Development of behavioral control: Analysis of performance and motor-related brain potentials
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Citation for published version (APA):
CHAPTER 6

Summary and conclusion
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The ability to control one’s behavior is essential in every day life. This control includes the execution of appropriate actions and the ability to interrupt or adjust these actions in order to meet external or internal demands. The execution and inhibition of action can be investigated using the stop-signal task (Logan & Cowan, 1984). This task allows for computing the latency of covert actions, in addition to latency and accuracy measures of overt actions. This dissertation examined the mechanisms involved in the execution and inhibition of actions in speeded response tasks and how action control change during the course of development from child- to late adulthood. The aim was to examine the temporal dynamics of response activation and inhibition by using performance measures as well as Laplacian transformed motor-related brain potentials. Here we review the main findings.

Exploring cognitive processing stages of global and selective inhibition

The study described in Chapter 2 examines the effect of additional stop-signal processing requirements on the inhibition latency by performing a chronometric analysis of the duration of global and selective inhibition. Mental chronometry assumes that the processing of information during the performance on speeded RT tasks consists of successive steps (stages) that entail, for example, the processes of signal detection and discrimination, response selection and the actual implementation of the response. The basic idea was that global inhibition (the inhibition of whatever response is activated by the go signal) is analogous to the go process in the Donders-a task (Donders, 1868/1969); there is only one stop signal and one stop response (the Stop-a task). The two selective stopping tasks corresponded to the Donders-b and -c tasks. In the Stop-c task there were two stop signals (the stop signal is either blue or pink) and only one stop signal required a stop response, whereas in the Stop-b task the two stop signals were mapped onto each hand and inhibition was required when the response indicated by the stop-signal corresponded to the response activated by the go-signal. The design of the present stopping tasks allowed us to assess the duration of distinct processing stages that might augment the lengthening of the selective inhibition process. Logan (1994) argued that the increase in stop-signal reaction time (i.e., SSRT) in selective stopping tasks compared to global stopping tasks is depended on the additional processing requirements that the inhibition process has to deal with to selectively stop the response. Thus, the inhibition latency associated with the Stop-c task was expected to be longer than the Stop-a inhibition latency because it requires the additional time to discriminate the two stop colors (is it blue or pink?). In addition, the Stop-b latency was expected to be
longer than the inhibition latency associated with the Stop-c task due to the added mapping requirement (is it blue-left or pink-right?).

The results revealed an orderly pattern of inhibition latencies; that is, the SSRT was longer in the Stop-c task compared to the SSRT of the Stop-a task, and the Stop-b SSRT was longer than the SSRT of the Stop-c task. This finding is consistent with previous studies investigating global and selective inhibitory control (e.g., Aron & Verbruggen, 2008; de Jong, Coles, & Logan, 1995; van den Wildenberg & van der Molen 2004a). Moreover, the stopping data reported in Chapter 2 revealed that the pattern of global and selective inhibition latencies appeared robust against manipulations of go-signal probability (see also Ramautar, Kok, & Ridderinkhof, 2004). The Donders’ subtraction method was applied to global and selective inhibition latencies to obtain the duration of two additional processing stages that were present when the response was to be selectively inhibited compared to global inhibition of the response. Thus, subtracting the SSRT attained in the Stop-a task from the SSRT in the Stop-c task provided an estimate of the duration of the signal-discrimination stage (34 ms), whereas the duration of the response-mapping stage was obtained by subtracting Stop-c latency from Stop-b latency (20 ms). This study shows that the Donders’ subtraction method is a useful tool for decomposing the stages involved in the processing of the stop signal – as has been shown previously for the processing of the go signal (e.g., Gottsdanker & Shragg, 1985; Hackley, Schäffer, & Miller, 1990; Vidal, Burle, Grapperon, & Hasbroucq, 2011). For the sake of comparison, the duration of the response-mapping stage attained from the b- and c-tasks, administered in the study by Hackley et al. (1990), contributed 6.5% to the go RT associated with the b-task, whereas the relative contribution of the response-mapping stage to the Stop-b inhibition latency in Chapter 2 was 8%. This suggests that the information-processing stages associated with the go process and with the inhibition process are highly similar in nature.

