Plasticity of Executive Control Across the Lifespan

Examining Cognitive, Motivational, and Neural Mechanisms of Task-Switching Training in Children and Older Adults

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„Einfach nur mal ‘ne kleine Pause machen…“

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List of Publications

Paper I

Kray, J. & Dörrenbächer, S. (in press). The effectiveness of training in task-switching: new insights and open issues from a lifespan view. In M. Bunting & J. Novick (Eds.), *Cognitive Training*. Oxford: Oxford University Press.

Paper II

Dörrenbächer, S., Müller, P. M., Tröger, J., & Kray, J. (2014). Dissociable effects of game elements on motivation and cognition in a task-switching training in middle childhood. *Frontiers in Psychology, 5*, 1275.

Paper III

Dörrenbächer, S. & Kray, J. (submitted). The impact of a game-based task-shifting training on motivation and executive control in children with ADHD.

Paper IV

Dörrenbächer, S., Wu, C., Zimmer, H., & Kray, J. (submitted). Compensation in brain activity dynamics after cognitive-control training in older adults.

Paper I –IV can be found in the appendix of this dissertation that will be provided upon request.

Author Note

Several parts of this work (i.e., text passages or figures) are also included in manuscripts already published or submitted for publication in international peer-reviewed journals. For these manuscripts, I am the first or second author, but other authors contributed to the work and, hence, are included in the author list. The specific paragraphs with similar content to the manuscripts are not highlighted specifically in the continuous text to enable smooth reading. Full manuscripts can be found in the appendix of this thesis. In keeping with the practice of these manuscripts, I use the term 'we' instead of 'I' throughout my thesis.

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List of Abbreviations

AAAS	American Association for the Advancement of Science
ACC	Anterior Cingulate Cortex
ADHD	Attention-Deficit/ Hyperactivity Disorder
ADHS	Aufmerksamkeitsdefizit-/ Hyperaktivitäts-Syndrom
ANOVA	Analyses Of Variance
AR	Alternating Runs
BG	Basal Ganglia
BOLD	Blood Oxygenation Level Dependent
CAT	Computation Anatomy Toolbox
cf.	See Respectively Compare
CRUNCH	Compensation-Related Utilization Of Neural Circuits Hypothesis
cSFS	Caudal Superior Frontal Sulcus
d. h.	Das Heißt
DA	Dopamine
DARTEL	Diffeomorphic Anatomical Registration using Exponentiated Lie algebra
DCCS	Dimensional Change Card Sort
DMC	Dual-Mechanisms Of Control
e.g.	For example
EF	Executive Functions
ELSA	Early To Late Shift In Aging
fMRI	Functional Magnetic Resonance Imaging
fMRT	Funktionelle Magnetresonanztomographie
FP	Frontal Pole
gc	Crystallized Intelligence
gf	Fluid Intelligence
GLM	General Linear Model
HAROLD	Hemispheric Asymmetry Reduction In Older Adults
i.e.	That Is
IFJ	Inferior Frontal Junction

IPL	Inferior Parietal Lobule
PASA	Posterior-To-Anterior Shift In Aging
PFC	Prefrontal Cortex
PPC	Posterior Parietal Cortex
ROI	Region Of Interest
S-R	Stimulus-Response
SDT	Self-Determination Theory
SPL	Superior Parietal Lobule
STAC	Scaffolding Theory Of Aging And Cognition
TD	Typically Developed
THC	Temporal Hypothesis For Compensation
vlPFC	Ventrolateral Prefrontal Cortex
vs	Versus
WM	Working Memory

Summary

The overarching goal of the present thesis was to investigate cognitive, motivational, and neural mechanisms of plasticity in response to training of executive control at the outer stages of the lifespan (i.e., in childhood and in old age). The ability to exert executive control is one of the most fundamental human capacities for the enduring guidance of goal-directed behavior. Executive control is hierarchically organized into global and local processes that can be well dissociated in the task-switching paradigm. In order to measure global mixing costs, mean performance for single-task and mixed-task blocks are contrasted, thereby reflecting efforts to maintain and select between task sets. Local switching costs express performance differences between switch and repeat trials within mixed-task blocks, and therefore measure the ability to flexibly shift between tasks. A coordinated interplay of global and local task-switching abilities aids the precise implementation of controlled behavior. Importantly, global and local task-switching abilities show differential developmental trajectories over the lifespan, hence are differentially prone to immaturity in childhood – especially in cases when children suffer from developmental disorders, such as attention-deficit/ hyperactivity disorder (ADHD) – or to senescent decline in advanced age. Specifically, it has been documented that global functions mature later in childhood, while showing an earlier decline in old age, than local functions. At the same time, repeated practice in task switching has been shown to enhance such reduced executive abilities in early and late age ranges, thus providing a means for compensation. Therefore, we applied specific age-appropriate variants of task-switching training in children and older adults to investigate the scope of lifespan plasticity in local versus global aspects of executive control.

The present dissertation consists of four manuscripts reporting theoretical and empirical evidence on the effectiveness of task-switching training over the lifespan. The first publication (*Paper I*) is a review chapter, where we discuss task-switching training and potential modulating influences on its effectiveness in different age groups in the light of a recent

theoretical framework on cognitive plasticity. Based on the conclusions derived from *Paper I*, we designed and empirically tested specific variations of training interventions for children and older adults that are presented in the subsequent papers (*Papers II – IV*).

Paper II and *III* set a focus on task-switching plasticity in childhood. It has been well documented that children often do not benefit from cognitive training to their full capability due to a lack of training motivation or of willingness to perform cognitive tasks. This is also associated with an increased sensitivity for reward due to the earlier maturation of the appetitive socio-emotional compared to the rational cognitive system. Children's resulting high need for reward is not adequately nurtured in low-rewarding standard settings of cognitive training. Importantly, in children suffering from specific developmental disorders, such as ADHD, the imbalance between motivational and cognitive factors appears even larger. As a result, ADHD children show not only a reduced willingness to train but also a fundamentally altered response style, such as rapid responding at the expense of accuracy or a general increase in response variability, while they perform repetitively on a cognitive task. Implementing a motivationally enriched training setting, such as adding video-game elements in children, especially in case when they suffer from ADHD, may be a useful manipulation to enhance their engagement in meeting the demands of cognitive training and to align their behavior. Therefore, in the course of two intervention studies, we empirically investigated the interaction of cognitive and motivational mechanisms underlying training-induced plasticity in healthy (*Paper II*) and in ADHD-diagnosed children (*Paper III*).

The results of *Paper II* suggested that in typically developed children, adding video-game elements to a task-switching training setting promoted training willingness and local task-switching performance. Specifically, we obtained a larger reduction of switching costs in the training task and in an untrained task switching situation. However, this incremental cognitive benefit did not generalize to global task-switching abilities (i.e., to the mixing-cost level) or to other task domains of executive control (i.e., to different inhibition or working memory tasks).

The results of *Paper III* indicated that in ADHD children, the addition of video-game elements to a training setting also clearly enhanced the willingness to train (i.e., voluntary motivational control), and had an even more sustainable effect than in healthy children, which was in line with the compensation view. However, at the same time, this setting condition also established a more severe level of behavioral inappropriateness, thus fueling an unintentional motivational drive. In turn, on the cognitive level, the high-motivational training setting did not enable any larger performance improvements than a standard setting in ADHD children. This was the case for both local and global task-switching processes, both on mean-level performance and performance variability.

Hence, regarding the use of cognitive interventions, such as task-switching training, during periods early in the lifespan, we endorse the consideration of an appealing motivational training setting in typically developed children. Such an enriched setting may enhance training willingness and boost cognitive development, at least in training-specific, local executive processes. However, in subclinical samples that become easily distracted, such as in children diagnosed with ADHD, one should only carefully manipulate the training setting to avoid an 'over-heating' or further distraction by the task layout. Hence, motivation-cognition interactions might follow an inverted U-shaped dose-response function in childhood – an insight that should be taken into account when trying to design adequate training interventions for early lifespan periods.

While a lack of motivation often prevents children performing to their full capability, at the other end of the lifespan, there are different important issues leading to deficient performance. In older adults, senescent changes in the brain appear to be a major contributor. Therefore, *Paper IV* focuses on an empirical investigation of the neural correlates of training-induced plasticity in older adults, based on a similar task-switching regime. Task switching is neurally subserved by spatio-temporal interactions of brain activation; that is, by a dynamic interplay of enduring, sustained (block-related) brain activation across fronto-striatal networks, and brief, transient (trial-related) brain activation across fronto-parietal networks. Older adults show large disturbances in this dynamic functional recruitment of brain activation. A few functional magnetic resonance imaging (fMRI) studies provided the first evidence that older adults can change the spatial distribution of brain activation across cortical and subcortical networks as a response to cognitive training. However, these studies failed to investigate such spatial changes depending on the timescale of brain signals. Therefore, we specifically analyzed the spatio-temporal dynamics underlying training-related functional plasticity of task activation in old age. *Paper IV* elucidates these mechanisms within the task-switching paradigm based on a mixed block-/ event-related fMRI design that helps to directly separate the changes on sustained and on transient brain activation within the same analysis. In this study, we were also interested in whether training would promote a more similar or dissimilar neural processing pattern during task switching compared to younger adults.

