Lifespan changes in motor activation and inhibition during choice reactions: A Laplacian ERP study

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ABSTRACT

Response speed improves from childhood to early adulthood and declines steadily with advancing age. The present event-related brain potential (ERP) study explored the contribution of the primary motor cortex (M1) to lifespan changes in response speed and accuracy using a choice reaction time (RT) task. Two groups of children (8 and 12 years) and two groups of adults (21 and 76 years) responded to left- or right-pointing arrows. RTs showed a typical U-shaped lifespan pattern. RT was segmented into pre-selection time, pre-motor time, and motor time by using the onset of the central motor command (i.e., LRP, and the negative Laplacian potential) and the onset of response-related EMG. Pre-motor time was most sensitive to age-related change. In addition, the positive Laplacian potential, assumed to be associated with inhibition of the incorrect response alternative, was absent in children. In adults, the onset of the ipsilateral positivity started before the onset of the contralateral negativity but in elderly the onsets occurred approximately at the same time. This pattern of findings is consistent with the observed differences in choice error rates between age groups. Taken together, the lifespan changes in motor potentials point to suboptimal motor response control in children and the elderly compared to young adults.

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1. Introduction

Adaptive behavior in response to environmental demands requires the selection of appropriate actions according to internal goals. Developmental and cognitive aging studies on action selection showed that children as well as the elderly respond considerably slower than adults across a variety of tasks (e.g., Cerella and Hale, 1994; Kail, 1993; Salthouse, 1996, 2000). Consider for example a choice situation that requires the discrimination of two visual signals (e.g., a circle and a square) by pressing a button with either the left or right hand. Typically, choice reaction time (RT) sharply decreases from childhood to adolescence, followed by a less pronounced decrease from adolescence to early adulthood (Kail, 1991). RT is shortest in early adulthood and steadily prolongs with advancing age (e.g., Cerella and Hale, 1994). This typical U-shaped pattern is observed for a wide range of RT tasks differing in complexity (e.g., Myerson et al., 1990). The processes that underlie this characteristic developmental change in response speed have been subject of several lines of investigation.

One such approach toward understanding age-related changes in response speed in normal development and healthy aging focused on processing stages (e.g., Band et al., 2002; Hale, 1990; Kail, 1993). According to this framework, information processing entails distinct stages that contribute to RT differences (Luce, 1986). For example, the discrete-stage model by Sternberg (1969) assumes that each processing stage develops over time in a consecutive manner and that the start of information processing at later stages of the RT process is dependent on the finishing time of the preceding stage. By contrast, Eriksen and Schultz (1979) conceptualized the reaction process in terms of a continuous flow of information. That is, information extracted from the stimulus primes the response system and response activation is held in check until sufficient information is available for executing the correct response.

The interpretation of age-related change in the speed of information processing has been the subject of much debate. Some theories postulate that the age-related changes in information processing speed are modulated by a global mechanism rather than by specific age-sensitive components (e.g., Cerella and Hale, 1994; Salthouse, 2000). The notion of such a global mechanism attracted

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different interpretations. The neural-noise hypothesis, for example, assumes that the neural signal-to-noise ratio throughout the central nervous system underlies lifespan changes in the speed of information processing (Crossman and Szafran, 1956, but see also Kail, 1997; Salthouse and Lichty, 1985). As a consequence, additional information processing steps lead to an increase in information loss and, thus, to the slowing of response speed (see Myerson et al., 1990). Therefore, it is not surprising that over the last two decades, much of the developmental and aging research focused on general processes, such as processing speed (Salthouse, 1991). Such attempts to identify general components that are most sensitive to the effects of advancing age include analysis of processing stages or psycho-physiological measures.

The interpretation of the U-shaped relation between information-processing speed and advancing age in terms of a global mechanism has been challenged by event-related potentials (ERPs) that represent cortical activity associated with cognitive performance. Lifespan studies have examined the relation between the speed of responding and the P300 (e.g., Bashore et al., 1989; Kutas et al., 1977; Travis, 1998), an ERP component that has been associated with stimulus processing and is little affected by response demands (Magliero et al., 1984). Thus, P300 latency has been used to test whether stimulus- vs. response-related stages of information processing are differentially sensitive to age-related change. Using this approach, a meta-regression analysis by Bashore et al. (1989) showed that the age-related slowing with advancing age during adulthood was more dramatic for RT compared to P300 latency, which seems to present a serious challenge to the notion of global slowing (see also Bashore et al., 1997a).

The aim of the present experiment was to dissect RT by using response-related brain potentials and to assess whether response-related stages of RT are differentially sensitive to age-related change along the lifespan. Studies using ERPs in healthy adults showed that when initiating a response, neurons located in the primary motor cortex (M1) reach a particular level of activation that is expressed by a negative potential recorded over the hemisphere contralateral to the responding hand. The difference in activation between the contralateral and ipsilateral M1 is expressed in the *lateralized readiness potential* (LRP, Coles, 1989; Coles et al., 1988; Gratton et al., 1988). The initial negative deflection of the LRP trace preceding the overt response is taken to reflect the start of the inter-hemispheric difference in motor activation. LRP onset has been used to bisect the RT in two differential processing parts: (1) the pre-selection interval; from stimulus onset to LRP onset, including stimulus-evaluation processes up to response selection, and (2) the post-LRP interval; from LRP onset to the overt response, indexing processes related to response activation (e.g., Osman et al., 1995). These intervals are sensitive to stimulus- and motor-related manipulations, respectively (Miller and Ulrich, 1998). Surprisingly, only a handful of LRP studies applied this technique to investigate the differential sensitivity of pre-selection vs. post-selection stages of RT to advancing age (Bryce et al., 2010; Ridderinkhof and van der Molen, 1995; Szucs et al., 2007, 2009). Ridderinkhof and van der Molen (1995) used a version of the Eriksen flanker task (Eriksen and Eriksen, 1974) that required responding to target stimuli while ignoring surrounding distracter stimuli. This setup activates two responses simultaneously; the activation of the correct response to the target and the activation of the competing incorrect response to the distractors that should be withheld. Their results showed that LRP onset varied with age, much like RT; the pre-selection interval was prolonged in the youngest child group and shortest in the adult group. The studies of Bryce et al. (2010) and Szucs et al. (2009) used a child version of the Stroop task that required a response to an animal picture that is larger in real-life compared to another depicted animal while ignoring the size of the figures. Stroop interference was more pronounced in children than adults. Importantly, the

timing of LRP onsets was consistent with the slower RT of children compared to adults, suggesting that the maturation of the motor system is crucial for inhibiting competing motor plans. Likewise, a prolonged interval from LRP onset to overt response has been found in older adults compared to young adults, using a mental rotation task (Band and Kok, 2000), simple and choice RT tasks (Yordanova et al., 2004) and a motion-onset task (Roggeveen et al., 2007). These results were interpreted in terms of a decline of cortical motor structures that are crucial for selecting the correct response thereby impairing performance in elderly individuals.

At this point, it should be noted that the LRP is a compound measure that does not take into account the specific contribution of the activation processes recorded over the contralateral M1 (related to the responding hand) and the ipsilateral M1 (related to the non-responding hand). An alternative procedure that attempts to separate motor-related activity between the two hemispheres is the Laplacian transformation of EEG signals (e.g., Tandonnet et al., 2005; Taniguchi et al., 2001; Vidal et al., 2003). The Laplace transform is a technique that reduces contributions from remote sources and decreases the blurring effect of the skull (Nunez et al., 1994). The signal at each electrode is first interpolated followed by computing the spatial second derivative of the interpolated signals (for further information regarding the calculations see Perrin et al., 1989). This procedure can improve the spatial resolution from 6–9 cm up to about 2–3 cm, depending on the quantity of spatial sampling, by removing the blurring effects of the currents evoked by the low conductance of the skull (Babiloni et al., 1998; Nunez, 1981). In this regard, the Laplacian transformation also improves the temporal resolution of the EEG potentials (Law et al., 1993).

Using the Laplacian transformation of ERP signals, Vidal et al. (2003) observed that the contra- and ipsilateral M1 show an opposite electrical pattern around the time of the overt choice response (e.g., Meynier et al., 2009; Tandonnet et al., 2003; Taniguchi et al., 2001). Specifically, they observed a phasic negative potential contralateral to the responding hand that reached its maximal amplitude just before the overt response. In addition, a positive wave was observed over the ipsilateral M1 with an onset that preceded the onset of the contralateral negative wave (see also Praamstra and Seiss, 2005). According to Tandonnet et al. (2003), the degree of contralateral negativity likely reflects the strength of the motor command associated with the correct response whereas the magnitude of the ipsilateral positivity was interpreted to reflect cortico-spinal inhibition of the incorrect response that prevents activation of the muscles controlling the incorrect response alternative (see for a review Burle et al., 2004).