A novel aspect of the study in Chapter 2 was the focus on the performance on invalid stop-signal trials. Invalid stop-signal trials are trials on which the stop signal should have been ignored. Selective stop-signal studies revealed that the speed of responding on invalid stop trials is considerably delayed compared to that of responding on go trials (e.g., Aron & Verbruggen, 2008; Claffey, Sheldon, Stinear, Verbruggen, & Aron, 2010; Coxon, Stinear, & Byblow, 2006; Majid, Cai, George, Verbruggen, & Aron, 2011). The findings in Chapter 2 were consistent with this literature, indicating that the invalid stop-signal might not have been ignored on a large subset of invalid stop trials despite explicit going instructions. The longer RTs on invalid stop-signal trials were interpreted to reflect the deployment of a global stopping strategy on a subset of invalid stop trials; that is, the response was initially inhibited upon a stop-signal, followed by
the reactivation of the response after classifying the signal as invalid. This implied that the processing of the invalid stop-signal includes processing stages similar to stages of the selective inhibition process (i.e., the signal-discrimination stage in the Stop-b and Stop-c tasks, and the mapping stage in the Stop-b task) and a reactivation stage (see also van den Wildenberg & van der Molen, 2004b). The results revealed that the performance on invalid stop-signal trials provided information regarding the deployment of a global vis-à-vis selective stopping strategy by the participant, i.e., participants stopped responses globally on a subset of trials at the cost of response speed associated with invalid stop-signal processing.

Distinct lifespan trajectories for global and selective inhibition

In Chapter 3 we examined lifespan changes in global and selective inhibitory control in four different age groups (8-year-olds, 12-year-olds, young adults of 21-years-old, and a group of elderly adults of 76-years-old). The lifespan study of global inhibition reported by Williams, Ponesse, Schachar, Logan, and Tannock (1999) revealed that the speed of response inhibition improves from early childhood with advancing age until young adulthood and declines during senescence. This lifespan pattern of inhibition latencies was also observed for selective inhibition, i.e., when inhibition was based on the discrimination of two stop colors (Bedard, Nichols, Barbosa, Schachar, Logan, & Tannock, 2002). The study presented in Chapter 3 provided a direct comparison of age-related changes in the speed of global vs. selective inhibition along the lifespan, to examine whether global and selective inhibition follow different developmental trajectories. One stop signal was used in the global stopping task that instructed the participant to inhibit whatever response was activated by the go signal (global inhibition), whereas two stop signals were used in the selective stopping task that required the inhibition of the response to one (valid) stop signal but to execute the response to the other (invalid) stop signal (selective inhibition). The results revealed that global SSRT sharply decreased during childhood, followed by a less pronounced decrease during adolescence. Global SSRT was found to be shortest in the group of young adults and gradually increased during senescence. The lifespan pattern of selective inhibition latencies was similar to the lifespan pattern of global inhibition latencies with two exceptions. Firstly, the developmental gain in selective inhibition was similar during childhood and adolescence. And secondly, the speed of selective inhibition did not decline during senescence, implying that the elderly have just as much difficulty in inhibiting the response selectively as young adults do.

The finding that selective inhibition matures slower than global inhibition was previously reported by van den Wildenberg and van der Molen (2004a). Contradictory to our
findings, selective SSRT in the study of van den Wildenberg and colleague (2004a) did not differentiate between the two child groups. This discrepancy was most likely due to differences in design. Selective inhibition in their study was based on the motor end of selective inhibitory processing (inhibit the response only if the response activated by the stop and go signals correspond), whereas selective inhibition in Chapter 3 of the present dissertation was based on the perceptual discrimination of stop signals. The selective Stop-b task used in the study presented in Chapter 2 was highly similar as the selective stop task in the study by van den Wildenberg and van der Molen (2004a). Chapter 2 revealed that selective inhibition based on signal-response mapping is slower than selective inhibition based on signal discrimination of the stop signal. From these findings, it would be predicted that selective inhibition based on the signal-response mapping matures slower compared to selective inhibition based on the perceptual discrimination of stop signals, and selective inhibition based on signal discrimination matures slower than global inhibition that is based on signal detection.

In contrast to the study of Bedard et al. (2002), selective inhibition did not show a pronounced difference between young and elderly adults. A possible explanation for the absence of an age effect in the speed of selective inhibition was that the ability to inhibit a response was not impaired in the present group of elderly adults. However, this seemed highly unlikely since global SSRT was longer in elderly adults compared to that of young adults. Another, and more likely explanation, is that elderly adults might have initially stopped all responses on most of the selective stop trials, followed by reactivation of the response after complete invalid stop-signal processing. The difference between global vs. selective inhibition in elderly adults might therefore be considerably less than that of young adults, diminishing the age difference between the two adult groups. Claffey, Sheldon, Stinear, Verbruggen, and Aron (2010) observed that when participants applied a global stop strategy in a selective stop task, SSRT decreased while the go RT on invalid stop trials increased. Indeed, responses on invalid stop trials were considerably delayed in elderly adults compared to those of young adults. Moreover, it has been found that elderly adults have increased difficulty to reinitiate the correct response following the suppression of neural motor circuits (e.g., Vallesi, 2011). Thus, the aging-related response slowing on invalid stop trials might be taken to assume that the reactivation of the response takes considerably more time in elderly adults than in young adults. The results indicate the deployment of a global stop strategy in elderly adults when performing the selective stop task that decreased SSRT. Such a strategy might be an approach adopted by the elderly to resolve the higher cognitive control demands in the selective stop task at the cost of response speed on invalid stop trials.
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Lifespan changes in proactive and reactive response adjustments