The results of *Paper IV* indeed revealed spatio-temporal interactions underlying neural plasticity after task-switching training in old age: that is, task-switching training promoted (1) a reduction of overall sustained responses in fronto-striatal circuits, perhaps to set resources free for precise transient modulations; (2) a fine-tuning of transient responses in fronto-parietal circuits, which was associated with larger performance improvements in global and local task-switching processes (i.e., with a larger reduction of behavioral mixing and switching costs); and (3) a dissimilar neural pattern to younger adults, which clearly pointed to a training-induced boost of neural compensation.

Hence, regarding the use of cognitive interventions in old age, the present thesis provides important new insights into the neural mechanisms underlying training-induced behavioral improvement in executive-control functioning. To uncover the latent potentials of the aging brain, one needs to consider interactions between spatial and temporal dynamics of brain activation. Another noteworthy finding is that training in older adults may not simply restore the neural processing pattern of younger adults. In contrast, training may help older adults establish an alternative, compensatory processing pattern that enables people to deal with executive-control demands even at an advanced age. Hence, our findings imply that training late in the lifespan should aim at the fine-tuning and boosting of still preserved mechanisms.

Altogether, the present thesis contributes to a more comprehensive understanding of the complex mechanisms underlying and modulating training-induced plasticity in executive control across the lifespan.

Zusammenfassung in deutscher Sprache

Im Fokus der vorliegenden Arbeit stand die Erfassung kognitiver, motivationaler und neuronaler Mechanismen trainingsinduzierter Plastizität nach einem exekutiven Kontrolltraining in unterschiedlichen Altersbereichen, hier speziell in den Endabschnitten der Lebenspanne (d. h. in der Kindheit und im höheren Erwachsenenalter). Das Vermögen zur Ausübung exekutiver Kontrolle ist eine der fundamentalen menschlichen Fähigkeiten zur Steuerung zielorientierten Verhaltens. Exekutive Kontrolle unterteilt man hierarchisch in globale und lokale Prozesse, die im sogenannten Aufgabenwechselparadigma dissoziiert werden können. *Globale Wechselkosten* werden als Differenz von Einzelaufgaben- und Wechselaufgabenblöcken berechnet und reflektieren den Aufwand für die Aufrechterhaltung und Selektion von Aufgabensets. *Lokale Wechselkosten* hingegen werden als Differenz von Wechsel- und Nicht-Wechsel-Durchgängen innerhalb von Wechselaufgabenblöcken berechnet und spiegeln den Aufwand für das flexible Alternieren zwischen Aufgabensets wider. Ein koordiniertes Zusammenspiel dieser globalen und lokalen Fähigkeiten zum Aufgabenwechsel ermöglicht eine präzise Implementierung von kontrolliertem Verhalten. Von besonderer Bedeutung sind die unterschiedlichen *Entwicklungstrajektorien* globaler und lokaler Fähigkeiten über die Lebensspanne. Diese bedingen eine unterschiedliche Anfälligkeit für relative Unreife in der Kindheit – besonders im Falle vorliegender Entwicklungsstörungen, wie dem Aufmerksamkeitsdefizit-/ Hyperaktivitäts-Syndrom (ADHS) – oder für Seneszenz im hohen Lebensalter. Im Speziellen konnte gezeigt werden, dass globale Funktionen in der Kindheit später ausreifen als lokale Funktionen, zugleich aber auch einem früheren, altersbedingten Abbau im hohen Lebensalter unterliegen. Demgegenüber hat sich gezeigt, dass bestehende Einschränkungen bei exekutiven Funktionen im frühen und späten Lebensalter durch gezieltes, wiederholtes Training im Aufgabenwechselparadigma eingedämmt werden können und somit ein entsprechendes Training kompensatorischen Nutzen bringen kann. Aus diesem Grund wurden im vorliegenden Dissertationsprojekt spezifische, altersangemessene Varianten von

Aufgabenwechsel-Trainings bei Kindern und älteren Erwachsenen eingesetzt, um die Reichweite der Lebensspannenplastizität in lokalen versus globalen Aspekten exekutiver Kontrolle zu erproben.

Die vorliegende Dissertation umfasst vier Artikel, in denen theoretische und empirische Evidenz für die Effektivität des Aufgabenwechseltrainings über die Lebensspanne berichtet wird. Bei der ersten Publikation (*Artikel I*) handelt es sich um ein Überblickskapitel, in dem gegenwärtige Literatur zum Aufgabenwechseltraining zunächst allgemein im Kontext eines theoretischen Rahmenmodells zur kognitiven Plastizität beleuchtet wird. Hiernach werden potenziell modulierende Einflussfaktoren auf die Effektivität dieser Trainingsform in unterschiedlichen Altersgruppen diskutiert. Ausgehend von den Empfehlungen dieses Überblicksartikels wurden spezifische Variationen von Trainingsinterventionen für Kinder und ältere Erwachsene entwickelt, die in den nachfolgenden Artikeln genauer dargestellt werden (*Artikel II – IV*).

Die *Artikel II* und *III* fokussieren auf die Plastizität von Aufgabenwechselfähigkeiten im Kindesalter. Kinder ziehen oftmals nicht den vollen Nutzen aus einem kognitiven Training, was auf eine mangelnde Trainingsmotivation bei fehlendem Belohnungskontext zurückzuführen ist. Diese reduzierte Trainingsbereitschaft hängt mitunter mit der früheren Ausreifung des belohnungssensitiven sozio-emotionalen Systems im Vergleich zur späteren Ausreifung des rationalen kognitiven Systems im Kindesalter zusammen. Dem resultierenden erhöhten Bedarf nach Belohnung wird in Standardsettings kognitiver Trainings im Kindesalter nicht adäquat Rechnung getragen. Bei Kindern, die unter Entwicklungsstörungen wie ADHS leiden, scheint das Ungleichgewicht aus motivationalen und kognitiven Faktoren besonders ausgeprägt zu sein. Folglich zeigen Kinder mit ADHS nicht nur eine mangelnde Trainingsbereitschaft, sondern auch ein fundamental verändertes Antwortverhalten, wie z. B. einen impulsiven Antwortstil (d. h. schnelles Antworten auf Kosten der Genauigkeit) oder eine generelle Zunahme der

Verhaltensvariabilität während der Bearbeitung weniger attraktiver kognitiver Aufgaben. Eine motivational angereicherte Trainingsumgebung, wie beispielsweise durch das Einführen von Videospielelementen, mag bei Kindern – insbesondere mit ADHS– Diagnose – eine nützliche Steuerungsmöglichkeit darstellen, um das Engagement zu steigern. Dieses kann dann in die Anforderungen kognitiver Trainings sowie in die Verhaltensregulierung bei der Aufgabenbearbeitung investiert werden. Daher wurde im vorliegenden Dissertationsprojekt im Zuge zweier Interventionsstudien die Interaktion zwischen kognitiven und motivationalen Mechanismen trainingsinduzierter Plastizität bei verhaltensgesunden Kindern (*Artikel II*) und solchen mit ADHS-Diagnose (*Artikel III*) empirisch untersucht.

Die Ergebnisse von *Artikel II* zeigen, dass *bei regulär entwickelten Kindern* die Anreicherung des Settings eines Aufgabenwechseltrainings mit Videospiel-Elementen bedeutsam die Trainingsbereitschaft sowie lokale Aufgabenwechselfähigkeiten fördern konnte. Letzteres wurde ersichtlich durch eine stärkere Reduktion der lokalen Wechselkosten in der Trainingsaufgabe und in einer ungeübten Aufgabenwechselsituation. Dieser kognitive Mehrwert eines spielerisch angereicherten Trainingssettings generalisierte jedoch nicht auf globale Aufgabenwechselfähigkeiten (d. h. auf die Ebene globaler Wechselkosten) oder auf andere Aufgabendomänen exekutiver Kontrolle (d. h. auf strukturell unähnliche Inhibitions- und Arbeitsgedächtnisaufgaben).

Die Ergebnisse von *Artikel III* zeigen, dass auch *bei ADHS-Kindern* die Anreicherung des Trainingssettings durch Videospiel-Elemente entscheidend die Trainingsbereitschaft (d. h. die willentliche motivationale Kontrolle) erhöhen konnte. Dieser Effekt war sogar zeitstabiler als bei regulär entwickelten Kindern, was auf einen motivationalen Kompensationseffekt hindeutet. Zugleich induzierte die Videospiel-Umgebung allerdings bei Kindern mit ADHS auch ein verstärktes Problemverhalten, regte nämlich außerdem unwillentliche motivationale Triebkräfte an. In der Folge führte das hoch-motivationale Trainingssetting auf kognitiver Ebene bei ADHS-Kindern nicht zu den erwarteten stärkeren

Leistungsverbesserungen als ein Standard-Aufgabensetting. Dieses Ergebnis bezog sich sowohl auf lokale als auch globale Aufgabenwechselprozesse, sowohl auf Ebene des mittleren Leistungsniveaus als auch auf Ebene der Leistungsvariabilität.

Schlussfolgernd wird für den Einsatz kognitiver Interventionen bei regulär entwickelten Kindern eine Empfehlung für eine motivationale Anreicherung kognitiver Interventionen ausgesprochen. Durch die Implementierung von Videospielsettings können sowohl Trainingsbereitschaft als auch kognitive Entwicklungsprozesse (zumindest trainingsspezifische, lokale Prozesse) angeregt werden. Demgegenüber sollten bei subklinischen Stichproben, wie bei Kindern mit ADHS, nur vorsichtige Manipulationen des Trainingssettings vorgenommen werden, um ein „Überhitzen“ oder eine zusätzliche Ablenkung durch das Aufgabenlayout zu vermeiden. Somit scheinen motivational-kognitive Interaktionen im Kindesalter einer umgekehrt U-förmigen Dosis-Wirkungs-Beziehung zu genügen – eine Einsicht, die bei der Konzeptionierung adäquater Trainingsinterventionen für Kinder Berücksichtigung finden sollte.