To date, no studies have applied Laplacian transformations to examine age-related change in RT during development and only few studies compared elderly adults to younger adults (Falkenstein et al., 2006; Kolev et al., 2006; Yordanova et al., 2004). Analyses of the contralateral negative potential in elderly adults during a choice response task suggested that the motor cortex was activated for a longer period of time and that activation levels were higher compared to young adults (Kolev et al., 2006; Yordanova et al., 2004). Based on the absence of age effects on components reflecting early stimulus processing (P100 and N100), the authors concluded that stages following response selection drive the observed behavioral slowing in choice RT. Yordanova and colleagues did not observe the ipsilateral positivity in elderly adults that has been reported previously in young adults.

1.1. The present study

Two child groups, a young adult group and a group of elderly participants engaged in a speeded choice-RT task that required the discrimination between left- and right-pointing arrows by pressing a button with the left or right hand, respectively. At the behavioral

level, we aimed at replicating the U-shaped relation between RT and advancing age (e.g., Cerella and Hale, 1994). We used motor-related brain potentials to assess whether RT differences between age groups are driven by pre-selection time, pre-motor time, or motor time. Based on previous findings (Ridderinkhof and van der Molen, 1995; Yordanova et al., 2004), we predict that RT slowing in children and the elderly is primarily related to post-selection time rather than pre-selection time (separated by onset of the LRP). Laplacian-transformed motor potentials were used to study the effect of advancing age on cortical activation (indexed by the contralateral negativity) related to the correct response and on cortical inhibition (presumably indexed by the ipsilateral positivity) associated with the incorrect response. We expected the ipsilateral positivity to start before the contralateral negative wave for young adults (Vidal et al., 2003); a pattern that yet remains to be confirmed for children and elderly adults.

2. Method

2.1. Participants

The study included 77 participants across four age groups; 18 young children (8 females, $M = 7.7$ years, SD = .5), 21 older children (7 females, $M = 11.9$ years, SD = 1.2), 17 young adults (9 females, $M = 20.6$ years, SD = 3.1), and a group of 21 elderly participants (9 females, $M = 75.4$ years, SD = 5.5). Four young children, three older children, and five elderly adults were excluded from analyses due to unreliable EMG onsets or excessive motion-related artifacts. This reduced the effective sample to 65 participants (see Table 1 for demographic data). All participants had normal or corrected-to-normal vision. Children were recruited from local elementary schools and received a small present for participation. Young adults were university students who received course credits for participation. Elderly participants were recruited from the metropolitan area and reported no history of perceptual, motor, or neurological disorder and received 40 euros for their participation. Informed consent was obtained and the study was approved by the local Ethics Committee.

A non-verbal IQ test was used to obtain an estimate of the level of intellectual functioning. The standard progressive matrices (SPM; Raven et al., 1985) were administered to children and elderly adults, whereas young adults completed the advanced progressive matrices (APM, Raven et al., 1993). Mean percentile scores did not differ significantly between age groups (see Table 1), suggesting comparable levels of fluid intelligence ($p > .10$).

2.2. Task and stimuli

Stimulus presentation was controlled by a computer running Presentation software (www.neurobs.com) using a 17-in. monitor screen (60 Hz refresh rate). Stimuli were presented centrally against a dark-grey background in a dimly lit, sound-attenuating room. The choice task started with the presentation of a white fixation cross (3 cm × 3 cm) followed by central presentation of a white arrow (2.2 cm × 1.8 cm) pointing to the left or to the right (subtending a 1.9° visual angle) that remained on screen for 1000 ms. The inter-trial interval varied randomly from 1750 to 2250 ms in steps of 50 ms, during which the white fixation cross is shown. The task consisted of 50 practice trials followed by 50 experimental trials, with an equal number of right- and left-pointing arrows that were preceded by five warming-up trials. The practice trials and warming-up trials were excluded from further analyses. The choice task lasted about 5 min and was administered with several other experimental tasks, which are not reported here.

Participants were instructed to fixate on the cross and to respond as quickly and accurately as possible by pressing a force sensor with the left- or right thumb according to the direction of the arrow. Responses were recorded using two zero-displacement force transducers (Honeywell, model FS03) that were attached at the end of the arm supports and individually adjusted in such a way that the thumbs were in a relaxed position when resting on the force sensor. Downward thumb pressure was recorded in a continuous polling loop for both channels with a Keithley KPCI-1902 analogue-to-digital converter. The polling method ensures maximum sample speed at the cost of less accurate sample intervals. Prior to the experiment, maximum force was determined for each thumb press separately. The 15% value of maximum force served as individual RT threshold (van Boxtel et al., 2001). In order for the participant to know if the response was effectively given, the participant heard a sound (click) during the practice session when the force pressure exceeded the 15% of their maximum force. The sound was turned off during the experimental session.

2.3. Electrophysiological recordings

EEG (Biosemi, Amsterdam) was recorded from 30 standard scalp sites (Fp1, Fp2, AF3, AF4, AFz, F3, F4, F7, F8, Fz, FC1, FC2, 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′) using pin-type active electrodes (Ag/AgCl) attached to an Electrocap (International 10/20 system, Jasper, 1958) with linked mastoids as reference channel. Two electrodes served to record activity from left and right M1 (the precentral sulcus, Shibasaki et al., 1980); C3′ and C4′, recorded 1 cm anterior of the standard C3 and C4 locations, and C1′ and C2′, recorded 1 cm posterior–lateral of the original C1 and C2 locations. It has been found that several parts of the precentral gyrus (i.e., upper part, and anterior and posterior wall) are associated with right and left hand movements (Gerloff et al., 1998). 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 by placing two electrodes at the left and right thumbs above the *abductor pollicis brevis*. Throughout the experiment, the EMG signal was closely monitored and, in case of excessive EMG activity, participants were reminded to relax their hand muscles and to move only one of the thumbs downward in response to the arrow direction.

2.4. Electrophysiological analyses

Signals were digitized online at 2048 Hz. EEG signals were down-sampled offline to 256 Hz and filtered using a low-pass filter of 30 Hz and high-pass filter of 0.1 Hz with 24 dB/octave (a Butterworth zero phase filter). Segments with artifacts defined by an amplitude criterion exceeding ±100 μV were rejected. Ocular artifacts were corrected using the algorithm reported by Gratton et al. (1983).

The LRP was obtained by subtracting ipsilateral M1 activity from contralateral M1 activity with respect to the responding hand (Coles et al., 1988). The LRP in the present study was computed using the following formula and electrodes[1]: $(C2' - C1') + (C1' - C2')/2$. The LRP was computed from monopolar recordings (monopolar LRP) and from recordings after Laplacian transformation (Laplacian LRP). The onset of LRP was attained by conducting a regression-based procedure on two segments of the individually averaged LRP wave, taking the intersection of the two lines as the onset (i.e., a line fits the LRP trace preceding the onset, whereas the second line fits the trace from the onset to the peak). The advantage of the segmented regression method to estimate LRP onset over baseline-deviation method (with or without jackknifing procedures) is that it minimizes the influence of signal fluctuations before and after the onset, which are especially pronounced in children (Schwarzenau et al., 1998). However, the estimated onset times on averaged waves might not correspond to the actual onset times of single trial-by-trial waves (see Meyer et al., 1988). Thus, the averaged onset latencies in present study might be an over-estimation of the actual averaged onset latencies when measured on each trial separately. This might be particular the case in individuals with high variability between ERP components. This issue will be addressed when age groups show different onset times.

Surface Laplacian transformations were conducted on averaged ERP signals by applying the spherical spline interpolation procedure of Perrin et al. (1989). The interpolation of the potential of each electrode was obtained by fitting the optimal interpolated values in a sphere reference. Second, the spatial second derivative was computed in two dimensions of space. The order of splines was set at three and the interpolation was computed using 15 for the Legendre polynomial (Tandonnet et al., 2005)[2]. After Laplacian transformation, signals were low-pass filtered at 15 Hz and high-pass filtered at 1 Hz. The Laplacian-transformed ERPs were baseline corrected using a 200 ms window (from 500 to 300 ms) preceding EMG onset. This interval appeared minimally sensitive to age-related signal fluctuations preceding EMG onset. Mean amplitudes of 200 ms interval of the Laplacian-transformed ERPs were submitted to univariate ANOVA and revealed no Age Group effects, all Fs < 1.29. The onset of the contralateral negative and ipsilateral positive Laplacian potential was estimated using the same regression procedure as described for the LRP.

