Development of behavioral control: Analysis of performance and motor-related brain potentials
Radovčić-van de Laar, M.C.

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CHAPTER 5

Development of response activation and inhibition in a selective stop-signal task

Abstract

To gain more insight into the development of action control, the current ERP study examined response activation and inhibition during stop-signal processing. Two child groups (8 and 12 years) and one adult group (21 years) performed on two tasks: a choice RT task that required a left- vs. right-hand response to go signals, and a selective stop task that presented go trials, valid stop-signal trials (requiring response inhibition) and invalid stop-signal trials (requiring response execution while ignoring the stop signal). The behavioral results revealed that children delayed their go response more than adults, suggesting the use of a compensatory strategy to increase inhibitory success. The latency of selective response inhibition decreased with advancing age. Analysis of response-related motor potentials revealed that children were less able to suppress cortical motor outflow resulting in increased partial inhibition and partial error rates. On invalid stop trials, responses were initially activated, subsequently inhibited, and then reactivated. Children were less efficient in implementing this ‘global stop-reactivation’ strategy. Analysis of contralateral and ipsilateral motor-related potentials indicated that older children are “response prone”; that is, they recruit motor responses to a greater extent than younger children or adults do. The current findings indicate that the dynamic interplay between response selection, activation and inhibition follows a protracted developmental course.
Introduction

The ability to interrupt and adjust actions in response to environmental changes is a key prerequisite of goal-directed behavior. Response inhibition is an act of cognitive control that prevents the execution of unwanted overt actions (Logan, 1994). Factors that influence individual stopping latency have been widely investigated using the stop-signal paradigm (Logan & Cowan, 1984; Verbruggen & Logan, 2008). In this task, participants respond to frequently presented go signals, typically two visual choice stimuli. For example, participants are instructed to execute a fast button-press response with the right-index finger when the letter ‘O’ is presented and a left-index finger response to an ‘X’ stimulus, while maintaining high levels of accuracy. In addition, they should withhold the go response upon an occasionally presented stop signal, usually a tone that shortly follows after the onset of the go signal with a variable delay (i.e., stop-signal delay). Inhibition of the ongoing response is more likely to succeed when stop-signal delay is relatively short and more likely to fail when stop-signal delay is long. Within the context of a formal race model (Logan & Cowan, 1984), stopping behavior can be conceptualized as the outcome of a race between go and stop processes that run independently. The race model allows for the computation of stop-signal reaction time (or SSRT), which provides an index of individual stopping proficiency.

Classical versions of the stop-signal paradigm require processing of only one stop signal, referred to as ‘global stopping’. In daily life however, environmental demands related to inhibitory control are often more complex. To study more fine-grained manifestations of inhibitory control, some studies implemented the so-called ‘selective stop-signal task’. In the selective stop-signal paradigm, a stop signal can be either valid, indicating the inhibition of the activated response, or invalid, indicating that the stop signal can be ignored (Bedard, Nichols, Barbosa, Schachar, Logan, & Tannock, 2002; van de Laar, van den Wildenberg, van Boxtel, & van der Molen, 2010). Typically, selective SSRT (i.e., the time it takes to conditionally stop a particular response) is substantially longer than global SSRT (i.e., the time it takes to unconditionally inhibit all responses, e.g., Logan, Cowan, & Davis, 1984; van den Wildenberg, van Boxtel, & van der Molen, 2003; Verbruggen & Logan, 2008).

Over the years, the stop-signal paradigm has been applied successfully to study developmental changes in inhibitory processing. A consistent finding in the developmental literature is that global SSRT decreases from childhood to early adolescence and from adolescence to early adulthood (e.g., Band, van der Molen, Overtoom, & Verbaten, 2000; Ridderinkhof, Band, & Logan, 1999; van den Wildenberg & van der Molen, 2004b; Williams, Ponesse, Schachar, Logan, & Tannock, 1999). The few studies that examined the development
of selective stopping showed that, like global SSRT, selective SSRT decreases with advancing age up to young adulthood (Bedard et al., 2002; van de Laar, van den Wildenberg, van Bostel, & van der Molen, 2011; van den Wildenberg & van der Molen, 2004b). Importantly, a more pronounced decrease was observed for global SSRT compared to selective SSRT during childhood, indicating that global and selective inhibition follow distinct developmental trajectories (van de Laar et al., 2011; van den Wildenberg & van der Molen, 2004b).

The main goal of the current study is to extend these behavioral findings by examining physiological correlates of the development of response activation and inhibition during selective stopping. Event-related potentials (ERPs) may provide more insight into the neuro-physiological underpinnings of the observed differences in stopping abilities between age groups. To date, only two studies examined the development of global inhibitory proficiency using the N200 and P300. These two ERP components, appearing respectively 200 ms and 300 ms after stop-signal onset, have been frequently used to investigate stop-signal processing in the adult population (e.g., Dimoska & Johnstone, 2006; Ramautar, Kok, & Ridderinkhof, 2004; van Boxtel, van der Molen, Jennings, & Brunia, 2001). Johnstone, Dimoska, Smith, Barry, Pleffer, et al. (2007) found that global SSRT and the associated latency and amplitude of the N200 and P300 did not change from 7- to 11-year old children. Dimoska, Johnstone, Chiswick, Barry, and Clarke (2007) reported that both the latency of responding to go stimuli (go RT) and global SSRT decreased from 11-year-olds to young adults. In addition, they reported a developmental reduction of the amplitude of the inhibition-related N200 and P300 components. The reduction in amplitudes was largest at frontal sites and was interpreted to reflect a generalized developmental effect on excitatory and inhibitory processes in frontal brain regions (Dimoska et al., 2007), which is consistent with the notion of a protracted maturation of prefrontal brain regions (Giedd, 2004; Nelson & Guyer, 2011; for a review see Casey, Tottenham, Liston, & Durston, 2005).

The two developmental stop-ERP studies reported above focused primarily on processing of the stop signal. In the current study we aim to provide more insight into the development of response selection, activation and inhibition by using response-related electrophysiological indices recorded over the primary motor cortex (M1). Electrophysiological examinations of the primary motor cortex (M1) often use the Lateralized Readiness Potential (LRP) as an electrocortical measure of preferential response activation (Gratton, Coles, Sirevaag, Eriksen, & Donchin 1988). There is a handful of stop-signal studies, investigating the adult population, showing that LRP amplitude is considerably reduced on successfully inhibited trials compared to trials on which response inhibition failed (de Jong, Coles, & Logan, 1995; de
Development of Response Activation and Inhibition

Jong, Coles, Logan, & Gratton, 1990; van Boxtel et al., 2001). De Jong et al. (1995) concluded, on the basis of LRP data, that the response can be inhibited even after the central motor command and therefore distinguished between centrally and peripherally operating inhibition mechanisms. Findings reported by van Boxtel et al. (2001), however, are not consistent with the notion of two inhibition mechanisms. They compared failed vs. partial inhibition trials; the former are stop-signal trials on which participants were not able to inhibit their response to the go signal and the latter are trials on which participants initially activated the response to the go signal, as indexed by subthreshold muscle activity recorded from the signaled hand, but still succeeded in stopping their motor response. Van Boxtel et al. (2001) observed that failed and partial inhibits differed only gradually; that is, partial inhibits were characterized by reduced and shorter above threshold LRPs compared to failed inhibits suggesting a shared inhibitory mechanism, presumably operating centrally at M1 (see also review of Band & van Boxtel, 1999). In addition, more recent cognitive neuroscience studies support the conjecture that M1 is a candidate region for the actual implementation of response inhibition upon a stop signal (Coxon, Stinear, & Byblow, 2006; Swann, Tandon, Canolty, Ellmore, McEvoy, et al., 2009; van den Wildenberg, Burle, Vidal, van der Molen, Ridderinkhof, & Hasbroucq, 2010).

Although LRP studies show that this measure may provide useful information regarding motor-related cortical processing, it should be noted that the LRP is a difference wave that does not distinguish between the relative contributions of the left and right motor cortex to the activation process. In contrast, Laplacian transformed ERPs (Law, Nunez, & Wijesinghe, 1993; Srinivasan, Nunez, Tucker, Silberstein, & Cadusch, 1996) may dissociate motor-related activity of the two hemispheres (Praamstra & Seiss, 2005; Tandonnet, Burle, Hasbroucq, & Vidal, 2005; Taniguchi, Burle, Vidal, & Bonnet, 2001). Another advantage of the Laplace transform is the enhanced spatial resolution reducing the contributions from remote sources and the blurring effect of the skull (Babiloni, Carducci, Babiloni, & Urbano, 1998; Nunez, 1981; Nunez, Silberstein, Cadusch, Wijesinghe, Westdorp, & Srinivasan, 1994). Vidal, Grapperon, Bonnet, and Hasbroucq (2003) observed a phasic negative Laplacian potential recorded over M1 contralateral to the hand that executed a choice response. The negative wave likely reflects the activation of the contralateral motor cortex. Furthermore, the onset of the contralateral negative wave was preceded by the onset of a positive Laplacian potential over the ipsilateral M1, presumably reflecting the suppression of the ipsilateral motor cortex associated with prevention of incorrect activation of the incorrect hand (see also Burle, Vidal, Tandonnet, & Hasbroucq, 2004; Meckler, Allain, Carbonnell, Hasbroucq, Burle, & Vidal, 2010).
In a previous study, we examined the pattern of contralateral negative and ipsilateral positive Laplacian activation in relation to developmental changes in choice RT (van de Laar, van den Wildenberg, van Boxtel, Huizenga, & van der Molen, 2012). In order to investigate whether stimulus- or response-related stages of information processing are subject to age-related changes in response speed, we partitioned the choice process into several processing stages, including a pre-selection time (i.e., from stimulus onset to the onset of the contralateral negative wave), pre-motor time (i.e., the time between the onset of the negative wave and EMG onset), and motor time (i.e., duration of EMG onset until overt response). Latency analyses of stages revealed that pre-selection time, and most prominently, pre-motor time and motor time decreased with age. ERP analysis revealed that the positive wave recorded over ipsilateral M1 was evident in young adults only. The absence of this positive wave in both child groups was linked to the disproportionally large number of choice errors in children compared to young adults. This finding indicates that immature cortical motor inhibition systems contribute to the suboptimal action control in children.