Während bei Kindern ein Mangel an Motivation meist zur Folge hat, dass diese nicht ihr volles Leistungspotenzial ausschöpfen, sind für Leistungsdefizite bei älteren Menschen oftmals andere Faktoren verantwortlich. Hier scheinen seneszente Veränderungen des Gehirns eine der Hauptursachen darzustellen. Daher fokussiert *Artikel IV* auf eine empirische Untersuchung der neuronalen Korrelate trainingsinduzierter Plastizität bei älteren Menschen auf Basis einer ähnlichen Aufgabenwechsel-Trainingsprozedur.
Die Aufgabenwechselfähigkeit wird neuronal durch Interaktionen zwischen dem *räumlichen* Verteilungsmuster und der *zeitlichen* Qualität von Gehirnaktivität getragen. Im Speziellen geht man von einem dynamischen Wechselspiel zwischen einer länger andauernden (d. h. zeitlich auf einen gesamten Aufgabenblock bezogenen) Gehirnaktivität in fronto-striatalen Netzwerken und einer kurzlebigen, transienten (d. h. zeitlich auf ein

einzelnes Ereignis bezogenen) Gehirnaktivität in fronto-parietalen Netzwerken aus. Ältere Erwachsene zeigen grundsätzliche Einschränkungen in der dynamischen funktionellen Rekrutierung von Gehirnaktivität. Einige Studien liefern jedoch unter Nutzung bildgebender Verfahren, wie der funktionellen Magnetresonanztomografie (fMRT), erste Evidenz dafür, dass ältere Erwachsene noch in der Lage sind, als Reaktion auf ein Training ihre Gehirnaktivität in kortikalen und subkortikalen Netzwerken räumlich umzuverteilen. Besagte Studien untersuchten dabei allerdings nicht die Abhängigkeit solcher räumlichen Veränderungen von der zeitlichen Qualität der Gehirnaktivität. Daher war es Ziel des vorliegenden Dissertationsprojekts, mögliche zugrundeliegende räumlich-zeitliche Interaktionen funktioneller Plastizität im höheren Lebensalter herauszustellen. In *Artikel IV* werden diese Mechanismen speziell innerhalb des Aufgabenwechselparadigmas untersucht und zwar mit Hilfe eines gemischten block-/ ereigniskorrelierten fMRT-Designs, welches ermöglicht, die andauernde von der transienten Gehirnaktivität innerhalb derselben Analyse zu entkoppeln. Außerdem wurde untersucht, ob solche trainingsinduzierten neuronalen Veränderungen ein eher ähnliches oder unähnliches Muster im Vergleich zu jüngeren Erwachsenen hervorrufen, wobei Letzteres auf ein Muster neuronaler Kompensation hindeutet.

Die Ergebnisse von *Artikel IV* lieferten empirische Evidenz dafür, dass funktionelle Plastizität nach einem Aufgabenwechseltraining im höheren Lebensalter in der Tat durch räumlich-zeitliche Interaktionen gekennzeichnet ist. Im Speziellen führte das Aufgabenwechseltraining nämlich (1) zu einer Reduktion des gesamten Niveaus der andauernden Gehirnaktivität in fronto-striatalen Schaltkreisen, möglicherweise, um mehr Ressourcen für eine präzisere Modulation transienter Gehirnaktivität freizusetzen; (2) zu einem Fein-Tuning der transienten Gehirnaktivität in fronto-parietalen Schaltkreisen, welches mit breiteren Leistungs-verbesserungen in globalen und lokalen Aufgabenwechselprozessen (d. h. mit einer breiteren Reduktion behavioraler globaler und lokaler Wechselkosten) assoziiert war; und (3) zu einem im Vergleich zu jüngeren Erwachsenen unähnlicheren neuronalen Verarbeitungsmuster, was auf einen trainingsinduzierten Boost auf neuronale Kompensationsmechanismen hindeutete.

Hinsichtlich des Einsatzes kognitiver Interventionen im höheren Lebensalter gewährt die vorliegende Dissertation somit neue Einsichten in die neuronalen Mechanismen, die trainingsinduzierten Verhaltensverbesserungen in exekutiven Kontrollfunktionen zugrunde liegen. Um die latenten Potenziale des alternden Gehirns zu erkennen, bedarf es der Betrachtung der Interaktionen zwischen räumlichen und zeitlichen Dynamiken von Gehirnaktivität. Zudem ergab sich der Befund, dass Training bei älteren Menschen nicht einfach das neuronale Verarbeitungsmuster von Jüngeren wiederherstellt, sondern eher dazu verhilft, ein alternatives, kompensatorisches Verarbeitungsmuster zu etablieren, welches auch im höheren Lebensalter zu einer erfolgreichen Bewältigung exekutiver Kontrollanforderungen befähigen kann. Somit implizieren die Ergebnisse, dass ein Training in späten Phasen der Lebensspanne darauf abzielen sollte, die noch erhaltenen Mechanismen zu fördern und feinzujustieren.

Zusammenfassend liefert die vorliegende Thesis somit einen entscheidenden Beitrag zu einem besseren Verständnis der komplexen Mechanismen, die trainingsinduzierte Plastizität in exekutiver Kontrolle über die Lebensspanne bedingen und modulieren.

Introduction

‘There can (…) be no doubt that changed conditions induce an almost indefinite amount of fluctuating variability, by which the whole [human] organization is rendered in some degree plastic’ (Darwin, 1882, p. 30). As already recognized by Charles Darwin in his ‘The Descent of Man’ in 1882, one of the most remarkable properties of human nature is the ability to adapt to the continuously evolving and rapidly changing conditions of the environment. This innate human feature is defined as *plasticity*, representing ‘evolution’s intention to enable the nervous system to escape the restrictions of its own genome’ (Pascual-Leone, Amedi, Fregni, & Merabet, 2005, p. 377) in order to become customized in distinct environmental settings (Denes, 2015). Therefore, behavior is not simply inscribed in genetic code, but can be modulated or – as derived from the Greek word Πλαστός (plastos) – ‘molded’ by physiological changes, experiences, learning, or practice. Importantly, the scope and constraints of plasticity vary by the period of development across the lifespan (Denes, 2015; Lindenberger & von Oertzen, 2006).

The childhood phase is assumed to be the most ‘sensitive’ period for learning and adaptation. However, due to the diversity and the varying pace of maturational processes during childhood, there is still an imbalance between cognitive and energetic (motivational) systems that may temporarily hinder adaptive responding.

The phase of advanced chronological age seems even dominated by such maladaptive instead of adaptive reactions, mainly due to a broad physiological decline throughout the brain that induces losses across a wide range of sensory and cognitive functions (for a recent review, see Verhaeghen, 2014). Even worse, traditional theories on human ontogeny assume these age-related declines to be irreversible and to affect cognitive functioning in a universal fashion. In contrast, modern lifespan theory (Baltes, Staudinger, & Lindenberger, 1999) articulates the concept of brain development as an ongoing dynamic of both constraints and gains throughout all age stages, pointing to indeed smaller but still retained opportunities in the brain’s senescent state and to different trajectories for different neurocognitive functions.

Either way, both the early and late lifespan periods are at risk of suboptimal cognitive functioning, whether due to immaturity or due to senescence. Hence, it is imperative to identify and, especially, to promote the (emerging or remaining) mechanisms of *adaptive plasticity*[1] in these age ranges.

To address this issue, one important tool is cognitive training[2] that allows us to determine the possible range of plastic changes in cognitive processing across various age groups (Heckhausen & Singer, 2001; Shing, Brehmer, & Li, 2008; Singer & Lindenberger, 2000). Therefore, the present thesis aimed to gauge plasticity in response to an executive-control[3] training in children and older adults. Why executive control? The ability to exert executive control is one of the most fundamental human capacities for the guidance of goal-directed behavior. It allows us to integrate internally-set, overarching goals with information from a current task context to select the most appropriate action from an almost infinite menu of behavioral possibilities (Miller & Cohen, 2001). In this vein, a variety of encompassed functions (e.g., the preparation of upcoming tasks, the maintenance and updating of task-relevant information, the flexible transition between different tasks, or the resistance to interfering information) enable us to master currently relevant task demands (Miyake & Friedman, 2012; Miyake et al., 2000). Importantly, executive control, or at least some of its core functions, seems intimately linked to general fluid intelligence (Duncan, Burgess, & Emslie, 1995; Duncan, Emslie, Williams, Johnson, & Freer, 1996; Friedman et al., 2006), both in children (e.g., Arffa, 2007) and in older adults (e.g., Kray & Lindenberger, 2007). Hence, executive-control training may tap into broad cognitive mechanisms, and in turn, serve as a useful intervention to boost the general intellectual

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[1] The term ‘plasticity’ will from here on be used interchangeably with ‘adaptive plasticity’, leaving aside its maladaptive subtype.

