Neuronal Signatures of Age Differences in Context Processing:

The Interplay Between Cognitive and Motivational Processes

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Contents

Summary

The dual mechanisms of control theory (DMC, Braver & Barch, 2002) assumes that goal-directed behavior requires the ability to actively maintain context representations and to flexibly update these representations whenever environmental conditions change. Based on the claim that increasing age reveals a shift from a proactive toward a reactive mode of context processing, the present thesis aimed at investigating the mechanisms underlying the time course of context updating in younger and older adults. Temporal differences between an early, anticipatory updating of context information in younger adults and a delayed, interference-based updating mechanism in older adults, respectively, were hypothesized to be reflected in event-related potentials (ERPs). Specifically, these ERP differences in the predominant manner of context updating should be a core component of cognitive aging independent of performance differences. Furthermore, as the DMC account postulates affective factors to influence the balance between employing pro- and reactive control (Braver, Gray, & Burgess, 2007), this thesis sought to shed light on the interaction between motivational factors and context processing.

This thesis is built upon three publications reporting behavioral performance measures and ERP components of context processing as measured with the AX-Continuous-Performance-Test (AX-CPT). In *Paper I,* the behavioral data show distinct age-related impairments whenever the updating of context information was required for correct task completion. In the ERP data, context updating in younger adults was reflected in a P3b-like component prompted by context cues indicating the need for information updating. In older adults, the P3b-activation was independent of the reliance on the context, but linked to perceptual changes in the context cue identity. Matching behavioral performance in the AX-CPT between younger and older adults, *Paper II* provides evidence that the mechanisms underlying age differences in context updating in ERPs were

independent of behavioral performance differences per se. Moreover, *Paper II* substantiates predictions of the DMC theory as those older adults showing equivalent performance to a group of younger adults exhibited a late N450 component linked to response conflict and the need for reactive control.

Whereas *Paper I* and *II* clearly illustrate age-related changes in context processing, *Paper III* investigates whether motivational cues signaling performance-contingent reward promote the updating of context information. The behavioral data show motivational cues to benefit context updating only in younger adults, although the ERP correlates suggest similar processing of motivational cues in both age groups. In the ERP data on context processing, younger adults showed reduced proactive context updating to avoid losing rewards, reflected in an attenuated P3b, but an increased need for reactive context updating before task execution. In older adults, P3b amplitudes differed for context conditions on motivational cues irrespective of valence suggesting improved context representation.

Altogether, the present thesis contributes to the understanding of age differences in context processing and is of high importance for theoretical models on the relationship between cognitive and affective processes. First, although younger and older adults prioritized different strategies in context updating, these are closely linked to age-differences in higher-order context representation and not exclusively due to a reactive shift with increasing age. Second, in line with the DMC theory, temporal differences in context updating underlie context processing in performance-matched age groups. Third, reward motivation reveals a strong impact on context updating at distinct processing stages in younger and older adults, who show differential sensitivity to motivational valence. This finding extends recent neuro-cognitive models and empirical data on the relationship between affective factors and cognitive control strategies and contributes to the understanding of this relationship in cognitive aging.

Zusammenfassung

Zielgerichtes Verhalten unterliegt im Rahmen der "dual mechanisms of control" - Theorie (DMC, Braver & Barch, 2002) der Fähigkeit, kognitive Repräsentationen von Kontextinformationen aufrechtzuerhalten und im Einklang mit sich ändernden Bedingungen zu aktualisieren. Da mit zunehmendem Alter eine Verlagerung von einem proaktiven zu einem reaktiven Muster der Aktualisierung von Kontextinformationen (kurz: Kontextaktualisierung) angenommen wird, ist das Ziel der vorliegenden Dissertation die zugrunde liegenden Mechanismen des zeitlichen Verlaufs der Kontextaktualisierung in jüngeren und älteren Erwachsenen zu untersuchen. Unterschiede zwischen einer frühen, antizipatorischen Kontextaktualisierung jüngerer und einem späteren, interferenzbasierten Modus der Kontextakualisierung älterer Erwachsener sollen sich in ereignis-korrelierten Potentialen (EKPs) widerspiegeln. Die EKP-Unterschiede werden als zentraler Bestandteil kognitiver Altersveränderungen unabhängig von Leistungsunterschieden zwischen den Altersgruppen angenommen. Da im Rahmen der DMC-Theorie affektive Faktoren das Überwiegen eines pro- bzw. reaktiven Kontrollstils beeinflussen, wird zudem der Einluss motivationaler Faktoren auf die Kontextverabeitung untersucht (Braver, Gray & Burgess, 2007).

Die Dissertation basiert auf drei Publikationen zu Verhaltens- und EKP-Daten in dem AX-Continuous-Performance-Test (AX-CPT). Die Verhaltensdaten in *Artikel I* zeigen Altersdefizite in Bedingungen, welche eine Kontextaktualisierung für die korrekte Aufgabenbearbeitung erforderten. In den EKP-Daten jüngerer Erwachsener ist die Kontextaktualisierung mit der Amplitude der P3b-Komponente assoziiert. Die P3b älterer Erwachsener ist hingegen unabhängig von der Notwendigkeit der Kontextaktualisierung, jedoch sensitiv gegenüber perzeptuellen Veränderungen der Kontextinformation. Durch den Vergleich jüngerer und älterer Probanden mit ähnlicher Verhaltensleistung liefert *Artikel II* den Nachweis, dass die EKP-Unterschiede der Kontextaktualisierung jüngerer

und älterer Erwachsenen unabhängig von Performanzunterschieden sind. Da diejenigen älteren Erwachsenen mit einer vergleichbaren Leistung zu jüngeren Erwachsenen eine späte N450-Komponente der Konfliktverarbeitung aufweisen, untermauert *Artikel II* die Annahme der DMC-Theorie hinsichtlich reaktiver Kontrolle älterer Erwachsener.

Während *Artikel I* und *II* deutliche Altersunterschiede in der Kontextverarbeitung demonstrieren, untersucht *Artikel III* den Einfluss motivationaler Hinweise, die eine Belohnung oder Bestrafung für die individuelle Verhaltensleistung ankündigen, auf die Kontextaktualisierung. In den Verhaltensdaten profitieren lediglich jüngere Erwachsene von diesen Hinweisen, obwohl die EKPs beider Altersgruppen eine verstärkte Verarbeitung der Hinweise gegenüber einer neutralen Bedingung nahe legen. Die EKP-Daten der Kontextverarbeitung jüngerer Erwachsenen zeigen eine verringerte P3b-Amplitude, sowie die Notwendigkeit für reaktive Kontrolle in Bestrafungs-Bedingungen. Die P3b-Amplitude älterer Erwachsenen hingegen differenziert in den Kontextbedingungen zwischen neutralen und motivationalen Durchgängen, jedoch unabhängig von deren Valenz.

Die vorliegende Dissertation trägt zum Verständnis von Altersunterschieden in der Kontextverarbeitung bei und ist für theoretische Annahmen über kognitiv-affektive Zusammenhänge von großer Bedeutung. Altersunterschiede in der Kontexterarbeitung zeigen sich nicht ausschließlich in zeitlichen Mustern, sondern auch in der kognitiven Repräsentation der Kontextbedingungen. Im Einklang mit der DMC-Theorie unterliegt die Kontextverarbeitung in Altersgruppen mit vergleichbarer Leistung zeitlichen Unterschieden der Kontextaktualisierung. Motivationale Hinweise weisen einen starken Einfluss auf unterschiedliche Prozesse der Kontextverarbeitung in jüngeren und älteren Erwachsenen auf, die zugleich unterschiedlich auf die Valenz des Hinweises reagierten. Dieser Befund erweitert aktuelle neuro-kognitive Modelle und empirische Daten über den Einfluss affektiver Faktoren auf kognitive Kontrollstile um die Altersperspektive.

List of Publications

This dissertation is based on three articles, which are published as 'original' articles in international peer-reviewed journals. I am the first author of the articles, but other authors contributed to the work and are listed below. The articles are not exactly presented in the dissertation, but single paragraphs of the introduction and discussion include content similar to the published articles.

Paper I

Schmitt, H., Ferdinand, N.K., & Kray, J. (2014). Age-differential effects on updating cue information: Evidence from event-related potentials. *Cognitive, Affective, and Behavioral Neuroscience, 14,* 1115–1131. DOI 10.3758/s13415-014-0268-9

The final publication is available at www.springerlink.com.

Paper II

Schmitt, H., Wolff, M.C., Ferdinand, N.K., & Kray, J. (2014). Age differences in the processing of context information: Is it age or is it performance? *Journal of Psycho-physiology, 28,* 202-2014. DOI 10.1027/0269-8803/a000126

The final publication is available at www.hogrefe.com.

Paper III

Schmitt, H., Ferdinand, N.K., & Kray, J. (2015). The influence of monetary incentives on context processing in younger and older adults: An event-related potential study. *Cognitive, Affective, and Behavioral Neuroscience, 15,* 416-434. DOI 10.3758/s13415-015-0335-x

The final publication is available at www.springerlink.com.

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List of Abbreviations

ACC	Anterior Cingulate Cortex
AX-CPT	AX-Continuous-Performance-Task
cf.	See respectively compare
CNV	Contingent Negative Variation
CTI	Cue-Target-Interval
CRUNCH	Compensational-Related Utilization Of Neural Circuit
DA	Dopamine
DL-PFC	Dorsolateral Prefrontal Cortex
DMC	Dual Mechanisms of Control
EEG	Electroencephalography
e.g.	For Example
ERP	Event-Related Potential
FMRI	Functional Magnetic Resonance Imaging
i.e.	That Is
lPFC	Lateral Prefrontal Cortex
ms	Milliseconds
NAc	Nucleus Accumbens
PFC	Prefrontal Cortex
SP	Sustained Potential
TMS	Transcranial Magnetic Stimulation
VTA	Ventral Tegmental Area
WM	Working Memory
WSCT	Wisconsin Card Sorting Test
µV	Microvolts

1 Introduction

For a long time, understanding individual goals as key determinants of behavior has attracted both philosophers and psychologists (Adler, 1998). In today's cognitive psychology, the ability to focus on goal representations has been recognized as being critical for guiding adaptive behavior (Miller & Cohen, 2001). Nevertheless, it becomes evident from daily life that personal goals differ widely in their motivational value (Chiew & Braver, 2011b). Some goals, such as preparing for an upcoming exam, will be potentially rewarded and strongly influence behavior. Thus, goal-directed behavior is the product of cognitive and affective processes, although the underlying mechanisms remain largely unknown (Pessoa & Engelmann, 2010). Investigating cognitive-affective interactions might be particularly important in old age as advancing age is followed by a decline in various facets of controlled behavior, while affective processes seem to be relatively preserved (Carstensen & Mikels, 2005; West, 1996). In a current framework, neurobiological age changes are assumed to cause a temporal shift in the updating of goal-relevant context information for controlled behavior (Braver & Barch, 2002). As anticipated reward is expected to prompt context updating, the question arises whether incentives are useful to promote context processing in older adults.

The present thesis adresses this question by utilizing the high temporal resolution of ERPs. In the first study, ERPs serve to establish the neural mechanisms of temporal dynamics in context processing. In the second study, ERP-correlates are used to uncover the impact of incentives on context processing in younger and older adults. Eventually, the results of this thesis will contribute to the understanding of neuronal processes of cognitive aging, offer potential means to influence goal-directed behavior in old age, and elucidate possible mechanisms of cognitive-affective interactions.

2 Theoretical and Empirical Foundations

The following section serves as a review of theoretical and empirical foundations. Beginning with the description of cognitive control processes and the neuronal mechanisms involved, the second part outlines senescent changes focusing on the dopamine system and the prefrontal cortex. Part three and four summarize age-related changes in cognitive control tasks with regard to recent aging theories. In particular, evidence to the claim is provided that increasing age reveals a shift from a proactive toward a reactive mode of context processing. Afterward, the fifth part introduces the AX-CPT that allows investigating temporal mechanisms of context processing. Part six reviews age differences in behavioral and ERP markers of task switching. Thereafter, current findings about motivational manipulations on cognitive control are reported. The section closes by outlining the objective of the present thesis.

2.1 Cognitive Control Processes and Their Neural Basis

One remarkable feature of the human mind is its ability to exert controlled behavior in changing environmental conditions by selecting goal-directed actions from an unlimited behavioral repertoire (Miller & Cohen, 2001). For instance, aiming to go to the gym after work requires selecting and monitoring a complex chain of actions, such as packing the bag and pursuing the way to the gym, as well as the flexible switching between actions to persist toward this aim (Miller, 2000). This is particular important whenever automatic actions (e.g., returning home) interfere with the intended

purpose (Braver et al., 2007). The term cognitive control[1] refers to the fundamental higher-order cognitive ability to select, maintain, and guide "lower-level" (Alvarez & Emory, 2006, p. 17) sensory and motor mechanisms in favor of goal-directed, adaptive behavior (Braver & Cohen, 2000; Karbach & Unger, 2014; Miller & Cohen, 2001). Thereby, cognitive control functions are assumed to enable the resistance against interference and distraction, support the updating and shifting of goals, and facilitate the planning of temporally extended actions (Karbach & Unger, 2014; Kopp, Lange, Howe, & Wessel, 2014; Miller, 2000; Miyake et al., 2000; Shallice, 1982).

In an influential theory on cognitive control by Miller and Cohen (2001), it is assumed that the ability to form "*task contingencies*" (Miller, 2000, p. 60), i.e., associations between environmental conditions, internal states, and behavioral actions related to goal achievement is essential for establishing goal-directed behavior. Psychophysiological research in healthy subjects, neurological impaired patients, and non-human primates suggest that the prefrontal cortex (PFC) and the midbrain dopamine (DA) system are the prerequisite underlying these task contingencies (D'Ardenne et al., 2012; Miller, 2000; Miller & Cohen, 2001).

Specifically, the PFC receives multiple pieces of (sub-) cortical sensory and motor information to build-up complex representations. Sustained activity of PFC neurons serves to maintain such complex, goal-relevant information against distraction (Braver et al., 2007; Miller, Erickson, & Desimone, 1996; Miller & Cohen, 2001), as it has been shown during delayed-response tasks in macaques (Miller et al., 1996). Sustained

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[1] *Note:* There is no general agreement whether the mechanism underlying controlled behavior is best described in the term "cognitive control" (cf. Miller & Cohen, 2001) or "executive functions" (cf. Alvarez & Emory, 2006). Some scholars seem to equate cognitive control and executive functions (Diamond, 2011; Luszcz & Lane, 2008), whereas others explain performance in complex *executive tasks* (e.g., planning, problem solving) by applying *cognitive control functions* (i.e., inhibition, working memory, shifting, cf. Miyake et al., 2000; see 2.3).

activitation along with its extensive connectivity allows the PFC to top-down control activity in domain-specific brain areas responsible for executing controlled, goal-driven actions (Desimone & Duncan, 1995; Miller & Cohen, 2001). In this role, the PFC is supported by a network of cortical and subcortical brain structures areas providing the means to guide goal-directed behavior (Miller, 2000). For instance, the anterior cingulate cortex (ACC) is assumed to support the monitoring of response competition and conflict (Botvinick, Cohen, & Carter, 2004; Carter et al., 1998). Critically, ACC projections to the PFC are supposed to indicate the need for supervisory regulation as a result of detecting ongoing conflict, and are accordingly important as a "performance-monitoring mechanism" (Braver et al., 2007, p. 78) to PFC-function (Miller & Cohen, 2001). Furthermore, a frontal-parietal network activated during tasks requiring the maintenance of task-relevant information serves the guidance of attentional top-down control (Cohen et al., 1997; Corbetta & Shulman, 2002; Madden, Whiting, & Huettel, 2005). Recriprocal connections between the PFC and the basal ganglia support the maintenance of task-relevant information against interference, particular by means of dopaminergic influences from the striatum (Cohen, Braver, & Brown, 2002; Gruber, Dayan, Gutkin, & Solla, 2006).

The DA influence on PFC activation is particularly critical for establishing task contigencies (Miller, 2000). Phasic DA release primarily from the midbrain ventral tegmental area (VTA) to reward not only encodes actual goal achievement (Miller, 2000; Schultz, 1998), but DA bursts can also undergo temporal changes and triggered by reward-predicting cues or inhibited if expected reward is hold back, thus being critical for learning stimulus-response associations (cf. Miller & Cohen, 2001; Schultz, 1998, 2010). The gating of DA to DA-innervated PFC neurons encoding the nature of the actual reward serves to support information maintenance in the PFC (Gruber, A. J.

et al., 2006) and to temporally connect PFC-activation elicited by reward with PFC-activity of preceding actions and environmental cues (Miller, 2000). Eventually, these task contingencies can be recalled to trigger goal-relevant behavior in a specific situation (Miller, 2000).

Taken together, the interplay between a subset of PFC-regions and the DA system and a can be regarded as a supervisory mechanisms controlling a broad network of posterior, lower-level brain regions in goal-directed action (Miller, 2000; Miller & Cohen, 2001; Shallice, 1982). Accordingly, as behavior becomes more practiced, the demand on control processes monitored by the PFC is diminished (Braver et al., 2007; Duncan & Owen, 2000; Miller & Cohen, 2001). Reports on patients with frontal brain lesions render support to the role of the PFC in controlled behavior, as these patients are often unable to maintain goal-relevant information to pursue goal-driven actions, but exhibit increased distractibility toward salient information eliciting automatic responses (Shallice & Burgess, 1991; Shallice, Burgess, Schon, & Baxter, 1989). At the same time, these patients fail to flexible adapt to changing environmental conditions or to acquire novel responses to ambiguous stimulus characteristics (Petrides, 1990). However, deficits in controlled behavior may also appear due to a decline in the PFC and the DA-system inherent in healthy aging (Cabeza, Nyberg, & Park, 2005; Li, Lindenberger, & Sikström, 2001). The following paragraph summarizes the most prominent senescent changes in the PFC and the DA system, before turning to age differences in cognitive control.

2.2 Senescent Changes in the PFC and the DA System

As described in the previous section, the PFC and the DA system are assumed to play an important role for cognitive control functions required in everyday life. Despite large individual differences and an age-related deterioration in other brain regions and neurotransmitter systems (for an overview, see Cabeza et al., 2005), increasing age has been associated with neuroanatomical and neurochemical alterations particularly pronounced in the PFC and the DA system (Dennis & Cabeza, 2008; Raz, 2005). Life-span studies reveal the earliest and steepest decline in neuronal gray matter volume in frontal areas (Braver et al., 2001; Resnick, Pham, Kraut, Zonderman, & Davatzikos, 2003). Within the frontal lobe, age-related neuronal loss is greatest in the PFC and regional differences indicate larger atrophy in the dorso-lateral than in the orbito-frontal PFC (Raz, 1997, 2005). Age-related atrophy of neuronal white matter seems to be pronounced in frontal areas (Raz et al., 1997; but see Resnick et al., 2003). Whereas the deterioration of prefrontal gray matter in aging occurs in a linear fashion, prefrontal white matter volume seems to follow an inverted U-function in longitudinal studies (Bartzokis et al., 2001; Jernigan et al., 2001; Raz et al., 2005). Nevertheless, reduced axonal integrity and myelin thickness in aging strongly affect white matter integrity, particularly in the PFC (Jernigan et al., 2001; Pfefferbaum, Adalsteinsson, & Sullivan, 2005).

Concerning the mesencephalic DA-system, three major separate albeit interacting DA-pathways have been identified (cf. Bäckman & Farde, 2005; see also Ashby, Isen, & Turken, 1999; Mirenowicz & Schultz, 1996). The nigro-striatal circuit involves neurons in the substantia nigra projecting to the striatum, which is densely innervated by DA-neurons of the caudate nucleus and the putamen (Green, 1994). Originating from

DA-neurons in the midbrain VTA, the meso-limbic pathway projects to the limbic system and the ACC, while the meso-cortical pathway continues into the neocortex including the PFC (Bäckman & Farde, 2005; Panksepp & Moskal, 2008). Aging is associated with a linear or even exponential loss of DA across the whole brain starting in middle adulthood (Bäckman & Farde, 2005; Dennis & Cabeza, 2008), but especially pronounced in the nigro-striatal system and the PFC (Bäckman & Farde, 2005; Li et al., 2001; Suhara et al., 1991). These age-related changes include a reduction of DA-neurons particularly in the substantia nigra, accompanied by a decrease in DA-synthesis rate, postsynaptic DA-receptor binding, and DA-transporter protein expression (Bäckman et al., 2000; Rinne, 1987; Suhara et al., 1991). As the striatum has reciprocal connections to the neocortex via frontal-striatal circuits (Li et al., 2001), age-related changes in the nigro-striatal DA-system are expected to impair performance on tasks relying on cognitive control supported by the PFC (Bäckman & Farde, 2005; Bäckman, Nyberg, Lindenberger, Li, & Farde, 2006, Li et al., 2001). The most prominent age differences in cognitive control tasks are summarized in the following paragraph.