The primary aim of the current study is to extend these findings by directly addressing developmental changes in the temporal dynamics of response activation and inhibition at the level of M1 associated with selective stopping. More specifically, we wanted to assess how response selection and activation are altered by occasionally presented stop signals instructing to stop either the left vs. right hand activated by the binary go signal. Three age groups participated in the current study: A young child group of 8-year-olds, an older child group of 12-year-olds and a young adult group of 21-year-olds. Additionally, a choice RT task was administered that required responding to left- and right-pointing arrows with the corresponding left and right hand. The selective stop-signal task involved responding to similar arrows with the additional requirement to inhibit upon one out of two stop signals (i.e., valid stop-signals) and to execute the go response when the other stop signal occurred (i.e., invalid stop-signals that could be ignored, see also van de Laar et al., 2010). Indices of inhibitory control are selective SSRTs and the proportion of partially inhibited responses. Central motor activation was assessed by the Laplacian transformation of response-related potentials, whereas peripheral motor processes were assessed using EMG. Like in our previous study (van de Laar et al., 2012), we examined motor time and pre-motor time, as well as activation levels (reflected by amplitudes) of peripheral and central motor processes during response execution. To study the effect of stop-signal processing on response activation, we directly compared: 1) responses on go trials in the selective stop task versus go responses in the choice RT task, 2) responses on valid stop-signal trials (failed inhibits) versus responses on go trials in the selective stop task, and 3) responses on
invalid stop-signal trials versus responses on go trials in the selective stop task. In a previous study, we observed a considerable delay in responding on invalid stop-signal trials (van de Laar et al., 2010). This delay was interpreted to reflect the initial inhibition of the go response (global stopping) followed by reactivation of the appropriate go response after classifying the stop signal as invalid. According to the race model (Logan & Cowan, 1984), fast responses on invalid stop-signal trials are likely to reflect processing of the go signal only, whereas slow invalid stop responses involve both the processing of the go signal and the processing of the invalid stop-signal. Therefore, we also compared fast vs. slow responses on invalid stop-signal trials with that of go trials. The analysis of performance associated with invalid stop-signal processing might reveal whether age groups differ in the deployment of a global vis-à-vis selective stopping strategy.

Predictions

Our predictions were threefold. First, it was predicted that all age groups would delay the response to go trials when stop signals are inserted and that the delay would be more pronounced in children (van de Laar et al., 2011; van den Wildenberg & van der Molen, 2004b) (comparison 1). This strategic delay has been interpreted in terms of proactive response adjustment to increase the chance of successful inhibition to stop signals (e.g., Verbruggen & Logan, 2009). Based on recent findings, we predict that the response adjustment is associated with a decrease in response-related potentials (reflected by amplitudes) in young adults (Cai, Oldenkamp, & Aron, 2011; Claffey, Sheldon, Stinear, Verbruggen, & Aron, 2010), an effect that remains to be determined in children.

Secondly, based on the independent race model (Logan & Cowan, 1984), we predicted that failed inhibit responses are faster than go responses (comparison 2). It is anticipated that each of the three age groups will reveal this pattern (van de Laar et al., 2011; van den Wildenberg & van der Molen, 2004b). Typically, fast go responses are associated with larger response-related potentials that have a shorter duration compared to those associated with slow go responses (see also Botwinick & Thompson, 1966; Osman, Moore, & Ulrich, 1995; Tandonnet, Burle, Vidal, & Hashbroucq, 2003; Vidal, Burle, Grapperon, & Hashbroucq, 2011). Thus, if failed inhibited responses escaped inhibition, we expect failed inhibition trials to be associated with shorter motor and pre-motor times and with higher EMG and contralateral negative amplitudes than that of go trials.

Thirdly, we predicted a delay in the speed of responding on invalid stop-signal trials compared to go trials in all age groups, but most prominently in children (see Band et al., 2000)
(comparison 3). We expect an increase in latency and a decrease in amplitude of response-related potentials associated with invalid stop compared to go trials, and with slow invalid compared to fast invalid stop-signal trials. This pattern remains to be determined in children.

Finally, we predicted an ipsilateral positive potential to precede the contralateral negative potential associated with the response to the go signal. The ipsilateral positive Laplacian potential has been interpreted in terms of inhibition of the competing response (e.g., Meckler et al., 2010; Vidal et al., 2003). Based on our previous findings (van de Laar et al., 2012), we predict that the ipsilateral positive wave is absent in young children; a result that is indicative of suboptimal action control.

Method

Participants

A total of 57 participants across three age groups participated, consisting of 19 young children (8 female, M = 7.7 years, SD = .51), 20 older children (7 female, M = 11.9 years, SD = 1.24), and 18 young adults (10 female, M = 20.7 years, SD = 2.99). The data of three young children, three older children and one adult were discarded because of unreliable scoring of EMG onsets or an excessive amount of EEG artifacts (EMG or EEG signals were too noisy). Details of the remaining 50 participants are presented in Table 1. Children were recruited from local elementary schools and received a small present for their participation. Adults were university students who received course credits for their participation. All participants had normal or corrected-to-normal vision. Informed consent was obtained prior to testing and the experimental procedure was approved by the local Ethics Committee. Children completed the Standard Progressive Matrices (SPM; Raven, Court, & Raven, 1985) to obtain a general index of fluid intelligence, whereas the Advanced Progressive Matrices (APM, Raven, Raven, & Court, 1993) was administered to adults.
Demographic data per age group. \( n \) refers to number of participants. Mean age in years (standard deviations between parentheses).

<table>
<thead>
<tr>
<th>Age group</th>
<th>( n )</th>
<th>Age (years) Mean (SD)</th>
<th>Gender (female/male)*</th>
<th>Preferred hand (right/left)</th>
<th>Raven progressive matrices score**</th>
</tr>
</thead>
<tbody>
<tr>
<td>Young children</td>
<td>16</td>
<td>7.79 (0.5)</td>
<td>8/8</td>
<td>15/1</td>
<td>83.6 (24.5)</td>
</tr>
<tr>
<td>Older children</td>
<td>17</td>
<td>11.78 (1.2)</td>
<td>5/12</td>
<td>17/0</td>
<td>79.3 (19.4)</td>
</tr>
<tr>
<td>Adults</td>
<td>17</td>
<td>20.7 (3.1)</td>
<td>10/7</td>
<td>17/0</td>
<td>86.9 (5.7)</td>
</tr>
</tbody>
</table>

*Gender distributions did not differ between groups, \( \chi^2 = 3.11, p = .21 \).
**Groups did not differ in Raven score, \( F < 1 \).

Tasks and stimuli

Participants were seated in a dimly lit, sound-attenuating room facing a computer screen (17-in monitor, 60 Hz refresh rate) at a distance of about 100 cm. Stimuli were presented centrally on a dark-grey monitor background and were controlled by Presentation software (www.neurobs.com). Responses were collected from two individually placed zero-displacement force transducers (Honeywell, model FS03) attached at the end of the arm supports. The transducers recorded downward thumb movements in a continuous polling loop after which the voltage signal was A/D converted online (Keithley, model KPCI-1802 using DrvrLINX4). The polling method ensures maximum sample speed at the cost of less accurate sample intervals. A criterion value of 15% of the maximum force was used as individual RT threshold (van Boxtel, van der Molen, Jennings, & Brunia, 2001). This value was individually determined from the maximum force for each thumb press separately at the start of the experiment. For the participant to know if the response was effectively given, a sound (click) was given when the force pressure exceeded the 15% of their maximum force during the practice session. The sound was turned off during the experimental session. Responses were recorded within 1200 ms from go stimulus onset. Participants completed two experimental tasks; a choice RT task and a selective stop task. Presentation order was counterbalanced across participants.

Choice RT task. Each trial started with the presentation of a white fixation cross (3 x 3 cm) followed by a white arrow (subtending a 1.9º visual angle) pointing to the left or to the right (2.2 x 1.8 cm), i.e., the go signal, that remained on screen for 1000 ms. Left and right arrows were counterbalanced. A white fixation cross was visible during the inter-trial interval that varied randomly from 1750 to 2250 ms in steps of 50 ms. Each block consisted of an equal number of right- and left-pointing arrows. Participants were instructed to respond as quickly and
accurately as possible to the direction of the white go arrow by pressing a left or right force sensor, respectively, with the left- or right thumb. The choice RT task consisted of two blocks of 50 experimental trials each, the first block served as practice. The first five trials of the second block were marked as warm-up trials that were excluded from the analyses.