[2] The terms ‘practice’ and ‘training’ have different connotations in the literature: while practice refers to performing a routine in a process-based manner or doing an exercise repeatedly, training refers to making use of an administered strategy that shows explicit ways to do things, such as in mnemonic instruction training (e.g., Derwinger, Neely, Persson, Hill, & Bäckman, 2003). In the present thesis, both terms will be used interchangeably, but see also chapter 1.1.6.

[3] It should be noted that there is no agreement on whether goal-directed, controlled behavior is better described in terms of ‘cognitive‘ or ‘executive control‘. Although some researchers (e.g., Hillman, Buck, Themanson, Pontifex, & Castelli, 2009) propose a distinction between more basic ‘cognitive-control‘ operations (i.e., inhibition, working memory, switching, cf. Miyake et al., 2000) as a subset of more complex ‘executive‘ functions (e.g., planning, problem solving), mostly, the terms are used interchangeably in the current literature (e.g., Miller & Wallis, 2009), and therefore we use them similarly in the present thesis.

development in childhood, while slowing down the pace of cross-domain cognitive decline in older adults. From an applied perspective, such interventions may also promote an increasingly autonomous and self-governed living in early stages of the lifespan, while prolonging independent living and delaying social dependence in late stages of the lifespan.

Outline of the present thesis

In the first chapter of this thesis (based on *Paper I*), we review current views on plasticity in executive control across the lifespan. We highlight the huge potential of task switching for age-appropriate training of executive-control functions.

In the second chapter, we present the empirical studies of this dissertation. First, we introduce our research agenda on the investigation of training-induced plasticity in task switching in children and older adults and present the main research goals of the present dissertation project. Then, we provide closer details for each age group in separate parts.

In the first empirical part (based on *Paper II* and *Paper III*), we tackle the specific training needs and potential of *children*. Hence, this chapter focuses on topics, such as motivation effects on learning and manipulations of the training setting as an important motivational enhancer in task-switching training. In particular, we also investigate subclinical populations, namely children suffering from ADHD, because the manifestation of such a developmental disorder may interact unexpectedly with motivational manipulations of cognitive training. Important theoretical and methodological considerations for the investigation of training-induced cognitive changes in child age groups are summarized. We then provide an overview of the research aims and of the results obtained in two empirical training studies that are discussed in the light of potential for plasticity in childhood.

In the second empirical part (based on *Paper IV*), we focus on the specific training needs and potential of *older adults*. We discuss a highly studied but still controversial topic, which is age-related neural compensation. In this realm, we examine the neural correlates of cognitive training that may support age-related compensation. We provide new insights into theoretical and methodological considerations when investigating training-induced neurocognitive changes in older adults. This is followed by a summary of the research aims and results obtained in an empirical training study that are discussed in the light of potential for plasticity in old adulthood.

In the third chapter of this dissertation, we close with an extensive discussion of the main current findings, bringing together the different empirical studies. Each study is presented in detail as original article.

1 General propositions on plasticity in executive control over the lifespan

The first publication of this thesis (Paper I) is a review chapter about the effectiveness of training in task switching from a lifespan view. In this chapter, we introduce a framework, which emphasizes the distinction between flexible and plastic changes by training. We apply this framework to the task-switching paradigm, which seems particularly suitable for age-appropriate training of executive control. We also depict lifespan changes in prefrontal lobe functioning, which is considered the main neural substrate of task switching. We review age differences in the effectiveness of task-switching training interventions regarding training, transfer, and long-term maintenance effects. Importantly, we describe findings on the training effectiveness at different lifespan stages as a function of different manipulations. The main themes of content of this chapter and its implications for the present thesis are summarized and extended in the following dissertation parts.

This chapter is based on Paper I:

Kray, J. & Dörrenbächer, S. (in press). The effectiveness of training in task switching: new insights and open issues from a lifespan view. In M. Bunting & J. Novick (Eds.), *Cognitive Training*. Oxford: Oxford University Press.

Cognitive plasticity as an attempt to adapt to environmental changes, such as in the course of cognitive training, ultimately implies alterations in the brain's chemistry and morphometry (Kühn & Lindenberger, 2016). As one can easily imagine, the instantiation of such profound changes is quite effortful and metabollically costly (Kuzawa et al., 2014). Thus, mechanisms of plasticity need to be held in check by mechanisms ensuring stability, such as the reliance on once learned functions. As put in a nutshell by Wenger (2014), the brain should at best be 'solid and reliable where it can be, and capable of adaptation where it has to be' (Wenger, 2014, p. 13). This stability-plasticity trade-off varies across the lifespan and can be biased by cognitive training.

1.1 A theoretical framework on cognitive plasticity

In a recent theoretical framework, Lövdén, Bäckman, Lindenberger, Schaefer, and Schmiedek (2010) propose the economic metaphor of balancing (cognitive and neural) supplies and (experiential) demands to describe the stability-plasticity relationship (see Figure 1).

Figure 1[4]. Schematic model of the mismatch between functional supply and training demands underlying training-induced cognitive and neural plasticity (adapted from Lindenberger, 2014). Copyright © by American Association for the Advancement of Science (AAAS).

The current supply of the brain is stretched along its momentary functional and structural constraints that determine the range of cognitive and

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[4] For licencing reasons, the original figure will not be provided here.

neural functions usable at a given time (integral of the area below the grey maximum function in Figure 1). Within this current supply, brain functioning is optimized over some unknown period towards a default level (blue default-level curve in Figure 1) that represents the actual compromise between stability and adaptivity. This equilibrium is far from being immutable but is dynamic, meaning that the default level is continuously calibrated to even further changes of environmental demands (i.e., red demand curve in Figure 1). Environmental demands, such as placed by cognitive training, could in theory directly match the default supply level, whereupon the brain would stay completely solid. However, more likely, they create a mismatch, even if only to a slight extent, whereupon the brain needs to react, either with slight, *flexible* deviations from the stable set point or with profound *plastic* changes. Hence, *flexibility* refers to temporary, small adaptations within the current range of the brain's supply, including an optimization of performance by the recruitment of given cognitive functions or brain states (e.g., the fine-tuning of a once learned skill). These flexible changes point to fluctuations of cognitive performance across different environmental conditions, such as across varying levels of difficulty in an experimental context. Changes based on flexibility, however, will not change the maximum of the current supply. In contrast, plasticity means overcoming the dynamic status quo of the current supply by expanding the outer limits of the preexisting repertoire of behavioral functions (e.g., the acquisition of a new skill). Hence, plastic changes point to a further range of performance improvement after extended periods of development or practice, such as succeeding in new, challenging tasks in an intervention context. Such plastic adaptation will greatly restructure the brain's functioning and will shift the entire equilibrium up to a higher level. Whether cognitive training will induce only flexible but also profound plastic changes is determined by polarity, intensity, and duration of the created mismatch.

1) *Mismatch polarity* refers to whether a mismatch is positive, in the case where the default supply exceeds the environmental demands (red area under the demand curve in Figure 1); or negative, in the case where the environmental demands exceed the default supply (orange area under the demand curve in Figure 1).

2) *Mismatch intensity* refers to whether a mismatch puts low demands (small amplitude of the demand curve in Figure 1) or high demands on the default supply (large amplitude of the demand curve in Figure 1).
3) *Mismatch duration* refers to whether a mismatch will last only a short time (short distance between starting and ending point of the demand curve in Figure 1) or will be prolonged over an extended time period (long distance between starting and end point of the demand curve in Figure 1).

Lövdén et al. (2010) suggest that, to induce profound plastic changes, a cognitive training intervention needs to produce a *negative supply-demand mismatch of a high but manageable intensity and duration*, pointing to a bell-shaped plasticity-mismatch function. Low-intense, short-lasting or overwhelmingly high-intense and unnecessary long training demands will trigger only flexible reactions. In contrast, sufficiently intense and prolonged negative mismatches are powerful to trigger even plastic reactions. However, plastic reactions are induced only sluggishly and often follow as a secondary reaction to primary flexible changes depending on the longevity of the mismatch. Due to their metabolic costs, plasticity is also only possible up to a certain degree that is defined by an intrinsic or latent potential. This latent potential is shaped throughout the lifespan by individual genetics and the personal learning history, and variations therein may account for age differences and individual differences in the scope and nature of plasticity.

Taken together, cognitive and brain functioning are considered to be malleable by cognitive training, first in a flexible, and second in a plastic manner. The nature of training-induced changes depends on polarity, intensity, and duration of the created supply-demand mismatch and the possible scope of plastic changes is determined by the individual latent potential that varies over the lifespan.

1.1.1 Lifespan changes in training-induced flexibility and plasticity

Regarding lifespan changes in flexibility and plasticity, Kühn and Lindenberger (2016) put forth a set of propositions: As can be seen from Figure 2, they propose that flexibility shows an inverted U-shaped trajectory over the lifespan, with a sharp increase from childhood to middle adulthood, but an accelerated decline thereafter. In contrast, overall plasticity, on average, may decrease from childhood to old age in a linear fashion. The latter trajectory can indeed be explained by the higher metabolic costs of plasticity in damaged biological systems, such as in the age-affected brain. However, another reason might be that compared to children, younger and older adults have accumulated a 'rich model of the world', which allows for a more flexible deployment of already existing repertoires (Kühn & Lindenberger, 2016, p. 107; Lindenberger, 2014). Hence, 'older adults are (…) less able (…) [but, similarly to younger adults,] less in need of reaction to a supply-demand mismatch with a plastic response, relative to the brains of normally developing children' (Kühn & Lindenberger, 2016, p. 107).