2.3   Age-related Changes in Cognitive Control Tasks

Whereas the acquired knowledge of cultural procedures has been shown to remain either unaffected, to decline only in very old age, or even to improve with aging (Baltes, Staudinger, & Lindenberger, 1999), the age-related decline in the PFC and the DA-system outlined in the previous section have been associated with behavioral deficits in tasks requiring the supervisory control of cognitive processes (Bäckman et al., 2006). However, what exactly defines cognitive control and whether cognitive control constitutes a unitary or a multidimensional construct is still a matter of debate (Luszcz

& Lane, 2008, Miyake et al., 2000; Salthouse, Atkinson, & Berish, 2003). Traditionally, the central executive component in Baddeley's model of working memory (WM; Baddeley, 1992) has been proposed as a candidate for the control of cognitive processes. WM refers to a resource-limited form of memory (Oberauer, 2005) that serves the online storage and manipulation of goal-relevant information in the service of flexible, controlled processing (Baddeley, 1992; Braver et al., 2007; D'Esposito, 2007; Kane, Conway, Hambrick, & Engle, 2007; Reuter-Lorenz & Sylvester, 2005). The central executive in particular has been associated with the regulation and manipulation of domain-specific short-term memory content to fulfill goal-directed actions and linked to frontal-lobe functioning (Baddeley, 1992; Braver et al., 2007; D'Esposito, 2007; Kane et al., 2007; Klingberg et al., 2005; Miyake et al., 2000).

Recent research assumes that cognitive control can be fractionated into different sub-functions including WM (Fisk & Sharp, 2004; Luszcz & Lane, 2008; Miyake et al., 2000; for a recent overview, see Karbach & Unger, 2014). In the study by Miyake and colleagues (2000), confirmatory factor analysis on tasks generally assumed to tap cognitive control revealed three underlying separable, but interrelated latent target functions, namely, the *updating and monitoring* of WM representations, the *inhibition* of predominant responses, and the attention *shifting* between tasks (cf. Miyake et al., 2000). Importantly, the factor structure was replicated in a sample consisting of a large age range (Fisk & Sharp, 2004). Performance reflected in the three variables showed a significant decline with increasing age (Fisk & Sharp, 2004). In the following, typical age-related changes in tasks loading on these factors will be reviewed. Whether the changes can be explained by an age-related impairment in a single underlying factor (e.g., Salthouse, 1996) will be discussed subsequently.

Concerning the ability to temporally maintain, monitor, and update WM content (Miyake et al., 2000), aging has been found to be accompanied with a performance decline across a variety of WM-tasks, for instance, in delayed item recognition, in the n-back task stressing the continuous updating and monitoring of memory (Reuter-Lorenz & Jonides, 2007), as well as in complex span measures involving item storage and processing from secondary tasks (Conway et al., 2005). Some studies reveal a larger age-related decline in WM for visuo-spatial than verbal material (Bopp & Verhaeghen, 2007; Hale, Myerson, Emery, Lawrence, & Dufault, 2007; Reuter-Lorenz & Sylvester, 2005; but see Park et al., 2002) and a larger decline as the demand on information manipulation in WM and the general task complexity increase (Braver & West, 2008; Reuter-Lorenz & Sylvester, 2005; Salthouse & Babcock, 1991). Age differences in the ability to monitor information are also related to conflict detection. In the Wisconsin Card Sorting Test (WCST; Berg, 1948), subjects sort carts to target categories whilst adapting the sorting behavior to the announcement of a change in target criterion (Miyake et al., 2000). Older adults show more perseveration errors than younger adults indicating a failure to monitor and use feedback for behavioral adaption (Gunning-Dixon & Raz, 2003; Zelazo, Craik, & Booth, 2004). The decline in the efficiency to learn from feedback seems to be related to age-related differences in psycho-physiological measures of error processing and feedback monitoring reflecting the interaction between the midbrain's DA systems and the ACC (e.g., Herbert, Eppinger, & Kray, 2011; Nieuwenhius et al., 2002)

Age-related impairments in the ability to inhibit the influence of task-irrelevant information have a tradition in explaining cognitive aging phenomena (Lustig, Hasher, & Zacks, 2007). The enhanced interference effect in older adults when naming the color of an incongruent stimulus (i.e., ''red'' written in blue ink) compared to a congruent

stimulus (e.g., ''red'' written in red ink) in the Stroop task (Stroop, 1935; Verhaeghen & Cerella, 2002; West, 2004; West & Alain, 2000b) renders support for an age-related decline in the inhibitory control of predominant responses. Older adults also show increased reaction times in the stop-signal task indicating a decline in the ability to withhold an ongoing response (Kramer, Humphrey, Larish, Logan, & Strayer, 1994). Moreover, age differences can be found in the antisaccade task measuring the inhibition of a reflexive saccade toward a suddenly emerging cue and the execution of an antisaccade to the opposite of the cue (Hallett & Adams, 1980; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001). A slower onset of correct antisaccades and augmented saccade errors in old age suggests an impaired suppression of the automatic orientation to the cue (Butler, Zacks, & Henderson, 1999).

Finally, a decline in the flexible shifting back and forth between tasks and mental sets to changing environmental conditions (Monsell, 2003) in older adults is related to increased perseveration errors in the WCST (for a review, see Rhodes, 2004; see also Fisk & Sharp, 2004; Zelazo et al., 2004). Older relative to younger adults also show larger reaction time costs when two tasks are performed concurrently compared to performance on a single task (Verhaeghen & Cerella, 2002, 2008). This increase in performance costs can also be obtained in task switching (Rogers & Monsell, 1995) requiring the permanent switching between task rules on successively presented trials relative to performance on single tasks without switching (Rogers & Monsell, 1995). However, the latter seems to be related to age differences in the maintenance and coordination of two task sets in WM when being in a switch situation than the switching per se (Kray & Lindenberger, 2000; Wasylyshyn, Verhaeghen, & Sliwinski, 2011; for a recent review, see Kray & Ferdinand, 2014).

2.4   Recent Theories of Cognitive Aging

The foregoing paragraph has outlined three factors critical to controlled behavior, namely the updating and monitoring of WM content, the inhibition of automatic responses, and the flexible shifting between mental sets (Miyake et al., 2000). An age-related decline has been found in all of these factors, which are moderately correlated to each other (Fisk & Sharp, 2004). It should be noted that complex cognitive control tasks, such as the WCST, are assumed to involve performance reflected in more than one factor (Fisk & Sharp, 2004; Karbach & Unger, 2014; Miyake et al., 2000). Recent aging theories questioned whether the age-related decline in cognitive control tasks can be explained by a limited number of underlying factors or even by a single mechanism (Braver et al., 2001; Craik & Salthouse, 2008; Kray & Ferdinand, 2014; Li et al., 2001; Lustig et al., 2007; Salthouse & Babcock, 1991). Importantly, any hypothesized mechanisms needs to encompass age-related changes in neuro-biological factors, brain mechanisms, and behavioral findings (Braver et al., 2001; Dennis & Cabeza, 2008; Li et al., 2001). Although a number of current cognitive aging theories involve a neurobiological framework (for a review, see Dennis & Cabeza, 2008; Hale et al., 2007; West, 1996), the following paragraph introduces the prominent processing-speed theory of cognitive aging (cf. Salthouse, 1996), before turning to the DMC theory (Braver et al., 2001), which is of most interest for the scope of the present dissertation.

2.4.1 The Processing-Speed Theory of Adult Age Differences in Cognition

One of the most influential theories on cognitive aging is the processing-speed theory of adult age differences in cognition (cf. Salthouse, 1996; see also Myerson, Hale, Wagstaff, Poon, & Smith, 1990; Verhaeghen & Cerella, 2008). By mechanisms of limited time and simultaneity (Hale et al., 2007), the well-documented age-related decline in speed with which perceptual, motor, or cognitive operations can be performed is assumed to account for age differences in multiple cognitive tasks (Dennis & Cabeza, 2008; Salthouse, 1996; Schaie, 1989). Age-related neuronal changes, such as diffuse cell loss, deteriorated myelin sheaths as well as reductions in the number of dendritic branches, active synapses, and neurotransmitters are proposed to account for slowed propagation of neuronal impulses and disrupted neuronal synchronization, underlying the decline in processing speed (Dennis & Cabeza, 2008; Miller, 1994; Myerson et al., 1990; Raz, 2005; Rypma & D'Esposito, 2000; Salthouse, 2000; but see Söderlund, Nyberg, Adolfsson, Nilsson, & Launer, 2003). Indeed, results showing that the decline in white matter integrity mediates the relationship between age and performance in cognitive tasks are in support of this notion (cf. Dennis & Cabeza, 2008; Madden et al., 2009).

In conditions of constrained time, decreased processing speed is assumed to lead to insufficient time available to perform single processing stages, with more time necessary for early operations limiting time for executing later operations (Dennis & Cabeza, 2008; Fisk & Sharp, 2004; Salthouse, 1996). This *"limited time mechanism"* (cf. Salthouse, 1996, p. 404) explains larger age differences in complex tasks consisting of a number of processing steps to perform than in tasks featuring low-level difficulty (i.e., *"complexity cost"*, cf. Li, Lindenberger, & Frensch, p. 879; Kliegl, Mayr, &

Krampe, 1994; Salthouse, 1996). In conditions of unlimited time, slowed processing reduces the amount of simultaneously available information in tasks requiring multiple processing steps. The de-synchronization occurs as information processed at earlier stages decays over time and is therefore unavailable or even outdated for later processing stages (cf. Salthouse, 1996). Deficits in the *"simultaneity mechanism"* (cf. Salthouse, 1996, p.405) may not only cause a higher rate of errors, but also the need for repeating critical operations (Salthouse, 1996).

The processing-speed theory has been influential to the research on cognitive aging by demonstrating an attenuated or even non-significant influence of age on numerous cognitive measures after statistical controlling for age differences in processing speed (Lindenberger, Mayr, & Kliegl, 1993; Salthouse, 1996). Hence, processing speed has been explained as a common mediator of age differences in cognitive tasks such as WM span, memory, reasoning, or spatial abilities to name only a few (Lindenberger et al., 1993; Luszcz & Lane, 2008; Salthouse, 1994; Schaie, 1989). Here, older adults' latencies have often been described as a linear function of younger adults' reaction times (Myerson et al., 1990; Verhaeghen & Cerella, 2002).

However, the impact of processing speed on age differences varies across cognitive tasks. Some age effects on performance remain stable after controlling for speed differences, such as for switching and dual-task performance (Braver et al., 2001; Verhaeghen & Cerella, 2002; Verhaeghen, Steitz, Sliwinski, & Cerella, 2003). Although age differences in many tasks share variance based on age-related slowing, cognitive tasks seem to differ in the reliance on the common speed factor. Following this line of thought, processing speed might not be the only mechanism accounting for age differences across cognitive tasks (West, 2004). Critically, the processing-speed theory predicts an age-related decline in the neuronal propagation of information to

underly reduced speed of processing, but it remains unclear by which means this deficit occurs (Braver et al., 2001). Particularly, distinct age effects on the PFC and the DA-system, and typical patterns of age-related differences in psychophysiological measures, such as task-related neuronal over-activations or activation overlap between different tasks (cf. Cabeza et al., 2005; Reuter-Lorenz & Sylvester, 2005) are not considered (see part 2.6.2).

2.4.2 The Dual Mechanisms of Control Theory

In common with the foregoing theory (Salthouse, 1996), the DMC theory strives to explain age differences in multiple cognitive tasks by a common underlying mechanism (Braver et al., 2001). In the DMC theory, it is proposed that the relationship between the PFC, more precisely its dorso-lateral part (DL-PFC), and the DA-system serves the processing of *context information* required for cognitive control. This relationship is supposed to be influenced by individual differences and non-cognitive factors (Braver et al., 2007). Hence, the DMC theory not only contributes to the understanding of age differences in cognitive control, but also offers a potential means to experimentally investigate and modulate the variability of cognitive control within subjects (for a review, see Braver, 2012; see section 2.7).

In the DMC framework, context processing involves the ability to internally represent, maintain, and update context information (Braver & Barch, 2002). Context information comprises any task-relevant information, such as goal representations, task instructions, or stimulus characteristics (Braver et al., 2001; Braver & Barch, 2002). In line with an earlier account on PFC-function (Miller & Cohen, 2001; see section 2.1), sustained activity of DL-PFC neurons serves the long-lasting representation of goal-

relevant context information in an accessible state (Braver & West, 2008). In situations claiming a high demand on cognitive control (see section 2.1), actively maintained context representations are assumed to top-down regulate activations of posterior and subcortical brain areas in order to influence the direct stimulus-response pathways consistent with internal goals (see Figure 1; Braver & Barch, 2002). Thus, context representations constitute a subset of WM-representations (Braver et al., 2007), but are assumed to modulate both the processing and the storage of goal-relevant representations within WM (Braver et al., 2001, 2007).

As controlled behavior requires the adaption to rapidly changing conditions (Miller & Cohen, 2001), a DA-guided gating mechanism is presumed to regulate the balance between the stable maintenance of context in the DL-PFC and its flexible updating to novel or unexpected information (see Figure 1; Braver & Barch, 2002; Cohen et al., 2002). In line with the role of the midbrain DA-system in learning based on reward achievement (Braver et al., 2007; Bromberg-Martin, Matsumoto, & Hikosaka, 2010; Schultz, 2002), phasic DA-projections to the DL-PFC after salient, i.e., novel and reward-predicting cues are associated with the updating of context information by gating external information into the PFC. In contrast, in the absence of phasic DA release, the gate is closed, thereby protecting context representations against access of distracting information (Braver et al., 2001; Braver & Barch, 2002).
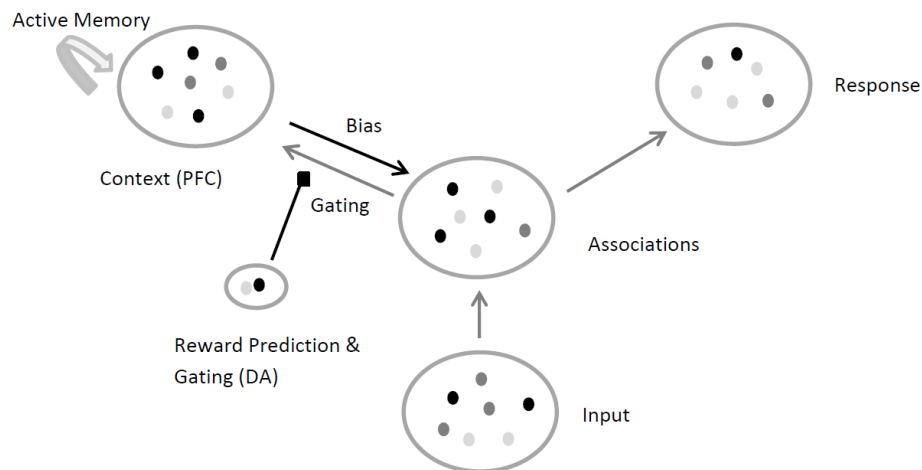
Figure 1. Schematic diagram of the context processing model (own depiction, modified and adapted from Braver et al., 2001).

Recurrent PFC-activation serves to maintain context information in order to top-down bias the direct pathway between input and response. Phasic DA-activity to reward prediction regulates the updating of context information in the PFC.

Support for the DMC theory is drawn mainly from computational modeling, but is also provided by recent neuroscientific research and studies on patient populations with disturbances in the DA-system and the PFC (Barch, 2004; Braver et al., 2001; Cohen et al., 2002). For instance, D'Ardenne and colleagues (2012) applied functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) to first identify and then interrupt DL-PFC-regions associated with the encoding and representation of context information in a WM-task. The fMRI data also indicated phasic DA-release from the VTA and the substantia nigra after the presentation of task-relevant context information. As this DA release was positively correlated to DL-PFC activation and behavioral performance, the study provides evidence for the gating of context representations into the PFC (D'Ardenne et al., 2012). Furthermore, the results of the study are in line with the beneficial effect of increased DA-release by pharmacological

substitutes on task tapping the use of contextual information (Barch, 2004). Moreover, the DMC may also account for cognitive control deficits in psychiatric disorders such as in Schizophrenia. Abnormalities in the PFC and the DA-system commonly observed in Schizophrenia may lead to impaired encoding, representation, and maintenance of context information (Braver, Barch, & Cohen, 1999). On the basis of these considerations, disturbancies in the DA-systems may lead to an imbalance in gating context information, i.e., on the one hand reduced updating and maintenance of task-relevant information, but one the other hand representation of task-irrelevant information. These changes on the neuronal level may lie at the core of poor interference control and behavioral perserveration in schizophrenic patients (Braver et al., 1999).

2.5 One Way to Measure the Nature of Context Processing: The AX-CPT

Regarding the decline in the PFC and the DA-system in healthy aging (Bäckman & Farde, 2005, see section 2.2), age-related deficits in context processing are expected and have been investigated by applying a specific variant of the AX-CPT (Paxton, Barch, Storandt, & Braver, 2006; Rosvold, Mirsky, Sarason, Bransome, & Beck, 1956; Servan-Schreiber, Cohen, & Steingard, 1996). In the task, subjects are confronted with letters presented one at a time in a series of cue-probe pairs (Braver et al., 2001; see Figure 2). A target response to the probe is required whenever the letter "A" (i.e., cue A) is followed by the letter "X" (i.e., probe X), whereas a non-target response is mandatory whenever either a cue other than the letter "A" (generally termed cue B) is followed by the letter "X", or whenever the letter "A" is followed by a letter other than

the letter "X" (generally termed probe Y). Thus, correct responses to probes require the trial-to-trial representation and maintenance of context information provided by the cue.
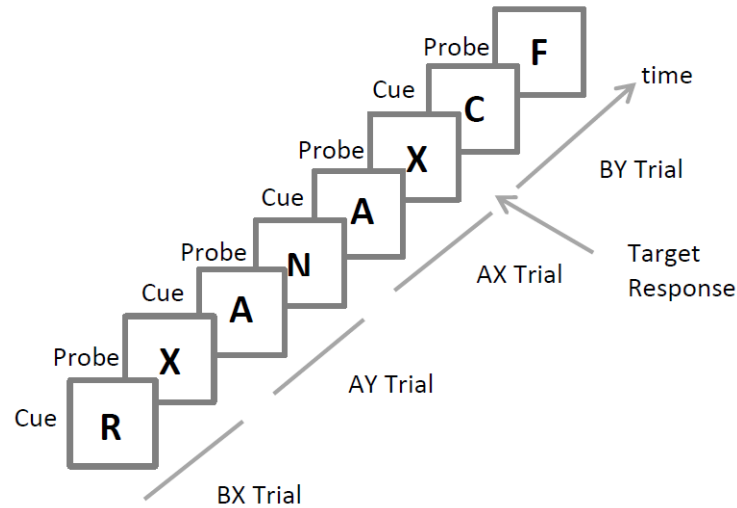
Figure 2. Trial procedure of the AX-CPT (own depiction, adapted and modified from Braver et al., 2001).

A target response is required, whenever the probe "X" immediately follows the cue "A" (i.e., AX-trial), whereas a non-target response is required on all other combinations of cues and probes (i.e., BX-, AY-, and BY-trials). Note that cue "B" refers to any letter except "A" and probe "Y" refers to any letter except "X".