Selective stop task. Like in the choice RT task, participants were presented with white arrows (go stimuli) pointing left or right with equal probability. However, in the selective stop task, the white arrow stimulus occasionally turned pink or blue, indicating a stop signal. When the white arrow changed to pink, the participant should refrain from responding to the go signal (valid stop). When the white arrow changed to blue participants should execute the go response (invalid stop). Stop signals occurred on 35% of the trials (18% valid and 17% invalid stop-signals). Half of the participants were instructed to stop to the pink arrow, whereas the other half stopped to the blue arrows. The presentation of stop signals followed the onset of the go signal with a variable stop-signal delay (i.e., SSD). During practice, the initial SSD was set at 225 ms and was dynamically adjusted after every valid stop signal in such a way that the SSD of the subsequent stop trial, either valid or invalid SSD, was shortened or lengthened according to the stopping performance of the participant. More specifically, SSD decreased by 25 ms when inhibition failed and SSD increased by 25 ms upon successful inhibition. SSD was continuously adjusted over subsequent blocks. This tracking procedure (Levitt, 1971) ensured approximately 50% failed inhibits in all age groups, which yields accurate estimation of stop-signal reaction time (i.e., SSRT, Band, van der Molen, & Logan, 2003). The selective stop task consisted of eight blocks of 100 trials each that were preceded by a practice block. The first five trials of each experimental block were discarded as warm-up trials.

Electrophysiological recordings
EEG was recorded with Biosemi system (Amsterdam) using pin-type active electrodes (Ag/AgCl) attached to an Electro-cap (International 10/20 system, Jasper, 1958) with 30 standard scalp sites (Fp1, Fp2, AF3, AF4, AFz, F3, F4, F7, F8, Fz, FC2, FC3, FC5, FC6, FCz, Cz, C5, C6, CP1, CP2, CP5, CP6, P3, P4, P7, P8, Pz, PO3, PO4, Oz) and six other scalp
locations (FC3', FC4', C1', C2', C3', and C4')\(^1\). Electrodes were referenced to linked mastoids. Vertical and horizontal eye movements (VEOG and HEOG, respectively) were recorded with flat-type active electrodes placed 1 cm above and below the left eye and 1 cm from the outer canthus of each eye.

Bipolar surface EMG was recorded from the left and right thumbs above the *abductor pollicis brevis*. EMG signals were closely monitored throughout the experiment and participants were told to relax their hand muscles in case of excessive EMG activity that was not related to the immediate response.

**Electrophysiological analysis**

Signals were amplified and digitized online at a 2048 Hz sampling rate. EEG and EOG signals were down-sampled to 512 Hz offline. EEG signals were filtered using a low-pass filter of 30 Hz and high-pass filter of 0.1 Hz (24 dB/octave) and signals exceeding an amplitude criterion of \(\pm 100 \, \mu \text{V}\) were rejected. Ocular artifacts were corrected using the algorithm proposed by Gratton, Coles and Donchin (1983).

The spherical spline interpolation algorithm described by Perrin, Pernier, Bertrand, and Echallier (1989) was applied to obtain the surface Laplacian. To compare the present results with previous motor Laplacian studies, we used exactly the same settings, i.e., three for the order of splines and the interpolation was computed using a maximum of 15 for the Legendre polynomial (Meckler, Allain, Carbonnell, Hasbroucq, Burle, & Vidal, 2010; Meynier, Burle, Possamaï, Vidal, & Hasbroucq, 2009; Tandonnet, Burle, Hasbroucq, & Vidal, 2005). Surface Laplacians were low-pass filtered at 15 Hz and high-pass filtered at 1 Hz. A baseline correction was applied using a 300 ms window (from 500 to 200 ms) preceding EMG onset. Univariate

\(^1\) The current electrode configuration differs slightly from the standard 10-20 placement system. Electrodes C3' and C4' recorded activity 1 cm anterior of the standard C3 and C4 locations, and C1' and C2' were positioned 1 cm posterior-lateral of the original C1 and C2 locations. The current focus is on electrode positions, C1' and C2'. The monopolar activity recorded using electrodes C3' and C4' showed a more diffuse and less timely pattern compared to C1' and C2': the contralateral activity at C3' and C4' peaked well beyond the response trigger. Laplacian activity recorded at C1' and C2' corresponds more precisely to the morphology and timing of activity found in motor Laplacian studies that typically focus on C3 or C3' and C4 or C4' electrodes (Vidal, Grapperon, Bonnet, & Hasbroucq, 2003). Therefore, the present study uses more posterior electrode positions to capture activity from the precentral sulcus (Mima, Steger, Schulman, Gerloff, & Hallett, 2000).
ANOVA of mean Laplacian amplitudes associated with the 300 ms interval revealed that this interval was not affected by age (all $F$s < 1.98). The onset of the contralateral negative and ipsilateral positive wave was estimated using a segmented regression method for each participant individually (Schwarzenau, Falkenstein, Hoormann, & Hohnsbein, 1998). That is, we first selected a time interval that contained both the period preceding a wave and the period until a wave peaked. The signal in this interval was described by a model that consisted of two regression lines, where both the coefficients of these lines as well as the breakpoint between the lines was estimated. The breakpoint yields an estimate of the onset of a wave.

EMG signals were down-sampled to 1024 Hz, high-pass filtered at 20 Hz, rectified, and low-pass filtered at 50 Hz. A procedure run on the rectified EMG signal searched for the time point at which the positive developing flank exceeded 30 $\mu$V. When this was the case, a trigger was placed at 5 $\mu$V backwards. All EMG onsets were visually inspected and manually adjusted if automatic onset detection failed (van Boxtel, Geraats, van den Berg-Lenssen, & Brunia, 1993).

Data analysis

Trial types. Go trials were classified into: 1) correct go trials; indicated by EMG activity and a button-press response, both associated with the correct hand, 2) partial error trials; a go trial characterized by sub-threshold EMG activity of the incorrect hand followed by a button press of the correct hand, 3) full choice error trials; EMG activity associated with the incorrect hand followed by an incorrect button press, and 4) omission trials; absence of both EMG activity and a button press on a go trial. Valid stop-signal trials were sorted into: 1) full inhibit trials; indicated by the absence of both EMG activity and a button press on a valid stop trial, 2) partial inhibit trials; presence of sub-threshold EMG activity of the hand associated with the go stimulus, but absence of a button press on a valid stop trial, 3) failed inhibit trials. This trial category was classified into: a) failed inhibit trials; presence of EMG activity and a button-press response, both associated with the go stimulus on a valid stop trial, b) partial error trials; a valid stop trial characterized by sub-threshold EMG activity of the incorrect hand followed by a button press of the correct hand, and c) full choice error trials; EMG activity associated with the incorrect hand followed by an incorrect button press on a valid stop trial. Invalid stop-signal trials were sorted into: 1) invalid stop-signal trials; presence of EMG and a button press associated with the go stimulus on an invalid stop-signal trial, 2) partial error trials; an invalid stop-signal trial characterized by sub-threshold EMG activity of the incorrect hand followed by
Performance measures. Reaction times (RTs) were calculated separately for correct go, valid failed inhibit, and invalid stop-signal trials. SSRT was estimated using the integration method (Logan & Cowan, 1984). Responses on go and invalid stop-signal trials in the selective stop-signal task were classified into fast and slow RTs with respect to the estimated finishing time of the stop process. RTs shorter than the finishing time were classified as fast responses, whereas RTs that exceeded this value were classified as slow responses. These will be referred to as fast vs. slow go RT and fast vs. slow invalid RT. This comparison allowed investigating the influence of the stop signal on go-signal processing.

Repeated measures ANOVAs were used to assess performance measures with Task (choice RT task vs. selective stop task), Stop Success (full inhibit vs. partial inhibit vs. failed inhibit), Trial Type (go vs. failed inhibit vs. invalid stop) and Trial Category (fast vs. slow), as within-subject factors, and Age Group (young children, older children, and adults), as between-subject factor. When the assumption of sphericity was violated, degrees of freedom and p-values were adjusted using a Greenhouse-Geisser correction. Error proportions are not normally distributed and therefore tests were performed on square rooted values. To correct for differences in baseline performance between age groups, the natural logarithm of RTs were calculated and analyzed when interaction effects included Age Group (Huizinga & van der Molen, 2010; Meiran, 1996).

Electrophysiological measures. Laplacian-transformed ERP and EMG signals were time-locked to EMG onset and averaged. Preliminary analysis indicated that ERP and EMG amplitudes did not differ significantly between hands ($F_s < 2.22$, $p_s > .12$). Therefore, data were collapsed across hands. The EMG peak was identified as the most positive value within 300 ms from EMG onset.

The peak of the contralateral negative Laplacian potential was captured by determining the most negative value in the interval ranging from -100 to 250 ms with respect to EMG onset. For three young children there was not a sufficient amount of trials for a reliable analysis of the contralateral negative wave and those were excluded (for one child there were insufficient fast go trials and for two others there were insufficient fast invalid stop-signal trials). The same applied to two older children (one had insufficient failed stop- and the other insufficient fast invalid stop-signal trials) and two adults (insufficient fast invalid stop-signal trials). Thus the number of participants was reduced to 13 young children, 15 older children, and 15 adults for the analysis of the contralateral wave when it included those set of trials. Repeated measures
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ANOVA were used to assess peak amplitudes and wave onset measures with Task, Trial Type and Trial Category as within-subject factors and Age Group as between-subject factor. Significant interaction effects including Age Group were additionally analyzed by transforming values (peak amplitudes and wave onsets) to the natural logarithm, to correct for baseline performance differences between age groups.

Visual inspection of ipsilateral traces revealed a large variability in the morphology of the waves at the ipsilateral side between age groups and trial types. To determine the presence of an ipsilateral positive wave, we performed statistical analyses on the slopes of the traces. Slopes were calculated for six epochs (50 ms each) of the ipsilateral traces for each Trial Type and Trial Category: 1) -150 to -100 ms, 2) -100 to -50 ms, 3) -50 to 0 ms, 4) 0 to 50 ms, 5) 50 to 100 ms, and 6) 100 to 150 ms. Slopes were submitted to ANOVA with Interval (6) as within-subject factor. The onset scoring procedure failed to detect the onset for some participants because of strong signal fluctuations prior to the positive deflection (for one adult this applied to go trials, for three other adults to fast invalids, and for five older children to slow invalids, young children did not reveal a positive wave). Timing differences between the onsets of the contralateral negative and ipsilateral positive Laplacian potentials were assessed by submitting onset values to ANOVA with Wave (contralateral negative vs. ipsilateral positive wave), Trial Type and Trial Category as within-subject factors.

