



Differences in response inhibition processes between adolescents and adults are modulated by sensory processes

Benjamin Bodmer, Julia Friedrich, Veit Roessner, Christian Beste*

Cognitive Neurophysiology, Department of Child and Adolescent Psychiatry, Faculty of Medicine, TU Dresden, Germany

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ABSTRACT

Response inhibition processes undergo strong developmental changes. The same is true for sensory processes, and recent evidence shows that there also within-modality differences in the efficacy to trigger motor response inhibition. Yet, modulatory effects of within-modality differences during age-related changes in response inhibition between adolescence and adulthood are still indeterminate. We investigated this question in a system neurophysiological approach combining analysis of event-related potentials (ERPs) with temporal EEG signal decomposition and source localization processes. We used the somatosensory system to examine possible *within-modality* differences. The study shows that differences in response inhibition processes between adolescents and adults are modulated by sensory processes. Adolescents show deficient response inhibition when stimuli triggering these mechanisms are processed via SI somatosensory areas, compared to SII somatosensory areas. Opposed to this, no differences between adolescents and adults are evident, when response inhibition processes are triggered via SII cortical regions. The EEG data suggests that specific neurophysiological subprocesses are associated with this. Adolescents seem to encounter problems assigning processing resources to integrate motor with tactile information in posterior parietal areas when this information is processed via SI. Thus, basic perceptual and age-related processes interactively modulate response inhibition as an important instance of cognitive control.

1. Introduction

The ability to inhibit prepotent or inappropriate motor responses has been studied widely (Aron et al., 2004; Bari and Robbins, 2013; Diamond, 2013), and is known to undergo strong developmental changes between children and adults (Brandeis et al., 1998; Hämmerer et al., 2010; Johnstone et al., 2007; Jonkman, 2006; Jonkman et al., 2007; Lewis et al., 2006; Liu et al., 2014; Smith et al., 2004; Woltering et al., 2013). However, only recently the importance of lower level sensory processes for motor response inhibition has been considered (Bodmer et al., 2018; Huster et al., 2010; Shedden and Reid, 2001; Stock et al., 2016; Verbruggen et al., 2006).

It has been shown that the somatosensory modality is particularly potent to trigger response inhibition processes (Bodmer and Beste, 2017), which has been explained by the strong structural neuroanatomical connections between the somatosensory cortex and prefrontal areas (Bodmer and Beste, 2017; Friedrich et al., 2017). Regarding developmental effects in response inhibition it is important to consider that especially the somatosensory system is subject to strong developmental effects in children (Taylor et al., 2016). Yet, even within the

somatosensory system (i.e. between the SI and SII somatosensory areas) differences exist how efficient response inhibition processes can be accomplished (Friedrich et al., 2017). Recent evidence suggest that response inhibition processes are better when being triggered via stimuli that are processed in area SI, compared to stimuli that are processed in area SII (Friedrich et al., 2017). This is also crucial regarding developmental effects, because functions of SI and SII cortical areas undergo transformations from childhood to adulthood (Uppal et al., 2016; Nevalainen et al., 2014). Several lines of evidence indicate that children are overresponsive to somatosensory inputs that are hardly noticed by adults (Uppal et al., 2016; Royeen and Mu, 2003; Dunn and Westman, 1997). It may therefore be hypothesized that due to the overresponsiveness to somatosensory (tactile) stimuli in children (Uppal et al., 2016; Royeen and Mu, 2003; Dunn and Westman, 1997) response inhibition is better in children than adults when these processes are triggered using somatosensory stimuli. However, it has also been shown that the connections to and the neurons in area SII are sufficiently developed at birth to produce somatosensory evoked potentials in cortical regions at a latency similar to the one in adults (Nevalainen et al., 2014; Hari and Forss, 1999). It therefore seems that already the

* Corresponding author.

E-mail address: christian.beste@uniklinikum-dresden.de (C. Beste).

neonatal SII area has some similar neurophysiological characteristics with the SII area in adults (Nevalainen et al., 2014). The SII region has been shown to encode cognitive aspects of tactile processing (Ackerley and Kavounoudias, 2015) that are crucial for behavioral decisions (Romo et al., 2002b, 2002a). Given all these considerations, it is possible that differences between children and adults in the efficacy to exert motor inhibitory control using somatosensory stimuli may be dependent on whether somatosensory stimuli are processed in different parts of the somatosensory system. Since neurophysiological processes in SII are very similar between children and adults, it is possible that no differences in response inhibition exist between children when response inhibition is triggered via SII. However, it is possible that such differences emerge when SI is used to trigger response inhibition processes: i.e., response inhibition processes are subject to stronger modulations when being triggered via SI or SII cortical areas in children than adults. This would suggest that within-modality differences to effectively trigger response inhibition are further subject to ontogenetic (age-related) modulations between adolescents and adults.