Figure 2[5]. **Putative trajectories of flexibility and plasticity over the lifespan** (adapted by Kühn & Lindenberger, 2016). Copyright © by Elsevier Inc.

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[5] For licencing reasons, the original figure will not be provided here.

These proposed lifespan trajectories for flexibility and plasticity allow the following three conclusions:

1) Children need to rely primarily on profound, albeit less efficient, plastic changes, because they have still narrow and immature flexibility ranges.
2) In contrast, younger adults firstly rely on flexible changes: Although they still have the potential for plasticity, they engage plastic changes in a more efficient manner, that is, only as a secondary reaction in case where such profound changes are really needed.
3) Older adults also heavily rely on flexible changes firstly. However, compared to younger adults, they are less able to engage plastic changes as a secondary reaction. In turn, their secondary reaction is often flexible as well, but in a compensatory manner. More specifically, older adults try to compensate for their reduced potential for plasticity with an *increased and more fine-grained* investment of flexibility. Hence, unlike in younger adults, in older adults, the 'secondary' reaction is associated with an *alternative, flexible utilization of preserved capacities* for compensation purposes (Kühn & Lindenberger, 2016).

1.1.2 The executive-control 'supply'

As already outlined in the introduction section, one of the most fundamental functions of our brain is the ability to exert executive control. Executive control is a generic term that refers to multiple general-purpose mechanisms that interact to enable individuals to guide their thoughts and actions in accordance with internal and external goals, tasks, and intentions (Miller & Cohen, 2001). Such control processes aid the orchestration of basal sensory, motor, emotional, and cognitive processes in support of producing intelligent behavior in novel and difficult situations or contexts (Kray & Schneider, 2012). Importantly, in the proposed framework by Lövdén et al. (2010), executive-control functions play a direct role for the modulation of flexible and plastic changes: while the brain's functional supply is assumed to be the sheer size of the behavioral repertoire at a given time point, executive-control functions are assumed to be the *basic mechanisms that implement the flexible use* of this repertoire (see also Kühn & Lindenberger, 2016). Hence, given that executive-control functions seem to mediate flexibility, and that flexibility may precede secondary plastic changes, executive control may, in turn, also indirectly enable plasticity. This drives us to explore these functions in the present thesis.

Regarding the structure of executive control, earlier models from a working memory (WM)[6] research tradition proposed a unitary or central authority system responsible for guiding the information stream across working memory, whether as a 'central executive' (Baddeley & Hitch, 1974) that coordinates the information exchange between different modality-specific subsystems and an amodal buffer, or as a 'supervisory attentional system' (Norman & Shallice, 1986) that biases automatic action tendencies in a contention-scheduling system towards a controlled processing mode.

In contrast, more recent approaches emphasize the modular nature of executive control. Relying on structural equation modeling, Miyake et al. (2000) were among the first to provide empirical evidence for three core components, namely the updating of task information within WM, the flexible shifting between multiple task requirements, and the inhibition of automatic response tendencies. Indeed, the robust unique variance portions of the extracted components spoke in favor of a modular view on executive control. However, all three functions still showed moderate interrelations, suggesting that they not only measured separable facets but also a common processing resource as claimed by traditional unitary views. Therefore, the Miyake approach seemed to reconcile controversial notions about the structure of executive control, by stressing both 'the unity and diversity' of executive functions (Miyake et al., 2000, p. 49). In their revised model (Friedman & Miyake, 2017, p. 49; Miyake & Friedman, 2012), the inhibition factor turned out to be isomorphic with the common resource, leaving

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[6] Working memory is defined as a capacity-limited cognitive function that allows us to keep a set of goal-relevant mental representations temporarily in an accessible state (i.e., 'online') for further processing and manipulation (e.g., Baddeley, 2012; Cowan, 1999; Oberauer, 2009; Zimmer, 2008). Importantly, the 'declarative' or memory part of WM is responsible for the short-term storage and exchange of representations, while the 'procedural' or working part of WM is responsible for doing the manipulation or processing (Oberauer, 2009).

no incremental variance after accounting for the fundamental variance portion common to all executive-control tasks. This merged ‘common executive functioning factor (common EF)’ was referred to as the ability to maintain or establish goal information in WM while protecting it from interfering information. The common EF factor is complemented by a *specific updating* function (i.e., replacing old by new representations in *declarative* WM)[7] and/or a *specific switching* function (i.e., disengaging from a previous task in order to flexibly change to another task in *procedural* WM) depending on current task requirements (Friedman & Miyake, 2017).

Importantly, this unity-diversity distinction has been also confirmed by neuroimaging findings. For example, a recent meta-analysis (Niendam et al., 2012) revealed an overlapping engagement of a ‘superordinate’ fronto-cingulo-parietal network, including dorsolateral prefrontal, anterior cingulate, and parietal networks, that were activated *across* different executive task domains (i.e., unity), while a process-specific engagement of distinct anterior prefrontal, anterior and midcingulate cortical as well as subcortical striatal and cerebellar regions depending on the specific task domain (i.e., diversity).

The unity-diversity distinction also resembles accounts that propose a hierarchical organization of executive control along gradients of abstraction. However, there have still been no agreements on what exactly is abstracted (Badre, 2008; Badre & D'Esposito, 2007; Badre & D’Esposito, 2009; Badre, Hoffman, Cooney, & D'Esposito, 2009; Botvinick, 2008; Christoff & Gabrieli, 2000; Koechlin & Jubault, 2006; Koechlin, Ody, & Kouneiher, 2003; Kouneiher, Charron, & Koechlin, 2009; O’Reilly, 2010).

Some researchers define more abstract information in terms of broader *semantic categories* (e.g., ‘fruits’) as compared to more specific categories (e.g., ‘apple’ or even ‘red apple’; Badre & D'Esposito, 2007).

Others define it in terms of higher *rule complexity*, referring to the number of different elements that need to be integrated to generate task-appropriate

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[7] It should be noted that the term ‘updating’ has been used with different connotations in the current literature. Updating as more general concept refers to the maintenance and refreshing of information in both declarative and procedural WM. However, updating in its narrow sense, such as the updating factor in Miyake et al. (2000), only refers to the refreshment of content of declarative WM.

responses (O'Reilly, 2010): that is, a higher-order set of multiple task rules (e.g., '*if food task and fruit picture, then left button press; if food task and vegetable picture, then right button press; if size task and large picture, then left button press; if size task and small picture, then right button press*') as compared to single stimulus-response (S-R) rules (e.g., *'if fruit picture, then left button press'*).

A direct hierarchical interpretation of the *unity-diversity* perspective on executive control takes a *process-oriented* view: that is, bottom-up domain-specific processes, such as switching or updating, are considered to be biased top-down by the domain-general common executive-functioning factor (e.g., Courtney, Roth, & Sala, 2007; Petrides, 2005; Sakai & Passingham, 2006).

Still others define abstraction *temporally* (Aben, Verguts, & van den Bussche, 2017; Koechlin et al., 2003), either in terms of a *sequential processing cascade*, assuming first a task-selection stage and second a response-selection stage (e.g., Banich, 2009; Koechlin & Summerfield, 2007; Sakai & Passingham, 2003, 2006), or in terms of the *temporal duration* of control signals (e.g., Braver, Reynolds, & Donaldson, 2003), distinguishing between 'sustained' (i.e., temporally extended processes, enduring over a longer time interval, such as a task block) and 'transient' processes (i.e., processes that span a short-lasting temporal episode, such as a task trial).

Taken together, hierarchical accounts on executive control vary widely in terms of whether representations ('WHAT?'), operations ('HOW?'), or temporal features ('WHEN' or 'HOW LONG?') are abstracted. Interestingly, these different hierarchical definitions are reflected by distinct neural signatures; that is, *spatially*, by separate sub-regions within the prefrontal lobe along a rostro-caudal axis subserving the processing of different levels of rule complexity (for a review, see Badre, 2008); or *temporally*, by sustained versus transient brain activation (e.g., Braver et al., 2003).

Either way, such hierarchical distinctions may help to separate executive control at a more *global* demand level and executive control at a more *local* demand level across various life stages.

1.1.3 Flexible adaptation to global and local executive-control demands in an experimental context: the task-switching paradigm

Lifespan researchers have mainly applied variants of the task-switching paradigm[8] to measure developmental changes of flexible executive control at global and local levels (for recent reviews on childhood development, see Kray & Ferdinand, 2013; and on adult development, see Kray & Ferdinand, 2014). The advantage of the task-switching paradigm is that it allows researchers to measure separately different executive-control processes, such as task maintenance, inhibition, and switching processes within the same experimental paradigm (for a review, see Kiesel et al., 2010). Although quite a number of different variants of the task-switching paradigm now exist, a majority of studies apply an experimental design in which participants have to perform only one of two tasks in isolation (i.e., single blocks) or to switch between the two tasks within the same block of trials (i.e., mixed blocks). For example, in an often applied task variant (Karbach & Kray, 2009; Kray, Karbach, Haenig, & Freitag, 2012b; Pereg, Shahar, & Meiran, 2013, see Figure 3), the first task is the 'food task', where participants have to decide whether a presented picture shows a fruit or a vegetable. The second task is the 'size task', where participants are required to decide whether the picture is given in a small or large size. In single blocks, participants have to perform only the food task *or* the size task, while in mixed blocks, they are required to flexibly alternate between the food *and* the size task.

