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Age-related changes in neural recruitment for cognitive control

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ABSTRACT

The dual mechanisms of control (DMC; Braver, Gray, & Burgess, 2007) framework postulates a distinction between proactive and reactive modes of cognitive control. Event-related brain potentials (ERPs) were used to examine age differences in the neural correlates of proactive and reactive control for task-switching. Whereas proactive control is associated with brain activity for anticipatory task preparation, reactive control is accompanied by reduced preparatory activity, but increased activation during task execution. Switching between tasks was based on feedback-based transition cueing which places particularly high demands on mechanisms for cognitive control. Older adults maintained good performance accuracy at the expense of slower response times. No age-related increase in behavioral switching costs was observed. The cue-locked ERP (P3a) data revealed an age-related decrease in neural activity related to the processing of switch cues. In the target-locked ERPs, there was an increased frontal focus of the P3b in older adults. These ERP data indicate an age-related neural under-recruitment for proactive cognitive control and an age-related neural over-recruitment for reactive cognitive control. They are consistent with the idea that older adults may not fully implement task settings before target onset, after which they need to catch up on the omitted preparatory task settings.

1. Introduction

The frontal lobes of the brain are affected by the process of aging earlier and at a more rapid pace than other brain areas (West, 1996). This frontal theory of normal aging has been very influential on recent models of neuropsychological changes with age (Braver & West, 2008). The theory proposes that many age-related changes in cognition are attributable to deterioration of the frontal lobes, although obviously age also affects a number of other brain regions that impact cognition, such as the medial temporal lobes (Dennis & Cabeza, 2008; Hedden & Gabrieli, 2004; Raz et al., 2005). Volumetric findings support the frontal theory of normal aging because brain changes with age are most prominent in the frontal lobes (Dennis & Cabeza, 2008; Hedden & Gabrieli, 2004; Raz et al., 2005). There is substantial agreement that the prefrontal cortex is involved in executive processing (Miller & Cohen, 2001; Stuss & Knight, 2013). Therefore, age-related changes should be most evident in cognitive tasks demanding executive function (Braver & West, 2008; Fabiani, Friedman, & Cheng, 1998; Phillips, MacPherson, & Della Sala, 2002). The present study aimed at elucidating how these changes manifest themselves on an electrophysiological level in cued task-switching paradigms.

A core function of executive processes is to enable adaptive behavior in response to changing environmental demands (Luria, 1973). As a consequence, mechanisms of cognitive flexibility have been studied using a variety of task-switching paradigms (see Kiesel et al., 2010, for review). Within these paradigms response speed and accuracy are typically reduced on repeat trials in mixed task blocks as opposed to single task blocks (mixing costs) and on switch trials relative to repeat trials in mixed task blocks (switching costs). When task-switching paradigms were applied to the effects of aging on cognitive flexibility (Verhaeghen, 2011; Wasylyshyn, Verhaeghen, & Sliwinsky, 2011), behavioral studies revealed that mixing costs are consistently larger for older adults than for young adults while the evidence concerning switching costs is more ambiguous (Karayanidis, Whitson, Heathcote, & Michie, 2011). Specifically, behavioral switch costs have been reported to be increased (Kray, Li, & Lindenberger, 2002), decreased (Kray, 2006) or relatively unchanged (Kray & Lindenberger, 2000; Mayr, 2001) by age.

This picture of age-related differences in task-switching performance is complemented by neuropsychological research using the Wisconsin Card Sorting Test (WCST, Heaton, Chelune, Talley, Kay, & Curtiss, 1993). Specifically, age-related impairments have

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been reported with regard to the number of perseverative errors committed on the WCST (Rhodes, 2004). However, the specificity of the age-sensitivity of perseverative errors is questionable because increased numbers of non-perseverative errors on the WCST were also reported in older adults relative to younger adults (Salthouse, Atkinson, & Berish, 2003). In a large group of older adults, a negative correlation between number of perseverative errors on the WCST and prefrontal volume was observed, suggesting a relationship between the age-sensitivity of the perseverative errors on the WCST and the integrity of the frontal lobes in older adults (Gunning-Dixon & Raz, 2003; Head, Kennedy, Rodrigue, & Raz, 2009; Raz, Gunning-Dixon, Head, Dupuis, & Acker, 1998).

In task-switching environments, successful performance requires mechanisms of cognitive control which allow not only to react appropriately to changes in task contingencies, but also to cope with them in proactive ways (Braver, Gray, & Burgess, 2007). Mechanisms of *proactive* control, based on sustained activation prior to imperative events which may enforce behavioral changes, are future-oriented; they make use of the available predictive contextual information and permit to attend, in a preparatory and selective manner, to relevant sources of information. In contrast, mechanisms of *reactive* control, based on transient activation following such an imperative event, are past-oriented. They are focused on the resolution of interference from irrelevant sources of information because they do not allow selecting relevant information in advance. The distinction between proactive and reactive mechanisms of executive control within the dual mechanisms of control (DMC) framework (Braver et al., 2007) seems to be fundamental to an understanding of age-related changes of the neural correlates of cognitive flexibility. Specifically, based on functional brain imaging, it has been shown that older adults may shift from a proactive to a reactive cognitive control strategy (Jimura & Braver, 2010; Paxton, Barch, Racine, & Braver, 2008), thereby placing greater cognitive load on the processing of imperative events (Velanova, Lustig, Jacoby, & Buckner, 2007).