To examine above hypothesis in a system neurophysiological approach, we combine high-density EEG recordings with signal decomposition and source localization methods. Previous results show that reliable differences between areas SI and SII to trigger response inhibition processes can best be detected when intermingled stimulus and response selection processes (codes) in the neurophysiological signal are dissociated using a temporal signal decomposition method (Friedrich et al., 2017). It has been shown that stimulus and response selection codes in the neurophysiological signal can be dissociated using residue iteration decomposition (RIDE) (Mückschel et al., 2017; Ouyang et al., 2011a). In the current study, this procedure is also important, because it accounts for intra-individual variability in the data (Mückschel et al., 2017; Ouyang et al., 2011a). This intra-individual variability is well-known to be strongly affected by developmental processes (Bielak et al., 2014; Garrett et al., 2012; Mella et al., 2015, 2016; Störmer et al., 2014; Tamnes et al., 2012) and that intra-individual variability is larger in children than in adults (Mella et al., 2015, 2016). Most important, it has been shown that differences in intra-individual variability can bias comparison between children/adolescents and adults (Bodmer et al., 2018) and lead to non-reliable insights in cognitive-neurophysiological mechanisms associated with age-related differences (Bodmer et al., 2018). Moreover, especially within-subjects modality differences to trigger response inhibition processes have been shown to be reliably detectable using this method (Friedrich et al., 2017). RIDE decomposes event-related potential (ERP) data into several component clusters with dissociable functional relevance (Ouyang et al., 2011b, 2015a): the S-cluster refers to stimulus-related processes (like perception and attention), the R-cluster refers to response-related processes (like motor preparation/execution) and the C-cluster refers to intermediate processes between S and R (like response selection) (Ouyang et al., 2011b). However, an R-cluster cannot reliably be calculated in Go/Nogo tasks (Ouyang et al., 2013), because of a lack of motor responses in correct Nogo trials. Any response-related processes (like motor preparation/execution) are therefore represented by the C-cluster.

Because the S-cluster reflects mechanisms involved in the processing of stimuli, and we expect that there are within-modality differences to effectively trigger response inhibition between adolescents and adults, we hypothesize that especially the S-cluster shows interactive effects between age groups and stimuli that are processed by SI or SII cortical areas. Previous findings in a dual visual and auditory Go/Nogo tasks suggest that especially mechanisms of resource allocation are modulated when variations in sensory input are likely to affect response inhibition (Witold X. Chmielewski et al., 2016a,b; Chmielewski et al., 2016a,b). These modulations in resource allocation processes and in attention resources are reflected by the P2 ERP and could be detected in tasks with auditory stimuli (Campbell and Sharma, 2013), somatosensory stimuli (Sugimoto and Katayama, 2013) and olfactory as well

trigeminal stimuli (Geisler and Murphy, 2000). Therefore we hypothesize that the S-cluster in the P2 time window is smaller in SI Nogo trials, than in SII Nogo trials in adolescents. In adults, no modulations are expected. These modulations are expected to be associated with superior parietal structures, as these are known to mediate sensory integration for the sake of behavioral control (Bizley et al., 2016).

However, the C-cluster has already been shown to be modulated by variations of somatosensory stimuli that are processed in SI and SII cortical regions (Friedrich et al., 2017). We therefore hypothesize that above-mentioned differential effects between adolescents and adults are reflected by modulations in the C-cluster amplitude. This is also the case because the C-cluster has been considered to reflect processes similar to the Nogo-P3, which has been attributed to the process of the motor inhibition itself (Beste et al., 2009, 2010, 2011, 2016; Huster et al., 2013; Wessel and Aron, 2015). Therefore, anterior cingulate and/or inferior frontal regions are expected to reflect modulations of the C-cluster.

Traditionally, response inhibition processes are considered to be reflected by two ERP components: the Nogo-N2 and the Nogo-P3. The Nogo-N2 reflects processes like conflict monitoring or updating of the response program during response inhibition (Beste et al., 2009, 2010, 2011, 2016; Huster et al., 2013; Wessel and Aron, 2015, 2015) or the activity of a modality-specific inhibition process at premotor level (Falkenstein et al., 1999). While another hypothesis at premotor level proposes that the N2 component in Go and Nogo conditions represents proactive inhibitory control and reflects activity of late motor-preparation processes in premotor areas. In this areas the activity might be equal between Go and Nogo conditions with smaller and more posterior N2 components in Go conditions than for Nogo conditions. These proactive processes are more affected in Go conditions through overlapped prefrontal positivity characteristic than in Nogo conditions. (Di Russo et al., 2017; Perri et al., 2015) However the Nogo-P3 ERP likely reflects the inhibition itself (Beste et al., 2009, 2010, 2011, 2016; Huster et al., 2013; Wessel and Aron, 2015). Since the C-cluster strongly reflects processes that are considered to be reflected by the Nogo-P3 (Ouyang et al., 2017; Verleger et al., 2014; Wolff et al., 2017), it is possible that also the Nogo-P3 ERP-component reflects age-dependent differential effects in response inhibition processes when being triggered via SII, compared to SI cortical area. However, especially in ERP components with longer latencies (like the P3 ERP component) variations in amplitude are confounded with a latency jitter (Ouyang et al., 2017). This, together with the high intra-individual variability of longer latencies ERP components (Ouyang et al., 2015a,b,b,a; 2017; Verleger et al., 2014) makes it unlikely, that reliable neurophysiological modulations in line with the behavioral data are obtained using standard ERP components.

2. Materials and methods

2.1. Participants

This study includes two groups with $N = 30$ adults between 20 and 30 years (mean age 23.70 ± 0.83) and $N = 30$ adolescents between 14 and 15 years (mean age 14.57 ± 0.18). All participants were right-handed, had a normal or corrected-to-normal vision and confirmed that they don't have any psychiatric or neurological disorders. The institutional review board of the Medical faculty of the TU Dresden approved the study and the participants obtained a written informed consent before the experiment started.

2.2. Task

To examine the effects of somatosensory stimuli being processes in the SI versus SII cortical areas on response inhibition processes we used a Go/Nogo task with vibro-tactile stimuli (Friedrich et al., 2017). It is well-known that slow frequencies predominantly activate the SI cortex

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