Table 2 Mean RTs (in milliseconds) and error percentages (%) associated with go trials in the choice RT task and the selective stop-signal task for each age group (standard deviations between parentheses).

<table>
<thead>
<tr>
<th>Age group</th>
<th>Choice RT task</th>
<th>Selective stop task</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Go RT</td>
<td>Full errors</td>
</tr>
<tr>
<td>Young children</td>
<td>511 (84.9)</td>
<td>10.0 (6.1)</td>
</tr>
<tr>
<td>Older children</td>
<td>369 (50.7)</td>
<td>10.4 (8.3)</td>
</tr>
<tr>
<td>Adults</td>
<td>299 (26.3)</td>
<td>3.3 (3.9)</td>
</tr>
</tbody>
</table>

Results

The results are presented in two parts, starting with the performance results. The second part includes the electrophysiological results that are presented in three sections: electromyographic (EMG) results, results associated with the contralateral negative Laplacian wave, and results associated with the ipsilateral positive Laplacian wave. The sections were mainly driven by
Development of Response Activation and Inhibition

three comparisons; that is: 1) go trials in the choice RT task vs. go trials in the selective stop task, (2) go trials vs. failed inhibition trials in the selective stop task, and (3) go trials vs. invalid stop-signal trials in the selective stop task. For EMG and the contralateral negative wave, a preliminary analysis for each trial type was performed to determine whether the insertion of stop signals affects age-related changes in central and peripheral motor processes (van de Laar, van den Wildenberg, van Boxtel, Huizenga, & van der Molen, 2012).

Behavioral data

Performance on go trials

Table 2 presents mean RTs and error percentages on go trials. Analyses of go RTs yielded a significant main effect of Task, $F(1, 42) = 111.70$, $p < .001$, that interacted with Age Group, $F(2, 42) = 5.54$, $p = .007$. Log-transformed RTs decreased from the younger child group to older children and up to adults ($p < .001$), a pattern that is in line with the developmental literature (e.g., Kail, 1993). All participants slowed their responses to go signals in the selective stop task compared to the choice RT task, $F(2, 42) = 3.4$, $p = .04$. Contrast analyses of log RTs indicated that the slowing was disproportionally larger for young and older children (who did not differ, $p = .68$) compared to adults ($p < .02$).

The percentage of full choice errors was below 10% for all age groups, indicating that all participants performed the tasks relatively well. Analysis of full choice errors on go trials revealed a significant main effect of Task, $F(1, 42) = 23.21$, $p < .001$, that interacted with Age Group, $F(2, 42) = 3.84$, $p = .03$. The two child groups committed more full choice errors than adults on both tasks ($p < .01$). Full choice error rate was higher for young compared to older children, but only on the selective stop task ($p = .006$). Full choice error rate tended to be lower on the selective stop task compared to the choice RT task for young children (marginal, $p = .06$) and older children ($p < .001$), but not for adults ($p = .22$). Partial EMG choice error rates of young and older children (who did not differ, $p = .91$) was higher compared to adults, $p < .001$ ($F(2, 42) = 17.54$, $p < .001$). Partial choice error rates did not differ between tasks ($F < 1$).

Omission rates on go trials were somewhat higher on the selective stop task compared to the choice RT task, $F(1, 42) = 6.45$, $p = .02$. There was a significant effect of Age Group, $F(2, 42) = 26.53$, $p < .001$, showing that omissions were more frequent in young children compared to older children and adults ($p < .001$), in both tasks ($F < 1$).

The first aim of the current study was to investigate if age groups delay the response to the go signal when stop signals are inserted into the trial series. The results confirm our prediction regarding comparison 1 (go RT in the choice RT task vs. go RT in the selective stop
task) and suggest that all age groups proactively slowed down in the selective stop task and the delay is most pronounced in children.

**Table 3** Mean percentages (%) of successful, partial and failed inhibition trials. Mean stop-signal reaction time (SSRT) and mean failed inhibit RT (in ms). Error percentages associated with failed inhibited trials in the selective stop task for each age group (standard deviations between parentheses).

<table>
<thead>
<tr>
<th>Age group</th>
<th>Stop percentage</th>
<th>Latency</th>
<th>Error percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Full inhibit</td>
<td>Partial inhibit</td>
<td>Failed inhibit</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Young children</td>
<td>15.2 (4.3)</td>
<td>33.3 (5.9)</td>
<td>51.4 (2.3)</td>
</tr>
<tr>
<td>Older children</td>
<td>16.1 (6.1)</td>
<td>32.7 (5.6)</td>
<td>51.2 (3.8)</td>
</tr>
<tr>
<td>Adults</td>
<td>23.1 (8.4)</td>
<td>26.1 (7.9)</td>
<td>50.7 (2.1)</td>
</tr>
</tbody>
</table>

**Performance on stop-signal trials**

*Valid stop-signal trials.* Performance measures associated with valid stop-signal trials are presented in Table 3. It can be seen that the tracking algorithm (targeting inhibition rates of about .50) worked quite well for all age groups, $F < 1$. Analysis of selective SSRT revealed a significant Age Group effect, $F(2, 47) = 32.6, p < .001$. Log-transformed SSRTs decreased with age group ($ps < .002$). The developmental gain was most pronounced from the young compared to the older child group. Analysis of partial inhibition rate also yielded a significant Age Group effect, $F(2, 47) = 6.75, p = .003$; the two child groups showed more partially inhibited trials compared to adults ($ps < .004$). This finding suggests that response-related activation on valid stop-signal trials progressed to later motor stages in children compared to adults. The two child groups did not differ in the proportion of partially inhibited trials ($p = .74$).

Analysis of failed inhibit RT revealed a similar age-related pattern as go RT, $F(2, 47) = 79.77, p < .001$ (see Table 3); that is, log-transformed failed inhibit RTs decreased with advancing age ($ps < .001$). A comparison between go RT and failed inhibit RT yielded a significant effect of Trial Type, $F(1, 47) = 62.76, p < .001$, that interacted with Age Group, $F(2, 47) = 20.63, p < .001$. Additional analyses revealed that failed inhibit RT was shorter than go RT for the two child groups ($ps < .001$), but not for adults ($p = .90$).

Full choice error rates did not differ between go and failed inhibited responses, $F(1, 47) = 1.56, p = .22$. However, a significant Trial Type effect was found on partial EMG error rates, $F(1, 47) = 12.12, p = .001$; participants committed less partial choice errors on failed inhibits...
relative to go trials (note that a partial EMG choice error with no overt response on a stop-signal trial is classified as a partial inhibit trial). As shown in Table 3, the age-related pattern of full and partial choice error rates on failed inhibited trials were comparable to that of go trials ($p > .22$).

In sum, selective stopping latency in young children is prolonged compared to older children, and older children were slower to inhibit than adults. With respect to comparison 2 (go RT vs. failed inhibit RT in the selective stop task), we predicted that failed inhibit RT is shorter than go RT. This prediction was confirmed for the two child groups only.

Table 4 Mean RT (in ms) of fast and slow go and invalid stop-signal trials and error percentages (%) associated with invalid stop-signal trials in the selective stop task for each age group (standard deviations between parentheses).

<table>
<thead>
<tr>
<th>Age group</th>
<th>Go trials</th>
<th></th>
<th>Invalid stop-signal trials</th>
<th></th>
<th>Error percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Latency</td>
<td>Error</td>
<td>Latency</td>
<td>Error</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fast RT</td>
<td>Slow RT</td>
<td>Fast RT</td>
<td>Slow RT</td>
<td>Full errors</td>
</tr>
<tr>
<td>Young children</td>
<td>467 (46.7)</td>
<td>690 (85.1)</td>
<td>460 (45.4)</td>
<td>763 (82.5)</td>
<td>6.6 (4.7)</td>
</tr>
<tr>
<td>Older children</td>
<td>373 (42.0)</td>
<td>524 (57.5)</td>
<td>365 (38.8)</td>
<td>560 (69.6)</td>
<td>3.0 (2.7)</td>
</tr>
<tr>
<td>Adults</td>
<td>297 (23.7)</td>
<td>372 (40.3)</td>
<td>292 (24.5)</td>
<td>459 (36.7)</td>
<td>1.0 (1.8)</td>
</tr>
</tbody>
</table>

Invalid stop-signal trials. Fast and slow responses on go trials and invalid stop-signal trials were compared to assess age effects on invalid stop-signal processing. Analyses yielded a significant main effect of Trial Type, $F(1, 47) = 173.11, p < .001$, indicating that invalid RT is longer than go RT (see Table 4). Trial Category (fast vs. slow) interacted with Trial Type, $F(1, 47) = 188.29, p < .001$, and with Age Group, $F(2, 47) = 68.85, p < .001$. Log-transformed analyses of RTs indicated that young children disproportionately delayed slow responses relative to fast responses more than the other age groups ($p < .001$). This delay was also larger in older children compared to adults ($p < .001$). This effect was most pronounced on invalid stop-signal trials ($p < .001$), indicating that the RT lengthening on invalid stop-signal trials is more prominent in children compared to adults.