As the target-combination (i.e., A-X trials) occurs with a frequency of 70%, whereas each non-target combination (i.e., A-Y, B-X, and B-Y trials) occurs with 10% frequency, subjects have a high expectation of exerting a target-response whenever the cue A or the probe X is presented. According to the DMC theory, this expectation can be used to examine intact versus impaired context processing and is statistically expressed by computing performance on BX- relative to AY-trials. Both trials violate the expectation of a target-response due to an invalid cue (i.e., BX-trials), or an invalid probe (i.e., AY-trials). Preserved context processing in younger adults is predicted to result in better performance on BX- than AY-trials. This is due to the assumption that the intact representation and maintenance of the cue B should be associated with the

advanced preparation of a non-target response to the probe X (Braver, Satpute, Rush, Racine, & Barch, 2005), whereas the representation of contextual information on AY-trials is assumed to result in a strong expectation and preparation of a target-response causing a tendency for false alarms to the probe Y (Braver et al., 2005). In contrast, impaired representation of contextual information in older adults is supposed to benefit performance on AY-trials but to impair performance on BX-trials. In AY-trials, the failure to maintain the cue information reduces interference during presentation of the probe Y linked to a non-target response. In contrast, deficits in representing and maintaining cue information will lead to relatively more false alarms on BX-trials, in which the strong tendency for a target response to the probe X needs to be overridden (Fröber & Dreisbach, 2014). However, apart from the trade-off between performance on AY- and BX-trials across the two control modes, it should be noted that due to the high frequency of AX-trials, proactive control is the optimal strategy in the AX-CPT (Redick, 2014).

In a number of behavioral studies, Braver and colleagues (2001, 2002, 2005) received support for age-related deficits in context processing, as younger adults showed better performance on BX- than AY-trials, whereas older adults showed the reciprocal pattern (Braver et al., 2005). Importantly, the age effect remained significant when controlling for processing speed, and older adults showed even faster reaction times than younger adults on AY-trials. Hence, the results speak against the hypothesis of age differences in processing speed as the single underlying mechanism (Salthouse, 1996). Instead, as the pattern is highly consistent with the DMC theory, Braver and colleagues claimed context processing to be the common factor underlying age differences in inhibition, WM, and attentional control often regarded as separable components of cognitive control (Braver et al., 2001; see section 2.3; Miyake et al.,

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2000). For instance, the active maintenance of task-relevant context information is not only essential to protect information against interference in WM-tasks. Context also reflects the representation of a contemporary task rule over a dominant response tendency in inhibition tasks, and supports goal-directed behavior by biasing the task-relevant and inhibiting the task-irrelevant response (Braver et al., 2001; Braver & Barch, 2002). Age differences in switching tasks might be due to the failure to update the current relevant task-set and to actively represent it in WM (Braver & West, 2008), which again serves the top-down implementation of the targeted behavior and the inhibition of behavior related to the currently irrelevant task-set. Following these considerations, instead of separating age differences in cognitive control into a decline of several sub-components, age differences in context processing are expected to lie at the core of age deficits in various measures of cognitive control (Braver et al., 2001). In further support of this notion are correlations between performance in the AX-CPT and other cognitive control tasks establishing the construct validity of the task (Braver et al., 2005).

2.5.1 Context Processing in a Proactive and in a Reactive Manner

Earlier versions of the DMC-theory on age differences in context processing have been described as the goal-maintenance or context-processing account (Braver et al., 2001; Braver & West, 2008). The DMC theory extents these accounts by assuming that aging specifically affects the predominant manner of context *updating* (Braver, 2012). This assumption is based on results of a study applying a variable delay between the presentation of the cue and the probe in the AX-CPT (Braver et al., 2005). Prolonging the delay between the presentation of the two stimuli offers the possibility to separately

investigate the core components of context processing, i.e*.,* context *updating* and context *maintenance* (West, 2004).

In case of intact context updating but impaired maintenance, extending the cue-probe delay is expected to exacerbate the age-related reciprocal performance on AY- vs. BX- trials, because 1) weak context representations in older adults should increasingly lose strength in a long delay condition and accordingly cause larger BX-errors (Braver et al., 2005) whereas 2) intact context representations in younger adults will reach the full activation strenght in a long delay and consequently cause increased AY-errors (Braver et al., 2005). The investigation of this assumption showed maintenance deficits only in oldest adults and subjects suffering from Alzheimer's disease. Hence it was concluded that age differences in context *updating*, but not maintenance, underlie the performance pattern in the AX-CPT. The result gave rise to the definition of "*dual mechanisms of control*" (DMC; Braver, 2012, p.106): Younger adults are supposed to exhibit *proactive control*, defined as a mode that fosters early updating and sustained maintenance of context information by the time context information is presented. Thereby, this "early selection" (Braver, 2012, p. 106) optimally triggers the top-down representation of task-relevant processes to anticipate upcoming events. In contrast, older adults tend to show transient context representation and therefore reactivate context information in a bottom-up fashion once interference is detected. This "just-in-time-manner" (Braver, 2012, p. 106), termed *reactive control,* serves the "late correction" (cf. Braver, 2012, p.106) and flexible activation of goal representations after conflict onset.

Although pro- and reactive control are flexibly applied to optimize cognitive control in daily life as they feature complementary costs and benefits (cf. Braver, 2012, see Braver et al., 2007, page 82), age-related differences in the predominant manner of

context updating perfectly explain the behavioral performance differences in the AX-CPT between younger and older adults. Moreover, the mechanisms underlying the relative predominance of proactive control in younger, and reactive control in older adults have been confirmed on the basis of a fMRI-investigation on the AX-CPT. Younger adults showed increased activation in lateral PFC after context cue presentation that sustained during the cue–probe delay. In contrast, older adults tend to exibit descreased PFC-activations to the cue, but larger transient lateral PFC activation to the onset of the probe (Braver, Paxton, Locke, & Barch, 2009; Braver & Bongiolatti, 2002; Paxton, Barch, Racine, & Braver, 2008; for a similar result in cued task switching, see Jimura & Braver, 2010).

Intermediate Summary and Implications for the Present Study

The DMC framework provides an explanation of age differences in a variety of cognitive control tasks by assuming *temporal* differences in the processing of task-relevant context information between age groups (Braver & Barch, 2002). Whereas younger adults usually show a preparatory, proactive mode of context updating to bias subsequent behavior, older adults engage in a delayed reactivation of contextual information to resolve interferenc (Braver et al., 2007; Kopp et al., 2014). Although the mechanisms underlying the age-differential time course of context updating has been confirmed on the basis of fMRI (Braver et al., 2009; Braver & Bongiolatti, 2002; Paxton et al., 2008), the main drawback of fMRI is its sparse temporal resolution. Hence, it would be more appropriate to investigate the neuronal mechanisms underlying the time course of context updating in younger and older adults by psychophysiological measures yielding a high temporal resolution (Friedman, Nessler, Johnson, Ritter, & Bersick, 2008).

To this end, the dissertation project aims at examing age differences in pro- and reactive control by an ERP-approach which allows the online measurement of updating processes (Friedman et al., 2008; Gajewski & Falkenstein, 2011; Kray & Ferdinand, 2014). The ERP-technique makes use of changes in voltage measured in the electro-encephalograph (EEG) by electrodes placed on the surface of the scalp. The voltage changes are the result of dipole generation by summation of synchronous neuronal postsynaptic potentials (Fabiani, Gratton, & Coles, 2000; Luck, 2005). ERPs are usually time-locked to an external or internal event, hence reflecting "event-related" brain responses of the EEG (Fabiani et al., 2000). Apart from exogenous ERPs (Fabiani et al., 2000), endogenous ERPs are thought to reflect cognitive information processing in response to the presentation of a stimulus (i.e., stimulus-locked ERPs) or due to the

execution of a response (i.e., response-relaed ERPs). In general, ERP components are defined by their peak latency in milliseconds (ms), their polarity and amplitude in microvolts (µV), and by the electrode position at which the amplitude is maximal. Although the ERP approach offers sparse spatial information, the high temporal resolution of ERPs allows to draw inferences about distinct processing stages elicited by experimenal manipulations (Luck, 2005). The present thesis will utilize the temporal charactersitic of the ERP-approach to track cognitive processing stages associated with pro- and reactive context updating in a paradigm described in the following section. As this paradigm has only been applied to investigate context updating in younger adults so far, the following section will also report ERP-correlates of task-switching studies in younger and older adults regarded as the basis for the ERP-hypotheses of the present dissertation.

2.6 ERP Correlates of Proactive and Reactive Control

The next paragraph will first introduce a paradigm that can be applied to measure context updating in ERPs. Then, age differences in cue- and probe-locked ERPs of task-switching studies will be reported before turning to a recent study investigating neuronal mechanisms of pro- and reactive control in younger and older adults.

2.6.1 ERP Correlates of Context Updating in Younger Adults

The study by Lenartowicz, Escobedo-Quiroz, and Cohen (2010) made use of the precise temporal information of ERPs to determine neuronal correlates of updating context information in a modified version of the AX-CPT in a student sample. In this version of the AX-CPT, the necessity to update context information can be manipulated on a trial-by-trial basis along context-dependent (c-dep) and context-independent (c-indep) conditions arranged in cue-probe pairs (see Figure 3; Lenartowicz et al., 2010; see Figure 5, Appendix, for an adapted version applied in the present dissertation). On c-dep trials, the correct response to one of two probes is dependent on the preceding context, as stimulus-response (S-R) mappings are exactly reversed for the two cue-probe combinations. Thus, correct responding on c-dep trials is expected to require updating and maintenance of the cue information as well as the reconfiguration of S-R rules (Lenartowicz et al., 2010). On c-indep trials in contrast, the correct response to probes is independent of the preceding context cue as S-R rules are exactly the same for the two cue-probe combinations. Hence, correct responding to probes on c-indep trials only relies on the assignment to one of two response buttons. The two context

conditions (c-dep, c-indep) have a 25% probability each and are intermixed with 50% control trials, which only consist of cue presentation. As these control trials do not require any response, they are included to control for ERP correlates reflecting the pure processing of perceptual cue information (Lenartowicz et al., 2010).
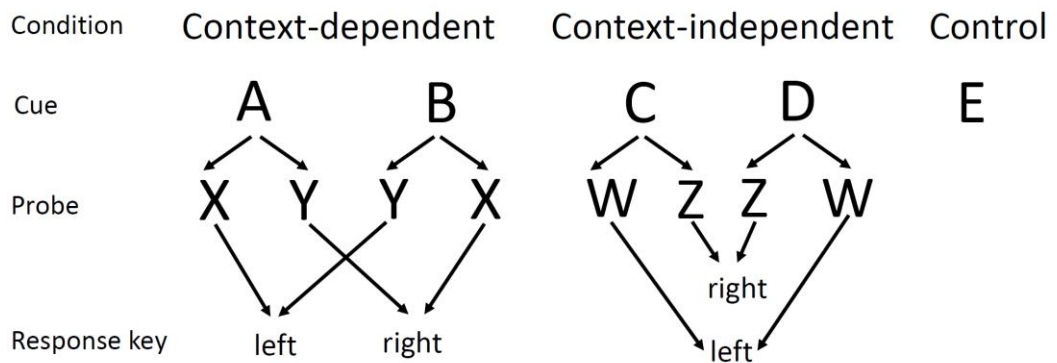
Figure 3. Schematic figure of the modified AX-CPT (own depiction; cf. Lenartowicz et al., 2010).

Context updating and maintenance provided by the cue is required on context-dependent trials as response-assignments are exactly reversed for the two probes. Correct responses on context-independent trials are independent of context information as correct responses to the probes are identical. Control trials serve the presentation of perceptual cue information without task requirements.

Results of this study showed a context effect, i.e., a difference between context conditions reflected in better performance on c-indep trials than on c-dep trials in behavioral data. Context updating in the ERP data was linked to a larger frontally distributed P2 component after context cue presentation on c-dep trials than on c-indep and control trials. The context effect in the P2 was followed by larger parietal P3b and a larger negative going component (i.e., reflecting a Contingent Negative Variation, abbr. CNV) on c-dep than c-indep and control trials associated with task-reconfiguration and context maintenance processes, respectively (Lenartowicz et al., 2010). Importantly, to

make sure that the frontal P2 was indeed related to context effects and not to cue switches found in previous studies (West, Langley, & Bailey, 2011), the study by Lenartowicz et al. (2010) included an analysis of sequence effects of c-dep, c-indep, and control trials to separate ERPs of actual context updating from ERP-effects linked to a perceptual change in the cue irrespective of context. This analysis revealed that the P2 was only sensitive to context updating, whereas the P3b and the CNV also reflected changes in context-cue identity independent of the context manipulation. Therefore, it was concluded that the P3b and the CNV might also indicate an effect of cue priming (Lenartowicz et al., 2010).

Hence, the modified AX-CPT by Lenartowicz and colleagues (2010) is well suited to determine the temporal dynamics of neuronal mechanisms underlying context updating and maintenance. However, the DMC account considers context updating in older adults as a late correction mechanism (Braver et al., 2007), occurring after the detection of interference (Braver, 2012). Thus, less efficient context updating in the cue interval in older adults should require the use of reactive control, particular on c-dep trials where ambiguous probes (and overlapping response rules) induce conflict concerning the correct response. Although this analysis was not included in the study by Lenartowicz et al. (2010), mechanisms of reactive control can be investigated by ERPs time-locked to presentation of the executive stimulus (i.e., the probe). Thus far, age differences in psychophysiological measures of control processes associated with cue- and probe-presentation have been examined in task-switching paradigms; therefore, the following section summarizes age differences in ERPs established in the task-switching literature.

2.6.2 Age Differences in ERP Correlates of Cue and Probe Processing

In task switching, subjects are instructed to successively alternate between two or more tasks afforded by a limited number of executive probe stimuli usually mapped to the same response set (for a review, see Jost, De Baene, Koch, & Brass, 2013; Kiesel et al., 2010; Kray & Ferdinand, 2014; Monsell, 2003). Behavioral performance in task-switching blocks (termed mixed task blocks) is compared to performance in blocks involving only one task to perform (termed single task blocks). The performance difference between single and mixed task blocks, labeled *mixing cost*, is assumed to reflect the ability to select and maintain multiple task sets in WM (Goffaux, Phillips, Sinai, & Pushkar, 2008; Karayanidis, Whitson, Heathcote, & Michie, 2011; Kray & Ferdinand, 2014; Kray & Lindenberger, 2000). In task switching, the term task set refers to cognitive processes supporting the selection, coordination, and execution of an appropriate response to accomplish the task instruction (Monsell, 2003; Rogers & Monsell, 1995)

In contrast to mixing costs, performance differences between a task switch and a task repetition *within* mixed task blocks, labeled *switching costs*, are thought to reflect the ability to perform a switch respectively the time taken by task-set reconfiguration (Rogers & Monsell, 1995)[2]. The majority of aging studies (for a meta-analysis, Wasylyshyn et al., 2011) has found reliable age differences in mixing costs after controlling for general slowing, whereas age differences in switching costs have revealed mixed results and seem to be smaller than age differences in mixing costs

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[2]Note that studies may differ in the calculation of mixing costs. While most studies compare performance in single to mixed-repeat trials, some calculate mixing costs as the difference between performance in single blocks relative to performance on the average of switch and repeat trials within mixed blocks (cf. Adrover-Roig & Barceló, 2009; Karayanidis, Whitson, Michie, & Heathcote, 2010).

(Kray & Lindenberger, 2000; Verhaeghen et al., 2003, but see Friedman et al., 2008). Thus, older adults seem to show impairments in dealing with dual-task demands in a switch situation, but the switching itself seems to be less affected by aging (Kray & Ferdinand, 2014; Verhaeghen et al., 2003; West & Moore, 2005; see section 2.3). However, the absence of age differences in switching costs may also be due to the fact that older adults have a deficit in task switching in conditions of high interference (Karayanidis et al., 2011). For instance, in case stimulus or response attributes of two tasks are overlapping (Kray & Ferdinand, 2014; Mayr, 2001), older adults tend to update the task sets all the time even when it is not required, i.e., even on repeat trials within mixed blocks (Mayr, 2001). Thus, the reliance on updating the task set leads to increased reaction times on repeat trials, and consequently reduces the difference between repetitions and switches (Friedman et al., 2008; Kray & Ferdinand, 2014).

In cued task-switching paradigms, the to-be executed task to the upcoming probe is announced by a preceding task cue (Monsell, 2003). Task cues typically diminish behavioral mixing and switching costs in younger and older adults, suggesting that subjects benefit from advanced preparation (Kray & Ferdinand, 2014). Nevertheless, residual switching costs in paradigms involving a long preparation interval (for a review, see Meiran, 1996) indicate that performance relies on not only cognitive processes associated with the cue (i.e., advanced preparation and configuration of the upcoming response), but also on control processes associated with the probe (i.e., interference from and inhibition of the preceding task set; cf. Kieffaber & Hetrick, 2005; Monsell, 2003). Therefore, cued-task switching paradigms allow the separation of cognitive processes in ERPs time-locked to the task cue reflecting task-preparatory, proactive processes from ERPs time-locked to the probe coupled to reactive processes (Eppinger, Kray, Mecklinger, & John, 2007; Friedman et al., 2008; Karayanidis et al.,

2011; West, Jakubek, Wymbs, Perry, & Moore, 2005; West & Moore, 2005). Aging has been found to be accompanied by differences in the latency, amplitude, and topography of these ERPs (Friedman et al., 2008; Karayanidis et al., 2011). Thus, the results of age effects in pro- and reactive control in cued task-switching studies are the background from which the hypotheses of the dissertation will be derived.

Cue-locked ERPs: The P3b and the CNV

In the cue-locked epoch, a posteriorly distributed positive component is commonly elicited approximately 300 ms after cue presentation, which is larger in mixed than single task blocks in younger adults (Karayanidis et al., 2011; West et al., 2011). This "mixing-cost positivity" (cf. Karayanidis et al., 2011) is assumed to be generated in frontal and parietal brain regions (Polich, 2007) and indexes the amount of resource allocation available for updating and revising WM-content to incoming stimuli, which is labeled as a P3b in Oddball paradigms (Donchin & Coles, 1988; Polich, 2007). Accordingly, the larger amplitude on mixed relative to single task blocks is interpreted as the updating of task-sets after task cue presentation essential on mixed but not on single blocks (Eppinger et al., 2007; Jost, Mayr, & Rösler, 2008; Kray, Eppinger, & Mecklinger, 2005; West, 2004; West & Travers, 2008). Older adults usually exhibit a temporally delayed or prolonged P3b, but no amplitude difference to younger adults (Karayanidis et al., 2011; Kray et al., 2005; West, 2004; but see West & Moore, 2005). This finding may either indicate a slowing of updating processes (Kray et al., 2005), or a tendency that older adults use the whole cue-target interval (CTI) for the encoding of the task context and the preparation of the upcoming response (i.e., prolonged WM-updating; Czernochowski, 2011; West, 2004). Younger adults also show a "switch cost positivity" (cf. Karayanidis et al., 2011), i.e., a larger positive

component on switch relative to repeat trials within mixed blocks (Jost et al., 2008; Nicholson, Karayanidis, Poboka, Heathcote, & Michie, 2005; West et al., 2011). This P3b emerges about 500 ms after task-cue presentation (Friedman et al., 2008; Karayanidis et al., 2011; West & Moore, 2005) and is interpreted as reflecting updating and anticipatory reconfiguration processes on switch trials (Eppinger et al., 2007). In older adults, the switch cost positivity is substantially smaller or absent relative to younger adults (Friedman et al., 2008). As this difference is mainly due an increase in P3b amplitudes on repeat trials, it reflects that older adults tend to update task-sets on both switch and repeat trials (Friedman et al., 2008; Kray & Ferdinand, 2014). This finding corresponds to the lack of behavioral age effects on switching costs (Eppinger et al., 2007; Friedman et al., 2008; Karayanidis et al., 2011; Mayr, 2001).