With regard to the study of age-related changes in cognitive flexibility, cued task-switching paradigms appear particularly useful for testing the hypotheses derived from the DMC framework (Braver et al., 2007). In these paradigms, a task cue is delivered permitting advance task preparation (supported by proactive control). The task cue is usually followed by an imperative stimulus (target) which requires the execution of a task (supported by reactive control). Hence, for the present study, we decided to use a task-switching paradigm based on external cuing to allow for a dissociation in time between cue-locked (proactive) and target-locked (reactive) event-related brain activity.

In a number of studies, event-related potentials (ERPs; see Fabiani, 2012; Friedman, 2012, for reviews) were used to examine age-related differences in the neural correlates of switching costs (De Sanctis, Gomez-Ramirez, Sehatpur, Wylie, & Foxe, 2009; Eppinger, Kray, Mecklinger, & John, 2007; Friedman, Nessler, Johnson, Ritter, & Bersick, 2008; Karayanidis et al., 2011; Kray, Eppinger, & Mecklinger, 2005; West & Moore, 2005; West & Travers, 2008). As opposed to repeat cues, switch cues tend to elicit a larger sustained posterior positivity (spP) and a larger sustained frontal negativity (sfN; see Karayanidis et al., 2010, for review). Aging has been reported to be associated with a reduction in the amplitude of both ERP correlates of switching costs (West & Moore, 2005; West & Travers, 2008). Friedman et al. (2008) used a cued task-switching paradigm in which cues and targets were presented simultaneously so that cue-locked and target-locked neural activities were not dissociable in time. They reported a decrease in anterior positivities in response to switch stimuli in older adults relative to young adults, but also an age-related increase in anterior positivities in response to repeat stimuli (see also Karayanidis et al., 2011).

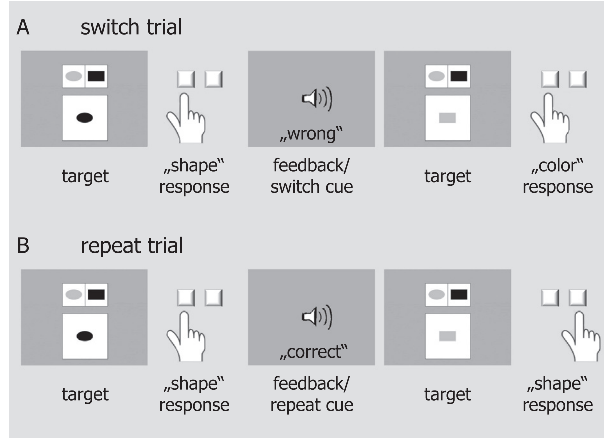

Fig. 1. (A) Illustration of an exemplary switch trial (A) and a repeat trial (B) in our attention switching paradigm. Switching from one sorting rule to the other (A) was guided by feedback-based transition cues ("wrong"-feedback stimuli).

The present study focused on age-related changes in the P300 component. In task-switching paradigms, cue-locked anterior (P3a-like) and posterior (P3b-like) positivities are typically more pronounced in response to switch cues relative to repeat cues (Barceló, Escera, Corral, & Periáñez, 2006; Barceló, Periáñez, & Knight, 2002; Gajewski & Falkenstein, 2011; Kopp & Lange, 2013; Kopp, Tabeling, Moschner, & Wessel, 2006). These cue-locked P3a switching effects occur in addition to the switching effects (spP, sfN) which are typically observed in response to prospective *task cues* (i.e., cues that provide explicit information about the currently effective task; Karayanidis et al., 2010). Importantly, prominent P3a amplitudes can only be observed when task switches are implicitly cued (via *transition cues*) but not when participants are explicitly informed about the correct rule on the upcoming trial (Adrover-Roig & Barceló, 2010; Kopp & Lange, 2013; Kopp, Moschner, & Wessel, 2005[1]; West, Langley, & Bailey, 2011). These cues can be delivered either at the beginning of each trial (*prospectively-signaled cuing*) or as feedback stimuli which are contingent on task performance (*feedback-based cuing*). Further, posterior (P3b-like) positivities are typically more pronounced in response to repeat targets relative to switch targets (Barceló et al., 2002). In the elderly, target-locked P3b activity has been shown to be shifted to more anterior sites (Adrover-Roig & Barceló, 2010; De Sanctis et al., 2009).

In the present task-switching study, feedback-based transition cuing was used to inform participants about changes in task contingencies (see Fig. 1). This type of (WSCT-like) cuing has previously been shown to be associated with substantial P3a switching effects (Kopp et al., 2005; Kopp & Lange, 2013) and increased involvement of the dorsolateral prefrontal cortex (Monchi, Petrides, Petre, Worsley, & Dagher, 2001). Taken together, the available data suggest that task-switching paradigms involving feedback-based transition cuing place particular demands on cognitive control processes (i.e., memorizing sets, performance monitoring; see Kopp & Wessel, 2011, for discussion, see also Fig. 2). Given the detrimental effects of aging on working memory (Braver & West, 2008; Hasher & Zacks, 1988) and on error processing

[1] This article was written in German language. Nevertheless, the reader can get an impression of the results by inspecting Fig. 3 (p. 81). ERP waveforms elicited by prospective task cues ("Wiederholung" = repeat cues; "Wechsel" = switch cues) are shown in the left panels (headed by the words "spezifischer Hinweis"). The central panels show ERP waveforms in response to prospective transition cues (headed by the words "nicht-spezifischer Hinweis"), whereas ERP waveforms elicited by retrospective transition cues can be found in the right panels (headed by the word "Rückmeldereiz").