Go accuracy may benefit from response delaying on invalid stop-signal trials. This hypothesis was examined by comparing error percentages between go and invalid stop-signal trials. The analysis revealed that full choice error rate was lower on invalid stop-signal trials.
relative to go trials in the selective stop task, \( ps < .001 \) (\( F(1, 47) = 17.02, p < .001 \) (see Table 4). Partial choice error rates did not differ between go and invalid stop-signal trials, \( F < 1 \). The age-related pattern of full and partial error rates associated with invalid stop-signal trials was comparable to that of go trials \( (ps > .19) \). The lower proportion of full choice errors on invalid stop-signal trials suggest that the accuracy of all age groups benefits from the longer processing time of the initial go signal preceding an invalid stop-signal.

In sum, these results indicate that each age group slowed on invalid stop-signal trials and this slowing is most pronounced in children. This finding confirms our prediction regarding comparison 3 (go RT vs. invalid stop RT in the selective stop task). Moreover, pronounced age effects were observed for slow invalid stop responses and this longer processing time benefited choice accuracy in each age group.

Electrophysiological data

Electromyography

Figure 1 shows rectified EMG activity of the responding hand, time-locked to its onset. Preliminary analyses of motor time (i.e., the interval from EMG onset to RT) and peak amplitudes of EMG activity were performed to examine developmental changes in peripheral response processing. Analyses of motor time on go trials of the choice RT and selective stop tasks revealed a significant Age Group effect, \( F(2, 42) = 18.24, ps < .001 \) (see Table 5); log-transformed motor time values decreased from young children to older children and up to adults \( (ps < .02) \). Similar age patterns of motor time were observed for failed inhibition trials and for invalid stop-signal trials, \( Fs > 21.67, ps < .001 \). These findings suggest that development of peripheral motor processes was not affected by the presence of the stop signal.
Electromyographic activity. Traces of EMG activity (in arbitrary units, recorded in microV) are averaged time-locked to its onset (0 ms, vertical bar). (A) EMG activity associated with go trials in the choice RT task (black line) and selective stop task (green line). (B) EMG activity associated with go trials (green line) and failed inhibits (red line) in the selective stop task. (C) EMG activity associated with fast go (blue line), slow go (orange line), fast invalid (light green line) and slow invalid (brown line) stop-signal trials in the selective stop task for each age group. Vertical dashed lines denote overt responses.

Figure 1
Analyses of EMG peak amplitudes associated with go trials yielded a significant main effect of Age Group, $F(2, 42) = 5.34, p = .009$ (see Table 5). Analysis of log-transformed values revealed disproportionately increased EMG amplitudes for older children and adults (who did not differ, $p = .99$) compared to young children ($p < .003$) (see Figure 1A). The observed age-related pattern of EMG amplitudes was similar for failed inhibition trials and for invalid stop-signal trials, $F > 5.29, p < .009$. It appears that the observed age differences in the recruitment of motor muscles were not affected by the presence of the stop signal.

*Go (choice RT task) vs. go trials (selective stop task).* Analyses of motor time on go trials revealed a significant Task effect, $F(1, 42) = 14.17, p < .001$. As shown in Figure 1A, motor time was longer on the selective stop task compared to the choice RT task; a pattern that did not differ between age groups ($p = .24$). This latter finding suggests that motor time did not contribute to the observed age-related RT pattern associated with proactive control.

Analyses of EMG peak amplitudes associated with go responses (see Table 5) yielded a significant main effect of Task, $F(1, 42) = 9.18, p = .004$, indicating a smaller EMG peak on go trials in the selective stop compared to the choice RT task. This effect did not differentiate between age groups, $F < 1$. This finding suggests less muscle output on go trials presented in a stop-task context for all age groups.

In sum, it appears that the proactive slowing in the selective stop task is expressed in both latency shifts as well as a reduced motor output that did not differ between age groups. This confirms our prediction regarding comparison 1 (peripheral response activation associated with go trials in the choice RT task vs. selective stop task).
Go vs. failed stop-signal trials (selective stop task). Motor time and peak amplitudes of EMG activity on failed stop-signal trials were compared to go trials of the selective stop task (see Table 5). Analyses of motor time revealed a significant Trial Type effect, $F(1, 47) = 28.61$, $p < .001$; motor time was longer on failed inhibit trials compared to go trials, a pattern that did not differ between age groups, $F < 1$. It appears that failed inhibits are associated with prolonged muscle activation before reaching the response criterion compared to go responses.

Analyses of EMG peak amplitudes yielded a significant main effect of Trial Type, $F(1, 47) = 29.84$, $p < .001$, that interacted with Age Group, $F(2, 47) = 7.34$, $p = .002$. As can be seen in Figure 1B, EMG amplitudes did not differentiate between go and failed inhibit responses in young children ($p = .10$), but EMG peak was lower on failed inhibits compared to go trials in older children ($p = .05$) and adults ($p < .001$). This reduction in EMG amplitudes on failed inhibits was disproportionate in adults compared to older children ($p = .03$). Although, it is typically assumed that failed inhibits escape inhibition, the current data suggest inhibitory control (indexed by reduced amplitudes) on failed inhibit trials, albeit ineffective. Furthermore, this (ineffective) inhibitory control was present in adults and older children but not in younger children.

In sum, and contradictory to what we hypothesized, failed inhibition trials are associated with longer motor times and lower EMG amplitudes compared to go trials. This may reflect an attempt to inhibit the response on failed inhibit trials.
Go vs. invalid stop-signal trials (selective stop task). Analyses of motor time associated with fast and slow go and invalid stop-signal trials (see Table 5) yielded a significant interaction between Trial Type and Trial Category, $F(1, 47) = 16.49, p < .001$ (see Figure 1C). Longer motor times were found for slow go compared to fast go trials ($p < .001$), whereas slow and fast responses associated with invalid stop-signal trials did not differ in motor time ($p = .83$). Trial Type and Trial Category also interacted with Age Group, $F(2, 47) = 3.28, p = .05$. Subsequent analyses of log-transformed motor times indicated that the relative difference in motor times between age groups was larger on slow go compared to fast go trials ($p = .003$). But the age-related pattern of motor times was comparable for fast and slow invalid stop-signal trials ($p = .10$). The latter finding suggests that motor time does not contribute to the observed (disproportional) developmental pattern of RT on slow invalid relative to fast invalid stop-signal trials.

Analyses of EMG peak amplitudes yielded a significant interaction between Trial Type and Trial Category, $F(1, 47) = 14.82, p < .001$. Amplitude values were higher on fast go compared to slow go trials ($p < .001$), but did not differ between fast and slow invalid stop-signal trials ($p = .19$). This effect was not altered by age, $F(2, 47) = 2.53, p = .09$.

In sum, and contradictory to what we predicted, motor time and EMG amplitudes associated with slow invalid stop-signal trials did not differ from fast invalid stop-signal trials, indicating the processing of invalid stop-signals in each age group.
**Figure 2** Laplacian transformed ERPs. Contralateral Laplacian traces (bold lines) and ipsilateral Laplacian traces (thin line) recorded from C1’/C2’.

(A) ERPs associated with go trials in the choice RT task (black line) and selective stop task (green line). (B) ERPs associated with go trials (green line) and failed inhibits (red line) in the selective stop task. (C) ERPs associated with fast go (blue line), slow go (orange line), fast invalid (light green line) and slow invalid (brown line) stop-signal trials in the selective stop task for each age group. Traces are averaged time-locked to EMG onset (vertical bar crosses at zero). Negativity is plotted upwards.
Chapter 5

Contralateral negative Laplacian wave

Figure 2 depicts grand-averaged Laplacian waves recorded from the contra- and ipsilateral M1 for each age group. As can be seen, all age groups exhibit a negatively developing wave at the time of EMG onset for all trials on which a response was observed. Preliminary analyses of pre-motor time (i.e., the interval between onsets of the negative wave and EMG) and peak amplitudes of the contralateral negative Laplacian wave were performed to examine developmental changes in central response activation. Onsets and peak amplitudes of the contralateral negative wave are presented in Table 6. Analyses of pre-motor time on go trials yielded a significant Age Group effect, \( F(2, 42) = 7.14, p = .002 \). Analysis of log-transformed pre-motor time values showed that this interval was disproportionally longer for young children compared to older children and adults (\( ps < .005 \)), who did not differ (\( p = .41 \)). The observed age-related pattern of pre-motor times was similar for failed inhibition trials and invalid stop-signal trials, \( F_5 > 3.79, ps < .03 \). Similar to motor time, the development of central motor processes was not affected by the presence of the stop signal.

Analyses of the amplitudes of the negative Laplacian wave associated with go trials yielded a significant main effect of Age Group, \( F(2, 42) = 15.07, p < .001 \) (see Table 6). Analyses of log values showed that the negative wave was disproportionally larger in older children compared to young children and larger in young children than in adults (\( ps < .03 \)) (see Figure 2A). A similar age pattern of peak amplitudes was observed for failed inhibition trials, \( F(2, 46) = 9.55, p < .001 \). For invalid stop-signal trials, log amplitude values did not differ between the two child groups (\( p = .35 \)), \( F(2, 40) = 7.20, p = .002 \). These findings indicate that children’s responses were associated with a stronger activation of M1 compared to adults, irrespective the presence of stop signals.

Go (choice RT task) vs. go trials (selective stop task). Analyses of pre-motor times yielded a significant main effect of Task, \( F(1, 42) = 22.69, p < .001 \), indicating longer pre-motor times for the selective stop relative to the choice RT task, a pattern that did not differ between age groups, \( F = 1 \). Similar to motor time, pre-motor time did not contribute to the observed age-related RT pattern associated with proactive control.