Distinct age differences have also been found in the scalp distribution of the P3b in mixing and switching costs: Whereas the P3b amplitude typically increases from frontal to posterior sites in younger adults and is largest at parietal electrodes, older adults exhibit a more evenly distributed P3b across the anterior-posterior plane due to an increase at frontal sites (Fabiani, Friedman, & Cheng, 1998; Karayanidis et al., 2011). Whether this frontal shift reflects a compensational mechanism to maintain good performance (Daffner et al., 2011; De Sanctis, Gomez-Ramirez, Sehatpour, Wylie, & Foxe, 2009), or less efficient frontal lobe functioning (Fabiani et al., 1998) is a matter of an ongoing debate. For instance, as a consequence of reduced efficiency in control processes, the more widespread P3b can be attributed to older adults' need to additionally recruit frontal areas to carry out the task (Daffner et al., 2011; Fabiani et al., 1998). In this regard, research from neuro-imaging in older adults helps to explain costs and benefits of increased brain activations (particularly at prefrontal sites; Reuter-Lorenz & Cappell, 2008). For instance, the compensational-related utilization of neural

circuit hypothesis (abbr. CRUNCH; cf. Reuter-Lorenz & Cappell, 2008) suggests that the age-related trade-off between neuronal over- and under-activations depends on the level of task demand and reflects general processing efficiency. Increased, bilateral PFC-activation in older adults (relative to unilateral activation in younger adults and age-related neuronal under-recruitment) correlated with high performance in a memory task in seniors (Cabeza, Anderson, Locantore, & McIntosh, 2002), suggesting compensatory brain activity to meet task demands. But, as task difficulty increased, PFC regions in the elderly become under-activated and performance declined relative to younger adults (Reuter-Lorenz & Cappell, 2008; see also Cabeza et al., 2005).

At the end of the cue-locked epoch, cued task-switching studies show a negative fronto-central CNV that emerges roughly from 600 ms after task cue onset, depending on the duration of the CTI (Adrover-Roig & Barceló, 2009; Kray et al., 2005; West 2004; West & Moore, 2005). The CNV is larger on mixed than single blocks as well as on switch relative to repeat trials and has been related to the retrieval and maintenance of task representations (Goffaux et al., 2008; Kray et al., 2005; West 2004). Whereas West (2004) and West and Moore (2005) found the CNV to be larger on mixed than single blocks in younger, but attenuated in older adults, the larger CNV on mixed than single blocks in Kray et al. (2005) was present in older adults only. This discrepancy might be due to the fact that the studies differed in the duration of the CTI which is critical to maintenance demands (Braver et al., 2005), as well as the electrodes involved in statistical analysis of the CNV (see Wild-Wall, Hohnsbein, & Falkenstein, 2007). Nevertheless, the age differences in the CNV across the aforementioned studies seem to be related to a larger effort or a failure to maintain the updated task-set until presentation of the executive stimulus in older adults (Kray et al., 2005; West, 2004; West & Moore, 2005).

Probe-locked ERPs: The P3b, the N450, and the sustained potential

Compared to the results of cue-locked ERPs in task switching, age differences in probe-locked components linked to interference processing, conflict resolution, or response preparation have only been rarely investigated (Eppinger et al., 2007; Gajewski & Falkenstein, 2011; Goffaux et al., 2008; Karayanidis et al., 2011; Kray et al., 2005; West & Travers, 2008). The processing of the executive stimulus in cued task-switching has been associated with a parietal P3b emerging about 300–800 ms after probe presentation (Gajewski & Falkenstein, 2011; Goffaux, Phillips, Sinai, & Pushkar, 2006; Periáñez & Barceló, 2009). In younger adults, the P3b is larger in single than in mixed blocks (Goffaux et al., 2006; Jost et al., 2008), and in repeat than switch trials (Gajewski & Falkenstein, 2011; Goffaux et al., 2006; Karayanidis et al., 2011). The former result has been suggested to reflect less post-probe interference on single blocks (cf. Karayanidis et al., 2011). The latter has been interpreted to reflect facilitated and efficient target processing, i.e., a larger amount of attentional resources and WM-capacity available for probe processing on repeat trials (Daffner et al., 2011; Goffaux et al., 2006; West & Travers, 2008). Studies on age differences in the probe-locked P3b have produced inconsistent findings. For instance, Goffaux et al. (2008) found no age differences in the probe-locked P3b of mixing costs between age groups. However, Adrover-Roig and Barceló (2009) and West and Travers (2008) found comparable probe-locked P3 amplitudes on single and mixed blocks in the elderly. Yet, Karayanidis and colleagues (2011) showed a larger difference between single and mixed blocks in the P3b in older than younger adults, although this finding might be due to a larger amount of task practice in the study (Karayanidis et al., 2011). In general, the reduced amplitude differentiation between single and mixed blocks suggests that both blocks might be equally difficult for older adults (Kray & Ferdinand, 2014; West & Travers,

2008). Again, as for the cue-locked data, the probe-locked P3b is more evenly and widespread distributed across the scalp in older adults, indicating a compensatory or inefficient resource allocation to probe evaluation supported by frontal brain regions (Adrover-Roig & Barceló, 2009; Kray & Ferdinand, 2014).

As the DMC-theory assumes the lack of proactive control to increase the need for reactive control once interference is detected (Braver, 2012), it would be helpful to investigate ERPs not only to linked to probe evaluation (as resembled by the P3b), but also to processes of conflict detection and response preparation. The N450 and the positive sustained potential (abbr. SP) have been associated with conflict-related processes, although not exclusively in task-switching studies (for a review, Larson, Kaufman, & Perlstein, 2009). The N450 is a negative going deflection assumed to have its origin in the ACC (labeled *Ni* in Kray et al., 2005; Liotti, Woldorff, Perez, & Mayberg, 2000) and usually obtained at fronto-central, central, and parietal electrodes in the time range between 200 ms and 650 ms after stimulus presentation (Eppinger et al., 2007; Kray et al., 2005; Liotti et al., 2000; West, 2004). Commonly, the N450 has been studied in the Stroop task (Rebai, Bernard, & Lannou, 1997; see section 2.3, see also Eppinger et al., 2007 and West, 2004). In younger adults, incongruent Stroop stimuli usually elicit a larger N450 than congruent stimuli (Rebai et al., 1997) even in the absence of response conflict. Therefore, the N450 has been associated with interference detection at the stimulus level (cf. Mager et al., 2007; Liotti et al., 2000; West, 2004). Interestingly, the effect of conflict in the N450 in the Stroop can be separated from the aforementioned probe-locked P3b and the SP which emerges from 500 ms post-probe (Liotti et al., 2000; Mager et al., 2007; West et al., 2005). Whereas the P3b might not be sensitive to conflict (West & Alain, 2000b), the larger parietal SP to incongruent trials in younger adults has been shown to correlate with reaction time

and accuracy in the Stroop, suggesting a role in conflict resolution (Liotti et al., 2000; West, 2004; West & Alain, 2000a), or response selection (Liotti et al., 2000; West et al., 2005). However, both the amplitude of the N450 and the SP increase as the demand on conflict processing rises, indicating that younger adults can transiently adapt to changes in contextual conditions (Eppinger et al., 2007; West & Alain, 2000b).

Older adults show a later onset of the N450 and a prolonged duration (Eppinger et al., 2007; Kray et al., 2005; Mager et al., 2007) associated with slowed and extended conflict processing (Kray et al., 2005). Some studies also found the N450 amplitude to be attenuated in older adults, which implies an age-related decline in the efficiency to detect conflict supported by the ACC (West, 2004; West & Alain, 2000a). Moreover, whereas the N450 in younger adults is particularly pronounced in situations of high conflict (West & Alain, 2000b), an increased N450 to incongruent stimuli in older adults can be found even in conditions of frequent conflict, indicating that they are less able to adapt to task demands (Eppinger et al., 2007). Concerning the SP, only two studies investigated the effects of aging on its amplitude. In West (2004), older relative to younger adults showed an attenuated SP on incongruent trials in the Stroop when color naming was claimed. In contrast, the SP to incongruent Stroop stimuli in the study by West and Alain (2000a) was larger in older adults. However, the larger SP in West and Alain (2000a) might resemble an prolongation of the SP-like component that was found in older, but not younger adults in the former study (West, 2004). Thus, the age-differential effect on the SP particularly in the color-naming condition, reflecting a condition of high interference, might indicate some first evidence for a functional reorganization of conflict processing in older adults (West, 2004).

In sum, the cued task-switching paradigm is a useful tool to establish age differences in the time course of cue- and probe-related control processes. The ERP-

results of task switching studies can be used as a background from which to examine whether younger adults indeed rely on proactive preparation, whereas older adults invest in reactive control in the AX-CPT. To this end, it would be necessary to compare temporal differences in ERP correlates of context processing between younger and older adults in the same paradigm. Moreover, the DMC account claims that employing pro- versus reactive control is accompanied by complementary costs and benefits, as indicated by the reciprocal behavioral performance on AY- and BX- trials in the AX-CPT (Braver et al., 2005). Thus, to substantiate the assumptions by DMC theory, it would be essential 1) to detect neuronal indices of age-related temporal dynamics in pro- and reactive control and 2) to show that the age difference in temporal dynamics of context processing reflects a trade-off in the reliance on pro- and reactive control in behavioral measures.

2.6.3 An ERP-Study on Proactive and Reactive Control in Younger and Older Adults

So far, the study by Kopp and colleagues (2014) investigated ERP correlates associated with proactive and reactive control in a task-switching version of the WCST in younger and older adults (Kopp et al., 2014). Participants were instructed to categorize cards of ambiguous probes either according to the probes' color or shape. The current categorization rule remained until feedback-based transition cues signaled a switch. The authors found larger central P3a amplitudes for cues announcing a subsequent rule switch than a rule repetition in younger, but not in older adults (Kopp et al., 2014; West et al., 2011). Older adults showed increased P3b amplitudes at frontal sites in ERPs time-locked to the probe. Hence, it was interpreted that younger adults

used the cue information in a proactive, preparatory manner, whereas older adults relied on probe-related information to prepare the upcoming response in a reactive manner. Importantly, and as predicted by the DMC account, the age-related shift from a proactive toward a reactive control mode was paralleled by equal behavioral task performance of the two age groups (Braver, 2012; Kopp et al., 2014). However, it should be noted that in the probe-locked P3b, older adults showed increased amplitudes on both switch and repeat trials. This finding could reflect that older adults exhibited a delayed updating of task-rules not only on switch trials, but also on repeat trials in which the categorization rule remained the same and hence interference should be reduced. This finding is similar to the absence of P3b-differences between switch- and repeat trials in older adults in task switching (Eppinger et al., 2007; Friedman et al., 2008; Kray & Ferdinand, 2014), although in task-switching studies this effect is usually found in cue-locked ERPs. One explanation for the result in the study by Kopp and colleagues (2014) could be the use of transition cues, which only signal a switch, but do not explicitly announce the upcoming task (Jost et al., 2013; Kray & Ferdinand, 2014). Hence, although this study found ERP evidence for reduced proactive control in the elderly, transition cues might have put a high demand on cognitive control in older adults, which in turned might have led to a nonselective over-recruitment of control processes at the time the probe was presented. Therefore, and in contrast to this study, the present thesis will investigate the age-related tradeoff between pro- and reactive control by applying the AX-CPT by Lenartowicz et al. (2010) in which context cues explicitly signal the need for context updating on c-dep and c-indep trials, respectively.

2.7   Motivational Influences on Cognitive Control

The previous sections outlined senescent changes in the predominant manner of context processing, the underlying neuronal mechanisms, and ERP correlates to track pro- and reactive control (Braver et al., 2007; Kopp et al., 2014). However, the DMC theory states that pursuing cognitive control pro- versus reactively (and vice versa; Braver, 2012) might not only trace back to advancing age, i.e., to individual differences *between* subjects, but may differ considerably *within* subjects. Individual differences in the predominant mode of cognitive control within subjects are claimed to occur due to situational demands (e.g., memory load, Braver et al., 2007) or due to non-cognitive factors such as affective emotional or motivational manipulations (Braver, 2012).

The later claim is based on lines of evidence that DA is critical for both cognitive and affective processes (Ashby et al., 1999; Braver et al., 2007; Chiew & Braver, 2011b; Schutz, 2010). In this respect, the remainder of the theoretical part is dedicated to the question whether motivation can be manipulated to modulate context processing in younger and older adults. To this end, the following sections will review affective definitions, report current considerations on the interaction between cognitive and affective processes, and summarize recent findings of emotion regulation in old age. It should be noted that affective influences on cognitive control have been studied in the light of motivational and emotional manipulations, such as mood induction or performance-contingent reward, respectively. Nevertheless, there is some evidence that the mechanisms underlying these modulations are different (cf. Chiew & Braver, 2014; Fröber & Dreisbach, 2014). As the dissertation aims at investigating motivational influences, section 2.9 will focus on empirical evidence of motivational effects on cognitive control in behavioral and ERP data.

2.7.1 The Relationship Between Affective and Cognitive Processes

Recent psychological perspectives assume that the traditional separation between processes primarily labeled as "cognitive" and processes viewed as "affective" ignores accumulating evidence that cognitive and affective processes are closely related in the control of behavior (Pessoa, 2008). While there seems to be a consensus that cognition involves processes such as reasoning, language, memory, attention, or cognitive control (Pessoa, 2008; Pessoa & Engelmann, 2010), affective processes are related to the more broadly, squishy defined concepts of emotion and motivation (Buck, 2000; Chiew & Braver, 2011b; Elliot, 2008; Pessoa, 2008). In an overview of current definitions of the constructs emotion and motivation, Chiew and Braver (2011b) suggest that both emotion and motivation describe the relationship between a person and the environment (for a general overview, see also Roseman, 2008). Motivation is characterized as an internal mechanisms focusing on the fundamental goal to obtain reward and to avoid punishment ("*approach and avoidance motivation*"; Elliot, 2008, p.3). Thus, motivation is closely linked to the direction of behavioral actions targeting a goal of "hedonic value" (Chiew & Braver, 2011b, p.2; Roseman, 2008). In contrast, emotions have been described as a subjective affective experience resulting from an evaluation of a situation or a stimulus (Chiew & Braver, 2011b; Dolan, 2002; Rolls, 2000; Scherer, 2005). Emotional states are comprised of physiological, expressive, cognitive, and behavioral changes (Chiew & Braver, 2011b; Ekman, 1992; Roseman, 2008; Scherer, 2005).

Some researchers argue that emotion and motivation can be dissociated in the extent to which they are subjective versus objective, impulsive versus deliberate and specific versus general (Roseman, 2008). In this view, emotions have been described as being rather subjective, impulsive, and more general with regard to motives, whereas

motivations are considered as objective, deliberate, and related to specific conditions (Roseman, 2008). Nevertheless, although these definitions attempt to dissociate motivation and emotion, they cannot cover that the two constructs reflect internal states or processes and may be inextricable linked (Chiew & Braver, 2011b). For instance, the experience of an emotional state is often (but not exclusively, see Laming, 2000) a result of the delivery of reward or punishment (Rolls, 2000) and emotional states themselve flexibly motivate behavior toward goal optimization (Chiew & Braver, 2011b). Hence, emotion and motivation seem to be "two sides of the same coin" (Buck, 2000, p. 196), i.e., they cannot be separated (cf. Chiew & Braver, 2011b).

In current neuro-cognitive theories, cognitive and affective processes are assumed to be integrated in terms of functional and neuroanatomical brain dynamics and collectively contribute to goal-directed behavior (Gray, 2004; Pessoa, 2008, 2009; Pessoa & Engelmann, 2010). In this regard, the lateral PFC (lPFC) has been proposed as one of the key brain regions for integration (Pessoa, 2008; for further brain areas incorporating affect-cognition interactions, see Pessoa & Engelmann, 2010; Watanabe, 2007). Patient studies provide evidence that PFC-lesions or specific forms of dementia affecting the frontal lobes are accompanied not only by deficits in controlled behavior (e.g., in WM-tasks), but also by dramatic changes in mood states, emotional and social behavior (Dalgleish, 2004; Damasio & Anderson, 2012). This finding is supported by neuromaging data showing subregions of the PFC to be engaged in different aspects of processing: While the lPFC (especially the DL-PFC) seems to be responsible for updating and maintaining goal-related information, the apprehension of emotional value and the processing of reward seems to depend on the orbitofrontal and the ventromedial part of the PFC (Braver & Barch, 2002; Dalgleish, 2004; Damasio & Anderson, 2012; Pessoa, 2008). Most importantly, these studies also support the assumed integration of

cognitive and affective influences in the lPFC (Pessoa, 2008). In an overview by Watanabe (2007), it is summarized that lPFC-neurons show increased firing for task-relevant information in WM, benefitting the maintenance of stimulus information. Moreover, these neurons also exhibit increased firing for reward, indicating the encoding of a stimulus' value. Critically, proof for the integration of reward- and maintenance-bound information was established by an enhancement of the WM-related activity by the expected reward value of the to-be maintained stimulus. Importantly, this enhancement was larger as predicted from adding WM- and reward-related activations (Watanabe, 2007). Similar affective influences on lPFC functions in cognitive control have been affirmed by showing a larger maintenance-related activity in DL-PFC for emotional than neutral information (Perlstein, Elbert, & Stenger, 2002; Pessoa; 2008), and a larger inhibition-related DL-PFC activation for negative than neutral words (Goldstein et al., 2007). Interestingly, affective stimuli affected DL-PFC activations only when they were critical for performance on the WM- or inhibition-task (Perlstein et al., 2002; Pessoa; 2008), suggesting an important role of the lPFC in processing affective significance in the service of goal-directed behavior (Perlstein et al., 2002; Pessoa, 2008).

The aforementioned findings contribute to the lPFC-theory by Gray and colleagues (Gray, 2004; Gray, Braver, & Raichle, 2002). Specifically, the authors claim that the affective influence on cognitive control abilities need to be highly specific to suggest a true cognitive-affective integration. It is hold that if a certain brain area (i.e., the lPFC) provides such an integration, this assumption would be corrobated by fMRI-data showing a combined contribution of neuronal affective and cognitive processes on behavior. In other words, specialised affective and cognitive subprocesses would be insaparable merged into a new function (cf. Gray et al., 2002). In statistical terms, this

hypothesis should be reflected by an "crossover interaction" (Gray et al., 2002, p.4115). of cognitive and affective factors with no main effects in the specific brain area (Goldstein et al., 2007; Gray et al., 2002). In support of this notion, Gray and colleagues (2002, 2004) found highly selective effects of positive and negative mood manipulations on task-related activation patterns of the lPFC in a spatial and a visual WM-task without main effects. Such highly specific affective modulations of cognitive control abilities (i.e., promoting some abilities while inhibiting others) may be particularly adaptive for behavior to fullfill specific situational requirements (for instance, to gain reward; Gray, 2004). Hence, the lPFC is regarded as a key brain region supporting highly specific affective influences on cognitive control and promoting adaptive behavior in changing environmental conditions.