Studies investigating performance adjustments in the stop-signal task observed that participants delay the response on go trials following a stop-signal trial (e.g., Rieger & Gauggel, 1999; Verbruggen, Logan, Liefoghe, & Vandierendonck, 2008), which is referred to as reactive response adjustments (Verbruggen & Logan, 2009). More specifically, the delay following successful inhibited stop trials was found to be due to the repetition effect of stimuli, i.e., the successful inhibited response automatically primes the inhibition process on the following go trial when the choice stimulus is repeated (the memory hypothesis, Verbruggen et al., 2008; see also Verbruggen & Logan, 2008). The delay following failed inhibition trials was attributed to the deployment of reactive control to increase inhibition success in case of stop-signal occurrence on the following trial (i.e., the goal priority hypothesis, see also Bissett & Logan, 2011). Another aim of the study presented in Chapter 3 was to investigate lifespan changes in reactive response adjustments in global and selective stop-signal tasks. Such investigation might provide valuable information regarding the development of the implementation of control procedures deployed by the participant when performing the stop-signal task. Age groups were compared on the speed of responding following successful inhibit, failed inhibit, and invalid stop trials relative to the speed of responding following go trials.

The results obtained for young adults revealed several interesting findings that seemed to be in line with the goal priority hypothesis proposed by Bissett and Logan (2011). Firstly, the delay of responses on go trials following stop-signal trials was more pronounced than the delay following go trials. This indicates that the slowing of the response is specifically related to the insertion of stop signals into the trial series. Secondly, response speed on go trials following stop-signal trials did not differentiate between successful inhibit vs. failed inhibit vs. invalid stop-signal trials. This finding suggests that the response delay is not related to the performance of the preceding stop trial, which rejects the memory hypothesis that suggests a larger response delay following successful inhibition compared to failed inhibition trials and only when the choice stimulus is repeated. This brings us to the third finding, i.e., the pattern of response adjustments was not altered by go-stimulus sequence. These findings were taken to suggest that the insertion of stop signals signaled the participant to be more cautious in responding by reducing their speed on go trials following stop-signal trials in order to increase inhibition success (e.g., Bissett & Logan, 2011).

Analysis of the developmental data revealed that child groups also delayed the response following stop-signal trials. However, and against to our expectations, the developmental findings did not differ from the young adult group in this regard. The absence of a
developmental effect in post-stopping adjustment indicated that this type of reactive control is already developed in children of 7 years of age. However, the inhibition results also revealed that reactive control to the stop signal (as reflected in SSRT) matures beyond the age of 12 years. Aron (2011) argued that the ability to implement reactive control procedures depends on the efficiency to recruit the neural mechanism associated with successful inhibition and the participants’ strategy when performing stop-signal tasks (for example, one might give priority to accuracy at the cost of response speed). Apparently, the developmental pattern of findings is difficult to interpret with the notion that reactive control associated with response inhibition vs. response execution matures at similar rates and point to the need for further developmental data in this field.

The findings associated with post-stopping adjustments obtained for the elderly differed somewhat from the results of the other age groups; that is, elderly adults did not delay the response on go trials following successful inhibited stop trials, but the slowing was considerably larger than the other age groups following failed inhibited and invalid stop trials. Moreover, elderly adults also delayed the response on go trials in the stopping tasks compared to the choice RT task considerably more than the other age groups. This type of control is referred to as proactive control and is interpreted in terms of a strategic response adjustment exercised by the participant to increase the chance of successful inhibition upon stop-signal occurrence (see also, Verbruggen & Logan, 2009). The pattern of results associated with aging indicated that the amount of proactive response adjustment exercised by the elderly affected the amount of reactive response adjustment following stop-signal trials. More specifically, the increase in go RT associated with proactive control in elderly adults was sufficient enough not to cautiously act on go trials following successful inhibited trials, indicating that the balance between proactive and reactive control is shifted more towards proactive control. However, the amount of proactive control was not sufficient on trials following failed inhibition and invalid stop trials. The response slowing on these trials might be another way for the elderly to prevent erroneous responses at the cost of response speed (e.g., Band & Kok, 2000; Ratcliff, Thapar, & McKoon, 2007). Therefore, the elderly might have exercised more proactive control in the stopping tasks and more reactive control following failed inhibited trials to increase the chance of successful inhibition. The reactive control elicited on go trials following invalid stop trials was suggested to be due to the extra time consumed by the reactivation processes of the response following global inhibition on invalid stop trials in the present group of elderly adults (e.g., Vallesi, 2011).
Lifespan changes in response processing on choice RT tasks