Analyses of the amplitudes of the negative Laplacian wave associated with go trials yielded a significant main effect of Task, \( F(1, 42) = 68.72, p < .001 \); lower amplitude values were found for the selective stop compared to the choice RT task. Task also interacted with Age Group, \( F(2, 42) = 3.53, p = .04 \). The relative difference in negative amplitude values between the selective stop and the choice RT task was larger in adults compared to young children, and larger in young children than older children (\( ps < .006 \)). The reduction of the contralateral
negative Laplacian wave observed for the selective stop task was less pronounced for the older children compared to the other two age groups.

The current findings show that proactive response slowing, as evidenced by longer RTs in the selective stop compared to the choice RT task, is associated with a reduced M1 activation of longer duration. This confirms our prediction regarding comparison 1 (central response activation associated with go trials in the choice RT task vs. selective stop task). Moreover, the relative M1 reduction was most pronounced in adults and less pronounced in older children.

Table 6 Contralateral negative Laplacian wave. Mean pre-motor time (in ms, relative to EMG onset), and peak amplitude (in microV) values of the negative wave on go trials in the choice RT and selective stop tasks, on failed stop-signal trials and on fast and slow go and fast and slow invalid stop-signal trials associated with the selective stop task for each age group (standard deviations between parentheses).

<table>
<thead>
<tr>
<th>Age group</th>
<th>Pre-motor time</th>
<th>Peak amplitudes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Go trials</td>
<td>Failed stop-signal trials</td>
</tr>
<tr>
<td></td>
<td>Fast</td>
<td>Slow</td>
</tr>
<tr>
<td>Young children</td>
<td>-76 (54.5)</td>
<td>-148 (124.6)</td>
</tr>
<tr>
<td>Older children</td>
<td>-49 (42.6)</td>
<td>-78 (30.7)</td>
</tr>
<tr>
<td>Adults</td>
<td>-20 (42.5)</td>
<td>-73 (35.9)</td>
</tr>
</tbody>
</table>

Go vs. failed stop-signal trials (selective stop task). Pre-motor time was compared between failed inhibits and go trials (see Figure 2B). A significant Trial Type effect was found, $F(1, 46) = 11.83, p = .001$; pre-motor time associated with failed inhibits was shorter than on go trials (see Table 6). This effect was comparable between age groups ($p = .23$).

Figure 3B shows a somewhat reduced contralateral negative wave for failed inhibit responses, but analyses did not confirm this visual impression, $F_s < 1$ (see Table 6).

In sum, failed inhibited responses are associated with shorter M1 activations compared to go responses. However and contradictory to what we hypothesized, failed inhibited responses were executed with similar magnitude of M1 activation as go responses. This latter finding suggests that failed inhibits are a different category than fast go responses.
Go vs. invalid stop-signal trials (selective stop task). Analyses of pre-motor time revealed a significant interaction between Trial Type and Trial Category, $F(1, 40) = 4.32, p = .04$ (see Table 6). As can be seen in Figure 2C, pre-motor time was longer for slow go compared to fast go trials ($p < .001$), but pre-motor time was comparable between fast and slow invalid stop-signal trials ($p = .10$). The pattern of pre-motor times for fast and slow responses was comparable between age groups, $F < 1$. Similar to motor time, pre-motor time associated with slow invalid stop-signal trials differs from the disproportional age-related pattern observed for slow invalid stop RTs.

Analyses of negative peak amplitudes yielded a significant interaction effect between Trial Type and Trial Category, $F(1, 40) = 4.52, p = .04$. Subsequent analyses indicated that negative amplitudes were reduced on slow go compared to fast go trials ($p = .001$). As shown in Table 6, negative amplitudes did not discriminate between slow vs. fast responses on invalid stop-signal trials ($p = .58$). This effect was comparable between age groups, $F < 1$.

Contradictory to what we predicted, fast invalid and slow invalid stop-signal trials revealed similar M1 activation and duration. Together with the EMG findings, it can be concluded that the invalid stop-signal was not ignored, and this was true for each of the three age groups.
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| Table 7 Ipsilateral positive Laplacian wave. Slope values of ipsilateral Laplacian activity with six time windows (zero of time point refers to EMG onset) and mean onset values (in ms, relative to EMG onset) on go trials in the choice RT and selective stop tasks, on failed stop-signal trials and on fast and slow go and fast and slow invalid stop-signal trials associated with the selective stop task for each age group (standard deviations between parentheses). |

<table>
<thead>
<tr>
<th>Interval</th>
<th>Young children</th>
<th>Older children</th>
<th>Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Go trials</td>
<td>Go trials</td>
<td>Fast</td>
</tr>
<tr>
<td>-150 to -100 ms</td>
<td>0.4 (2.7)</td>
<td>-0.3 (1.0)</td>
<td>1.0 (2.3)</td>
</tr>
<tr>
<td>-100 to -50 ms</td>
<td>0.0 (2.7)</td>
<td>0.1 (1.2)</td>
<td>0.2 (2.0)</td>
</tr>
<tr>
<td>-50 to 0 ms</td>
<td>-0.9 (2.3)</td>
<td>-0.4 (1.1)</td>
<td>-0.6 (2.1)</td>
</tr>
<tr>
<td>0 to 50 ms</td>
<td>0.8 (2.6)</td>
<td>-0.3 (1.2)</td>
<td>-0.4 (2.5)</td>
</tr>
<tr>
<td>50 to 100 ms</td>
<td>-0.9 (3.0)</td>
<td>0.3 (0.9)</td>
<td>-0.4 (1.7)</td>
</tr>
<tr>
<td>100 to 150 ms</td>
<td>-0.3 (2.8)</td>
<td>-0.5 (1.5)</td>
<td>0.8 (2.2)</td>
</tr>
<tr>
<td></td>
<td>Go trials</td>
<td>Failed stop-signal trials</td>
<td>Fast</td>
</tr>
<tr>
<td>-150 to -100 ms</td>
<td>-0.0 (1.9)</td>
<td>1.3 (2.2)</td>
<td>0.1 (1.3)</td>
</tr>
<tr>
<td>-100 to -50 ms</td>
<td>-1.1 (2.6)</td>
<td>-0.7 (0.8)</td>
<td>-0.6 (2.2)</td>
</tr>
<tr>
<td>-50 to 0 ms</td>
<td>-1.4 (2.4)</td>
<td>-0.4 (0.9)</td>
<td>-1.0 (2.5)</td>
</tr>
<tr>
<td>0 to 50 ms</td>
<td>-3.0 (3.0)</td>
<td>-0.3 (1.2)</td>
<td>0.1 (2.0)</td>
</tr>
<tr>
<td>50 to 100 ms</td>
<td>-0.7 (2.9)</td>
<td>0.1 (1.1)</td>
<td>0.1 (2.1)</td>
</tr>
<tr>
<td>100 to 150 ms</td>
<td>0.9 (1.8)</td>
<td>0.8 (1.1)</td>
<td>0.3 (2.0)</td>
</tr>
<tr>
<td></td>
<td>Go trials</td>
<td>Invalid stop-signal trials</td>
<td>Fast</td>
</tr>
<tr>
<td>-150 to -100 ms</td>
<td>-0.7 (1.1)</td>
<td>-0.1 (0.4)</td>
<td>-0.4 (0.7)</td>
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<td>-100 to -50 ms</td>
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<td>0.1 (0.5)</td>
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<td>1.0 (0.7)</td>
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<tr>
<td>0 to 50 ms</td>
<td>0.8 (2.1)</td>
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<td>100 to 150 ms</td>
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<td>0.0 (0.7)</td>
<td>0.8 (1.4)</td>
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<table>
<thead>
<tr>
<th>Onset latencies</th>
<th>Young children</th>
<th>Older children</th>
<th>Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>—</td>
<td>—</td>
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<td>-72 (31.8)</td>
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<td>—</td>
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<td>—</td>
<td>-87 (26.4)</td>
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<td>—</td>
<td>—</td>
<td>—</td>
<td>-102 (36.9)</td>
</tr>
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<td>—</td>
<td>—</td>
<td>—</td>
<td>-66 (28.4)</td>
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<td>—</td>
<td>-101 (32.8)</td>
</tr>
<tr>
<td>—</td>
<td>—</td>
<td>—</td>
<td>-48 (45.4)</td>
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**Ipsilateral positive Laplacian wave**

Figure 2 presents ipsilateral Laplacian traces for each age group and reveals a positive developing wave around EMG onset in adults on all trial types except on slow invalid stop-signal trials. The ipsilateral positivity is absent in the two child groups, except in the older child group on slow invalid stop-signal trials.

Analyses of the slopes of the six intervals (see Table 7) indicated that the ipsilateral trace deflects positively around EMG onset in adults on go trials in both the choice RT and selective stop tasks, $F > 5.18, p < .004$ (see Figure 2A), on failed stop-signal trials, $F(5, 80) = 2.73, p = .03$ (see Figure 2B), on fast and slow go trials, $F > 3.06, p < .01$, and on fast invalid stop-signal trials, marginal $F(5, 80) = 2.79, p = .06$ (see Figure 2C); i.e., interval from -50 to EMG onset revealed steeper positive slopes compared to the intervals -150 to -100 ms and 50 to 100 ms ($ps < .05$). The positive deflection is absent on slow invalid stop-signal trials, $F(5, 80) = 1.19, p = .33$.

Similar analyses were done on the slopes of the six intervals of the ipsilateral traces in children. As shown in Figure 2, a systematical change of the ipsilateral trace is absent on all trial and response types in the group of younger children, $F < 1.81, p > .12$ (see Table 7).