EMG signals were high-pass filtered at 20 Hz, rectified, and low-pass filtered at 50 Hz. After down-sampling to 1024 Hz, a procedure run in BrainVisionAnalyzer placed a trigger at the start of the rectified EMG signal when the positive-going flank exceeded 30 μV. Then, the trigger moved backwards to 5 μV. All EMG signals were visually inspected and EMG-onsets were manually adjusted if needed (van Boxtel et al., 1993).

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[1] The present study used activities recorded from electrodes C1′ and C2′ for the analysis of M1 modulations, since the contralateral Laplacian ERP trace confined to C1′ and C2′ for young adults is highly similar in morphology and timing to the Laplacian ERP observed in Laplacian motor cortex studies using C3 and C4. Activity recorded from C3′ and C4′ in present study was more diffuse and peaked approximately 50 ms later than C1′ and C2′.

[2] The Laplacian enhances spatial resolution. Under optimal circumstances, i.e., a realistic head model and over 64 channels, it has been claimed that the spatial resolution may reach 2–3 cm (Nunez, 1981). This resolution will not be attained in the present study since we did not use a realistic head model and the quantity of spatial sampling was 36.

Table 1
Demographic data for participants in each age group. *n* refers to number of participants. Mean age in years (standard deviations between parentheses).

Age group	*n*	Age	Gender (female/male)[a]	Preferred hand (right/left)	Raven progressive matrices score
Young children	14	7.80 (0.4)	4/10	13/1	82.0 (25.8)
Older children	18	11.77 (1.2)	5/13	18/0	79.8 (18.9)
Young adults	17	20.59 (3.1)	9/8	17/0	86.9 (5.7)
Elderly adults	16	76.25 (5.9)	5/11	15/1	91.9 (5.4)

[a] Gender distribution did not differ between groups, $\chi^2 = 3.15$, $p = .37$.

2.5. Statistical analyses

2.5.1. Behavioral measures

Trial types were classified according to the presence of EMG activity and a button-press response with the correct or incorrect hand. A correct response trial contained EMG activity associated with the correct hand followed by a correct button press within 1200 ms from stimulus onset and the absence of response-related EMG of the incorrect hand preceding the correct button press. Choice errors were classified into two trial types: (1) a partially incorrect EMG trial, characterized by the presence of sub-threshold EMG activity of the incorrect hand with the presence of the correct button press, and (2) a full incorrect EMG trial, defined as the presence of EMG activity of the incorrect hand followed by the incorrect button press response (irrespective of the presence of EMG activity and button press response of the correct hand). Omissions were separated into two categories: (1) a partial omission trial, i.e., the presence of EMG activity of the correct hand without a correct button press response (the correct response was initiated but the 15% force criterion was not reached, this trial type occurred fewer than 2% in each group, see Table 2), and (2) a full omission trial, i.e., no EMG activity associated with the correct or incorrect hand was present within 1200 ms from stimulus-onset.

Mean RT (defined as the interval between stimulus-onset and button-press response) was calculated on correct trials and full incorrect trials. RT and square rooted error percentages were submitted to ANOVA with Age Group as between-subjects variable. Post hoc tests were used to confirm group differences.

2.5.2. Electrophysiological measures

ERP and EMG signals on correct response trials were response-locked with respect to EMG onset. Rectified EMG on correct response trials was then averaged over left- and right-hand responses. It has been found that the steepness of EMG activity from its onset reflects variability in the initiation of motor units (Meijers et al., 1976) and might therefore provide valuable information concerning the nature of the motor command. Slopes were calculated on two sections of the leading edge of EMG activity: (1) 0–40 ms and (2) 40–80 ms. EMG peak amplitudes and latencies were determined by capturing the peak of the EMG trace within 300 ms from EMG onset.

Laplacian-transformed ERPs (i.e., the contralateral negativity and ipsilateral positivity) were pooled for left and right hand responses, as preliminary analyses did not reveal differences across hands. This was done by averaging signals over M1 contralateral to the right-hand response with activity contralateral to the left-hand response. Pooled ipsilateral M1 signals were achieved in similar manner. The peak of the contralateral negative potential with respect to EMG onset was identified as the most negative value relative to the baseline in the interval ranging from −100 to 250 ms using the automatic peak-picking procedure as implemented in BVA. Visual inspection of ipsilateral traces revealed a large variability between age groups in the morphology of the waves at the ipsilateral side. Slopes of the ipsilateral traces were calculated for six sections (50 ms each) around EMG onset: (1) −150 to −100 ms, (2) −100 to −50 ms, (3) −50 to 0 ms, (4) 0–50 ms, (5) 50–100 ms, and (6) 100–150 ms. The peak-picking procedure as implemented by BVA searched for the largest positive value associated with the ipsilateral positive potential relative to the baseline in the interval ranging from −100 to 200 ms. If the procedure failed to detect a negative or positive potential at, respectively the contralateral or ipsilateral side of the responding hand, the Laplacian data of that participant was excluded from analysis. The time course of contralateral negativity and ipsilateral positivity was statistically tested using onset latency values relative to the EMG onset. Statistical analyses were performed on slopes, peak amplitudes, peak latencies, and wave onsets by submitting the values to ANOVA with Interval (in the slope analyses) and Timing (in the time-course analysis) as within-subjects factors and Age Group as the between-subjects factor. Onsets will be analyzed using both the monopolar LRP and contralateral negative Laplacian wave for comparison with literature.

RT was segmented into three intervals using either the onset of the monopolar LRP or the onset of the contralateral negative Laplacian wave: (1) the pre-selection time, from stimulus onset to negativity onset, (2) the pre-motor time from negativity onset to EMG onset, and (3) the motor time from EMG onset to RT. To correct for baseline differences in the speed of responding between age groups, the latencies of the three intervals were transformed by taking the natural logarithm (Meiran, 1996). Latency values of log-transformed segments were submitted to ANOVA with Segment as within-subjects factor and Age Group as between-subjects factor. To compare the estimates of the pre-motor interval based on the monopolar LRP vs. Laplacian LRP vs. the contralateral negative Laplacian wave, a final

analysis was conducted which included Negativity (monopolar LRP, Laplacian LRP and contralateral negative Laplacian wave) as within-subjects factor and Age Group as between-subjects factor.

3. Results

3.1. Behavioral data

Performance results are presented in Table 2. Analysis of accuracy yielded a significant effect of Age Group on the percentage of partially incorrect EMG trials, $F(3, 61) = 12.78$, $p < .001$, and the percentage of full incorrect EMG trials, $F(3, 61) = 8.23$, $p < .001$. Post hoc analysis indicated that children committed more full and partial incorrect responses than the two adult groups ($ps < .02$). The proportion of partial and full EMG responses did not differentiate between the child groups ($ps > .42$). Young adults and elderly adults did not differ in the proportion of full incorrect EMG trials ($p = .85$). Remarkably, elderly adults committed more partially incorrect responses compared to young adults ($p = .03$). Analysis of omission trials indicated that the youngest children occasionally failed to respond to the arrow stimulus in contrast to the other age groups, $F(3, 61) = 11.81$, $p < .001$.

Analysis of RTs on correct response trials confirmed a U-shaped age-related pattern, $F(3, 61) = 39.65$, $p < .001$; young adults showed the shortest latencies while young children responded slowest, followed by the elderly and, in turn, the older children (all $ps < .04$). This finding replicates the RT pattern that is consistently found in lifespan studies (see Cerella and Hale, 1994).

For older children, young adults, and elderly adults, RT on full incorrect response trials was substantially shorter compared to correct response RTs ($Fs > 5.83$, $ps < .03$). Full incorrect and correct response RTs did not differ for young children ($F < 1$).

3.2. Electrophysiological data

3.2.1. Correct response activation

3.2.1.1. Electromyography. As shown in Fig. 1, the EMG is characterized by a large wave in all age groups. Analyses of motor time (i.e., the interval between EMG onset and RT, see Fig. 1) revealed a significant age-related pattern, $F(3, 61) = 10.05$, $p < .001$ (see Table 4 for motor time values relative to the contralateral negative Laplacian wave), that in part resembled the RT data. The longest latency was found for young children whereas motor time was shortest for young adults ($ps < .05$). The older children and elderly adults did not differ in this regard ($p = .19$).