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[8] In early and middle childhood, researchers have often applied a specific non-computerized task switching variant, namely the dimensional change card sort test (DCCS; for a review, see Zelazo, 2006). However, the analysis of this task variant is often restricted to response accuracy. In the present studies, we preferred computerized paradigm versions in all age groups that allow for the extraction of both accuracy and latency measures given that reaction times may capture a huge amount of cognitive variability in children.

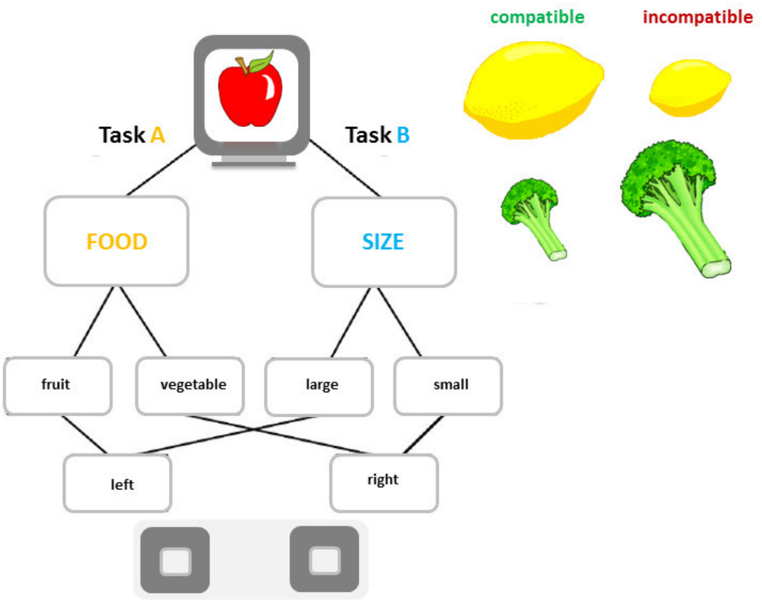

Figure3. Schematic of the task-switching paradigm.

In cued task switching, the indication when to switch from one task set[9] to another task set is given by task reminders (cues) that announce explicitly the upcoming task set from trial to trial, thereby lowering memory requirements. Another variant of the paradigm that puts even higher demands on WM is task switching in alternating runs (AR), where it is required to alternate between tasks on every other trial (for a review, see Cragg & Chevalier, 2012). Importantly, in the AR variant, participants have to internally keep track of the task sequence. Another important feature of the task-switching paradigm is that it contains bivalent stimulus material; that is, overlapping stimulus features for both tasks. Moreover, the responses for both tasks are mapped onto overlapping response keys. Based on such ambiguous response formats, one can separate compatible trials, where responses for both tasks require the same response key (i.e., in the case of a large fruit or a small vegetable, see Figure 3), and incompatible trials, where each task requires a different response key (i.e., in the case of a small fruit or a large vegetable). Such incompatibility at the stimulus-

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[9] A task set can be defined as a ‘set of representations and processes capable of performing a task, including the parameterization of those processes and the identification of their neural substrates’ (Schneider & Logan, 2014; p. 34).

and response level induces a high amount of cross-task competition (for a recent review, see also Gade, Schuch, Druey, & Koch, 2014)

. Extracting different types of costs from this task arrangement allows determining the separate contributions of global and local executive control components to task-switching performance (Cepeda, Kramer, & Gonzalez de Sather, 2001; Kiesel et al., 2010; Kray & Lindenberger, 2000). First, *demands on maintenance* are reflected in the difference in performance between single blocks and mixed blocks. These mixing costs (also termed global or general switch costs; cf. Kray & Lindenberger, 2000; Mayr, 2001)[10] refer to the ability to sustain multiple task set representations and to select between them. In the AR task switching variant, mixing costs also capture the ability to keep track of the alternating sequence (Kray & Lindenberger, 2000). In terms of hierarchical models of executive control, mixing costs may reflect costs of meeting global task demands and have been temporally assigned to sustained, block-related control efforts (Marí-Beffa & Kirkham, 2014). Second, *demands on switching* are reflected in the difference in performance between repeat trials (i.e., a repetition of the same task, such as food task → food task or size task → size task) and switch trials (i.e., a change of tasks, such as food task → size task or size task → food task) within mixed blocks. These switching costs (also termed local or specific switching costs) refer to the ability to flexibly reconfigure the task. In terms of hierarchical models of executive control, specific switching costs may reflect costs of meeting local task demands and have been temporally assigned to short-lived, transient control efforts from trial to trial (Marí-Beffa & Kirkham, 2014).

Global mixing and local switching costs are the most intensively studied performance-cost measures in task-switching research. A third measure, however, are incompatibility costs, that reflect the difference between performance on compatible and incompatible trials (for a review, see Gade et al., 2014). This cost measure captures *demands on inhibition* (in terms of Miyake's

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[10] It should be noted that there are different definitions of mixing costs (Cragg & Chevalier, 2012; Marí-Beffa & Kirkham, 2014): mixing costs referred to as 'general' or 'global' are measured as the difference in performance on single-block trials and mixed-block trials (i.e., the latter encompassing both switch as well as repeat trials); mixing costs referred to as 'repeat-specific', however, are measured as the difference between single-block trials and only repeat trials from mixed blocks. In the present dissertation, we refer to 'global mixing costs'.

original three-factor solution, see section 2.2), that is, the different needs for resolving interference[11] between overlapping rule-set representations.

Important for the present dissertation project is that global and local components of task switching show different trajectories over the lifespan and, hence, are differentially prone to plastic change.

1.1.4 Lifespan changes in global and local task-switching functions

Regarding lifespan changes in task switching, it is now well documented that global mixing costs show a clear U-shaped development across the lifespan that is less pronounced for local switching costs.

Comparing younger and older children, nearly all studies find larger age-related changes in mixing costs than in switching costs, suggesting that the ability to switch between task rules develops earlier than the ability to maintain and select task sets (e.g., Cepeda et al., 2001; Crone, Ridderinkhof, Worm, Somsen, & van Der Molen, 2004; Dibbets & Jolles, 2006; Huizinga & van der Molen, 2007; Karbach & Kray, 2007; Kray, Eber, & Karbach, 2008; Kray, Eber, & Lindenberger, 2004; Kray, Karbach, & Blaye, 2012a; Manzi, Nessler, Czernochowski, & Friedman, 2011; Reimers & Maylor, 2005). More specifically, the maturational trajectories peak in 11 years old children for set-switching abilities, and in 15 years old children for set-maintenance abilities (Huizinga & van der Molen, 2007). However, compared to typically developed children, children who suffer from developmental disorder, such as ADHD, show still in preadolescent age ranges increased local task-switching costs (Cepeda, Cepeda, & Kramer, 2000), especially in situations when there is a high concurrent need to resolve task-set interference, such as in incompatible task-switching trials (Cepeda et al., 2000).

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[11] It should be noted that the terms ‘inhibition’ and ‘interference’ have different connotations in the literature. While interference refers to the source of disturbances, inhibition denotes the *active* process to resist or control these disturbances. More specifically, such ‘interference control’ (Nigg, 2000) reflects only one subcomponent of inhibition, namely the ‘resistance to distractor interference’ (Friedman & Miyake, 2004) at the ‘access’ stage (Hasher, Lustig, & Zacks, 2007). Inhibition may also include ‘cognitive inhibition’ (Nigg, 2000), referring to the ‘resistance to proactive interference’ (Friedman & Miyake, 2004) or the ‘deletion’ (Hasher et al., 2007) of information at the processing stage; and ‘behavioral inhibition’ (Nigg, 2000), referring to the ‘inhibition of prepotent responses’ (Friedman & Miyake, 2004) or ‘restraint’ at the response stage (Hasher et al., 2007).

Comparing younger and older adults, the majority of task-switching studies report substantial age differences in mixing costs, suggesting age-related impairments in maintaining and selecting between task sets (Buchler, Hoyer, & Cerella, 2008; Cepeda et al., 2001; Kray, 2006; Kray et al., 2008; Kray et al., 2004; Kray & Lindenberger, 2000; Lawo, Philipp, Schuch, & Koch, 2012; Lien, Ruthruff, & Kuhns, 2008; Mayr, 2001; Meiran, Gotler, & Perlman, 2001; Reimers & Maylor, 2005; van Asselen & Ridderinkhof, 2000). Importantly, such age differences in global mixing costs in adult age ranges cannot be simply explained by age-related differences in general slowing, as they are still reliable after controlling for speed of processing (e.g., Kramer & Kray, 2006; Verhaeghen & Cerella, 2002). Although some studies also found age differences at the local level, that is, in switching costs (e.g., Meiran et al., 2001), most of these studies revealed smaller age differences in switching than in mixing costs (e.g., Karayanidis, Jamadar, & Sanday, 2013; Karayanidis, Whitson, Heathcote, & Michie, 2011; Kray et al., 2008; Kray et al., 2004; Kray, Eppinger, & Mecklinger, 2005; Kray & Lindenberger, 2000; Lien et al., 2008; Mayr, 2001; Mayr & Liebscher, 2001; Reimers & Maylor, 2005; Whitson et al., 2013; Whitson, Karayanidis, & Michie, 2012), that often disappear after controlling for age differences in general slowing (for a review, see Kray & Ferdinand, 2014). This may indicate that older adults show fewer process-specific limitations in executing a task switch per se, but show concerns when they are in a task switching situation requiring the maintenance and selection between tasks (for a meta-analysis, see Wasylyshyn, Verhaeghen, & Sliwinski, 2011).