In the older child group, the ipsilateral trace turned positive around EMG onset on slow invalid stop-signal trials, $F(5, 80) = 3.82, p = .004$: slopes of the intervals -50 ms to EMG onset and EMG onset to 50 ms were more positive compared to the intervals -100 to -50 ms and 50 to 100 ms ($ps < .02$) (see Figure 2C lower panel). Figure 2 shows a negative ipsilateral wave in older children for the other trial types. As can be seen in Table 7, on all go trials, the slopes of the intervals -50 ms to EMG onset and EMG onset to 50 ms were more negative compared to the intervals -150 to -100 ms and 100 to 150 ms ($ps < .05$). Slope values did not differ between intervals for failed and fast invalid stop-signal trials, $F < 2.00, p > .09$.

These slope analyses confirm the visual impression of Figure 2. That is, young children did not show an ipsilateral positive wave around EMG onset. The ipsilateral trace of go trials in older children is characterized by a negative developing wave and, for slow invalid stop-signal trials only, by a positive developing wave. Finally, adults showed an ipsilateral positive wave on go, failed stop- and fast invalid stop-signal trials that appeared absent on slow invalid stop-signal trials.

**Comparing the onsets of the positive and negative potentials**

A final set of analyses was performed on the relative onsets of the contra- (see Table 6) and ipsilateral Laplacian waves (see Table 7). In adults, Task interacted significantly with Wave.
onset on go trials, \(F(1, 14) = 4.56, p = .05\); the ipsilateral positivity started well before the contralateral negativity in the choice RT task, \(F(1, 14) = 13.83, p = .002\), a pattern that is consistently found on correct go trials in adults (e.g., Meynier, Burle, Possamaï, Vidal, & Hasbroucq, 2009). The onsets did not differ on go trials in the selective stop task, \(F(1, 15) = 2.48, p = .14\). On failed stop-signal trials, the ipsilateral positive wave started well before the contralateral negative wave, \(F(1, 16) = 30.88, p < .001\), whereas onsets did not differ between fast and slow go vs. fast invalid stop-signal trials, \(Fs < 1\). In older children, the analysis of the onsets of the contralateral negative and ipsilateral positive wave on slow invalid trials failed to reveal a significant effect of Wave, \(F(1, 10) = 3.12, p = .11\) (see Table 7).

Discussion

The primary aim of the present study was to gain more understanding of the developmental changes in stop-signal task performance by examining response activation using response-related brain and EMG potentials. Two child groups and one adult group performed two tasks: a choice RT task and a selective stop task. The discussion section is mainly guided by the following issues: 1) the use of proactive response strategies, 2) responses that escaped inhibition, and 3) the effect of invalid stop-signal processing on the execution of invalid stop responses. A final section discusses the suppression of the competing (incorrect) response (reflected by the ipsilateral positive wave) vis-à-vis age-related changes in action control.

Go RT decreased sharply from the younger child group to the older child group with a more gradual improvement to young adulthood. This pattern is consistent with a host of studies investigating age-related change in response speed (e.g., Cerella & Hale, 1994; Kail, 1993). Previously, we observed that both central and peripheral motor processing on go trials in a choice RT task is prolonged in children compared to young adults (van de Laar, van den Wildenberg, van Bokxel, Huizenga, & van der Molen, 2012). This pattern of results is extended by the current developmental pattern of response-related stages on go trials in the selective stop task. That is, pre-motor and motor times were disproportionally longer in young children compared to the other age groups. Motor time, but not pre-motor time, was longer in older children than young adults. This shows that the phasic recruitment of response-related muscles matures beyond the age of 12 years, whereas the latency of the cortical motor command to activate response-related muscles was similar in older children and young adults (Ridderinkhof & van der Molen, 1995; van de Laar et al., 2012). Moreover, it appears that stopping context does not modulate the dynamics of motor response execution, which is consistent with the
independence assumption underlying the race model of stop-signal processing (Logan & Cowan, 1984; Logan, 1994).

Developmental changes in stopping efficiency were studied using selective SSRT and partial inhibition rates. The latency of the covert selective stopping process, selective SSRT, followed a developmental pattern that is consistent with the literature; selective SSRT decreased with advancing age (Band, van der Molen, Overtoom, & Verbaten, 2000; Bedard, Nichols, Barbosa, Schachar, Logan, & Tannock, 2002; van de Laar, van den Wildenberg, van Boxtel, & van der Molen, 2011; van den Wildenberg & van der Molen, 2004b). Children showed an increase in the proportion of partial inhibits, as indexed by the rate of subthreshold EMG activity. Presumably, this increase in partial inhibition rate results from difficulties that children experience in inhibiting cortical motor outflow to the response hand and can be viewed as suboptimal response control (see also Bryce, Szucs, Soltesz, & Whitebread, 2010; Cragg, Fox, Nation, Reid, & Anderson, 2009).

**Proactive response slowing on go trials in the selective stop task**

A typical finding in the stop-signal processing literature is that responses to go signals in stop tasks are considerably slower than in choice RT tasks, even though explicit speed instructions and the tracking algorithm discourage adopting a strategy of delaying the response to the go signal (e.g., Bissett & Logan, 2011; Logan & Burkell, 1986; Ramautar, Kok, & Ridderinkhof, 2004; van de Laar, van den Wildenberg, van Boxtel, & van der Molen, 2010). This delay is also observed in the current study and can be considered as a ‘proactive’ control strategy in an attempt to increase the chance of successful inhibition upon stop-signal occurrence (e.g., Verbruggen & Logan, 2009). Two recent TMS studies showed that when participants knew that the upcoming response hand might have to be stopped, the cortico-spinal excitability associated with that response was reduced before go-signal presentation (Cai, Oldenkamp, & Aron, 2011; Claffey, Sheldon, Stinear, Verbruggen, & Aron, 2010). The current findings add to this literature by showing that EMG and contralateral M1 activation associated with the responding hand are also reduced during response execution on go trials in the selective stop task compared to the choice RT task. The results indicate that participants apply proactive response adjustments by reducing the excitability of the motor system to increase the chance to withhold the response when a stop signal appears (see also Cai et al., 2011).

Most importantly, the response slowing associated with the insertion of stop signals was also apparent in children, and even more so than in adults. In addition, children revealed a more pronounced contralateral negative wave than adults and might therefore need to delay the
response to the go signal relatively more compared to adults, to increase stopping success when confronted with a stop signal. However, children exhibited more partial inhibitions compared to adults, suggesting that the amount of proactive control exercised by children might not have been sufficient to suppress all central motor outflow to the responding hand. Moreover, developmental findings revealed that the relative reduction of the contralateral negative wave associated with proactive control in children was less pronounced than in adults. Apparently, the balance between proactive and reactive response adjustments might be shifted towards proactive control in children (see also van de Laar et al., 2011). Remarkably, the older child group did not differ from the younger child group in the amount of proactive response adjustment as evidenced by RT slowing. In both tasks, however, older children exhibited a larger contralateral negative wave than the younger child group. Thus, the need for delaying the go response could be even stronger for older relative to younger children, thereby reducing the age group difference in the strength of proactive control. Moreover, the delay in peripheral and central response processing associated with proactive control was not affected by age, suggesting that processes occurring upstream of M1 primarily contribute to the development of proactive control. Apparently, children proactively delayed the onset of M1 activation relative to stimulus onset to maintain the ability to inhibit on stop-signal trials.

**If inhibition failed**

According to the race model (Logan & Cowan, 1984), failed inhibits represent fast go responses that escaped inhibition and, thus, mean failed-inhibition RT should be shorter than mean go RT. The current findings are consistent with this prediction with one exception; failed-inhibition RT did not deviate from go RT in the young adult group. Analyses of response-related potentials revealed that fast go trials were associated with shorter pre-motor and motor times and with larger contralateral negative amplitudes compared to those associated with slow go trials (see also Tandonnet, Burle, Vidal, & Hasbroucq, 2003; Vidal, Burle, Grapperon, & Hasbroucq, 2011). In contrast, the analyses of response-related potentials revealed that motor time was longer on failed inhibits compared to go trials, which contributed to the RT lengthening on failed inhibit trials in adults. A recent study by Ko, Alsford, and Miller (2012) showed reduced response force associated with failed inhibits compared to go trials indicating that responses to the go signal do not escape inhibition but rather inhibition is insufficient to prevent response execution (see also van Boxtel, van der Molen, Jennings, & Brunia, 2001). The current results extends these findings showing that failed inhibits are also associated with reduced EMG output compared to go trials and, furthermore, the amplitudes of the contralateral negative wave did not
differ between failed inhibits and go trials. This pattern of findings might be indicative of an ultimate stopping attempt that nevertheless failed in the end. The reduction of EMG output associated with failed inhibition was more pronounced in adults compared to older children and appeared even absent in young children. Children also responded faster on failed inhibit trials relative to go trials unlike adults, indicating that their responses were too fast for the action control system to recruit inhibition. For successful inhibition of the response, the stop signal should have triggered the action control system to suppress M1 activity before the central motor command activates the muscles associated with the responding hand (Coxon, Stinear, & Byblow, 2009; van den Wildenberg, Burle, Vidal, van der Molen, Ridderinkhof, & Hasbroucq, 2010).

**Age-related differences in selective stopping strategy?**

The analysis of invalid stop-signal trials (i.e., trials on which the stop signal was to be ignored) revealed that invalid stop RT was substantially longer than go RT. Previously, we argued that this delay might be due to the initial arrest of all responses (global stopping) followed by stop-signal discrimination (is it blue or pink?) and the reactivation of the appropriate go response (van de Laar et al., 2010). The strategy of a ‘global stop followed by reactivation’ can be evaluated by examining response-related processes associated with fast invalid vs. slow invalid RTs. Typically, slow go responses are associated with prolonged pre-motor and motor times relative to fast go responses (see also e.g., Botwinick & Thompson, 1966; Osman, Moore, & Ulrich, 1995; Tandonnet et al., 2003). In contrast, the current findings revealed that motor and pre-motor times associated with slow invalid stop-signal trials did not significantly differ from fast invalid stop-signal trials. If the participant ignored the invalid stop-signal, one would expect longer duration of response-related processes on slow invalid stop-signal trials compared to fast invalid stop-signal trials. However, we observed similar durations of response-related processes associated with fast and slow invalid stop-signal processing, indicating that the invalid stop-signal was not ignored completely on those trials. Tandonnet et al. (2003) observed a decrease in pre-motor and motor times when the go response is prepared just prior to go-signal onset (optimal preparation condition) compared to when the response was prepared earlier relative to go-signal onset (suboptimal preparation). Concerning the present study, the go signal indicated response preparation on invalid stop-signal trials, resulting in a shorter duration of central and peripheral motor processes associated with slow invalid stop responses.