Analysis of the slopes of the two sections of the leading edge of EMG activity (see Table 3) yielded a significant Interval effect, $F(1, 61) = 9.24$, $p = .003$, that interacted with Age Group, $F(3, 61) = 2.85$, $p = .05$. The EMG trace associated with the interval from 0 to 40 ms was steeper in the two adult groups, who did not differ ($p = .71$), compared to the two child groups ($ps < .06$), who did not differ ($p = .47$). The EMG trace associated with the interval from 40 to 80 ms was steeper in older children and young adults, who did not differ ($p = .99$), compared to young children and elderly adults ($ps < .04$), who did not differ ($p = .41$) (see Fig. 1). The reduced slopes of the EMG burst in children and elderly adults suggest a higher

Table 2
Percentages of omissions, partial incorrect and full incorrect response trials. Mean RT (in milliseconds) and within-subject RT variability of correct and incorrect response trials in each age group (standard deviations between parentheses).

Age group	Error proportion (%)				Latency measures (ms)			
	Partial incorrect responses	Full incorrect responses	Partial omissions	Full omissions	RT		SD (w-s)	
					Correct responses	Incorrect responses	Correct responses	Incorrect responses
Young children	27.1 (12.7)	9.3 (6.2)	1.9 (2.4)	1.9 (2.4)	518 (82.7)	490 (186.5)	129.7	150.6
Older children	31.0 (12.5)	10.1 (8.1)	0.1 (0.5)	0.0 (0.0)	368 (49.5)	309 (117.1)	85.4	57.1
Young adults	10.1 (7.0)	3.2 (3.8)	0.0 (0.0)	0.0 (0.0)	301 (26.5)	247 (19.6)	39.1	33.8
Elderly adults	17.3 (11.4)	3.5 (4.1)	0.1 (0.5)	0.1 (0.5)	434 (64.4)	297 (70.4)	64.1	45.1

Table 3
Slope values of the EMG trace associated with two time windows (zero of time point is EMG onset). Peak amplitude (in arbitrary units) and latency (in milliseconds and relative to EMG onset) values of EMG in each age group. Mean RT (ms) associated with different segments of the reaction process for the monopolar LRP (pre-selection time, i.e., the interval from stimulus to start of negative wave, pre-motor time, i.e., interval from onset negative wave to EMG onset, and motor time, i.e., interval from EMG onset to button-press response). Pre-motor time values for the Laplacian LRP are presented for each age group (standard deviations between parentheses).

Age group	EMG				Monopolar LRP			Laplacian LRP
	Slope values		Peak amplitudes	Peak latencies	Segment			Segment
	Interval				Pre-selection time	Pre-motor time	Motor time	Pre-motor time
	0–40 ms	40–80 ms						
Young children	7.3 (3.8)	8.7 (7.4)	0.3 (0.2)	159 (41.7)	250 (98.9)	143 (92.9)	138 (34.6)	51 (20.8)
Older children	9.1 (5.4)	26.2 (17.3)	0.5 (0.3)	130 (20.4)	150 (75.6)	101 (55.4)	114 (21.0)	49 (72.7)
Young adults	14.8 (10.0)	26.3 (20.4)	0.5 (0.2)	93 (26.6)	156 (30.6)	61 (27.5)	84 (20.6)	75 (41.7)
Elderly adults	13.8 (7.3)	13.8 (18.3)	0.3 (0.2)	93 (31.3)	172 (54.5)	154 (46.7)	101 (18.8)	170 (55.0)
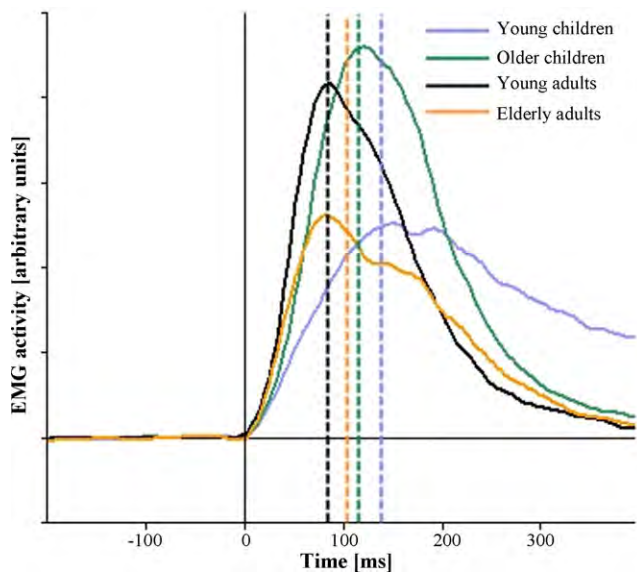
Fig. 1. Grand averaged electromyographic (EMG) activity (in arbitrary units) associated with correct response trials for young children (purple), older children (green), young adults (black), and elderly adults (orange). Traces are averaged time-locked to EMG onset (vertical bar). Vertical striped lines indicate latency from EMG onset till overt response (i.e., motor time, in milliseconds) for each age group.

variance in motor unit onset times relative to young adults (Meijers et al., 1976).

The ANOVA performed on peak amplitudes revealed an effect of Age Group, $F(3, 61) = 5.80$, $p = .001$ (see Table 3). As shown in Fig. 1, the EMG peak is larger in older children and young adults, who did not differ ($p = .66$), compared to young children and elderly adults ($ps < .009$), who also did not differ ($p = .93$).

The analysis on EMG peak latency showed an age-related pattern, $F(3, 61) = 16.84$, $p < .001$. As can be seen in Table 3, the peak of the EMG response occurred later in younger compared to older children ($p = .01$) whose EMG signal peaked later than that of young

adults and elderly adults ($ps < .001$). Peak latency did not distinguish between the two adult groups ($F < 1$).

3.2.1.2. Lateralized readiness potential. Unfortunately, onsets of the monopolar LRP could not be detected for 14 participants (eight young children, five older children and one elderly participant)[3]. The LRP waveforms for the remaining participants, time-locked to EMG onset, are presented in Fig. 2. For all age groups, the LRP started well before EMG onset, peaking after EMG onset.

Pre-motor time (i.e., the interval between the onsets of the monopolar LRP and EMG, see Table 3) was longer for the elderly compared to young adults and older children ($ps < .008$) (overall ANOVA; $F(3, 47) = 9.86$, $p < .001$). As shown in Fig. 2, pre-motor time was also longer for young and older children (who did not differ, $p = .11$) than for young adults ($ps < .04$). The finding of longer pre-motor times for children and elderly is compatible with the findings reported by Ridderinkhof and van der Molen (1995) and Yordanova et al. (2004). Pre-motor time did not differentiate between young children and elderly adults ($p = .64$). In sum, the time between the start of inter-hemispheric lateralization and peripheral motor activation of the correct response is longer in both child groups and in elderly participants compared to young adults.

3.2.1.3. Contralateral negative Laplacian potential. Fig. 3 shows Laplacian-transformed ERPs (bottom) time-locked to EMG onset, with corresponding Laplacian maps (top), all participants included. For all age groups, the negative wave at the contralateral M1 starts before EMG onset and reaches its maximal amplitude after EMG onset. The negativity is followed by a large positivity for the children (i.e., the post-response motor-related potential, Gerloff et al., 1998) but is strongly reduced for young adults and elderly adults

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[3] The LRP is not always manifested in children: 12 out of 45 children in Ridderinkhof and van der Molen (1995), and 16 out of 30 children in Szucs et al. (2007). Also in adults the LRP is not always found. For example, Band and Miller (1997) reported that 4 out of 28 young adults did not show a LRP.
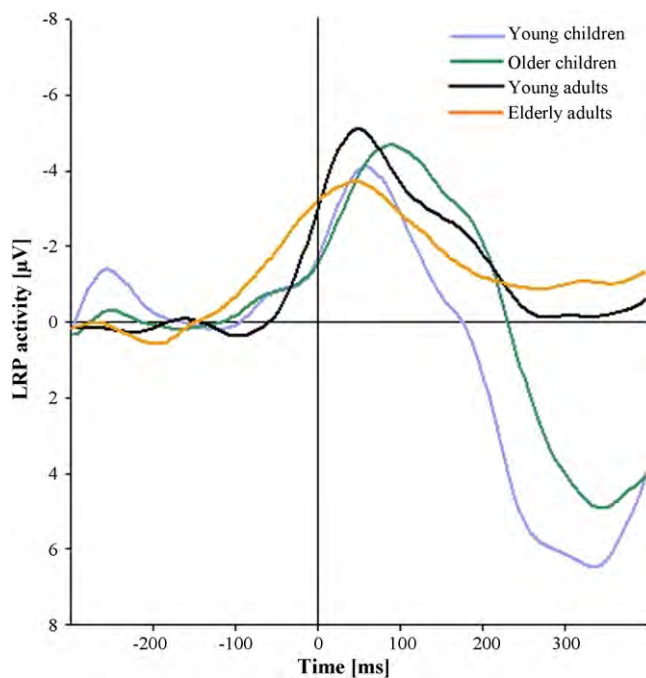
Fig. 2. The monopolar lateralized readiness potential (LRP) associated with correct response trials for young children (purple line), older children (green line), young adults (black line), and elderly adults (orange line). Only participants who showed a LRP were included in the figure. Time zero corresponds to EMG onset (vertical bar). Negativity is plotted upwards.

