplitude did not significantly differ between the conditions at T1 in the younger group and only differed between congruent and incongruent conditions at T1 in the older group \( p = .007; \) congruent < incongruent). At T2, there were significant differences in N2 amplitude between the conditions in the younger group \( p < .001; p = .007; \) congruent < reversed and incongruent <
reversed, respectively) and in the older group ($p = .046; p = .008$; congruent < incongruent and congruent < reversed, respectively).