Importantly, invalid stop-signal processing was disproportionally longer in young children compared to older children, and longer in older children than adults. Band, van der
Molen, Overtoom, and Verbaten (2000) argued that age groups differ in stopping strategy when performing on a stop-change task (stop one response hand indicated by the go signal, but execute the opposite response hand); that is, children initially stopped all responses (global stopping) followed by reactivation of the opposite (appropriate) response. Conversely, young adults were able to stop one response hand selectively, resulting in a relatively short RT of the opposite response hand. The current data, however, are compatible with the notion that age groups differ in terms of the efficiency of the ‘stop-all first followed by reactivation’ strategy rather than in adopting different stopping strategies (see also Aron & Verbruggen, 2008; Cai et al., 2011; Claffey et al., 2010). In addition, it should be noted that the comparison of RTs associated with fast invalid vs. slow invalid stop-signal trials revealed that age effects on the duration of slow invalid stop responses was more pronounced relative to fast invalid stop responses. Such a disproportional age effect was not observed for pre-motor and motor times reflecting response-related processes. The pattern of results indicates that processes occurring upstream of M1 contributed to disproportional RT lengthening on invalid stop-signal trials in children. In sum, the results that emerged from the analysis of invalid stop-signal trials suggest that, compared to adults, young children are less efficient in the implementation of the ‘global stop followed by a reactivation’ process.

**Suppression of the incorrect response alternative**

An additional focus of the current study was on the positive Laplacian wave recorded over the ipsilateral M1 in relation to developmental changes in action control. Recent choice RT studies showed that the onset of the positive Laplacian wave preceded the onset of the negative Laplacian wave and was interpreted to reflect early inhibition of the ipsilateral M1 to prevent the execution of an incorrect response (Burle, Bonnet, Possamai, Vidal, & Hasbroucq, 2002; Burle, Vidal, Tandonnet, & Hasbroucq, 2004; Carbonnell, Hasbroucq, Grapperon, & Vidal, 2004; Meynier, Burle, Possamai, Vidal, & Hasbroucq, 2009; Vidal, Grapperon, Bonnet, & Hasbroucq, 2003). This pattern was replicated for adults in the choice RT task (see van de Laar et al., 2012).

A recent study by Meckler, Allain, Carbonnell, Hasbroucq, Burle, and Vidal (2010) showed that when the probability of responding in a block of trials was high (e.g., more right-hand responses than left-hand responses), pre-motor time was shorter and error rate was higher compared to the low response probability condition. Importantly, the onset of the ipsilateral positivity preceded the onset of the contralateral negativity despite probability condition. In the present study, analyses of the motor-related ipsilateral positivity in the selective stop task in
adults revealed several interesting findings. First, on go trials, the ipsilateral positivity started on average simultaneously with the onset of the negative wave. Second, failed inhibit trials revealed that the ipsilateral positivity preceded the contralateral negativity. Third, slow invalid stop-signal trials did not reveal a positive wave developing over the ipsilateral M1. Assuming that the ipsilateral positivity is a manifestation of the inhibition of the response alternative, the relative late implementation of inhibition onto the ipsilateral M1 indicates that the incorrect response was not inhibited prior to the built-up of the central motor command to the correct response. Consequently, this reduced error rate differences between go trials in the choice RT task (shorter pre-motor times) vs. selective stop task (longer pre-motor times) and between go trials (longer pre-motor times) vs. failed inhibits (shorter pre-motor times) in the selective stop task. These findings show the importance of the timing of the ipsilateral positive wave relative to the contralateral negative wave in preventing errors (e.g., Burle et al., 2004; Meynier et al., 2009). With regard to slow invalid stop-signal trials, the absence of a positive wave suggests that there was no inhibition of M1 that controls muscle activity associated with the incorrect (competing) response. Most likely, the incorrect response does not require inhibition during reactivation of the invalid stop response, since the go signal informed the adult regarding hand direction. Indeed, error rate was lower on invalid stop-signal trials compared to that of go trials. This interpretation is consistent with the findings reported previously by Carbonnell et al. (2004) and suggests that a choice RT trial is reduced to a simple RT trial when information is provided prior to the respond signal regarding hand direction (see also Burle et al., 2004; Meckler et al., 2010).

The absence of a positive wave on go trials in both child groups and the increased number of incorrect responses compared to adults supports the functional role of the positivity at the ipsilateral M1 to prevent motor activity to the incorrect hand (e.g., Burle et al., 2004; Meynier et al., 2009; van de Laar et al., 2012). The ipsilateral positive wave is likely a consequence of an active implementation of inhibition through higher-order functional brain areas that are responsible for top-down control, for example the preSMA (e.g., Kasess, Windschitlberger, Cunnington, Lanzenberger, Pezawas, & Moser, 2007; Nachev, Kennard, & Husain, 2008), that are not fully developed until adulthood (e.g., Casey, Giedd, & Thomas, 2000; Giedd, 2004; Nelson & Guyer, 2011; for a review see Casey, Tottenham, Liston, & Durston, 2005). How the exertion of control by the prefrontal cortex onto the motor cortex develops cannot be determined on the available data here and remains to be investigated.

A positive wave was clearly present on slow invalid stop-signal trials in the older child group. This indicates the ability of older children to implement inhibition at the ipsilateral M1
given additional time for response processing. Contrary to adults, older children displayed a negative developing wave at both the ipsilateral and contralateral M1 on go trials in both tasks (see also van de Laar et al., 2012). Negative activation recorded over the contralateral M1 is generally interpreted as a manifestation of cortical activity associated with the correct response (e.g., Tandonnet, Burle, Vidal, & Hasbroucq, 2006; Vidal et al., 2011). Presumably, older children were less able to select the correct response on go trials and, thus, the ipsilateral M1 requires inhibition on invalid stop-signal trials to prevent incorrect responses. The finding of simultaneous onsets for the contralateral negativity and ipsilateral positivity associated with slow invalid stop-signal trials in older children suggest that the implementation of inhibition at the ipsilateral M1 is still developing at the age of 12 years. It would be of considerable interest to examine developmental change in response accuracy in relation to the ipsilateral positive wave by speed vs. accuracy instructions.

The last point worth discussing refers to the pronounced negative developing waves at the contralateral and ipsilateral M1 on go trials observed in the older child group. In our previous study, we interpreted this pattern in terms of an enhanced focus on response speed of older children when performing the choice RT task (van de Laar et al., 2012). Previously, it has been found that response proneness to appealing incentives disrupts the ability to inhibit inappropriate actions during adolescence as compared to childhood and adulthood (e.g., Casey, Jones, & Hare, 2008; Somerville & Casey, 2010). In the present study, participants received feedback, regarding response speed and error rate associated with go trials. Thus, giving their response proneness, older children might have attempted to decrease RTs on go trials by recruiting motor responses, relatively, stronger and faster than the other age groups. This might have altered successful suppression of motor activity from cortical to peripheral motor structures. Indeed, the proportion partial EMG errors and partial inhibits did not discriminate between child groups while response speed did.

Summary and conclusions

Behavioral as well as electrophysiological examination of response activation and inhibition shows suboptimal action control in children. Three processes were identified contributing to the observed age-related changes in selective stop-task performance. First, children were less efficient in the implementation of inhibitory control than young adults. This was reflected by (i) longer selective stopping latencies (SSRT) in children compared to adults, (ii) a less efficient implementation of proactive control in children, as evidenced by pronounced response slowing and less reduction of M1 activity compared to adults, (iii) a smaller decrease in the amplitude of
response-related potentials associated with failed inhibit vs. go trials in children, and (iv) the absence of the ipsilateral positive wave in young children and the relatively late timing of the ipsilateral positive relative to the contralateral negative wave in older children. These findings indicate that children were less able to suppress cortical motor outflow to peripheral motor structures compared to adults, as evidenced by the high rate of partial inhibit and partial EMG errors in children.

Second, age groups did not differ in the deployment of a global vis-à-vis selective stopping strategy, but rather in the ability to implement a ‘global stop-reactivation’ strategy that was less efficient in children.

Third, older children were characterized by response proneness, which may have contributed to the absence of a developmental effect on proactive control and erroneous responses during childhood. This was reflected by pronounced contralateral and ipsilateral negative waves during go responses in older children that increased the chance of incorrect response inhibition. However, to maintain the ability to inhibit on stop-signal trials, older children proactively adjusted the response as much as young children.

The results that emerged from this study show that developmental change in action control reflects immature response activation and inhibition mechanisms in children and conform well with developmental literature showing that action control develops beyond childhood (e.g., Casey, Tottenham, Liston, & Durston, 2005; Friedman, Nessler, & Cycowicz, 2009; Szucs, Soltesz, Bryce, & Whitebread, 2009). Moreover, the findings also point to a different response strategy in older children that contributes to recent adolescence literature showing that motivational processes modulate developmental trajectories of cognitive control and provides useful direction for future work (e.g., Ernst, Romeo, & Anderson, 2009; Somerville & Casey, 2010).