(this wave will not be analyzed). All participants exhibited a negative developing wave at the contralateral M1.

Pre-motor time varied significantly with Age Group, $F(3, 61) = 13.64$, $p < .001$ (see Table 4). Post hoc analyses revealed that pre-motor time was significantly longer for the elderly compared to older children and young adults (both $ps < .001$), but was only marginally longer when compared to young children ($p = .06$). The finding of increased pre-motor time for elderly adults is compatible with previous aging studies (e.g., Yordanova et al., 2004). As shown in Fig. 3, young children showed a longer pre-motor time compared to older children and young adults ($ps < .03$). Finally, this interval tended to be longer for older children relative to young adults ($p = .08$). This pattern suggests that the cortical motor command issued by the contralateral M1 is slower to build up and activate the motor units that control the responding hand in young and older children, and elderly adults relative to young adults.

Fig. 3 shows a somewhat reduced contralateral negativity for elderly adults, which is larger for the older children compared to the other age groups. The ANOVA on negative peak amplitude values confirmed this observation, $F(3, 61) = 21.17$, $p < .001$ (see Table 4); negative amplitudes were enhanced for children and lower values were obtained for the elderly, with intermediate amplitude values for young adults (all $ps < .02$)[4]. Older children also showed

enhanced amplitudes compared to young children ($p = .005$). This finding indicates that M1 associated with the correct response is more strongly activated in children and less activated in elderly adults compared to young adults.

Peak latency analysis with respect to EMG onset revealed a prolonged interval for young and older children compared to elderly adults ($ps < .03$) (overall, $F(3, 61) = 2.89$, $p = .04$). Peak latencies of the child and elderly groups did not differ from the young adult group ($ps > .13$).

3.2.2. Age-related differences in RT segments

A schematic representation of segments of the RT process is presented in Fig. 4. Segment analysis will be done on the monopolar LRP.

3.2.2.1. Lateralized readiness potential.
ANOVA on log-transformed pre-selection, pre-motor time and motor time values revealed a significant main effect of Segment, $F(2, 94) = 22.64$, $p < .001$. Pre-selection interval was longer than the pre-motor and motor intervals ($ps < .001$). Age Group interacted also with Segment, $F(6, 94) = 2.79$, $p = .04$ (see Table 3 for latencies). The pre-selection interval was disproportionally longer for young children compared to the other age groups ($ps < .02$). Elderly adults showed a disproportionally longer pre-motor time compared to older children ($ps = .008$) and young adults ($ps < .001$), but did not differ from young children ($p = .54$). Pre-motor time was also disproportionally longer for young and older children, who did not differ ($p = .13$), compared to young adults ($ps < .03$). Finally, age had a substantial effect on motor time, $F = 10.49$, $p < .001$. The interval between EMG onset and button-press was disproportionally longer for young children compared to the other age groups ($ps < .04$). Older children and elderly adults, who did not differ ($p = .13$), also displayed longer motor times than young adults ($ps < .03$).

#### 3.2.2.2. Contralateral negative Laplacian potential.
The ANOVA on log-transformed segments using the onset of the negative Laplacian wave revealed a significant interaction between Age Group and Segment, $F(6, 122) = 19.60$, $p < .001$ (see Table 4 for latencies). The analysis performed on the pre-selection and motor intervals revealed similar findings as the pre-selection and motor time intervals identified on the basis of the LRP, respectively, $F(3, 61) = 12.83$, $p < .001$ and $F = 10.11$, $p < .001$. Pre-motor time varied also disproportionally with age, $F = 14.19$, $p < .001$, and was relatively longer for elderly adults compared to the other age groups ($ps < .04$). As shown in Fig. 4, pre-motor time was also disproportionally longer for young children compared to older children ($p = .03$) and young adults ($ps < .001$), but the difference between the latter two age groups failed to reach significance ($p = .10$).

3.2.3. Comparing segments between LRP and Laplacian procedures

To exclude potential effects of the amount of participants included in the monopolar LRP vs. contralateral negative Laplacian wave analysis of the age-related pattern of pre-motor times, the pre-motor interval was compared between the two methods that included the same participants as in the monopolar LRP analysis (see section 'age-related differences in RT segments'). An additional factor Negativity (monopolar LRP and contralateral negative Laplacian wave) was included. The analysis yielded a significant Negativity effect, $F(1, 47) = 21.96$, $p < .001$; pre-motor time was longer for the monopolar LRP compared to the contralateral negative Laplacian wave. A significant Age Group effect was found, $F(3, 47) = 20.11$, $p < .001$; elderly adults and young children (who did not differ, $p = .39$) showed longer pre-motor times than older children and young adults ($ps < .03$). Older children showed also a longer pre-motor interval compared to young adults ($p = .005$).

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[4] Yordanova et al. (2004) reported higher instead of lower negative peak values for elderly adults compared to young adults. They selected correct response trials by deleting trials that contained a full incorrect response but not those that contained a partially incorrect response (trials containing EMG activity associated with the incorrect hand were included). To resolve these discrepant findings, we conducted a similar analysis on peak amplitudes of the contralateral negativity for correct response trials including partially incorrect response trials (ERP traces not shown here). However, this did not change the age-related pattern of contralateral peak amplitudes in present study ($F = 15.82$, $p < .001$): highest amplitudes were found for older children ($-94.9 \, \mu V/cm^2$) and lowest for the elderly ($-31.3 \, \mu V/cm^2$), with young adults ($-51.0 \, \mu V/cm^2$) and young children ($-72.8 \, \mu V/cm^2$) having intermediate amplitude values (all $ps < .05$).
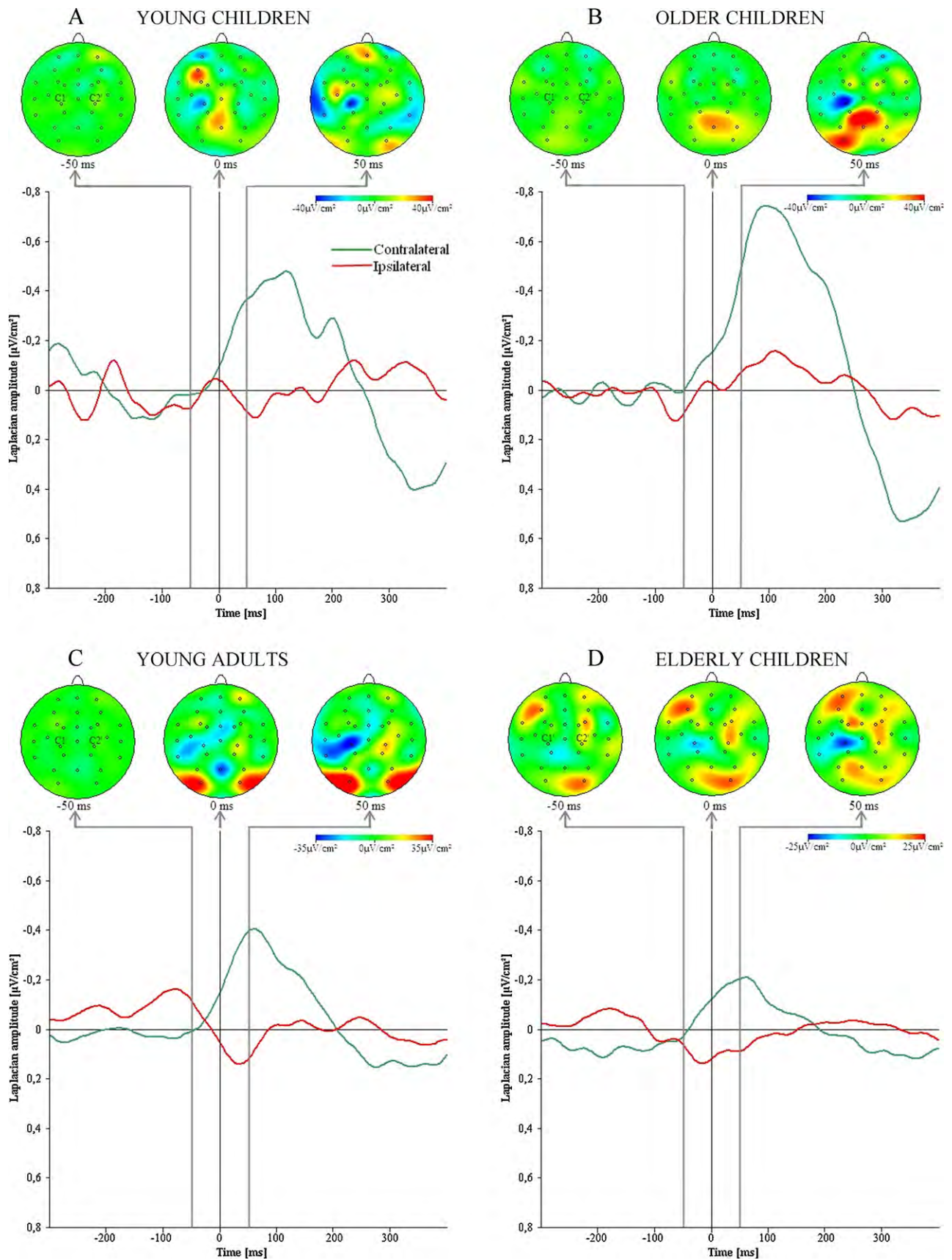
Fig. 3. The Laplacian-transformed ERPs with corresponding topographical maps. Contralateral (green line) and ipsilateral Laplacian traces (red line) associated with correct response trials for young children (A), older children (B), young adults (C) and elderly adults (D). Traces are averaged time-locked to EMG onset (vertical bar crosses at zero). Negativity is plotted upwards. Maps associated with right hand responses are drawn at three time points (−50, 0 and 50 ms) for each age group. C1′ denotes contralateral Laplacian activity associated with the right hand response, whereas C2′ activity at the ipsilateral side.