2.7.2 The Role of Dopamine in Cognitive and Affective Processes

Although the integration of cognitive and affective processes in lPFC might be beneficial to adaptive behavior, the critical question of how this integration is specifically achieved remains to be answered (Pessoa, 2008). Current theories about affective influences on cognitive control functions bring the midbrain DA system (see section 2.2 for anatomy) into focus (Ashby et al., 1999; Braver, 2012; Braver et al., 2007; Chiew & Braver, 2011b; Cohen et al., 2002; Hoebel, Avena, & Rada, 2008; Panksepp & Moskal, 2008; Pessoa, 2008). In the affective literature, it is well-known that chemical stimulants inducing feelings of euphoria and approach motivation, such as amphetamines, enhance extracellular DA transmission particular in the nucleus accumbens (NAc) of the ventral striatum (Di Chiara et al., 2004; Grace, Floresco, Goto, & Lodge, 2007). This finding corresponds to rewarding effects of DA release by lever

pressing of electrodes implanted in the VTA or substantia nigra in studies on intracranial self-stimulation in rats (cf. Garris et al., 1999; Panksepp & Moskal, 2008; Schultz, 2010). The midbrain DA system has even been described as the neuronal correlate of the reward system (cf. Schultz, 1998; see also Schultz, 2010 for a definition of rewarding events). While some DA neurons exhibit slow, tonic activity, the majority of neurons in the mesencephalic DA system exhibit fast, phasic activations to afferent influences, particularly reward (Bromberg-Martin et al., 2010; Grace et al., 2007; Schultz; 2010). As can be seen in Figure 4A (adapted from Schultz, 2010), DA neurons initially exhibit phasic bursts of activity after unpredicted primary reward, such as food or liquids (Bromberg-Martin et al., 2010; Schultz, 2010). However, by pairing reward with sensory stimuli, the phasic DA activation will no longer occur by the time the initial reward is actually delivered, but will be triggered by conditioned stimuli predicting later reward (see Figure 4B, Schultz, 2010). As DA neurons only show activity if the delivery (or absence) of reward is different to expectation, it is assumed that the phasic increase in DA activation is critical for reinforcement learning (Di Chiara et al., 2004; Mirenowicz & Schultz, 1996; Schultz, 2010): If a delivered reward is better than predicted from previous experience, DA neurons will be activated, whereas if the predicted reward fails to appear, DA activity will be inhibited (Bromberg-Martin et al., 2010; Chiew & Braver, 2011b; Schultz, 2010). Accordingly, these DA signals can be used to reinforce or weaken reward-preceding actions critical for establishing associative learning (Bromberg-Martin et al., 2010; Chiew & Braver, 2011b).
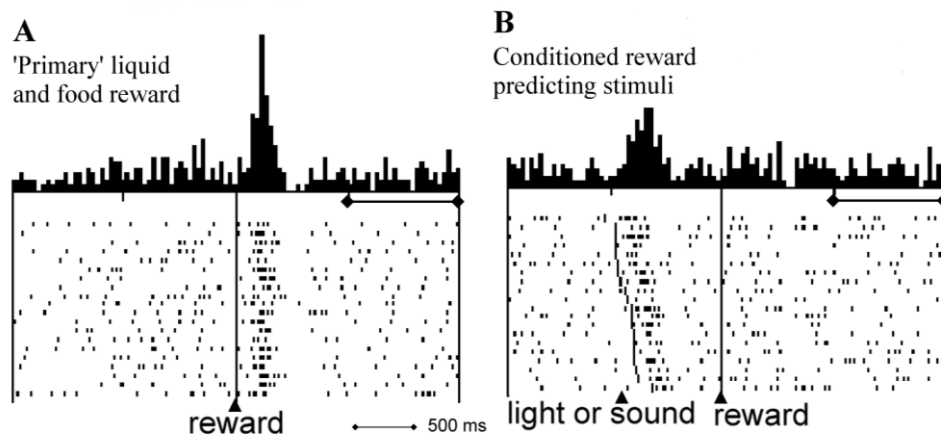
Figure 4. Schematic figure of DA activity (adapted and modified from Schultz, 2010). Copyright by BioMed Central.

A. Phasic DA bursts (represented by dots), indicated by an increase in the activity distribution after delivery of primary reward announced by the triangle. **B.** During learning, increased DA release (represented by dots) is temporally shifted to conditioned stimuli announced by the triangle predicting later reward.

Although the role of midbrain DA in reward has been established (Schultz, 2010), recent theories suggest that DA neurons display phasic activity also to aversive or salient events in general, although the former might be conveyed by a smaller number of DA neurons and a weaker DA response (Bromberg-Martin et al., 2010; Ikemoto & Panksepp, 1999; Mirenowicz & Schultz, 1996). Some DA neurons respond to reward while at the same time exhibiting firing to aversive events (i.e., penalty; Mirenowicz & Schultz, 1996). Therefore, it has been assumed that appetitive and aversive events possess a similar *"motivational salience"* because both are behaviorally relevant, although they may differ in their *"motivational value"*, being positive for reward and negative for penalty (cf. Bromberg-Martin et al., 2010, p.815). Accordingly, so-called motivational value coding DA-populations can be stimulated by reward and inhibited by

penalty, whereas motivational salience coding DA-populations are excited by both reward and penalty but inhibited by neutral events. The latter are thought to be critical for orienting to and processing of important stimuli and situations of behavioral relevance (cf. Bromberg-Martin et al., 2010).

Given the fundamental role of DA neurons in reward processing and associative learning, it is particularly noteworthy that further lines of evidence emphasize the role of DA in cognitive control (cf. Chiew & Braver, 2011b). Herein, it has been put forward that as midbrain DA can be send to frontal cortices (for details, see section 2.2), DA may alter specific control functions subserved by the PFC (Chiew & Braver, 2011b; Cohen et al., 2002; Pessoa & Engelmann, 2010). In pharmacological studies, computational modeling, and single-cell recordings in non-human primates, the DA influence to the PFC is assumed to enhance the signal-to-noise ratio of neuronal responses by suppressing spontaneous firing, but enhancing neuronal activity to afferent input (Cohen et al., 2002; Miller et al., 1996; Li et al., 2001; Pessoa & Engelmann, 2010). At the same time, this modulatory function of DA supports sustained activity of PFC neurons, which in turn benefits short-term storage of information for controlled behavior (Cohen et al., 2002), for instance in WM-tasks (Goldman-Rakic, 1995; Sawaguchi & Goldman-Rakic, 1991; Watanabe, 1996, 2007).

However, the role of the PFC in rote memory storage has been challenged (Cohen et al., 2002; D'Esposito, Cooney, Gazzaley, Gibbs, & Postle, 2006; Reuter-Lorenz & Sylvester, 2005). Instead, recent models suggest that phasic DA-release regulates the balance between maintenance and updating of stimulus representations within the PFC (see also section 2.4.2; Braver et al., 2007; Gruber, A. J. et al., 2006). In these models, midbrain DA-bursts from D2-receptors to salient and reward-predicting cues are assumed to be forwarded to the PFC in order to signal the need for gating information

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into the PFC (Gruber, A. J. et al., 2006). In contrast, in the absence of salient and reward-predicting information, phasic DA release will be inhibited by tonic DA levels possibly from D1-receptors which ensure the stability of information maintenance (Cohen et al., 2002). Overall, DA activity has been attributed to play a key role in mediating affective influences on cognitive control performance, but so far, the precise mechanisms, and the differential impact of motivational salience and value coding DA-neurons seem to be only poorly understood.

2.8   The Positivity Effect in Old Age

Given that DA seems to play a crucial role in the effects of aging (see section 2.2) and anticipated reward (Chiew & Braver, 2011b) on cognitive control, affective-cognitive interactions might be especially important in advancing age (Carstensen & Mikels, 2005; Mather & Carstensen, 2005). Although it is well known that aging is accompanied by a decline in various facets of cognition (see section 2.3), there is increasing evidence that affective functions, for instance, emotional regulation and the processing of affective stimuli, might be relatively preserved or even improved in old age (Carstensen & Mikels, 2005; Mather & Carstensen, 2005; Reed & Carstensen, 2012). These age differences have been explained in the so-called socioemotional selectivity theory (cf. Mather & Carstensen, 2005) hypothesizing that personal goals have to be regarded within temporal constraints. Specifically, if individuals perceive future time horizons as enduring, they will focus on goals related to the future, such as gaining knowledge. In contrast, if individuals recognize future time as restriced, as it likely occurs in aging, they will focus on immediate, meaningful goals, such as emotional regulation (Carstensen, Isaacowitz, & Charles, 1999). Accordingly, it has

been found that in order to enhance well-being, older adults invest more cognitive resources than younger adults in emotional regulation. This can be seen by heightened processing of positive, gratifying information in contrast to negative or neutral information in cognitive task assessing attention or memory performance (Carstensen & Mikels, 2005). It should be noted that the critical factor leading to this age-related "*positivity effect*" (cf. Reed & Carstensen, 2012, p.1) is the individually perceived time, and not age per se. Hence, differences in how a respective task is framed (limited or unlimited time) may explain inconistencies in the positivity effect across studies (Reed & Carstensen, 2012). This finding also suggests that emotional regulation can be flexible applied in old age, ruling out age differences in neural markers of affective processing (Carstensen & Mikels, 2005). Connecting with the previous paragraphs, and the assumptions of the DMC theory (Braver & Barch, 2002), it might therefore be interesting to examine whether preserved affective processing, and even increased processing of positive information in old age, might be beneficial to cognitive control in older adults, for instance by triggering context processing.

Intermediate Summary and Implications for the Present Study

Anatomical and functional data suggest that the major role of the PFC in integrating affective and cognitive functions may be subserved by midbrain DA release initiated by reward and reward-predicting stimuli (Cohen et al., 2002). Given its precise temporal characteristic, DA release serves the updating of PFC representations to guide behavior toward reward achievement (Cohen et al., 2002; Schultz, 2010; Watanabe, 2007). This idea has been incorporated in the DMC-model as reward-predicting stimuli are assumed to trigger updating of context information for goal-directed behavior (Braver & Barch, 2002). Hence, giving the temporal differences in processing context information between age groups (Braver & Barch, 2002), it might be interesting to examine whether reward-predicting cues are able to modify the temporal dynamics of context processing or even to promote proactive context updating in older adults (Braver et al., 2007). This line of thought is supported by evidence showing reward anticipation to increase voluntary preparation for an upcoming stimulus, which can be reflected in ERPs (Gruber & Otten, 2010; Gruber, Watrous, Ekstrom, Ranganath, & Otten, 2013; Halsband, Ferdinand, Bridger, & Mecklinger, 2012).

However, as initial evidence suggests that DA activity might not only be triggered by reward, but by salient cues in general (Bromberg-Martin et al., 2010), the question arises whether context updating can be triggered by DA release to behavioral relevant salient positive (i.e., reward) and negative (i.e., penalty) manipulations in general. Although this differentiation has been largely neglected so far, it might be especially important in older adults who seem to focus on positive information (Mather et al., 2005). Therefore, the second aim of the dissertation is to investigate the influence of motivational salient cues on the time course of context updating in younger and older adults reflected in ERPs. Moreover, ERPs help to reveal whether motivational effects

on context processing in the AX-CPT are associated with context updating, task-reconfiguration, or maintenance associated with proactive control (Lenartowicz et al., 2010), with processes of conflict detection and response selection reflecting reactive control (Krebs, Boehler, Applebaum, & Woldorff, 2013; West & Alain, 2000a, 2000b; West et al., 2005), or both. So far, motivational manipulations on mechanisms of context processing have mainly been conducted in younger adults, and the following paragraph summarizes these studies regarding behavioral and ERP-results.

2.9 Behavioral and ERP-Studies of Motivational Manipulations on Cognitive Control

In accordance with the DMC theory, recent studies on cue processing in task-switching paradigms and the AX-CPT report reward prediction to fasten reaction times relative to baseline blocks without reward. As this effect cannot be attributed to a speed-accuracy tradeoff, the reward effect on cognitive control seems to be highly specific (Braver et al., 2009; Jimura, Locke, & Braver, 2010; Kleinsorge & Rinkenauer, 2012; Locke & Braver, 2008; Pessoa & Engelmann, 2010). In the AX-CPT under reward conditions, the relationship between performance on AY- and BX-trials suggests reward to foster context cue processing in a preparatory, proactive manner (Chiew & Braver, 2013, 2014). Larger effects of reward incentives on mixed than single task blocks in task switching indicate an effect of reward incentives particular in situations of increased cognitive control demands (Kleinsorge & Rinkenauer, 2012).

Compared to results on reward incentives on cognitive control, only a few studies investigated the influence of penalty manipulations (Braver et al., 2009; Krawczyk & D'Esposito, 2013). In the AX-CPT, anticipated penalties caused a slowing in reaction

times, and a reduction of errors (Braver et al., 2009), suggesting increased reactive control. However, in this study, penalties were only applied after errors on no-go trials and hence the comparison to the reward-related effect is missing. In contrast, both reward and penalty fastened reaction times in a cued attention task which was not at the cost of errors, interpreted as improved perceptual sensitivity and sharpened exogenous attention on motivationally salient trials (Engelmann & Pessoa, 2007). In sum, different lines of evidence suggest that anticipated rewards and probably also penalties might benefit cognitive control in younger adults.

Only a handful of studies investigated the effect of anticipated reward on ERP correlates of cognitive control. In a study on the Stroop task, Krebs and colleagues (2013) found larger P3b amplitudes to reward-predicting cues preceding the presentation of the executive Stroop- stimulus. This finding was interpreted as reflecting increased preparatory attention toward the upcoming ambiguous Stroop stimulus which was essential to obtain later reward. In a task-switching study, larger P3b amplitudes on reward trials during response execution (probe-locked) were supposed to reflect a larger investment of available WM benefitting fast responding (Capa, Bouquet, Dreher, & Dufour, 2013). In addition, the CNV has also been associated with reward processing, as larger CNV amplitudes were found on trials indicating reward for fast and correct responses (Capa et al., 2013; Falkenstein, Hoormann, Hohnsbein, & Kleinsorge, 2003; but see Goldstein et al., 2006). Finally, in the Stroop study by Krebs and colleagues (2013), reward incentives modulated conflict-related components, such as the N450 and the SP. Although amplitude modulations were not reported, the two components peaked earlier during reward trials. This temporal shift might indicate an earlier onset of conflict processing triggered by enhanced attention allocation toward the presentation of the Stroop stimulus linked to the preceding cue-locked P3b (Krebs et al., 2013).

Taken together, previous research in younger adults has outlined highly selective effects of reward conditions on cognitive control especially when enhanced controlled processing was demanded. Interestingly, although some of the aforementioned studies used slightly different paradigms to assess cue processing, motivational influences were found in all ERP components in younger adults that have been linked to context processing in a pro- and reactive manner (see section 2.6.2). Despite these previous results, the impact of motivational manipulations on context processing in old age has been largely neglected. Also largely unclear from the literature is the effect of penalty manipulations on cognitive control performance. In this regard, it would be particularly necessary to conduct ERP studies assessing the effect of reward and penalty on context processing in the same paradigm.

Summary and Research Objectives

Considerable evidence suggests that as people age, they are confronted with a decline in goal-directed behavior (Baltes et al., 1999; Fisk & Sharp, 2004). Apart from monitoring age-related deficits on the behavioral level, current research attempts to elucidate the underlying mechanisms, and to connect behavioral and neurobiological changes of advancing age (Braver & Barch, 2002; Li et al., 2001; Salthouse, 1996; West, 1996). Particularly in an aging society (Pack et al., 2000), research on the nature of age differences in cognitive processes is important as components of cognitive control seem to be strongly related to intellectual functioning (Friedman et al., 2006) and essential to performing everyday life activities (Vaughan & Giovanello, 2010). Understanding the precise age-related changes therefore contributes to the early differentiation between normal and pathological aging (Braver et al., 2005), and paves the way for developing and implementing age-appropriate facilities and effective interventions to promote successful cognitive aging. Hence, the knowledge on the mechanisms of cognitive control is fundamental to support sustained autonomy in older adults (for a review on aging and intervention, see Daffner, 2010).

Paper I and II[3]

As a framework to reveal the core mechanisms of age differences in cognitive control, the DMC theory (Braver & Barch, 2002) claims that the well-known neuro-biological decline in the PFC and the DA system with advancing age causes a temporal shift in the gating of context information required for controlled behavior. Although the expected age differences in pro- and reactive control have been established on the basis

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[3]Note that the data set in paper I and II was drawn from the same experiment and therefore constitutes results of one study.

of behavioral data, the precise neuronal mechanisms underlying the time course of context processing in younger and older adults remain largely unknown.

Therefore, based on the theoretical assumptions of the DMC theory (Braver, 2012) and on the experimental design by Lenartowicz and colleagues (2010), the first study of the thesis aims at investigating context updating in both younger and older adults in an ERP approach allowing the online measurement of control processes. Although Lenartowicz and colleagues (2010) found context updating, but not cue switching, to be announced by a frontal P2 component in younger adults, this finding strongly contrasts with results of cued task-switching studies. Herein, the parietal P3b has usually been linked to the updating of task-cue information (Kray & Ferdinand, 2014; Kray et al., 2005; West, 2004). The frontal positivity has only rarely been reported or specifically associated with an upcoming switch signaled by transition cues (West et al., 2011). Thus, the first study (*Paper I*) offers an important insight into the questions of whether 1) age-related differences can already be found in early (i.e., the P2), or only in late (i.e., the P3b and CNV) cue-related potentials of context and task cue-related processing (Kray et al., 2005; Lenartowicz et al., 2010), and 2) whether the effects reflect context processing rather than cue priming (Lenartowicz et al., 2010).

Understanding the age-related shift from pro- toward reactive control requires investigating cue- and probe-based mechanisms at one time tied to age differences in task performance (Steffener, Barulli, Habeck, & Stern, 2014). As only one study so far shed light on the neuronal mechanisms of pro- and reactive control in old age (Kopp et al., 2014), data of the first study are reanalyzed (*Paper II*) in order to examine whether the lack of proactive preparation in older aduls is accompanied by a relatively increase in reactive control indexed by ERP correlates of conflict processing (i.e., the N450).

Moreover, the first study contains a further crucial consideration (*Paper II*): Research on cognitive aging is challenged by accumulating evidence that between group differences in neuroscientific correlates of cognition can vanish after statistical controlling for age, suggesting that age differences on the neuronal level are modulated or confounded by individual differences, such as in actual performance (Riis et al., 2008; Rugg & Morcom, 2005). Hence, a second aim was to approve whether the age-related shift in the temporal dynamics of context updating in ERPs indeed lies at the core of cognitive aging (Braver & Barch, 2002). Although this aim has been largely neglected so far (for an exception, see Daffner et al., 2011; De Sanctis et al., 2009; Goffaux et al., 2008), it can be achieved by investigating ERP correlates of pro- and reactive control in performance-matched age groups and may yield several important conclusions: First, in case ERP correlates show a relatively predominance of pro- to reactive control in younger than older adults when performance is matched, this finding would reveal that reactive control in old age is beneficial or even compensatory to performance. Second, age differences in ERPs of pro- and reactive control would also suggest that the psychophysiological processes underlying overlapping performance in younger and older adults are not identical (De Sanctis et al., 2009; Oberauer, 2005). Finally, investigating ERP differences within the sample of older adults might also indicate neural recruitment of distinct processes contributing to behavior in well- and poor-performing subjects (Daffner et al., 2011), which is important for inventing strategies to promote successful cognitive aging (De Sanctis et al., 2009).

Paper III

Based on overlapping reliance on the midbrain DA system between cognitive and affective processes, the second ERP-study in younger and older adults investigated the claim by the DMC theory that motivational cues may impact the time course of context

processing (Braver & Barch, 2002). Specifically, as affective processing is relatively preserved in old age (Carstensen & Mikels, 2005), the crucial question was whether one can manipulate individual differences in context processing within subjects (e.g., by motivational cues) to influence temporal differences in context processing between subjects (i.e., age groups). Given that anticipated reward may enhance neuronal mechanisms for processing of subsequent information reflected in ERPs (Gruber & Otten, 2010), motivational cues indicating performance-contingent reward and penalty in the second study preceded presentation of context cue information in the AX-CPT. Although previous research has already examined the effect of reward, it remains unclear from the literature whether context updating may only be benefited by reward cues, or also by motivationally salient cues in general (being positive or negative) that have been associated with DA-release (Bromberg-Martin et al., 2010; Schultz, 2010). This question might be particularly important in older adults, as research on the positivity effect indicates a focus of positive relative to negative and neutral events in the elderly (Carstensen & Mikels, 2005). Moreover, there is also some first evidence that motivational salience and valence effects might be reflected in different ERP components (Ferdinand & Kray, 2013). Hence, the ERP approach on the influence of motivational cues on context processing in the second study allows determining 1) whether motivational cues impact context processing in younger and older adults as expected by the DMC theory and whether this impact is related to cue- or probe-related processes in the respective age group, 2) whether motivational value and salience effects differentially affect behavioral and ERP correlates of context processing, and 3) whether younger and older adults differ in the impact of positive information on context processing. In general, this study has the potential to illustrate certain means to promote context updating important to cognitive control in older adults.

3 Overview of Publications

Paper I

Schmitt, H., Ferdinand, N.K., & Kray, J. (2014). Age-differential effects on updating cue information: Evidence from event-related potentials. *Cognitive, Affective, and Behavioral Neuroscience, 14*, 1115-1131.

This article reports age differences in behavioral and ERP data on context processing and cue switching in a modified AX-CPT in younger and older adults.

      Theoretical background. Based on the claim that age differences in the temporal dynamics of updating and maintaining context information are fundamental to cognitive aging (Braver & Barch, 2002), this study investigated age differences in ERP correlates context processing. A modified AX-CPT was applied (cf. Lenartowicz et al., 2010), consisting of trials in which context updating and maintenance were mandatory for correct responding on a subsequent probe (i.e., c-dep trials), and trials in which correct responses to probes were independent of the preceding context cue (i.e., c-indep trials). In a previous study in younger adults, context updating on c-dep trials has been associated with an early frontal P2 followed by a parietal P3b, and a central CNV linked to task-set reconfiguration and context maintenance, respectively (Lenartowicz et al., 2010). Importantly, context updating in the P2 in the mentioned study was not by virtue of perceptual changes in context cue per se (Lenartowicz et al., 2010).