In Chapter 2 we dissected the inhibition process into several processing stages using Donders’ subtraction method. In the study presented in Chapter 4, we fragmented the reaction process using response-related electrophysiological indices to examine the contribution of the primary motor cortex (M1) to lifespan changes in response speed. Only a handful of developmental and aging studies dissected the reaction process using response-related ERP components. The developmental studies mainly focused on age-related changes in the ability to resist interference, i.e., a task that activates two responses simultaneously while only one response is appropriate (Bryce, Szucs, Soltesz, & Whitebread, 2010; Ridderinkhof & van der Molen, 1995; Szucs, Soltesz, Bryce, & Whitebread, 2009; Szucs, Soltesz, Jarmi, & Csepe, 2007). The studies that investigated age-related changes in response speed using response-related potentials compared a group of young adults with a group of elderly adults only (Falkenstein, Yordanova, & Kolev, 2006; Kolev, Falkenstein, & Yordanova, 2006; Yordanova, Kolev, Hohnsbein, & Falkenstein, 2004). The results that emerged from the aging studies revealed that the response-related stages of the RT process contributed most significantly to the age-related response slowing.

Chapter 4 examined whether response-related stages of RT are differentially sensitive to age-related change along the lifespan using a choice RT task. This task required a left- vs. right-hand response to left- and right-pointing arrows, respectively. Response-related electrophysiological indices were obtained from four age groups (8-, 12-, 21-, and 76-year-olds). The onset of the central motor command (derived from either the Lateralized Readiness Potential, i.e., LRP, or the contralateral negative Laplacian wave) and the onset of peripheral motor muscles (EMG) associated with the correct response were used to dissect the RT into three intervals: 1) the pre-selection time, from stimulus onset to the onset of the central motor command, 2) the pre-motor time being the interval between the onset of the central motor command and EMG onset, and 3) the motor time, from EMG onset to overt response. The results revealed the typical U-shaped lifespan pattern of RTs on go trials (e.g., Cerella & Hale, 1994); that is, go RT sharply decreased from the younger child group (8-year-olds) to the older child group (12-year-olds) with a less pronounced decrease from the older child group to young adults (21-year-olds). RT increased again from the young adult group to the group of elderly participants (76-year-olds). Analyses of processing stages revealed that pre-selection time was prolonged in the younger child group compared to the other age groups. Furthermore, pre-motor was longest in elderly participants while being shortest in young adults. Additionally, motor time was longest in young children while being shortest in young adults. The age-related pattern of findings suggested distinct developmental trends in the duration of the processing stages.
Moreover, the pre-motor and motor intervals showed most pronounced age effects, indicating that response-related stages contribute most significantly to lifespan changes of the reaction process. The age-related pattern associated with the pre-motor interval revealed little difference between the LRP and Laplacian ERP procedures. However, the Laplacian method was favored over the LRP, since all of the children showed a negative Laplacian wave at the contralateral M1, whereas only half of the children exhibited a LRP. The data of the younger child group were interpreted to suggest slowness in stimulus processing and a less efficient response recruitment and preparation system. The data pattern obtained for the older children suggested that the motor system is still developing beyond the age of 12 years. The findings of the elderly were consistent with previous reports implying slowness in response activation processes (partly) due to their precautious response strategy that favors accuracy over speed (e.g., Starns & Ratcliff, 2010). The findings of the ipsilateral positive Laplacian wave provides support for the deployment of a conservative response strategy in elderly and will be discussed further in the section “A lifespan analysis of the ipsilateral positive wave vis-à-vis erroneous reactions”.

**Developmental change in action control: A response processing perspective**

The results reported in Chapter 4 revealed that response-related stages of information processing contributed most significantly to the age-related changes in response speed. Moreover, the Laplacian procedure was favored over the LRP due to the presence of a negative developing Laplacian wave over M1 in all children. These findings were used to guide the examination of the development of response activation and inhibition in a selective stop-signal task. This study is presented in Chapter 5. The main goal was to assess the impact of the insertion of stop signals on response activation. Such an analysis might reveal potentially interesting differences between children and adults in action control. The only two developmental studies that investigated age-related change in inhibitory control using ERPs focused on N200 and P300 components associated with stimulus processing in a global stop-signal task, but they did not focus on response-related motor potentials (Dimoska, Johnstone, Chiswick, Barry, & Clarke, 2007; Johnstone, Dimoska, Smith, Barry, Pleffer, Chiswick, & Clarke, 2007). The few stop-ERP studies that include an analysis of M1-related activity often report the LRP and focused primarily on comparing the outcomes of successful vs. failed stop-signal processing in a group of young adults only (de Jong, Coles, & Logan, 1995; de Jong, Coles, Logan, & Gratton, 1990; van Boxtel, van der Molen, Jennings, & Brunia, 2001). The results that emerged from these studies showed that the LRP associated with failed inhibit trials is larger than that of successful
inhibit (i.e., the absence of hand muscle activity, reflected in EMG activity, and overt button press on a stop trial), indicating that an inhibition mechanism exerted suppression on M1 activity during stop-signal inhibition.