Table 4
Mean RT of segments of the reaction process computed using the contralateral negative Laplacian wave (pre-selection time, i.e., interval from stimulus to start of negative wave, pre-motor time, i.e., interval from onset negative wave to EMG onset, and motor time, i.e., interval from EMG onset to button-press response). Peak amplitude (in $\mu V/cm^2$) and latency (in milliseconds and relative to EMG onset) values of the contralateral negative Laplacian wave are presented for each age group and the values associated with the ipsilateral positive Laplacian wave are given for the two adult groups. Mean onset latency values (in milliseconds and relative to EMG onset) for the ipsilateral positive wave are presented also for the two adult groups (standard deviations between parentheses).

Age group	Laplacian-transformed ERP							
	Contralateral negativity					Ipsilateral positivity		
	Segment			Peak amplitudes	Peak latencies	Onset latencies	Peak amplitudes	Peak latencies
	Pre-selection time	Pre-motor time	Motor time					
Young children	299 (56.9)	82 (52.4)	137 (39.5)	−0.7 (0.3)	92 (56.5)	–	–	–
Older children	205 (52.9)	47 (42.7)	116 (28.9)	−1.0 (0.4)	97 (35.7)	–	–	–
Young adults	195 (32.4)	20 (41.2)	84 (20.6)	−0.5 (0.2)	72 (39.5)	−73 (31.0)	0.2 (0.2)	31 (29.9)
Elderly adults	216 (51.8)	114 (45.8)	103 (19.6)	−0.3 (0.1)	53 (57.7)	−120 (55.8)	0.2 (0.2)	−9 (31.7)

Most importantly, Negativity and Age Group did not interact, $F < 1$. It appears that the onset-scoring procedure applied on the monopolar LRP and contralateral negative Laplacian wave yielded a longer pre-motor interval for the monopolar LRP compared to the contralateral negative Laplacian wave, but the age-related pattern of pre-motor times was comparable between the two methods.

The analysis above revealed that the difference in pre-motor time between the monopolar LRP and contralateral negative Laplacian wave is not due to differences in sample size. Therefore, a separate analysis was conducted on pre-motor time to compare procedural differences between the monopolar LRP and contralateral negative Laplacian wave. This was done by including the pre-motor time of the Laplacian LRP to the analysis with an additional factor Negativity (monopolar LRP, Laplacian LRP and contralateral negative Laplacian wave, see Table 3) (the figure of the Laplacian LRP is not presented). The Negativity x Age Group analysis was performed on participants who did reveal a monopolar LRP. The analysis yielded a significant Negativity effect, $F(2, 94) = 10.56$, $p < .001$. Pre-motor time was longer based on the monopolar LRP compared to the Laplacian LRP and contralateral negative Laplacian wave ($ps < .008$). Negativity interacted also with Age Group, $F(6, 94) = 4.26$, $p = .001$. For the two adult groups, pre-motor time was longer for the monopolar and Laplacian LRP (that did not differ, $ps > .28$) compared to that of the contralateral negative Laplacian wave ($ps < .02$). In children, the pre-motor interval was longer for

Fig. 4. Schematic representation of mean latencies of RT segments using the onset monopolar LRP or contralateral negative Laplacian potential for each age group. Vertical lines denote onset times of stimulus presentation (orange), negative wave (green) and EMG activity (purple). Horizontal lines represent the latencies of the pre-selection interval (orange), pre-motor interval (green) and motor interval (purple). Black squares denote finishing times of the RT process. Note that RTs differ between monopolar LRP and contralateral negative Laplacian procedures, because of an unequal number of participants in age group.

the monopolar LRP compared to that of the Laplacian LRP ($ps < .08$). Pre-motor time was also longer for the contralateral negative Laplacian wave compared to that of the Laplacian LRP but only in young children ($p = .05$). These findings show that the latency of the pre-motor interval differs between procedures and, most importantly, these procedural differences interact with age.

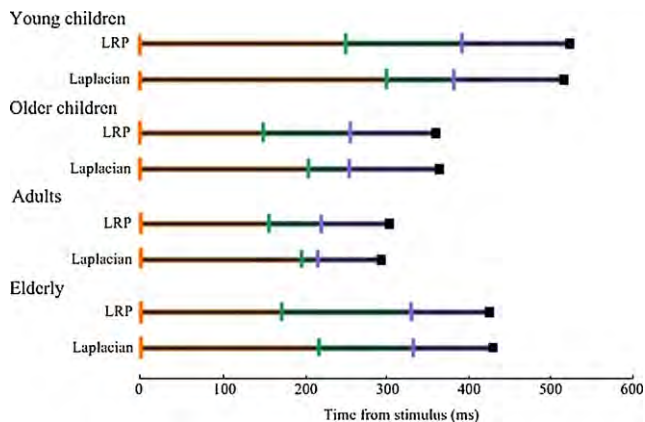### 3.2.4. Incorrect response activation
3.2.4.1. Ipsilateral positive Laplacian potential. Ipsilateral traces are presented in Fig. 3 and seem to suggest that a positive wave is present for the two adult groups only, starting considerably earlier before EMG onset in elderly adults than in young adults. Data of one participant in the older child group was excluded from the analysis because of artifacts at the ipsilateral side.

The slope analysis on the ipsilateral traces revealed a significant interaction between Interval and Age Group, $F(15, 300) = 2.23$, $p = .01$. Slope values are presented in Table 5. The analysis on the slopes associated with the ipsilateral trace in young adults yielded a significant Interval effect, $F(5, 80) = 5.35$, $p = .003$; the slope of the interval from −50 ms to EMG onset was positive, whereas the slopes of the intervals from −150 to −100 ms, from 50 to 100 ms and 100 to 150 ms were negative ($ps < .002$). The slope of the interval from EMG onset to 50 ms was also positive and significantly different from the intervals that extend from −150 to −100 ms and 50 to 100 ms ($ps < .04$). The slope of the interval −100 to −50 ms was only significantly different to the interval 50 to 100 ms ($p = .01$). This pattern of findings is consistent with the ipsilateral data reported previously by Vidal et al. (2003) and the findings indicate the presence of a positive wave at the ipsilateral M1 in young adults.