      Hypotheses. According to previous studies showing an age-related decline in the ability to update context information, prolonged latencies and higher error rates on c-dep than c-indep trials for older than younger adults were expected (Braver & Barch, 2002; Kray et al., 2005). In the ERP data of younger adults, larger frontal P2 and

parietal P3b amplitudes for c-dep than c-indep trials, associated with context updating and task reconfiguration, respectively, as well as a larger negative-going CNV on c-dep trials indicating context maintenance were predicted. The decline in context processing in older adults was assumed to result in reduced P2- and P3b-amplitudes on c-dep trials (Braver & Barch, 2002; Lenartowicz et al., 2010; Kray et al., 2005), and a more widespread P3b-scalp distribution (Fabiani et al., 1998). Age differences were also expected in context maintenance in the CNV (Kray et al., 2005; West, 2004). Finally, since perceptual changes in the context cue on c-dep, but not on c-indep trials were assumed to elicit context updating, an analysis of ERP-correlates was applied to separate changes in cue identity from changes in context (Lenartowicz et al., 2010).

Main results and conclusion. In line with previous studies, an age-related decline in context updating was obtained in longer latencies and higher error rates on c-dep than c-indep trials for older than younger adults (Braver & Barch, 2002, Kray et al., 2005). In the ERP data, the P2 showed no effect of context conditions, neither in younger nor in older adults. Since the P2 amplitude in the previous study was reduced on no-go trials with 50% probability which were not included in the present study (Lenartowicz et al., 2010), the P2 seems to reflect stimulus repetition and task relevance rather than context updating (Falkenstein et al., 2003; Potts, 2004).

Age differences in ERPs were clearly observed in the P3b. In accordance with oddball- and task-switching studies (Donchin & Coles, 1988; Kray et al., 2005), younger adults showed larger parietal P3b amplitudes on c-dep than c-indep trials, indicating that the parietal P3b reflects the updating of context information. Although P3b amplitudes in older adults were similar on c-dep and c-indep trials and evenly distributed across the scalp, older adults exhibited larger P3b amplitudes whenever the identity of the context cue changed relative to when it was repeated. Importantly, this

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effect occurred irrespective of the actual context condition. Thus, older adults seem to encounter difficulties in representing higher-order context conditions and therefore update context information whenever there was a perceptual cue change. Interestingly, this finding is in line with previous studies showing a strong reliance on visual information in the elderly (Spieler, Mayr, & LaGrone, 2006). In line with a behavioral study showing context maintenance to be relatively spared in old age (Braver et al., 2005), younger and older adults did not differ in the larger CNV on c-dep than c-indep trials, reflecting higher demands on context maintenance in the former (Kray et al., 2005; Lenartowicz et al., 2010). Hence, age differences in context updating and maintenance seem to be dissociable on the basis of ERPs. Although the study did not reveal direct evidence for an age-related shift in the temporal dynamics of context updating, it formed the basis for a consecutive report on pro- and reactive control by analyzing context effects in probe-locked data (Schmitt, Wolff, Ferdinand, & Kray, 2014).

Paper II

Schmitt, H., Wolff, M.C. Ferdinand, N.K., & Kray, J. (2014). Age differences in the processing of context information: Is it age or is it performance? *Journal of Psychophysiology, 28*, 202-214.

This study investigates age differences in ERP correlates reflecting pro-and reactive control in the AX-CPT independent of performance differences between the age groups.

Theoretical background. In the first study, age differences in ERP correlates of context processing were tightly linked to age differences in the cue-locked P3b

(Schmitt, Ferdinand, & Kray, 2014), but these might also reflect behavioral performance differences between the age groups. To rule out this issue, the second study analyzed age-related differences in ERP correlates of context conditions in performance-matched age groups. Moreover, dividing the sample in high- and low performing younger and older adults indicated further context effects in the N450 component of the probe-locked ERP, which has previously been linked to conflict detection and conflict processing (Liotti et al., 2000; West et al., 2005) and might therefore indicate the need for reactive control (Braver & Barch, 2002; Kopp et al., 2014). Thus, to examine whether age differences in pro- and reactive control are attributable to individual differences in age or in performance, context effects were analyzed in the cue-locked parietal P3b and the probe-locked central N450 in four groups of high and low performing younger and older adults.

Hypotheses. Based on the first study (Schmitt, Ferdinand, & Kray, 2014), we expected high performing younger and older adults to show larger P3b amplitudes on c-dep than c-indep trials than low performers (Adrover-Roig & Barceló, 2009; Lenartowicz et al., 2010; Schmitt, Ferdinand, & Kray, 2014). Context effects in the N450 indicating the need to resolve response conflict were expected in larger amplitudes on c-dep trials, containing reversed S-R mappings, than c-indep trials (Eppinger et al., 2007; Liotti et al., 2000; Mager et al., 2007). If older adults do not fully engage in proactive cue processing reflected in the P3b, but instead rely on reactive control, then conflict processing indicated by the N450 should larger in older than in younger adults (Braver & Barch, 2002; Kopp et al., 2014). However, in case high-performing older and low-performing younger adults show comparable cue-locked P3b amplitudes, then the need for reactive control in high performing elderly should be reduced. Finally, if low-performing elderly fail to update context information and to

reconfigure S-R mappings in a proactive manner (reflected in the P3b), but instead rely on reactive control, then the N450 should be enhanced particularly on c-dep trials.

Main results and conclusion. After dividing the age groups into four performance groups on the basis of a behavioral index, behavioral context effects were comparable between the groups of low-performing younger and high-performing older adults. However, the performance-matched groups continued to differ in their reliance on proactive control: Low-performing younger, but not high-performing older adults showed larger P3b amplitudes on c-dep than c-indep trials reflecting context updating. In contrast, high performing older adults showed larger amplitudes of the N450 on c-dep than c-indep trials, indicating conflict detection and the need to reactivate context information before task execution. Thus, the study substantiates predictions by the DMC theory that temporal differences in context processing are a core component of cognitive aging (Braver & Barch, 2002) independent of individual performance. Since high-performing older adults performed equivalently to low-performing younger adults the study renders further support for the DMC theory assuming older adults to compensate the lack of proactive control by applying reactive control (Braver, 2012).

Paper III

Schmitt, H., Ferdinand, N.K., & Kray, J. (2015). The influence of monetary incentives on context processing in younger and older adults: An event-related potential study. *Cognitive, Affective, and Behavioral Neuroscience.*

This study investigates the impact of performance-contingent reward on the time course of context processing in the AX-CPT in younger and older adults.

Theoretical background. Recent models on cognitive control (Gray, 2004) assume that subjects pursue behavioral goals carrying a high motivational value such as reward. Reward-predicting cues are able to modulate DA input into the PFC (Schultz, 2002) and may hence benefit proactive context updating (Braver & Barch, 2002). Previous research revealed enhanced neuronal activity to reward cues promoting the processing of subsequent stimuli (Gruber, M. J. et al., 2013). Since (1) the impact of penalty on cognitive control has only been rarely investigated (Locke & Braver, 2008), but (2) the motivational valence of information seems to be reflected in distinct ERP components of cognitive control (Ferdinand & Kray, 2013), and (3) the valence of information is thought to influence emotion-regulation in old age (Mather & Carstensen, 2005), we compared motivationally salient gain and loss with neutral cues preceding context information in the AX-CPT on their impact on temporal dynamics of context updating (uncovered by ERPs) in younger and older adults.

Hypotheses. Motivationally salient cues were expected to benefit behavioral performance especially on c-dep trials in which cognitive control demands are high (Bromberg-Martin et al., 2010; Chiew & Braver, 2013; Kleinsorge & Rinkenauer, 2012). Based on the DMC theory (Braver & Barch, 2002) and recent findings on DA function (Bromberg-Martin et al., 2010), gain and loss cues in younger adults were expected to enhance proactive context updating, reflected in larger context effects in the P3b and CNV than neutral cues. Since older adults seem to focus on positive events (Mather & Carstensen, 2005), it was an open question whether older adults would display a valence effect, i.e., a greater performance benefit and a modulation of probe-related context effects on gain relative to loss trials. Alternatively, as suggested by the DMC theory (Braver & Barch, 2002) reward trials could promote proactive control linked to increased cue-related context effects (i.e., the P3b and CNV).

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Main results and conclusion. Motivationally cues revealed a strong impact on context processing in reaction times and ERPs. Younger adults showed shortened latencies whenever motivational cues indicated possible reward, indicating enhanced proactive context processing to benefit fast and accurate responses. In contrast, older adults exhibited larger context effects on both gain and loss cues, interpreted as cautious responding whenever motivational cues signaled potential gains or losses. Both age groups showed attention capture by and information updating of task-relevant gain and loss relative to neutral cues, indicated by larger a P2 and P3b to motivationally salient cues. In the ERPs on context processing, younger adults showed increased effort to maintain context information (reflected in the cue-locked CNV) and a reactivation of context information (reflected in the probe-locked N450 and SP) on loss trials. This finding corresponds to an earlier study showing a reactive shift in conditions of potential loss in younger adults (Locke & Braver, 2008). Older adults showed context effects on motivationally salient cues in cue-and probe-locked P3b amplitudes. Compared to our previous study, these context effects might indicate that motivationally salience sharpens context representations, although older adults continued to reactive context information during response execution on motivationally salient trials.

In sum, the results indicate a flexible modulation in the predominant manner of context updating by motivational cues. They contribute to previous fMRI-results revealing changes in motivational state in the AX-CPT to shift context updating toward reactive respectively proactive control (Braver et al., 2009). Finally, the study did not render support for a positivity effect in old age, but strong evidence for age-differential motivational valence and salience effects; therefore it is of high importance to neuro-cognitive models assuming functionally specialized cognitive and affective processes to interact with cognitive control.

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4 Discussion

The aim of the dissertation was to determine age differences in component processes of context processing and its modulation by motivational incentives. In the first study, in line with previous results and theoretical considerations, the age-related decline in context updating in the AX-CPT was expected in attenuated amplitude modulations of the parietal P3b and central CNV of context processing (Braver & Barch, 2002; Kray et al., 2005). It was of specific interest whether age differences would be detected in the frontal P2 of context updating revealed in a prior study (Lenartowicz et al., 2010). A posteriori, to consider core age effects, the first study also analyzed ERP correlates of context processing in performance-matched age groups. Since the shortfall of proactive control is assumed to evoke conflict during response preparation (Braver, 2012), increased need for reactive control in conflict-related potentials (i.e., the N450; West, 2004) was expected in older adults. In the second study, motivational cues were predicted to promote updating of subsequent context cues reflected in behavioral performance and aforementioned ERPs particularly in older adults. Largely unclear from the literature, it was an open question whether motivational cues modulate pro- and/or reactive control processes, and whether age-differential valence or salience effects would be detected (Mather & Carstensen, 2005).

The general discussion is structured into five parts. The first part is dedicated to the contribution of individual differences in age and performance to behavioral and ERP markers of context processing (*Paper I and II*). The second part discusses the impact of motivational cues on age-related changes in pro- and reactive control *(Paper III)*. Afterward, an overall synopsis, as well as limitations of the present studies and future research directions are provided. The thesis closes with a general conclusion.

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4.1 Age and Individual Differences in Context Processing

Behavioral age differences in context processing. As expected and in line with previous reports on age differences in context processing (Braver, 2012; Braver & Barch, 2002), the first study showed larger error rates and longer reaction times for older than younger adults primarily on trials requiring the updating and maintenance of context information. Importantly, the age differences in the context effect remained after statistically controlling for processing speed (Kray & Lindenberger, 2000; Salthouse, 1996), suggesting that context processing is a key issue to cognitive aging (Braver & Barch, 2002). Moreover, it should be noted that the first study applied a slight modification of the AX-CPT (Braver et al., 2005) in order to investigate a more pure form of context updating (Lenartowicz et al., 2010). Whereas the traditional AX-CPT requires processing of context cues on each trial to choose between target and non-target responses (see section 2.5), context updating in the modified AX-CPT in the present studies was only required on c-dep, but not on c-indep trials. Hence, c-indep trials seem to resemble single task blocks in cued switching tasks, in which the cue is irrelevant for the response assigned to the subsequent probe. In contrast, c-dep trials are akin to mixed blocks requiring the updating of cue information for responding to the upcoming probe. Since older adults exhibit increased costs (in terms of error rates and reaction times) on c-dep trials consisting of ambiguous probes and overlapping response-sets, the results of the present study are fully in line with age differences in task switching showing older adults to be particularly sensitive to task interference (Kray & Ferdinand, 2014; Mayr, 2001).

ERP correlates of context updating. The DMC framework (Braver, 2012; Braver et al., 2001, 2007) assumes that increasing age reveals a shift in the temporal dynamics of context updating, hence the ERP-study in *Paper I* can be seen as a first step to investigate this assumption. In contrast to the previous results by Lenartowicz and colleagues (2010), the current study could not reveal effects of the context manipulation in the frontal P2 of the ERP, and also no age differences therein. One post-hoc explanation for this discrepancy could be a slight modification of the paradigm in the present study. Specifically, to control for neuronal correlates of cue presentation without demands on context processing, the AX-CPT in Lenartowicz et al. (2010) included 50% control trials consisting of cue-only presentations, intermixed with 25 % c-dep and 25 % c-indep trials. Since the amplitudes of the frontal P2 in this study had been shown to be larger for c-dep than c-indep trials and largely reduced on control trials, the latter were excluded from the present study. However, the P2 seems to be particularly sensitive to task requirements and stimulus characteristics, as larger P2 amplitudes can be found for infrequent targets and trials requiring effort mobilization (Falkenstein et al., 2003; Luck & Hillyard, 1994; Potts, 2004). Hence, whereas c-dep and c-indep target trials occurred with 50% frequency in the present study and were equally salient, the most difficult c-dep trials in the foregoing study were quite rare and required high occasional effort (Falkenstein et al., 2003). Accordingly, effects of stimulus frequency, salience, and processing effort on c-dep and c-indep trials might underlie amplitude differences in the P2 in the previous study, rather than context updating per se (Astle, Jackson, & Swainson, 2008; Potts, 2004). In this regard, it is also noteworthy that prior studies found larger frontal P2 amplitudes for both task cues, precisely indicating the upcoming task, as well as for transitions cues, signaling an unspecific switch of tasks, compared to cue repetitions (Rushworth, Passingham, & Nobre, 2002, 2005; West et al.,

2011). It was concluded that the frontal P2 reflects a "change detector" by the ACC (West et al., 2011, p. 621), for instance to promote general switching demands (Adrover-Roig & Barceló, 2009). Although the study by Lenartowicz et al. (2010) involved a control analysis ruling out that the P2 is sensitive to cue switches, it seems that further work is needed to clarify the function of the frontal P2 in context updating.

Compared to the frontal P2, context effects were clearly obtainable in the parietal P3b and the central CNV, with age differences restricted to the former. Since the larger P3b to c-dep than c-indep trails if fully in line with updating requirements in cued task switching and oddball studies (Donchin & Coles, 1988; Kray et al., 2005; West, 2004), it is reasonable to conclude that the amplitude of the parietal P3b reflects the updating of context information. At odds with the hypotheses, older adults showed comparable P3b amplitudes on c-dep and c-indep trials, which were evenly distributed across the scalp. The increased P3b amplitudes to c-indep trials which should not elicit context updating is in line with ERP results of task switching, showing a diminished or absent "switch cost positivity" in older adults (cf. Karayanidis et al., 2011) due to increased P3b amplitudes on repeat trials (Friedman et al., 2008). At first sight, this finding suggests that older adults invest the same amount of processing resources on the updating of context information on both c-dep and c-indep trials and additionally recruit frontal areas to do so, for instance, as a compensational or non-selective strategy to update context information on any trial (e.g., Cabeza et al., 2005; Czernochowski, 2011; Daffner et al., 2011; Karayanidis et al., 2011; Kray & Ferdinand, 2014; Mayr, 2001; Whitson, Karayanidis, & Michie, 2012). This suggestion is corroborated by results of a fMRI study (DiGirolamo et al., 2001) showing that during task switching, older adults activate DL-PFC and medial frontal cortex not only on mixed, but also on single blocks. Although the topography of ERPs does not allow drawing conclusions concerning the

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underlying neuronal generator(s), the frontal shift in older adults' P3b scalp distribution might indicate an additional recruitment of frontal areas for performance on the task (Daffner et al., 2011). This assumption is substantiated by a recent study showing widespread activation of prefrontal brain regions to benefit performance in older adults (De Sanctis et al., 2009). Nevertheless, and as pointed out in section 2.6.2, the interpretation of the additional recruitment of frontal areas in older adults is still subject to debate (Cabeza et al., 2005; De Sanctis et al., 2009; Fabiani et al., 1998; Reuter-Lorentz & Sylvester, 2005) and may vary with task demands (see Daffner et al., 2011).

Interestingly however, the control analysis in the present thesis provided important new insights in the mechanisms underlying context processing in older adults. By comparing ERP correlates of switches in context conditions to switches in cue identity, it turned out that younger adults' internal representation of the task only differentiated between context conditions (i.e., larger P3b amplitudes on c-dep than c-indep trials; see Appendix, Figure 5), whereas older adults were sensitive to cue switches in general, irrespective of changes in context (i.e., larger P3b amplitudes for cue switches than cue repetitions on both c-dep and c-indep trials). In other words, older adults seemed not to represent the two context conditions according to c-dep and c-indep trials (see Figure 5) as suggested by ERP data in younger adults, but each cue-probe combination was internally represented by an own S-R mapping, leading to four different task conditions (see Appendix, Figure 6 for a schematic illustration). In line with this differential representation, the P3b-data suggest that older adults updated context information whenever *perceptual* changes in the environment (here: the context cue) suggested a change in task rules, and not due to changes in context representations. However, given the task structure (see Figure 3), a change in the context cue from one trial to the other should only require context updating on c-dep trials, but not on c-indep

trials. Thus, depending on the internal representation of the task, the term "context information" has a differential meaning in younger and older adults, with older adults updating context information whenever there was a change in any task cue as suggested by ERP data.

The strong reliance on perceptual information in the elderly has already been reported in an elegant study design including eye tracking by Spieler and colleagues (2006). In this study, older adults continued to rely on the inspection of redundant task cues on single-task trials directly following an initial cued task-switching phase prompted, suggesting that older adults struggle to shift into a more efficient, low-control mode (Spieler et al., 2006). Although age differences in the flexible selection of control modes are unlikely to explain the results of the present study as the task remained identical through the experiment, the two studies have in common that older adults seem to outsource task requirements to external cue information (here: perceptual switches) when available instead of relying on internal representations (here: context conditions). Put another way, rather than updating context information following internal representations of context conditions and task requirements as in younger adults, context updating in older adults seems to be guided by salient, external cue switches. This finding may have been caused by inhibited access to (Zelazo et al., 2004) or a degradation of context representations in older adults (Braver et al., 2001) Moreover, it could also reflect task instructions, as the present study refrained from explicitly pointing out the two context conditions but instructed subjects on four different task rules. Hence, to fully understand the mechanisms underlying context processing and context representations in the AX-CPT, it would be interesting to examine whether age differences in the P3b disappear in case task instructions highlight the dependency on cue information and thus different context conditions.

Comparable to the P3b, CNV amplitudes were larger for c-dep than c-indep trials. The amplitude of the CNV has been interpreted as reflecting the extent of maintaining of goal-relevant information and of task preparation (Karayanidis et al., 2011; Lenartowicz et al., 2010; Wild-Wall et al., 2007). Thus, larger CNV amplitudes on c-dep, requiring maintenance of context information for responding to the probe, than on c-indep trials, not requiring context maintenance, accord with the expectations and earlier results on the AX-CPT (Lenartowicz et al., 2010). Recent studies on the effects of aging on the amplitude of the CNV have revealed mixed results (for a summary, see Wild-Wall et al., 2007). In this regard, the lack of age differences in the present study contrasts with age effects in the CNV in the studies by West (West, 2004; West & Moore, 2005) and Kray and colleagues (2005), who found increasing age to go along with deficits in goal-maintenance and a larger effort in maintaining cue information as reflected in the CNV. The absence of age effects in the CNV is also in contrast to a previous fMRI study on the AX-CPT, showing reduced activation of the lPFC for maintaining goal-relevant information during the CTI in older adults (Paxton et al., 2008).