This pattern of finding (i.e., large global mixing costs, while small local switching costs) has also been interpreted in terms of a tendency in older adults to update the task set on every trial, even when it is not required; that is, for example, even on repeat trials within mixed blocks (see Mayr, 2001), thus reducing the difference between repeat and switch trials (i.e., switching costs) by increasing the difference between single and mixed trials (i.e., mixing costs; see also Kray & Ferdinand, 2014). Importantly, this tendency may provide an example for the *flexible over-recruitment* of still preserved local control processes to compensate for declines in global processes in older adults as described in chapter 1.1.1.

Age-related changes in hierarchical executive control as measured by task-switching performance have been mainly attributed to the maturation of the prefrontal lobe and associated (sub-)cortical structures in the striatum (Anderson & Spencer-Smith, 2013; Bunge & Wright, 2007; Bunge & Zelazo, 2006; Cabeza & Dennis, 2012; Casey, Tottenham, Liston, & Durston, 2005; Enriquez-Geppert, Huster, & Herrmann, 2013; Giedd, Raznahan, & Lenroot, 2013; Karbach & Unger, 2014; Luna, Padmanabhan, & O'Hearn, 2010; Luna et al., 2001). The volume and structural integrity of the prefrontal cortex (PFC) show an inverted U-shaped trajectory over the lifespan, with a steep structural growth in childhood, a maturational peak in young adulthood, and a steady decline in older age (e.g., Blakemore, Burnett, & Dahl, 2010; Hedden & Gabrieli, 2004).

More importantly, the hierarchical organization of executive control is reflected in the staggered development of different parts of the prefrontal lobe. For example, Bunge and Zelazo (2006) proposed a brain-based framework to account for the functional development of rule processing depending on the maturation of different PFC regions. They suggest that successive changes on rule use in childhood (from using a single rule to switching between compatible rules to switching between incompatible rules) emerge from an age-related progress in the ability to represent increasingly complex rule hierarchies that are neurally supported by distinct parts of the prefrontal cortex. Specifically, orbitofrontal parts develop in early infancy and support only simple stimulus-reward contingencies. Lateral parts of the PFC continue to develop into late adolescence and specialize in representing rules of increasingly higher complexity levels (e.g., ventrolateral and dorsolateral parts represent rules of medium complexity, while rostrolateral parts, that show the most protracted maturation, represent rules of highest complexity). Hence, the hierarchical rule system that may enable the coordination of local versus global task rules, such as in a task-switching situation, evolves along the (structural and functional) maturation of distinct networks of the forebrain in childhood (Bunge & Zelazo, 2006).

In childhood, the subcortical networks supporting the socio-emotional system may also play a prominent role. This system is portrayed as being sensitive to reward and appetitive goals, thus amplifying the general arousability (e.g., Luciana & Collins, 2012). As proposed by dual-systems theories (e.g., Casey, Jones, & Hare, 2008; Steinberg, 2008), until mid-adolescence, the striatum shows a disproportionately steeper and faster maturational trajectory compared to cortical networks in the prefrontal lobe, suggesting that motivational and emotional dynamics may outweigh controlled behavior in middle to late childhood. In children diagnosed with ADHD, alterations along cortico-striatal loops (for a review, see Cubillo, Halari, Smith, Taylor, & Rubia, 2012) cause even more dramatic shifts in the ratio of motivational and cognitive control. Hence, such an increased responsiveness to rewards in children, especially when they suffer from ADHD, can interact unexpectedly with local or global control processes in early lifespan periods.

In late lifespan periods, it is the prefrontal lobe that is among the first brain regions to show age-related decline (for a recent review, see Cabeza & Dennis, 2012; Moscovitch & Winocur, 1992; West, 1996), a circumstance which has inspired the prominent frontal-lobe hypothesis of cognitive aging (West, 1996). The age-related deterioration in the PFC is expressed in volume shrinkage, reduced integrity of white matter, as well as in a functional de-differentiation across prefrontal sub-regions that become apparent disproportionately larger in dorso-lateral than in orbito-frontal parts (Braver et al., 2001; Double et al., 1996; Raz, 2004). In turn, these alterations successively diminish the ability of complex rule switching (as opposed to the ability to process simple stimulus-response rules, which is retained for longer).

At the same time, large age-related alterations have been determined in fronto-striatal neuronal pathways, suggesting impairments in the dopaminergic system, such as decreases in dopamine (DA) concentration, synthesis, receptor density, or transporter availability (for reviews, see Bäckman, Nyberg, Lindenberger, Li, & Farde, 2006; Hedden & Gabrieli, 2004). These declines in DA availability and function across subcortico-cortical loops may, in turn, hamper the balance between robust rule maintenance (subserved by a recurrent activation of the PFC) and local rule gating or updating mechanisms (subserved by a modulating influence of DA projections onto the PFC; Braver & Barch, 2002; Cohen, Braver, & Brown, 2002; McNab & Klingberg, 2008; O'Reilly, 2006).

It is an important link that these quadratic changes of both the ability to adapt to task switching demands and of prefrontal lobe functioning over the lifespan highly resemble the inverted U-shaped lifespan curve for the flexibility construct in Lövdén's framework (Kühn & Lindenberger, 2016; Lövdén et al., 2010; see chapter 1.1.1). According to these lifespan changes, the periods of childhood and old age seem particularly sensitive periods to incoming demands, as the immature or over-mature supply of the frontal lobe may create large mismatches. Interventions aiming at the improvement of prefrontal lobe functions within these developmental trajectories, such as task-switching training, thus might accelerate the maturation in childhood and decelerate the decline in older age (Wass, Porayska-Pomsta, & Johnson, 2011; Watson, Lambert, Miller, & Strayer, 2010). Hence, the identification of effective task-switching training variants for these age ranges is essential to exploit their plastic potential.

1.1.5 Plastic adaptation to global and local executive-control demands in an intervention context: general principles and application to task-switching training

General principles for cognitive interventions. Referring back to the framework of Lövdén et al. (2010), a critical precondition for plasticity is a training-induced mismatch between initial functioning and experienced training demands. Prior to the intervention, there is a dynamic equilibrium between supply and demand, that is, the demand curve employs about equal proportions of positive (current supply > demand) and negative mismatches (demand > current supply). The training intervention ideally produces a strong negative mismatch between the demands of training and the current constraints of the brain supply that is far from the routine demand. With increasing practice (i.e., with a prolonged training duration), the brain adapts to the high task demands by functional and perhaps even structural changes. This is the manifestation of training-induced plasticity, expanding the range for flexible functioning.

However, critical from a lifespan perspective is that the training-related mismatch needs to be induced *relatively* to the respective life period. Considering the constraints of brain functioning in children and elderly people as compared to young adult age, we need a mismatch that is activating and challenging but not overtaxing the age-specific initial supply to achieve an optimal level of requirement. Hence, the training demands must be tailored to the particular needs of the target age group. The scope of a training-induced mismatch depends also critically on the initial supplies of the trainees, which is of concern for different life stages. Regarding such interactions between initial supplies and treatment success (i.e., treatment-aptitude interactions), two likely outcome patterns have been proposed: first, the *magnification account* claims that those individuals, who are already performing well at the beginning, gain the most from an intervention. From a lifespan view, this account would imply that younger adults gain more from training than children and older adults. In contrast, the *compensation account* proposes that a cognitive intervention enhances the abilities of those who are performing worse at the beginning. From a lifespan view, this account would imply that children, especially, when they suffer from developmental disorder, and older adults gain more from training than younger adults. Hence, an adequate mismatch for children, especially when they are diagnosed with ADHD, and older adults may be one that promotes compensation.

Typically, a training intervention aimed to create a supply-demand mismatch is designed as a longitudinal pretest-training-posttest experiment, sometimes complemented by a follow-up session to measure long-term stability of the obtained effects. The intervention should optimally include an active control group who faces a smaller supply-demand mismatch than the critical training group, by receiving low-intense training demands on similar cognitive processes. For example, in the context of task-switching training, researchers have used as an active control group a group that performs exactly the same tasks as the treatment group but practices the tasks in single-task block conditions instead of mixed-block conditions (see Minear & Shah, 2008). Hence, single-task (active control) training and task-switching training differ in terms of intensity of the training-induced mismatch, while less in terms of polarity or duration. Selective improvements in the critical training group compared to such an active control group then speak clearly in favor of the effects being due to the intervention, ruling out general test-retest or task familiarization effects.

The efficiency of the intervention can be measured in terms of the scope of mismatch-induced effects: that is, by direct training benefits (i.e., improvements in task performance during the practice sessions) and by indirect transfer effects. Transfer refers to training-induced gains in similar or different task domains from those performed in the training sessions. Hence, by transfer, we determine whether the training had tapped into generalizable processes. Selective training benefits reflect a better deployment of existing repertoires, hence pointing to changes in cognitive *flexibility*. Selective transfer effects, however, reflect an expansion of the range of existing repertoires, especially if associated with functional or structural brain changes, hence pointing to cognitive *plasticity*. We distinguish between several transfer scopes. *Near transfer* refers to the generalization of training-induced improvements to a new but structurally similar task to the trained one, while *far transfer* refers to a broad generalization of training-induced benefits to dissimilar task domains (cf. Karbach & Kray, 2009). Transfer is assumed to occur in case when training and transfer tasks engage overlapping cognitive and neural resources (Karbach & Kray, 2016).