The slope analysis on the ipsilateral trace in the group of elderly participants revealed that the elderly exhibited also a positive developing wave at the ipsilateral side, $F(5, 75) = 2.96$, $p = .02$; the slope of the interval from −50 ms to EMG onset was positive, whereas the slopes of intervals from EMG onset to 50 ms and from 50 to 100 ms were negative ($ps < .04$).

The analysis on the slopes of the ipsilateral trace in young children did not reveal a significant Interval effect, $F(5, 65) = 1.23$, $p = .30$. This indicates that the positive wave is absent in the younger child group and might suggest that the incorrect hand was not activated or inhibited.

The analysis of the data associated with older child group showed that the slopes of the ipsilateral trace tended to differ significantly, $F(5, 80) = 2.14$, $p = .07$; the slope of the interval from −50 ms to EMG onset was *negative* compared to the intervals extending from −100 to −150 ms and from 100 to 150 ms ($ps < .03$). As can be seen in Fig. 3B, a negative wave developed around EMG onset in older children, which might reflect activity associated with the incorrect response.

Table 5
Slope values of the ipsilateral positive Laplacian wave associated with six time windows in each age group. Zero of time point refers to EMG onset (standard deviations between parentheses).

Age group	Interval					
	−150 to −100 ms	−100 to −50 ms	−50 to 0 ms	0–50 ms	50–100 ms	100–150 ms
Young children	0.5 (2.6)	−0.02 (2.7)	−1.2 (2.4)	1.1 (2.5)	−0.9 (2.8)	−0.3 (2.6)
Older children	−0.01 (1.9)	1.1 (2.6)	−1.4 (2.4)	−0.3 (3.0)	−0.7 (2.9)	0.9 (1.8)
Young adults	−0.7 (1.0)	0.1 (1.4)	1.3 (1.8)	0.7 (2.1)	−1.2 (1.6)	−0.2 (1.0)
Elderly adults	0.7 (1.1)	−0.02 (1.4)	0.7 (1.1)	−0.2 (0.8)	−0.6 (1.2)	−0.04 (1.2)

The onset- and peak-scoring procedure was done on the two adult groups only. One participant in the young adult group and one elderly participant did not reveal a positive wave around EMG onset and were excluded from analyses.

The ANOVA on onset latencies confirmed the visual impressions created by Fig. 3C and D, $F(1, 29) = 8.27$, $p = .007$ (see also Table 4). That is, the interval between the start of the positive wave and EMG onset was longer for elderly adults compared to young adults.

The ANOVA on peak amplitudes did not reveal a significant Age Group effect, $F < 1$ (see Table 4). But the ANOVA on EMG-locked peak latencies of the positive wave yielded a highly significant Age Group effect, $F(1, 29) = 12.68$, $p = .001$, indicating that the interval was longer for young adults compared to elderly adults.

3.2.5. Comparing onsets of contralateral negative and ipsilateral positive Laplacian potentials

A separate set of analyses was performed to study the dynamic interplay of contra- and ipsilateral activation (see Table 4 for latency values). The ANOVA performed on the onsets of the contralateral negative and ipsilateral positive Laplacian waves yielded a significant Wave effect, $F(1, 29) = 9.0$, $p = .005$, that interacted with Age Group, $F(1, 29) = 4.14$, $p = .05$. For young adults, the ipsilateral positivity started before the contralateral negativity ($p = .001$), a pattern that replicates the findings reported by Vidal et al. (2003). In contrast, the onset latencies of the ipsilateral positivity and the contralateral negativity did not differ in elderly adults ($p = .55$). Assuming that the ipsilateral positivity is a manifestation of the inhibition of the incorrect response, the latter finding might suggest that the start of cortical inhibition relative to activation occurred later in elderly adults compared to young adults.

4. Discussion

The primary objective of the present study was to investigate the motor system in relation to lifespan differences in accuracy and speed of responding in choice situations. Four age groups performed a choice task that required fast and accurate left- and right-hand responses to left- and right-pointing arrows, respectively.

Taniguchi et al. (2001) transformed ERP signals recorded over M1 using the Laplacian procedure (Nunez, 2000) and observed a negative developing wave at the side of the M1 contralateral to the responding hand and a positive wave at the ipsilateral side. They interpreted this pattern to reflect, respectively, the activation of the correct response and the inhibition of the incorrect response alternative. Next to the onset of the negative Laplacian wave, LRP onset has been used to bisect choice processing in a stimulus and a response-related segment (e.g., Miller and Ulrich, 1998; Osman et al., 1995). Lifespan analyses of these segments in present study revealed that cortical as well as peripheral response processes contribute substantially to age-related changes in response speed. The following sections will focus first on the activation of the correct response before interpreting the observed age-related changes in the suppression of the incorrect response alternative.

4.1. Activation of the correct response

The behavioral results replicated the typical U-shaped developmental pattern of RT showing that the speed of executing a manual choice response improves from childhood to adulthood and then gradually declines when people grow older (e.g., Cerella and Hale, 1994; Noble et al., 1964; Williams et al., 1999). All age groups showed a comparable pattern of interval latencies when segmenting the RT using the onsets of cortical (monopolar LRP and contralateral negative Laplacian wave) and peripheral activation (EMG); the duration of the pre-selection interval (interval between stimulus and negative wave onsets) was relatively longer than the pre-motor time (interval from onset negative waves to EMG onset) and motor time (time interval from EMG onset and overt response). This pattern replicates previous findings using LRP onsets (e.g., Leuthold, 2003; Osman et al., 1995) and shows that processes occurring before the activation of M1 contribute most to the RT process.

The current findings indicate that the duration of pre-motor interval is longer when computed using the monopolar LRP onset compared to the onset of the negative Laplacian wave, although both measures are assumed to capture the cortical motor command (Osman et al., 1995; Tandonnet et al., 2003). The Laplacian procedure acts as a high-pass spatial filter reducing blurring effects of the cortical potential distribution (Babiloni et al., 2001). This might have induced a shift toward EMG onset of the contralateral negative Laplacian wave; the start of the contralateral negativity is closer relative to EMG onset. However, the pre-motor time of the Laplacian LRP was not different from the monopolar LRP in adults, whereas the duration of the pre-motor interval of the Laplacian LRP was shorter compared to the monopolar LRP in children. The LRP captures also activity from the ipsilateral M1 associated with the correct response and if ipsilateral M1 activity deflects positive prior to the negative deflection at the contralateral M1, the pre-motor time of the LRP will correspond to the onset of the positive deflection relative to EMG onset. Thus, initial positive deflections of ipsilateral activation might contribute to the latency of pre-motor interval when computed relative to LRP onset (Tandonnet et al., 2003). Most importantly, although pre-motor times differed in duration between the LRP and Laplacian methods, the lifespan pattern was highly comparable between the two procedures when using the same participants in the statistical analysis; that is, pre-motor time was considerably shorter for young adults compared to the other age groups and was also shorter for older children than for elderly adults.

The increase in sample size in the analysis of the contralateral negative Laplacian wave caused a slightly different age-related pattern of pre-motor times compared to that of the monopolar LRP. The pre-motor time of the contralateral negative Laplacian wave decreased disproportionally from young children to older children and young adults and increased again with advancing age from young adulthood. Pre-motor time was not significantly different between older children and young adults. The longer motor processing time might have been caused by a higher variability in the built up of the motor command (Meyer et al., 1988). The age-related

pattern of findings resembles the findings of the developmental LRP study of Ridderinkhof and van der Molen (1995) where they showed that the latency of the LRP onset varies as a function of age, i.e., the latency from stimulus onset to the LRP onset decreased from childhood with advancing age to adulthood. The prolonged pre-motor time observed in children is consistent with the literature on the maturation of the corticospinal tract reporting that the neuronal signal speed increases progressively during childhood (Koh and Eyre, 1988). In addition, the observed aging effect replicates an EEG study by Yordanova et al. (2004), showing prolonged pre-motor time in elderly adults compared to young adults in a four-choice RT task.