However, in line with the current results, there is evidence from fMRI that the neuronal mechanisms supporting simple storage of information in WM tasks are less affected by aging (Reuter-Lorenz & Sylvester, 2005; Rypma & D'Esposito, 2000). Moreover, the lack of age differences in the CNV in the present study is in accordance with behavioral data on the AX-CPT (Braver et al., 2005, see section 2.5.1), indicating that context updating, but not maintenance is affected by aging. Hence, ERP correlates are able to confirm the behavioral results and precisely reveal dissociable age differences in updating, but not maintenance abilities, which may not be afforded by an fMRI design (Paxton et al., 2008).

Nevertheless, it can also be hypothesized that the seeming discrepancy in age effects on maintenance capabilities in the CNV across studies traces back to the use of different CTIs. For instance, Braver and colleagues (2005) demonstrated that only increased duration of the CTI (i.e., 5000 ms) and hence larger maintenance demands produced behavioral deficits in old-old (>75 years of age) adults relative to young-old (<75 years of age) adults and a short (i.e., 1000 ms) CTI. However, Redick and Engle (2011) found no maintenance deficits in younger adults with low WM capacity in a long CTI in the AX-CPT, but did not investigate ERPs. Therefore, to support the notion of the DMC theory that the mechanisms underlying context updating and maintenance are separable and differentially affected by increasing age, further studies should systematically vary the CTI in the AX-CPT and measure age differences in the CNV.

Age and individual performance differences in pro- and reactive control. In line with a large literature on performance differences among older adults (Braver et al., 2005, Daffner et al., 2011, De Sanctis et al., 2009; Fabiani et al., 1998; Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012; Riis et al., 2008), the analysis on the composite index of context processing revealed a large performance variability within older adults. Separating the age groups based on a common index of context processing disclosed no performance differences between high performing older and low performing younger adults. This result is comparable to the studies by Daffner and colleagues (2011) and Goffaux and colleagues (2008) showing that older adults with high WM ability to exhibit equivalent performance to a group of (low performing) younger adults in either reaction times or error rates. In extension to these reports, a subgroup of older adults in the present study seems to be able to exhibit similar

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performance to younger adults when examining performance differences in a joint measurement of *both* reaction times and error rates as in the current study.

Rerunning the analysis on context effects in the cue-locked P3b - the only component for which age differences had been observed - in the four subgroups revealed that both, high and low performing younger adults showed the aforementioned context effect in the parietal P3b, reflecting context updating. This effect was absent in both performance groups of older adults. The results are important as the DMC theory makes the strong claim that age differences in the neuronal mechanisms supporting context updating underlie the age-related decline in a wide variety of cognitive tasks (Braver et al., 2001). Hence, the thorough analysis in the performance-matched groups ensures that the alterations in the P3b of context updating revealed in the first article are indeed due to mechanisms of increasing age, and not due to performance differences per se (Rugg & Morcom, 2005), suggesting a key determinant of cognitive aging (Braver & Barch, 2002).

Interestingly, the analysis of probe-locked data indicated a context effect in the N450 component in high performing older adults. In general, the amplitude of the N450 is interpreted as reflecting conflict detection supported by the ACC (Liotti et al., 2000; West, 2004). Therefore, it seems as if the lack of proactive engagement (i.e., in the cue-locked P3b) in high performing older adults is followed by increased conflict concerning the correct response particularly for reversed S-R mappings on c-dep trials, for which the N450 was largest. This interpretation is consistent with the results of a fMRI study on the AX-CPT revealing larger probe- than cue-related activation in lPFC in older than younger adults (Paxton et al., 2008). Moreover, the ERP results corroborate the assumption by Braver et al. (2007), who speculated that the lack of

proactive control supported by the PFC leads to a strong involvement of further brain regions in reactive control, particularly the ACC.

The ERP results of the analysis in Paper II can only be discussed in light of a limited number of studies to date investigating the relative contribution of individual differences in age and performance to cognitive control (see Adrover-Roig & Barceló, 2009; Goffaux et al., 2008 for approaches). Though, the results indicate that the mechanisms underlying equivalent behavioral performance in younger and older adults not necessarily need to be the same (Oberauer, 2005). In line with the study by Kopp et al. (2014), the shift toward reactive control in old age as indicated by ERPs seems to be compensational as high performing older adults did not differ in the behavioral data from low performing younger adults. In the present study, reactive control reflected in the N450 was particularly increased for c-dep trials, while the allocation of reactive control in Kopp et al. (2014) was independent of the experimental condition and hence rather unspecific. Besides, in extension to the study by Kopp et al. (2014), the current study uncovers that the mechanisms of reactive control were only present in high, but not in low performing elderly.

The latter point warrants further discussion. In the cue-related ERPs, low performing older adults showed a more widespread distribution of the P3b than high performing older adults, reflecting the frontal shift in poor performers in a previous report (Fabiani et al., 1998). However, the difference in the P3b distribution did not interact with the experimental context manipulation. Hence, to gain insight not only into sources of differences between younger and older adults (Daffner et al., 2011), but also into the critical mechanisms distinguishing high from low performing elderly, the cue-related analysis allows no clear conclusion. In contrast, the probe-related N450 undoubtedly differentiated older subjects on different performance-levels: While the

high performers showed a context effect in the N450, no such effect was observed in the low performers. Thus, the analysis on ERP differences *within* the group of older adults reveals that successful performance in older adults might especially take place during processing stages of reactive control.

At this point, however, it remains unclear how increased and even comparable performance to younger adults can be achieved through mechanisms of reactive control. Although the N450 is associated with conflict detection generated in the ACC (Liotti et al., 2000), it remains open whether and how detected conflict can be resolved. Within the conflict theory on the ACC (Botvinick et al., 2004), it is suggested that ACC-activations serve as a "control signal" (West & Moore, 2005) to the (DL-) PFC. This signal modulates activity within the (DL-) PFC necessary to implement and regulate attentional top-down control in posterior brain regions for conflict resolution (Botvinick et al., 2004; Braver et al., 2007; Miller & Cohen, 2001; West & Moore, 2005). Nevertheless, as Botvinick et al. (2004) point out, the precise mechanisms allowing the translation of detected conflict into compensatory changes remain unclear. From the ERP-literature, a possible candidate related to mechanisms of conflict resolution is the probe-related SP (see section 2.6.2; West et al., 2005); however, no such potential could been detected in high performing older adults. Hence, future research on reactive control needs to precisely investigate mechanisms providing the transfer from conflict detection into adjustments of cognitive control, for instance by means of ERPs.

Finally, it should be noted that not only high performing older, but also low performing younger adults showed a context effect in the probe-locked N450. It remains unclear, why low performing younger adults exhibited reactive control given the proactive preparation reflected in the cue-locked P3b. One post-hoc explanation is that low performing younger adults also had to process residual conflict during probe

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presentation, which may account for their worse performance relative to high performing younger adults in the composite index. This finding is supported by results of the study by Redick (2014), showing mechanisms of reactive control in younger adults with low WM capacity. In sum, the results suggest that more work is needed to disentangle the contribution of age and behavioral performance on the temporal dynamics of processing context information.

4.2 Motivational Influences on Context Processing

Behavioral age differences in motivational influences on context processing. The behavioral data of the second study lend support to the prediction of motivational influences on cognitive control, which turned out to be different for younger and older adults. Although both age groups showed an effect of motivational salience on context effects in reaction time data, the effect in younger adults draws back to a benefit, i.e., fastened responding when motivational cues signaled potential gains, whereas older adults exhibited larger context effects on both, gain and loss trials.

The younger adults' reduced context effect on gain trials was caused by faster responding on c-dep trials, which replicates results of previous studies showing fastened reaction times under reward conditions even when performance at baseline (i.e., no reward condition) was already good (Chiew & Braver, 2013; Falkenstein et al., 2003). Moreover, similar to a previous report, the speed-up in the present study was not at the cost of errors, as no influence of motivational cues on error rates was detectable (Chiew & Braver, 2013; Kleinsorge & Rinkenauer, 2012), suggesting a true enhancement of cognitive control by motivational cues (Pessoa & Engelmann, 2010). This finding corresponds to predictions of the DMC theory (Braver & Barch, 2002), as gain cues

might have triggered proactive context updating specific for c-dep trials and hence supported fast and correct responding to the probe (Chiew & Braver, 2013). The results also address recent models on cognitive-affective integration (Gray, 2004; Pessoa, 2009). Therein, it is assumed that motivational influences regulate behavior to be adaptive in a specific situation (Gray, 2004). In the present study, gaining money was particular important for younger adults, and hence gain cues increased cognitive control to determine behavioral outcomes (Pessoa, 2009).

A further aim was to compare the impact of reward and penalty manipulations on cognitive control within the same task (Locke & Braver, 2008). Younger adults showed a larger improvement in context processing under gain than loss conditions. Again, this finding could be interpreted in terms of theories on affective-cognitive interactions (Gray, 2004; Gray et al., 2002; Pessoa, 2008, 2009). As younger adults performed relatively well in the task and committed few errors, gaining money by fast responding might have been more relevant respectively adaptive than losing money by incorrect responding. However, in the "dual competition framework" (Pessoa, 2009, p.160), motivational influences on cognitive control are considered to occur by means of altered perceptual processing. Hence, the analysis on ERP correlates of the valence effect in the subsequent section is particularly helpful to investigate the neuronal mechanisms underlying the processing of motivational cues in younger adults more thoroughly.

In contrast to the valence effect in younger adults, cognitive control in the elderly was affected by motivational cue salience. Slowed performance on c-dep gain and loss trials caused a larger context effect relative to neutral trials, but motivational cues did not affect error rates. Hence, older adults' performance may be best described in a more "cautious" responding whenever motivational cues indicated the possibility to win or lose money. The dual competition model (Pessoa, 2009) assumes that enhanced sensory

processing of motivational stimuli might negatively affect control performance, because increased resources devoted to sensory processing limits "common-pool resources" (Pessoa, 2009, p.162) available for cognitive control. Hence, drawing attention to motivationally salient stimuli might have taken away limited processing resources in old age. In turn, as processing ressources were particularly required for performance on the cognitively demanding c-dep trials, this may have caused the slowed responding on motivational trials. Nevertheless, current research demonstrating that the negative impact of motivational and emotional stimuli on cognitive control to depend on the level of affective significance speaks against this assumption (Pessoa, 2009). Here, it has been shown that particularly highly arousing stimuli (Verbruggen & De Houwer, 2007; Vogt, De Houwer, Koster, Van Damme, & Crombez, 2008) impair cognitive control performance. As the present study used stimuli low in affective significance (i.e., pictures of money bags), it is unlikely that the processing of motivational stimuli compromised cognitive control performance.

Instead, the salience effect in older adults might reflect explicit task instructions that both gain and loss cues are equally important for the monetary bonus given when starting the experiment. This suggestion may also account for the absence of a positivity effect, as the positivity effect seems to be most reliable whenever experimental situations do not explicitly place situation-specific constraints on affective processing (Reed & Carstensen, 2012), such as favoring explicit aspects of information. Thus, as the present study emphasized that gain and loss cues were equally relevant, older adults may have equally focused on their processing (Mather & Carstensen, 2005). Alternatively, the age-related positivity effect has been shown to be strongly linked to cognitive resources, as it is most evident in older adults with high levels of cognitive control ability but diminished in pathological aging (i.e., Alzheimer's disease) or

whenever cognitive resources are diverted to task demands (i.e., dual-task procedures; Reed & Carstensen, 2012). Since the AX-CPT was fairly challenging for older adults as inferred from behavioral data in the first study, cognitive resources might have been occupied in the primary tasks, and not available for processing motivational information and particularly positive information. As the first study already revealed large performance variability among older adults, one possibility to rule out this concern would be to examine the impact of motivational cues on context processing in high- and low performing elderly. Another is to look at ERPs reflecting the cognitive processing of motivational cues, which are presented in the following.

ERP correlates reflecting processing of motivational cues. So far, only a limited number of studies investigated age differences in ERP correlates of basic affective processing (Olofsson, Nordin, Sequeira, & Polich, 2008; Samanez-Larkin et al., 2007; Wood & Kisley, 2006). The current study provides evidence that both age groups were strongly affected by the salience of motivational cues reflected in larger P2 and P3b amplitudes relative to neutral cues. In line with previous work on processing affective-laden items, larger central P2 amplitudes to gain and loss cues may reflect automatic attention capture by salient stimuli (Carretié, Hinojosa, Martín-Loeches, Mercado, & Tapia, 2004; for a review, Olofsson et al., 2008), whereas larger parietal P3b amplitudes to salient cues have been linked to the controlled updating of task-relevant stimulus information and the amount of attentional resources for stimulus processing (Briggs & Martin, 2009; Donchin & Coles, 1988; Krebs et al., 2013; Polich, 2007; Olofsson et al., 2008).

Whereas the P2 amplitudes did not differ between the age groups, the effect of motivational salience on the P3b amplitude was more pronounced in younger than older

adults, probably due to an increase in the frontal proportion of the P3b in older adults. Age differences in the anticipation of motivational events have only rarely been investigated and are not well understood (Olofsson et al., 2008; Samanez-Larkin et al., 2007; Wood & Kisley, 2006). Hence, the results of the study suggest that older adults exhibit slightly reduced attentional allocation to gain and loss cues, while the automatic processing of salient information is utterly preserved. Again, in contrast to previous studies (Mather & Carstensen, 2005; Samanez-Larkin et al., 2007), but in accord with the behavioral data, older adults showed comparable P2 and P3b amplitudes to gain and loss cues and hence no positivity effect. However, as discussed, gain and loss cues were equally salient and instructed to be important for the monetary outcome, which may have diminished valence effects in the elderly.

The finding of larger P2 and P3b amplitudes to salient cues in both younger and older adults is relevant for the rational of the second study, as it aimed to promote context updating by motivational cues. First, the ERP results suggest that both younger and older adults indeed processed the meaning of the motivational stimuli as they were behaviorally relevant. This assumption is supported by results of an so far unpublished follow-up study in our lab, illustrating that the effect of motivational salience in ERP correlates dissapears by presenting the motivational cues blockwise instead of randomly within blocks. Second, the processing of motivational relevance is highly important as Gruber and Otten (2010) found enlarged P2 and P3b amplitudes to reward cues preceding to be-remembered items to benefit later recollection. As the effect was specific for high compared to low monetary reward in Gruber and Otten (2010), younger adults seemed to voluntarily exercise control over anticipatory and preparatory processes to benefit updating and encoding of a subsequent event (Gruber, M. J. et al., 2013; Gruber & Otten, 2010). In the present study, evidence is provided that increased

voluntary preparation may not only occur after reward, but also after salient cues in general (i.e., reward and penalty) as well as in older adults. Third, transferred to the aim of the present study and the assumptions of the DMC theory (Braver & Barch, 2002), the long-lasting preparation for task-relevant information may have been useful for the gating of subsequent context information. In extension to the DMC theory, the results suggest that also penalty-predicting cues enhance prestimulus activity and hence might be able to trigger context updating. However, whether neuronal acitivty to reward and penarly observed in both age groups actually translates into context processing will be discussed hereafter.

ERP correlates reveal age-differential salience and valence effects on context processing. The analysis of ERPs on context processing in cue- and probe-locked data reveals differential modulations by motivational cues in the two age groups. Whereas younger adults seem to focus on the impact of negative events (i.e., losses), context processing in older adults was generally affected by salient cues (i.e., gains and losses). Of most importance for the research question, the age-differential modulations took place at different stages in the time course of context processing.

In the cue epoch, younger adults showed context effects in the parietal P3b and the central CNV replicating the results of the first study. Additionally, cue valence modulated CNV amplitudes, which were largest for loss trials. This finding might reflect that younger adults strongly engage in maintaining context information in the CTI whenever incorrect and slowed responses would be penalized. This interpretation fits with the description of a prior result that the amplitude of the CNV mirrors the short-term mobilization of effort (Falkenstein et al., 2003). However, in the study by Falkenstein and colleagues (2003), CNV amplitudes were increased during reward as

compared to neutral trials. One reason for the discrepancy to the present results could be that Falkenstein et al. (2003) applied a simple choice reaction time task and the impact of penalties (i.e., for incorrect responding) was not assessed at all. Moreover, as outlined in the discussion of the previous results, the functional significance of the CNV seem to depend on multiple factors, such as the delay manipulation and the demands on maintenance capability. Therefore, more work is needed to understand how effects of cue valence, task demands, effort mobilization, and context maintenance interact. At the moment, the behavioral results provide some first evidence that gain cues led to fastened responding, while the CNV data suggests that younger adults more likely invest effort in the avoidance of losses.

In the probe epoch, negatively valenced cues continued to influence context processing in younger adults. In the early time-window, context effects were found only in a fronto-centrally distributed negative deflection on loss trials, bearing resemblance to the N450 of conflict processing in the first study and earlier reports (Liotti et al., 2000; West et al., 2005). In the later time-window, context effects in a parietally distributed slow positive component were reduced on loss trials only. This component might reflect the sustained positive potential (Krebs et al., 2013; West & Alain, 2000a), indicating conflict resolution and response selection (West et al., 2005). Taken together, the results of the entire probe epoch suggest that anticipated losses in younger adults give rise to more response conflict on trials with reversed S-R assignments (i.e., c-dep trials) and subsequently enhanced processing demands for its resolution. This idea is fully in line with the reaction time data, indicating a larger context effect for loss than for gain trials. Moreover, the ERP results correspond to a recent fMRI study investigating neuronal activations indicating the tradeoff between pro- and reactive control under blockwise neutral, reward, and penalty conditions in the AX-CPT (Braver

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et al., 2009). On reward blocks, younger adults exhibited increased sustained activity in a prefrontal network, reflecting increased proactive control. On penalty blocks, the time-course of activity shifted within these brain regions to the presentation of the probe, i.e., reflecting increased reactive control. Thus, the current ERP-results together with the previous fMRI-findings raises the interesting possibility that the avoidance of monetary losses moves context processing in younger adults toward a reactivation of context information before task execution (Braver et al., 2009). This view is strengthened by the study by Unger, Kray, and Mecklinger (2010) showing that (self-relevant) failure inductions may cause a shift toward mechanisms of reactive control in younger adults, which can be reflected in ERPs of cognitive control. Critically, in the present study, context information might have been updated in the cue-probe epoch as well, as suggested by the context effect in cue-locked P3b and CNV amplitudes. Nevertheless, to avoid self-relevant monetary penalty on loss trials, experienced response conflict and interference lead to an *additional* reactivation of context information in younger adults (Braver et al., 2009).

In the aforementioned fMRI-study, potential gains increased cue-related activity in prefrontal brain areas (Braver et al., 2009). In contrast, gain cues in the present study affected behavioral data but not ERPs. A closer look at the results of the mentioned fMRI study indicates that the increase in cue-related activity seems to depend on personality factors, as it was largest in highly-reward sensitive subjects (Braver, 2012; Locke & Braver, 2008). This assumption is corroborated by research on cognitive-affective interactions, suggesting that affective influences on cognitive control, in particular for low-arousing stimuli as applied, might also vary with state-dependent effects such as mood and anxiety (Pessoa, 2009). In self-report data, it has been revealed that the stronger subjects are affected by affective manipulations, the larger the

impact on performance and underlying mechanisms (Gray, 2001, 2004; Locke & Braver, 2008; Pessoa, 2009). As state-dependent effects and individual differences in personality factors have not been assessed in the current design, future studies should therefore disentangle the effects individual differences in approach (and avoidance) motivations (Elliot, 2008), temporal differences in context processing, and the underlying neuronal mechanisms.

An important new insight of the present study is that the analysis of cue- and probe-related ERPs indicates a differential modulation of context processing by motivational cues for younger than older adults. In the cue-locked epoch, context effects in P3b amplitudes were found only on motivationally salient trials in older adults, repeating the salience effect in older adults' behavioral data. In adherence to the hypothesis, the absence of context effects in the P3b during neutral trials suggests deficits in proactive context processing (Braver & Barch, 2002). Hence, it replicates the interpretation of the first study, namely that impaired context representations cause the updating of context information on any trial. However, the salience effect in the cue-locked data in the second study raises the interesting possibility that motivationally salient cues seem to modify context processing in older adults by sharpening representations about context conditions (Pessoa, 2009).