The study presented in Chapter 5 provided a detailed analysis of response selection, activation and inhibition processes to uncover age-related differences in selective stopping performance. Two child groups (8- and 12-year-olds) and a group of young adults (21-year-olds) performed a choice RT task and a selective stop-signal task. The choice RT task involved left- and right-hand responses to left- and right-pointing arrows (go signals), respectively. The selective stop task involved responding to similar go signals, but on some trials the go signal was followed by either a ‘valid’ stop signal, that required the inhibition of the response to the go signal, or by an ‘invalid’ stop signal that required a go response indicated by the go signal. Invalid stop-signal could be ignored. Response-related motor potentials were analyzed using the negative Laplacian wave over the contralateral M1 and EMG associated with the correct response. Responses on go trials in the selective stop task were directly compared with (i) go responses in the choice RT task, (ii) go responses on valid stop trials (failed inhibited trials), and (iii) go responses on invalid stop trials. According to the findings reported in Chapter 2 (see the section ‘Processing of global and selective stop signals’), we divided invalid stop-signal responses into a fast response and a slow response part. We then compared these trial categories with fast and slow responses on go trials to capture invalid stop-signal processing. The study presented in Chapter 5 is the first to reveal evidence for the impact of stop-signal processing on central and peripheral response activation in relation to development.

The results of go trials replicated and extended the developmental pattern of findings of response-related potentials in Chapter 4, showing that pre-motor time was longer in young children compared to those of older children and young adults in the choice RT task as well as in the selective stop task. This shows that the development of motor response execution was not affected by the anticipation of stop signals. Additionally, the comparison between tasks on RTs of go trials showed that all age groups delayed their go response in the selective stop compared to the choice RT task, an effect that is referred to as proactive response adjustment exercised by the participant to increase the chance of successful inhibition upon stop-signal occurrence (see also, Verbruggen & Logan, 2009). Most importantly, and in line with literature, this strategic response adjustment was most pronounced in children (van den Wildenberg & van der Molen, 2004a). This developmental effect was additionally examined by analyzing response-related potentials associated with proactive response adjustment. The analysis revealed a reduction of cortical motor activity (reflected in lower contralateral negative amplitudes) during response
execution on go trials in the selective stop compared to the choice RT task in each of the three age groups. This finding indicates that proactive control strategy exerted on response-related potentials, presumably to reduce the excitability of the motor cortex to prevent inhibition failure (see also Cai, Oldenkamp & Aron, 2011; Claffey, Sheldon, Stinear, Verbruggen, & Aron, 2010). However, this reduction was larger in adults than in children. This points to age-related differences in the implementation of proactive control; whereas adults were able to reduce their levels of cortical motor output (as reflected in reduced contralateral negative Laplacian amplitudes), children seem to delay the response in the stop context due to a less efficient suppression mechanism (as evidenced by RT slowing).

The inefficiency of the suppression mechanism in children was also manifested in the developmental pattern of response-related potentials associated with failed inhibit trials. According to the horse-race model (Logan & Cowan, 1984), failed inhibit responses are fast go responses that escaped inhibition. Fast go responses are typically associated with higher response-related potentials compared to that of slow go responses (e.g., Tandonnet, Burle, Vidal, & Hasbroucq, 2003; Vidal, Burle, Grapperon, & Hasbroucq, 2011). However, the analysis of response-related potentials revealed that EMG amplitudes associated with failed inhibits were lower compared to that of go trials. In this regard, at least a category of failed inhibits can be viewed as signs of inhibition insufficient to prevent overt responding because central motor processes progressed too far (van Boxtel, van der Molen, Jennings, & Brunia, 2001). Moreover, young children showed relatively less reduction and adults more reduction of EMG amplitudes associated with failed inhibits. This finding was interpreted to reflect the implementation of an inhibition mechanism that was insufficient in adults as well as immature in children (van Boxtel et al., 2001).

Invalid stop-signal trials were analyzed to investigate whether age groups differed in global vis-à-vis selective stopping strategy. Band, van der Molen, Overtoom, and Verbaten (2000) argued that age groups differed in stopping strategy when performing a stop-change task. They suggested that children initially inhibited the response to the go signal (global stopping) followed by reactivation of the opposite response, whereas adults were able to stop one response hand selectively while maintaining response speed with the opposite response hand. The results presented in Chapter 5 are not in agreement with this literature. Moreover, the analysis of response-related potentials associated with invalid stop trials revealed that age groups differed in terms of processing efficiency of the ‘global stop followed by a reactivation’ process, rather than stopping strategy. First, response-related potentials did not differ between fast and slow invalid stop trials, indicating that the invalid stop-signal was not ignored in each of the three age
groups (slow response trials are typically associated with longer pre-motor and motor times than fast response trials, e.g., Botwinick & Thompson, 1966). Second, slow invalid RT was more affected by age than fast invalid RT, and this age effect was not observed for the duration of response-related processes. This latter finding indicates that processes occurring upstream of M1 contributed to the age-related invalid RT lengthening. These findings were carefully interpreted to indicate age differences in the implementation of the ‘global stop followed by a reactivation’ process (see also Aron & Verbruggen, 2008; Cai et al., 2011).