The pre-selection interval (the time from stimulus onset to the onset of the negative wave of the monopolar LRP or contralateral negative Laplacian wave) was longer for young children compared to the other age groups, indicating that processes occurring before M1 activation contribute to RT lengthening in young children. Ridderinkhof and van der Molen (1995) reported that P300 latency, reflecting the evaluation processes of congruent and incongruent stimuli arrays in the Eriksen flanker task, was prolonged for 7–8-year olds compared to 10–12-year olds and, in turn, adults. Thus, young children seem to initiate the central motor command later compared to the other two age groups. Typically, it is assumed that the duration of overt responding relative to its onset (reflected in the pre-motor and motor time) decreases when stimulus processing accumulates over time (Eriksen and Schultz, 1979). Besides the long pre-selection time in young children, they also showed that the overt response is late relative to the onset of the contralateral negative Laplacian wave. This suggests that they were less efficient in using the information conveyed by the stimulus in order to prepare the correct response. In conclusion, young children might be more passively involved in performing on the choice task reflected in the slowness of stimulus processing, and when action is required, they show a deficient response recruitment and preparation system. Furthermore, the variability in motor unit onset times of hand muscles, reflected in the less steep slope of the EMG burst than young adults, and variability of the motor command, reflected in duration of pre-motor interval, provides additional support for the notion of an immature motor system in young children.

A study by Koh and Eyre (1988) showed that the latency of the evoked muscle response reaches adult levels at the age of 11 years. The current EMG findings regarding motor time, however, showed that the interval between EMG onset and the overt response was disproportionally longer for older children compared to young adults. This finding suggests that peripheral motor processes contribute to RT lengthening in older children (Ridderinkhof and van der Molen, 1995) and, together with the findings of the initial slope of EMG activity, the current study indicates that the recruitment of motor muscles in choice behavior continues to mature beyond the age of 12 years.

Elderly participants showed a pronounced increase in pre-motor time; cortical negativity triggered EMG activity of the correct response in a considerably longer time window or with more variable delay in the elderly compared to the other age groups. The time from EMG activity to overt response was longer compared to young adults, but the initial activation of muscles was similar between the two adult groups suggesting that aging-related changes of peripheral muscles activation constitute only a small fraction of the lengthening of response time in elderly adults (e.g., Birren and Fisher, 1995). However, after muscle initiation, elderly participants showed difficulty in keeping muscle activation at an optimal level. The pre-selection interval that captures processes occurring before M1 activation was not lengthened in elderly adults compared to young adults. This finding is in line with studies showing that stimulus-related processes are not affected in elderly individuals (Band and Kok, 2000; Ratcliff et al., 2007; Roggeveen et al., 2007),

suggesting that response activation processes from central motor command to muscle activation of the response are delayed in the elderly (e.g., Levin et al., 2011), even more so than in young children. The increased pre-motor time in elderly adults compared to the other age groups might reflect a precautious response strategy that benefits response accuracy (Ratcliff et al., 2007; Smith and Brewer, 1995; Starns and Ratcliff, 2010); it prevents incorrect activation of the incorrect hand developing into an overt choice error. The relatively high proportion of partial EMG errors in elderly adults and the timing of the ipsilateral positive wave that will be discussed in the next section vis-à-vis a compensatory mechanism in elderly adults confirm this conjecture.

The currently observed age effects on pre-motor and motor time clearly support the notion that response-related stages of the response-choice process contribute most significantly to lifespan changes of the RT process. Age-related changes in the pre-selection interval were also present, but less pronounced compared to the changes observed on response-related stages. This conclusion is compatible with various studies of age-related changes in the speed of information processing (Bashore et al., 1989, 1997b; Szucs et al., 2009). Furthermore, the disproportional findings regarding different sections of the RT process seem to support the hypothesis of specific age sensitive components underlying the lifespan changes of information processing (e.g., Bashore et al., 1997a,b; Baltes et al., 1980).

The amplitude of the contralateral negative Laplacian wave was considerably enhanced for older children and was smallest in the group of elderly participants. The age-related activation pattern of the magnitude of the contralateral M1 might reflect strategic differences across age groups. A study by Geier et al. (2010) found increased activity along the precentral sulcus during response preparation in adolescents compared to adults, but only during reward anticipation. Older children in the present study might have been more focused on response speed than accuracy. To achieve fast responses, older children might have enhanced motor cortical activation during response processing (Geier et al., 2010). The speculation that older children are more "action-focused" is consistent with the finding that the older child group exhibited a negative developing wave at the ipsilateral M1 at the time of a correct response. In contrast, elderly participants may have adopted more emphasis on accuracy than on response speed to avoid responses with the incorrect hand (Smith and Brewer, 1995) and this precautious strategy might have lowered M1 activation.

4.2. Suppression of the incorrect response

A novel aspect of the present study is the focus on the positive Laplacian wave that is recorded over ipsilateral M1 in relation to age-related changes in choice behavior. Recent evidence suggests that this positivity may reflect an early inhibition of the ipsilateral M1 to prevent the execution of a choice error (Meckler et al., 2010; Meynier et al., 2009; Vidal et al., 2003). Carbonnell et al. (2004) obtained the activation–inhibition pattern in a choice RT task but not in a simple RT task (the positive wave at the ipsilateral M1 associated with the simple RT task was much smaller compared to that of the choice RT task), and they concluded from these findings that the positivity refers to an active implementation of inhibition to overcome premature incorrect choice responses. Analyses of the motor-related ipsilateral positivity in present study revealed several interesting findings. First, both child groups did not reveal a positive wave, whereas almost all young adults and elderly participants did. The older child group even displayed a negative going wave over both contralateral and ipsilateral M1 at the time of the button press, which may indicate simultaneous activation of both correct and incorrect responses. The increased proportion of overt response errors observed in children compared to young

adults may be driven by the absence of functional inhibition of the incorrect response. Second, the onset of the positivity in young adults preceded the onset of the negative wave, an onset difference that is consistently reported in the literature (e.g., Carbonnell et al., 2004; Tandonnet et al., 2006; Vidal et al., 2003). Third, the ipsilateral positivity in the elderly started on average simultaneously with the onset of the negative wave. According to the notion that the positivity reflects inhibition, the current finding of a relative late positivity onset in the elderly might suggest that, on a majority of trials, the incorrect response was not inhibited prior to the built-up of the central motor command associated with the correct response hand, thereby increasing the chance of an incorrect response.

The absence of a positive developing wave in both child groups suggests that the inhibition to prevent incorrect responses is still developing beyond the age of 12 years. It has been suggested that the early implementation of inhibition at the ipsilateral M1 is regulated upstream of the M1 (e.g., Burle et al., 2004; Meynier et al., 2009). A candidate area for implementing top-down action control is the supplementary motor area (e.g., Nachev et al., 2008), part of the frontal cortex that is not fully developed until adulthood, both in terms of structure (Giedd et al., 1999) and function (Casey et al., 2000). A peculiar finding is that error rates did not differ between the two child groups. The older children and the two adult groups showed the typical latency pattern of incorrect responses that are faster than correct responses (Wood and Jennings, 1976). The substantial increase in fast incorrect responses for older children and the negative developing wave at the ipsilateral side associated with the correct response might suggest that they trade accuracy for response speed. This "action-focus" might contribute to the observed number of choice errors in older children.

Elderly adults showed simultaneous onsets for contralateral negativity and ipsilateral positivity. However, the activation–inhibition pattern in the elderly is not related to an increase in overt choice error rates. Although overt errors in elderly adults did not differ from young adults, the elderly displayed significantly more partial EMG errors. To prevent incorrect activation of the incorrect hand developing into an overt choice error, elderly participants may have adopted a relatively precautious response strategy to maintain a full incorrect response percentage (similar to young adults) at the cost of a lengthening of the RT. Such a strategy might be adopted by the elderly to compensate for potential performance deficits due to the neuro-degeneration of motor pathways (see for review Ward, 2006).

5. Conclusion and limitations

Analyses of temporal aspects of the RT revealed that cortical as well as peripheral response processes contribute significantly to the lifespan changes in response processing that drive choice behavior. Because only half of the children showed an LRP, whereas all exhibited a negative developing wave at the contralateral M1 of the responding hand, the Laplacian transformation procedure has a considerable advantage over the traditional LRP. The ipsilateral positive wave revealed a lifespan development of response inhibition, which is immature in young children, insufficient in older children, and fully developed in adulthood, with a slow decline when people grow older. The relationship between the ipsilateral positive wave and the development of accuracy are speculative. Clearly, more data is needed to determine whether the observed lifespan pattern is representative for the population or was a result of high within-subject variability or low sample size. Also, the age-related response activation and inhibition pattern over the M1 when performing a spatially compatible stimulus–response mapping task in present study should be replicated using, for example,

a task involving an arbitrary stimulus–response mapping rule. Last, the present study shows lifespan changes in response-related processes but future studies should address in which way areas upstream of the M1 controls response activation. Our results of the maturational change of cortical motor activation and inhibition, along with the developmental and aging literature on the speed of motor responses, support the notion of suboptimal motor response control in children and elderly adults.

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