In order to fully understand temporal mechanisms of context processing and the impact of motivational cues in older adults, the results of the cue-locked epoch have to be discussed in light of the probe-locked data. In the probe-locked ERPs, older adults showed larger frontally and parietally distributed context effects only for motivationally salient cues in the early phase, and this effect became more posterior in the late epoch. The waveform might reflect a prolonged P3b-like component across the two time windows. Thus, unlike the N450 and SP of conflict detection and resolution in younger

adults, the probe-locked P3b in older adults suggests increased WM recruitment required for context updating and task reconfiguration before response execution (Daffner et al., 2011; Goffaux et al., 2006; West & Travers, 2008). This finding suggests that the temporal shift of context processing toward reactive control reported in old age (Braver & Barch, 2002; Braver et al., 2005; Paxton et al., 2008) is particularly engaged whenever the correctness of the response is important for the behavioral outcome, i.e., during gain and loss trials. Again, as for the behavioral and ERP data of the motivational cue, the ERPs of the cue- and probe-locked epoch lend no support for a positivity effect in old age.

Taken together, the ERP and behavioral data in older adults displayed a consistent pattern, as context processing in all temporal stages was modulated by motivational cue salience. First, behavioral context effects were larger during gain and loss trials. Second, older adults similarly processed the salient information provided by gain and loss cues in the motivational cue interval, and third, differential cue- and probe-locked P3b amplitudes for context conditions were found only on motivationally salient trials. Compared to the first study in which (1) the amount of (proactive) context updating was similar for c-dep and c-indep trials, and (2) context effects were only apparent in probe-locked ERPs, the present results suggest that under conditions of high motivational salience, older adults show a temporal shift toward a sharpened representation of context conditions when context cues were inititally presented in the cue epoch. This finding fits nicely with a previous fMRI-study revealing a flexible change from a probe- toward a cue-based PFC-activations in the AX-CPT after strategy training in older adults (Braver et al., 2009). Moreover, as anticipated motivational cues have been shown to benefit encoding of subsequent information (Gruber, M. J. et al., 2013; Gruber & Otten, 2010), and older adults showed salience effects in ERPs of the motivational

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cues, this shift might have been triggered by increased prestimulus activity before the presentation of contextual information. One possibility could be that increased prestimulus activity reflects increased attention to goal-relevant information (Krebs et al., 2013), but the precise mechanisms underlying this benefit clearly warrant future investigation.

Finally, regarding the assumptions of the DMC theory (Braver & Barch, 2002; Braver et al., 2005) and the aforementioned shift from reactive to proactive control after strategy training (Braver et al., 2009), the cue-locked context effects on motivationally salient trials in older adults are not assumed to reflect a normalization of age-related differences underlying context updating. Rather, the results suppose that motivational cues led to an early representation of context conditions occuring *in addition* to the probe-locked context effects. As the probe-locked context effects were particularly pronounced during gain and loss trials, older adults might have still experienced response conflict and the need to reactivate context conditions during probe presentation. Eventually, this interpretation might also explain the larger behavioral context effects during gain and loss cues in older adults.

4.3   Synopsis

The present thesis investigated fundamental mechanisms of age differences in context processing which are of high importance to recent theories on cognitive aging. Moreover, the susceptibility of context processing by incentives will not only be of interest for the DMC framework and neuroscientific models on cognitive-affective interactions, but might also have practical implications.

In line with the DMC theory (Braver & Barch, 2002), the two studies revealed reliable age differences in context processing that cannot be explained by age-related slowing as the single underlying mechanism (Salthouse, 1996). Considering older adults as a whole group, differences in the internal representation of context information and the task may have caused a strong reliance on perceptual information, resulting in context updating on both context conditions. This unexpected finding contrasts with the assumptions by the DMC theory, but might explain why some studies fail to detect a decline of proactive control in older adults (Kray, Schmitt, Heintz, & Blaye, in press).

Alternatively, the assumed age-related trade-off between proactive and reactive context updating (Braver et al., 2005) might only be detected when investigating a subgroup of older adults. Hence, contributing to the DMC theory, the dissertation project unveils that only high-performing older adults indeed relied on a late correction mechanisms suggesting reactive control. In addition, this finding provides important new insights into the mechanisms of cognitive aging. First, within different performance groups of older adults, the study emphasizes the importance of intact reactive control for successful cognitive aging. Second, as high performing older adults showed equivalent performance to a subgroup of younger adults, but relied on a different control strategy, high performing older adults cannot simply be described as low performing younger adults. Instead, it suggests fundamental differences in context processing between age groups (cf. Oberauer, 2005). The latter will be of considerable interest for theoretical models on cognitive aging, and challenges the view that cognitive age differences only reflect individual performance differences. To the best of our knowledge, the present thesis is the first to disentangle the contribution of variability in age and performance on the mechanisms of context processing.

It is also worth considering that the present study confirms the hypothesis that context updating and maintenance are separable constructs differentially affected by increasing age. Hence, the fine-grained ERP approach applied in the dissertation project helps to substantiate the dissociation between the age-related decline in context updating and maintenance, which could not be afforded by functional brain imaging measures (Paxton et al., 2008). Therefore, in order to modify context processing in older adults, cognitive interventions (Daffner, 2010) should start with promoting particularly the aspects of context updating and the reliance on contextual representations, rather than context maintenance. In this regard, the results of the second study can be viewed as a first approach.

Contributing to the idea and previous results of reward-related gating (Braver & Barch, 2002; Chiew & Braver, 2011b; Watanabe, 2007), proactive control in the second study was fostered under conditions of anticipated gains. However, unlike expected from the DMC theory, this interpretation only holds for younger adults. In all temporal stages of context processing, older adults were strongly affected by the salience of motivational information. Although this finding is surprising in light of the age-related positivity effect (Mather & Carstensen, 2005), it substantiates recent findings of a reduced positivity effect under explicit task instructions and cognitively demanding conditions. Again, the ERP approach was able to precisely unveil the temporal stages of cognitive control and the mechanisms underlying the age-differential valence and salience effects. In extension to basic affective research (Oloffson et al., 2008), salient cues were followed by enhanced attention and task-relevant processing, and this pattern was relatively preserved in old age. First and foremost, this finding suggests that the experimental manipulation worked out. Beyond that, it will be of considerable importance to theoretical considerations on affective influences on goal-relevant

behavior. As prior research showed that attention to and processing of reward-related information can be voluntarily used in the service of subsequent stimulus processing (Gruber & Otten, 2010), the results indicate that pre-stimulus activity not only benefits memory performance, but it might also contribute to cognitive control in younger adults. Moreover, the voluntary control over pre-stimulus activity reflected in ERPs might also be engaged in penalty conditions and in older adults.

Obviously, the conclusion of pre-stimulus activity influencing cognitive control warrants further research. Nevertheless, the ERP results of motivational influences on context processing might already now open a wide field for applications. For the first time, the study showed that impaired goal-representations in the elderly can be sharpened by motivational cues. Hence, to promote goal-directed behavior in old age, important, necessary, and essential information has to be made fairly salient.

In addition to the beneficial effect of salient cues to context representations, older adults seemed to continue to apply mechanisms of reactive control under incentive conditions. Therefore, in contrast to the DMC theory (Braver et al., 2005), context updating may not be either proactive or reactive, but at least in conditions of salient information, older adults seem to recruit proactive mechanisms in addition to delayed control. Hence, as with the different mechanisms underlying comparable performance in younger and older adults in the first study, promoting context processing in older adults might not necessarily result in a similar pattern to that of younger adults. This assumption is supported by the fact that context processing in younger adults was more strongly affected by cue valence. Given the lack of previous studies investigating the impact of reward *and* penalty incentives under matched conditions of cognitive control, the present thesis reveals a relatively larger impact for penalty in younger adults. This effect might reflect a larger relevance of negative consequences for younger adults'

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outcomes in the present study. In this regard, inconsistencies in the current literature regarding the effect of reward and penalty incentives could also mirror the impact of personality factors and state-dependent effects on cognitive-affective interactions. Finally, differences in the subjective sensitivity to the kind of incentives applied might also account for age-differential valence and salience effects.

4.4   Limitations and Future Research Directions

Although the present dissertation provided considerable insights into the neural mechanisms of context processing, some limitations of the two studies should be addressed in future research directions.

First, the rational of the present thesis was based on the assumptions that the age-related decline in DA transmission to the PFC causes specific deficits in context processing (Barch, 2004; Braver & Barch, 2002), while DA release to incentive cues triggers the gating of goal-relevant context information (D'Ardenne et al., 2012; Gruber & Otten, 2010; Schultz, 2010). Clearly, as DA activity was not assessed, no conclusion can be drawn about the causal role of DA release in age- and incentive-related effects on context processing. Hence, to strengthen the functional role of DA in context updating, future work should directly measure DA activity in different age groups and experimental conditions, for instance by means of molecular imaging studies. Although much progress has been made on this topic, current inconsistencies regarding individual differences in DA in genetic (Barnett, Scoriels, & Munafò, 2008; Laukka et al., 2013; Nagel et al., 2008) and molecular imaging studies (Bäckman & Farde, 2005; Nyberg et al., 2012) may trace back to cross-sectional analyses (Nyberg et al., 2012), individual performance differences (Bäckman & Farde, 2005), or genotype characteristics (Laukka

et al., 2013). Hence, particularly for context processing, more longitudinal work is needed focusing on the interaction between individual performance differences, increasing age, and changing DA levels.

Secondly, and related to the first caveat, the present study was not designed to clarify whether DA itself implements the gating signal into the PFC or whether DA-release initiates a neuronal signal to other brain areas and neurotransmitter systems in order to accomplish context updating (see D'Ardenne et al., 2012 for a similar consideration). As research concerning this question is still in its infancy, the means by which DA activity is translated into context updating need to be strictly investigated. This aspect will also be of particularly interest for understanding the mechanisms underlying context processing modulated by incentives (Chiew & Braver, 2011b). Previous work has shown that presenting the same kind of reward at several times reduces the dopaminergic response (Schultz et al., 2010). However, the EEG approach in the current study required a large number of trials and accordingly a large number of incentive repetitions. Without understanding the precise functional principles of DA, it might therefore speculative to conclude whether the detected valence and salience effects on context processing were indeed linked to DA activity.

It is also noteworthy that the motivational manipulation in the second study comprised monetary gains (and losses) depending on the behavioral accuracy, while response speed was irrelevant to the monetary outcome[4]. Although this approach was chosen to put older adults not under (time) pressure, it might render the comparison to previous studies on incentive-related effects difficult. For instance, prior work on younger adults usually applied adaptive response-time procedures, penalizing both slowed and incorrect responses in cognitive control tasks (Chiew & Braver, 2011b,

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[4] See details in Paper III. Only responses exceeding 5000 ms were excluded from the analysis.

Kleinsorge & Rinkenauer, 2012; Krebs et al., 2013; Locke & Braver, 2008). Hence, in the present study, it cannot be ensured that with increasing task practice (and hence reduced error rates), younger adults were still motivated by incentive cues. Therefore, the current study can only be regarded as a first step to investigate the effect of motivational cues particularly in older adults. For reasons of comparability and motivational effects, follow-up studies in different age groups should use adaptive task procedures and assign incentives depending on behavioral performance in both error rates and reaction times. In this regard, it could also be useful to analyze diffusion models, which are able to track changes in speed-accuracy-tradeoffs between experimental groups and incentive conditions (for a discussion, see Chiew & Braver, 2011a, and Dambacher, Hübner, & Schlösser, 2011).

Besides limitations of the study design, a further critical point concerns the interpretation of the control analysis. The ERP-results of switches in context and in cue identity were interpreted as age differences in higher-order context representations. However, it should be noted that only the P3b data was sensitive to this dissociation and hence the conclusion is bound to restricted data. This constraint is important as prior research in younger adults revealed cognitive processes related to task (respectively context) and cue switches to constitute distinct phenomena (for a review, Jost et al., 2008, 2013) which can be separated on temporally and topographically properties of specific ERPs (Jost et al., 2008, 2013; Nicholson, Karayanidis, Bumak, Poboka, & Michie, 2006) and neuronal generators revealed by fMRI (Brass & von Cramon, 2004; De Baene & Brass, 2011). Thus, the view that older adults are more sensitive to external switches in cue than to switches in context representations should be substantiated by further work investigating the neuronal basis of this dissociation. This line of research would also contribute to the understanding of age differences in the reliance on

perceptual information. In the present study, it was argued that representations might have been impeded by the manner with which the context conditions were instructed (see discussion page 68/69). Moreover, cognitive resources required for processing cue switches in younger adults can be reduced by practice (Mayr & Kliegl, 2003). Hence, it would be interesting to see whether older adults might built up context representations when explicitly pointing to the two context conditions in the AX-CPT, and whether electrophysiological correlates of cue switches are modulated by extensive practice in older adults.

The final issue concerns the interpretation of individual differences in older adults with regard to mechanisms of successful cognitive aging. In the present studies, individual performance differences were considerably larger in older than younger adults (see Laukka et al., 2013 for a discussion). It can be argued that the younger age group consisted of a homogenous sample of university students from one age cohort, whereas the sample of older adults included a random population selection (see Rugg & Morcom, 2005). However, apart from behavioral and ERP-differences in the AX-CPT, no differences in demographic or control variables separated the group of high and low performing older adults at first sight. Hence, then questions arise of what exactly constitutes the difference between subgroups of older adults (Daffner, 2010), whether high performance in old age is rather flexible or persistent, and how intact cognitive control in high performing older adults translates into successful aging observed in every-day life. On the basis of these considerations, the understanding of mechanisms underlying individual age differences in the future might be a fruitful approach to promote successful cognitive aging in daily life.

4.5   Conclusion

Taken together, the present dissertation shed light on the mechanisms and modulations of age differences in goal-directed behavior. Aimed to determine the time course of context processing in younger and older adults, it turned out that the updating of goal information is not only a question of "when", but also of "how". Specifically, the ERP approach reveals that depending on *how* context is represented, changes in internal representations in younger adults versus salient perceptual switches in older adults seem to trigger the updating of goal information. Although this conclusion seems to be at odds with the assumptions of the DMC theory (Braver & Barch, 2002), it is in line with recent findings suggesting a strong reliance on perceptual information in older adults (Spieler et al., 2006). Further work on the impact of experimental manipulations, such as task instructions and task practice, will be desirable to uncover the underlying mechanisms.

Crucially, investigating performance-matched subjects supported the assumed temporal shift from pro-toward reactive control in advancing age (Braver & Barch, 2002). The younger adults constituted a homogenous group, whereas subgroups of older adults differed widely in performance (Nyberg et al., 2012). Above-average performing older adults indeed relied on a late correction mechanism, although it remains a future research question how this correction is translated into adaptive behavior (Botvinick et al., 2004). Hence, from a methodological point, the present thesis stresses the analysis of individual differences to precisely disentangle the mechanisms of successful cognitive aging (Daffner, 2010; Oberauer, 2005; Rugg & Morcom, 2005).

The dissertation project also contributes to the understanding of affective influences on cognitive control. Motivational cues modulated performance when

cognitive control demands were highest (Chiew & Braver, 2013; Kleinsorge & Rinkenauer, 2012) suggesting a true integration of cognitive and affective processes (Gray, 2004).

Importantly, the ERP approach was able to advance the understanding of cognitive-affective interactions in aging, as contrasting salience versus valence effects took place at differential processing stages in younger and older adults. Given the high relevance of losses for the monetary outcome, younger adults exhibited increased processing efforts and reactive conflict under conditions of penalty. Although this result substantiates prior work on the hitherto less examined influence of penalty, it also contrasts with research on reward-related gating (Braver et al., 2009). Progress in the understanding of individual sensitivity to reward and penalty, as well as experimental "pay-off schemes" (Dambacher et al., 2011, p.4) might reveal important new insights.

The strong impact of motivational salience on context processing in old age also sheds light on the age-related positivity effect. Both reward and penalty benefited the representation of context information in older adults, although salient information did not promote proactive control. Instead, in extension to the DMC theory (Braver, 2012), both control modes might be equally and concurrently applied in older adults. Given the complex nature of the task, and its explicit reference to salient cues, future work on the positivity effect needs to examine effects of task difficulty, individual performance, and automatic processing of motivational information (Reed & Carstensen, 2012).

In summary, the present thesis contributes to the understanding of age, individual differences, and motivational influences on the mechanisms of goal-related context processing. Eventually, and contributing to the introduction, it would also be interesting for future research to examine the reverse issue, i.e., how cognitive control ability might impact motivation in advancing age (Gray, 2004; Gay et al., 2002).

5 References

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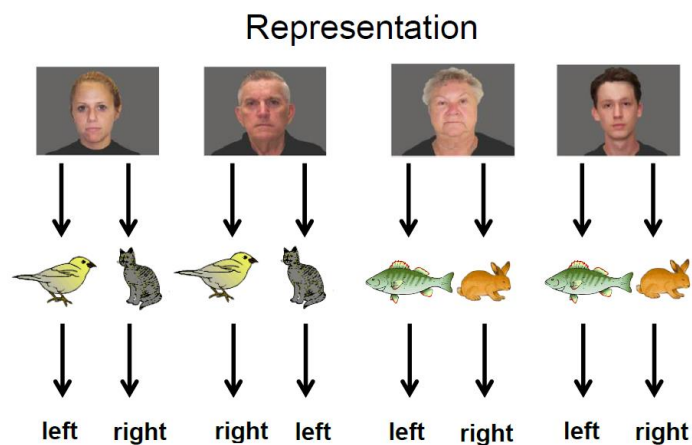
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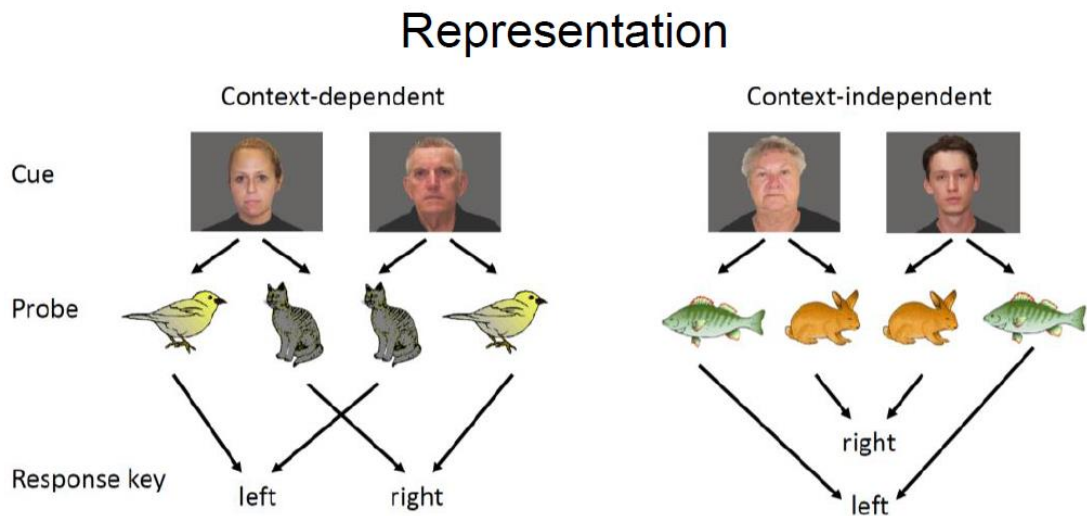
Figure 5. Assumed representation of the task rules in the AX-CPT in younger adults.

Younger adults seem to internally represent the task rules according c-dep and c-indep conditions as suggested by ERP data. Note that the task instruction refrained from explicitly pointing to the two context conditions. Figure adapted and modified from Schmitt, Wolff et al., 2014. Stimuli from Minear and Park (2004) and Rossion and Poutois (2004).

Figure 6. Assumed representation of the task rules in the AX-CPT in older adults.

Relative to younger adults (see Figure 5), ERP data suggest that older adults internally represent each cue-probe combination separately, and not according to higher-order c-dep and c-indep conditions. Note that this representation mirrors task instructions. Stimuli from Minear and Park (2004) and Rossion and Poutois (2004).