The results that emerged from Chapter 5 showed that suboptimal action control in children underlies age-related changes in selective stopping performance. Moreover, the findings show that the immature suppression mechanism and the less efficient implementation of the ‘global stop followed by a reactivation’ process in children underlie performance differences between age groups in a selective stop task.

A lifespan analysis of the ipsilateral positive wave vis-à-vis erroneous reactions

An additional focus of Chapters 4 and 5 was on the positive Laplacian wave recorded over the ipsilateral M1 in relation to age-related changes in response activation. Recent choice RT studies observed a phasic positive Laplacian wave developing over the ipsilateral M1 approximately 100 ms prior to the overt correct response, and this positive wave precedes the onset of the negative Laplacian wave recorded over the contralateral M1 (e.g., Taniguchi, Burle, Vidal, & Bonnet, 2001; Vidal, Grapperon, Bonnet, & Hasbroucq, 2003). This early positive deflection is interpreted to reflect early inhibition of the ipsilateral M1 to prevent the execution of an incorrect response during choice reactions (e.g., Burle, Vidal, Tandonnet, & Hasbroucq, 2004; Carbonnell, Hasbroucq, Grapperon, & Vidal, 2004; Meynier, Burle, Possamaï, Vidal, & Hasbroucq, 2009). One of the aims of Chapters 4 and 5 was to examine the development of the control of the incorrect response alternative using the onset of the ipsilateral positive wave relative to the onset of the contralateral negative wave. Chapter 4 focused on lifespan changes of the ipsilateral positive wave during choice reactions in a choice RT task, whereas Chapter 5 examined the ipsilateral positive wave during choice reactions in a selective stop task in two child groups and a group of young adults. The studies presented in Chapter 4 and 5 were the first in providing data regarding the ipsilateral positive wave in children and elderly adults.

The choice RT data obtained from young adults reported in Chapter 4 is in agreement with previous reports showing that the onset of the ipsilateral positive wave precedes the onset of the contralateral negative wave (e.g., Vidal et al., 2003). Most importantly, the ipsilateral
positive wave was absent in the two child groups, whereas the positive wave started simultaneously with the onset of the negative wave in elderly adults. Children also committed more choice errors than adults. The absence of the ipsilateral positive wave together with more choice errors were interpreted as manifestations of the inefficiency of the inhibition mechanism in children.

The two adult groups did not differ in overt error rates, but elderly adults displayed a larger proportion of partial EMG errors compared to young adults. The latter finding may be due to the relative late implementation of ipsilateral inhibition. The similar overt error rate between the two adult groups was interpreted to reflect a precautious response strategy in elderly adults that increased RTs in favor of accuracy (Mattay, Armand, Kirkwood, Yang, Davis, et al., 2002). These findings indicate the functional significance of the ipsilateral positive wave in preventing motor activity from the ipsilateral M1 to the hand muscles associated with the incorrect response alternative (see for a review Burle, Vidal, Tandonnet, & Hasbroucq, 2004) and contribute to the maturational change of action control in children and elderly adults.

The analysis of the ipsilateral positive wave in the study described in Chapter 5 revealed several interesting findings. First, young adults displayed a clear positive Laplacian wave over the ipsilateral M1 during response execution on go trials and failed stop trials, indicating that ipsilateral M1 activity was suppressed prior to response execution. Second, young children did not show a positive wave, indicating that ipsilateral M1 activity was not suppressed prior to correct response execution. And third, the positive wave was also absent in the older child group, except on slow invalid stop trials. The absence of ipsilateral M1 inhibition likely contributed to the increased number of choice errors in children compared to adults, showing again the important role of ipsilateral M1 inhibition in preventing choice errors, also when the task has a stopping requirement. Remarkably, older children revealed a positive wave at the ipsilateral M1 on slow invalid stop trials, indicating that they were able to inhibit the ipsilateral M1 prior to correct response execution. Presumably, the late response on invalid stop trials gave the older child some time for the suppression mechanism to come into play and suppress ipsilateral cortical activity. However, the finding of simultaneous onsets for the contralateral negative and ipsilateral positive waves suggests that the suppression mechanism is still developing at the age of 12 years. The implementation of inhibition onto the ipsilateral M1 is likely top-down controlled (e.g., Burle et al., 2004) by frontal brain mechanisms that are not fully developed until adulthood (e.g., Casey, Tottenham, Liston, & Durston, 2005).
Are young adolescents response prone?

The adolescence stage is a transitional period in human development with an average onset between the ages of 10 to 13 years (Spear, 2000). The behavioral changes that occur during the adolescence stage have received increased interest over the past decades. For example, it has been found that adolescents have a heightened responsiveness to stimuli that are of a personal relevance, which disrupts the ability to inhibit inappropriate actions (e.g., Casey, Jones, & Hare, 2008). The findings of Chapters 4 and 5 seem to point to an enhanced focus on response speed in the group of older children, which might have affected their efficiency of response inhibition. Firstly, the negative developing wave recorded over the contralateral M1 was more pronounced in older children compared to those of the other age groups, indicating that older children activate M1 more than the other age groups prior to response execution. Furthermore, the proportion of partial inhibits (i.e., stop-signal trials with subthreshold EMG activity) did not discriminate between child groups while the speed of responding did (Chapter 5). Secondly, older children also revealed a pronounced negative wave recorded over the ipsilateral M1. This likely reflects the manifestation of cortical activation associated with the incorrect response alternative. Likewise, the two child groups did not differ in partial EMG error rate while response speed did (Chapters 4 and 5). This pattern is suggestive for a relative overactivation of M1 in older children. Thus, older children are response prone which affected their ability to exert inhibition of alternative responses in the case of a go signal and inhibiting correct responses in the case of a stop signal.

Conclusion

The research described in this dissertation contributes to the developmental literature, augmenting the understanding of developmental changes in action control; most notably in response selection, activation and inhibition. Several conclusions can be drawn from this dissertation. First, the processing of the stop signal is highly similar in nature as the processing of the go signal (see also Logan, 1994). Donders (1868/1969) applied the subtraction method on reaction processes derived from three tasks that ought to differ with respect to one processing stage. By applying this method to inhibition latencies (Chapter 2), we were able to capture the latency of two distinct inhibitory processing stages, namely the processing duration of (i) the signal-discrimination stage obtained when inhibition was required based on the discrimination of two stop colors (selective inhibition) compared to a stop-all response task (global inhibition) and (ii) the response-mapping stage that was included in the condition when inhibition was
based on correspondence of stop and go signals compared to the signal-discrimination condition. This shows that the prolonged inhibition process, like that of the go process, is due to additional stages of information processing (van den Wildenberg & van der Molen, 2004a). In Chapter 4 we used the onsets of response-related potentials to fragment the reaction process in three processing stages and we examined whether stimulus- and response-related stages of RT are differentially sensitive to age-related change along the lifespan. The findings fit well with the developmental and aging literature showing that response-related stages of the reaction process contributed most significantly to age-related change in the speed of response execution (e.g., Bashore, Ridderinkhof, & van der Molen, 1997; Szucs, Soltesz, Bryce, & Whitebread, 2009). Furthermore, age differences cannot be explained by a generalized age effect on information-processing speed. The lifespan findings indicated suboptimal action control in children and elderly that affected their performance.

Second, this dissertation contributed to the stop-signal literature by providing a lifespan analysis of age-related change in global vs. selective inhibition. Van den Wildenberg and van der Molen (2004b) observed that the speed of global and selective inhibition is slower in children compared to adults, however selective inhibition matured slower than global inhibition. The present dissertation confirmed and extended these findings by showing that the developmental gain of global inhibition during childhood was larger than that of selective inhibition, but, with advancing age from young adulthood, the speed of global, but not selective, inhibition declines during senescence. The finding that global and selective inhibition followed different developmental trajectories was interpreted to indicate that selective inhibition imposed higher cognitive control demands in children and elderly adults than global inhibition, but the elderly resolved this issue by deploying a global stop strategy (canceling all responses to whatever stop signal appears) that benefits selective response inhibition. The global vis-à-vis selective inhibition strategy was evaluated by examining invalid stop-signal trials in Chapters 2, 3 and 5. The considerable delay in the speed of responding on invalid stop trials compared to on go trials was more pronounced in the elderly compared to children, and more in children than in adults. This indicates that the ‘global stop followed by a reactivation’ process was particularly time-consuming in the elderly (e.g., Vallesi, 2011) (Chapter 3). It was argued by Band, van der Molen, Overtoom, and Verbaten (2000) that children and adults differ in global vs. selective inhibition strategy. However, the analysis of response-related potentials associated with invalid stop processing suggested that adults also applied a global stop strategy on a proportion of invalid stop trials (Chapter 5). In addition, children were less efficient than adults in the
implementation of the ‘global stop followed by a reactivation’ process that underlies performance differences between age groups during selective inhibition.

Third, this dissertation provided a lifespan perspective on the implementation of proactive and reactive control procedures. We observed that all age groups delayed the go response (i) in stop-signal tasks compared to a choice RT task (Chapters 2, 3, and 5) and (ii) following stop-signal trials compared to go trials in stop-signal tasks (Chapter 3). This delay was attributed recently to the deployment of, respectively, proactive and reactive control in stop-signal tasks to increase inhibition success (e.g., Bissett & Logan, 2011; Verbruggen & Logan, 2009). The lifespan findings revealed that the amount of proactive control and reactive control following failed inhibited trials was more prominent in elderly adults compared to the other age groups, indicating the deployment of a precautious response strategy in elderly adults to prevent inhibition failure. In children, the amount of reactive control following stop-signal trials did not differ from adults, suggesting that the deployment of this type of reactive control is already in place and fully developed in children of 7 years of age. The development of proactive control until early adulthood was additionally examined using response-related potentials (Chapter 5). The results that emerged from this analysis contributed to the work of Cai, Oldenkamp and Aron (2011) and Claffey, Sheldon, Stinear, Verbruggen, and Aron (2010), showing a reduction of the excitability of M1 to prevent inhibition failure. The reduction of response-related potentials associated with proactive control was less pronounced in children, indicating a less efficient suppression mechanism. The response adjustment associated with the insertion of stop signals was more prominent in children however, M1 was also stronger activated in children than in adults during response execution. Thus, pronounced response slowing in children was to maintain the ability to inhibit on stop-signal trials at the cost of the efficiency of proactive control.

Fourth, this dissertation is the first in providing a lifespan analysis of ipsilateral M1 activity that controls the incorrect response alternative. The results were consistent with previous reports showing the functional significance of the positive Laplacian wave in inhibiting ipsilateral M1 to prevent incorrect response execution. Although the positive wave was clearly present in elderly adults, its timing was relatively late compared to young adults indicating a decline in temporal efficiency of the inhibition mechanism in the elderly. However, to prevent incorrect responses, elderly adults applied a conservative response strategy that benefits accuracy over response speed. In young children, the positive wave was absent, indicating that they did not implement inhibition onto the ipsilateral M1 to prevent incorrect responses. These findings support theories suggesting that ipsilateral M1 inhibition is top-down controlled (i.e.,
Summary and Conclusion

Burle, Vidal, Tandonnet, & Hasbroucq, 2004), presumably the frontal cortex that is not fully developed in children (Casey, Tottenham, Liston, & Durston, 2005). Older children were able to implement inhibition but only with postpone responding. The findings associated with the older child group indicate that their action focus disrupted the efficiency of response inhibition.

This dissertation shows that Laplacian transformation of ERP signals provides a useful tool to study motor cortical processes underlying age-related changes in response activation and inhibition, and may specify physiological correlates of performance differences between age groups. The results of the empirical chapters show that developmental change in action control does not only reflect inhibitory deficits but also varying response strategies across age groups. This may have consequential effects on studies investigating inhibitory processing between age groups or between groups of individuals with inhibitory deficiencies. Differences in strategy might be hidden in developmental or clinical data and results should be explained in light of the task-related inhibitory components, and should also consider strategic differences between groups of individuals. Future research needs to actively address these issues, perhaps in conjunction with motor-related electrophysiological indices to capture information regarding how the response is executed. A valuable follow-up study would be one that manipulates the frequency of correct and incorrect responses together with response speed manipulations to assess age-related response strategies. This dissertation focused primarily on motor structures. Future studies focusing on areas upstream of M1 are needed to confirm and investigate top-down M1 control. The results of the studies of Vidal and colleagues (2003/2011), which linked activation of the presupplementary motor area (preSMA) and M1 to activations of hierarchically organized systems with SMA acting upstream in the hierarchy of the motor command, provides promising directions for future work. Subsequently, an examination of the development of this hierarchically organized system, during stop task performance, might help to elucidate action control processes in normal developing children, however it might also be useful in atypical developing children, for example those suffering from Attention Deficit Hyperactive Disorder (i.e., ADHD) so as to solve the debate whether the core deficit of the disorder is purely attention related or is also inhibition related.

In closing, the present dissertation provided a behavioral and electrophysiological analysis of response activation and inhibition to uncover age-related changes in action control. The results indicated suboptimal action control in children and elderly that might cause failure to prevent inappropriate behavior in everyday life situations, especially under increased environmental demands. Over the course of development, people change their focus towards the behavior that appears to be for themselves of the most relevance. Young children are more
passively involved when action is required and when they do act, they do it relatively uncontrolled. Young adolescents tend to have an enhanced focus on action and therefore are more prevalent to acting before they give a thought about the consequences. Whereas the elderly act in an overcautious manner by decelerating their reaction to prevent inappropriate behaviors. However, this may not always be the proper course of action, as life sometimes requires us to react rapidly to make sure the appropriate behavior is carried out.

...So *think* before you jump, however, do jump *quickly*!