Application of the framework principles to task-switching interventions. By way of example, taking a lifespan approach, Karbach and Kray (2009) compared benefits of task-switching training (versus single-task active control training) between children (8 – 10 years), younger adults (18 – 26 years), and older adults (62 – 79 years). In all age groups, reductions of task-switching costs in the training task were substantially larger for the task-switching training groups than for the single-task training groups. More importantly, the researchers found larger transfer gains for children and older adults than for younger adults in a task-switching task that was different from the trained ones, indicating a compensation pattern (see also chapter 2.3). Specifically, the reduction of age differences was more pronounced for global mixing costs than for local switching costs.

How do the principles of the Lövdén et al. (2010) framework fit to this pattern of results? The larger reduction of global mixing costs for children and older adults can be explained in terms of a larger induced mismatch between initial supplies and training demands in these age ranges. Given that age differences in task switching are also initially more reliable at the global level than at the local level (see chapter 2.1.4) and given that the prefrontal lobe shows the latest maturation and the earliest decline in specifically those parts that underlie more complex rule switching, the selective improvements on mixing costs in these age groups seem plausible and point to age-related compensation. Given that the improvements had expanded to an untrained task-switching task (i.e., transfer) in children and older adults, this may point to plastic changes as a response to the experienced large supply-demand mismatch.

This is also in accordance with the lifespan trajectories of flexibility and plasticity proposed by Kühn and Lindenberger (2016), at least when comparing children and younger adults: As a reminder, flexibility may reach its peak during young adulthood (for a recent review, see also Buttelmann & Karbach, 2017). Hence, younger adults may work best to deploy already existing repertoires in a flexible manner. In turn, they are less in need for a metabolically costly plastic response to incoming demands, and achieve the same or better performance levels as children merely by flexible investment. In contrast, children have a high need to compensate for their less matured flexibility range by more expensive plastic modifications.

1.1.6 Manipulations of the training mismatch

The effectiveness of training may critically depend on specific manipulations of the nature, sustainment, duration, or interface of the training-induced mismatch at different life stages.

Manipulations of the nature of the training mismatch. A training mismatch can either be evoked by *process-based* training or by *strategy-based* training forms. Process-based training means performing a certain task repeatedly (i.e., ‘practice’ in its narrower sense; e.g., repeated practice on a task-switching task), while strategy training refers to ‘training’ based on the application of an instructed strategy that shows explicit ways to do things (i.e., ‘training’ in its narrower sense; e.g., using a mnemonic strategy). Although strategy-based training may result in higher effect sizes of training benefits than process-based training, it may at the same time only induce lower effect ranges; that is, lower transfer to other executive-control tasks (Karbach & Kray, 2016; Karbach & Verhaeghen, 2014; Rebok, Carlson, & Langbaum, 2007; Verhaeghen, Marcoen, &

Goossens, 1992). Important from the lifespan perspective is that the specific training form may also interact with magnification versus compensation effects: More specifically, magnification effects are primarily obtained in strategy-based training regimes (e.g., Baltes & Kliegl, 1992; Brehmer, Li, Müller, von Oertzen, & Lindenberger, 2007; Rebok et al., 2007; Verhaeghen et al., 1992; Yesavage, Sheikh, Friedman, & Tanke, 1990), while compensation effects are primarily obtained in process-based training regimes (e.g., Cepeda et al., 2001; Karbach & Kray, 2009; Kramer, Hahn, & Gopher, 1999; Kray & Lindenberger, 2000; Minear & Shah, 2008; Zinke et al., 2014).

Within the latter process-based interventions, also including task-switching training, the intensity of the training mismatch may vary with (a) the demand on working-memory abilities (e.g., cued versus un-cued paradigm variants); and (b) the demand on the ability to resolve cross-task competition (e.g., with ambiguous stimulus material, overlapping response formats, or changing task modalities; Anguera et al., 2013; Karbach & Kray, 2009; Karbach & Kray, 2016). In early stages of the lifespan, alternating-runs variants of task switching (i.e., high memory load) with ambiguous stimuli and overlapping responses (i.e., high inhibition load) have been shown to establish a suitable intensity of mismatch to induce transfer, both in typically developed children (Karbach & Kray, 2009) and in children suffering from developmental disorders, such as ADHD (Kray et al., 2012b). In older adults, the challenge on the ability to resolve interference seems even more critical (Anguera et al., 2013; Kray & Fehér, 2017). A recent study of Kray and Fehér (2017) revealed that task-switching training with high inhibition load (i.e., bivalent instead of univalent stimuli) worked best (i.e., largest amount of near transfer) for older adults when it was coupled with low memory load (i.e., cued instead of AR task switching), thus allowing the participants to outsource the demand on keeping track of the task.

Manipulations of the sustainment of the training mismatch. To keep the intensity of a training-induced mismatch challenging throughout the training period, one can apply either *adaptive* or *variable* training forms. Adaptive training means to adjust the task difficulty to individual performance throughout the training until individuals reach an asymptotic performance level. Such adaptive training has proven useful to promote training benefits across different life ranges, but especially in children (Brehmer, Westerberg, & Bäckman, 2012; Dunning, Holmes, & Gathercole, 2013; Holmes, Gathercole, & Dunning, 2009; Klingberg, 2010; Klingberg et al., 2005; Shipstead, Redick, & Engle, 2012). In a meta-analysis on executive-control and WM training in older adults, however, Karbach and Verhaeghen (2014) did not find a clear advantage for adaptive training regimes. An alternative to adaptive training is provided by variable training. During variable training, participants are confronted with a new task situation in each of the training sessions, that is, with new sets of stimuli and tasks (e.g., Karbach & Kray, 2009; Pereg et al., 2013). Most interesting from a lifespan view is that transfer gains to a new switching task were substantially larger for younger and especially for older adults after variable training due to practice in adapting to new sets of stimuli und tasks (Karbach & Kray, 2009). However, for the child age group, the variable training condition seemed to be too demanding as transfer gains here were strongly reduced compared with a training condition in which the same stimuli and tasks were practiced (Karbach & Kray, 2009).

Manipulations of the duration of the training mismatch. In general, short-term interventions dominate the area since they are of high importance from an applied perspective, because they are likely to be more easily implemented in real-life contexts than prolonged interventions (see also Zinke, 2012). Moreover, such a relatively short practice time, between three and four sessions on a weekly basis with an intensity of less than one hour, has been sufficient to induce considerable training and transfer effects both in typically developed children, children with developmental disorders, such as ADHD, and older adults (Karbach & Kray, 2009; Kray et al., 2012b). However, more prolonged practice may be needed in cases when one aims to detect profound changes at the neural level. To this end, for example Klingberg (2010) recommended a minimum amount of eight hours of practice. However, the optimal session length, number, or spacing of cognitive interventions remains a matter of debate.

Manipulations of the interface of the training mismatch. One may also consider motivational modulations of the trainings mismatch. Motivation is closely linked to the concept of executive control (Braver, 2016; Kouneiher et al., 2009; Locke & Braver, 2008, 2010; Pessoa, 2009) and may have a specific impact on the outcomes of respective training, such as task-switching training. One possibility to keep motivation and willingness high during training is to manipulate the interface or setting of training. From a lifespan view, an appealing training setting seems particularly important for children who show an imbalance between the maturation of cognitive and motivational systems (e.g., Casey et al., 2008; Luna & Wright, 2015; for a review, see Shulman et al., 2016; Steinberg, 2008;). There might be an even greater value of appealing settings for subclinical samples, such as children diagnosed with ADHD, who show clinically relevant dysfunctions in both executive and motivational control (e.g., Sonuga-Barke, 2002, 2005). However, the specific influence of a motivational manipulation of the training setting on separate outcomes in motivation and executive control has rarely been investigated in previous research.

1.2 Intermediate summary and implications for the present dissertation

To summarize, the ability of executive control is one of the most fundamental human capacities for enduring adaptive, goal-directed behavior. Executive control is hierarchically organized, covering both global and local functions, whether in terms of representations, processes, or timescales. For example, one important distinction is made temporally between global, sustained (enduring, block-level) and local, transient (brief, trial-level) control that both are required to act together in the task-switching paradigm. In this paradigm, efforts to meet global, sustained executive demands are captured by mixing costs, while efforts to meet local, transient executive demands are captured by switching costs. A coordinated interplay of global and local executive-control functions aids the precise implementation of flexibility (i.e., the optimal deployment of given repertoires) in a task switching situation. Importantly, local and global task-switching abilities show differential trajectories over the lifespan that are paralleled by the maturation of sub-regions of the prefrontal lobe and associated cortical and sub-cortical structures: global functions may mature later in childhood, while showing an earlier decline with advanced age. Taking a compensation view, such reduced task-switching abilities are especially susceptible to learning or training across various age ranges. Specific training may enable plastic changes; that is, an expansion of the outer limits of the cognitive system. Therefore, in the present dissertation project, we applied task-switching training in children and older adults to investigate the scope of lifespan plasticity in local versus global aspects of executive control. To induce an adequate training mismatch for these age ranges, we followed some design considerations that have proven useful in previous research:

(1) *considering the nature of the training mismatch*, we aimed first, to apply process-based training in both children and older adults, which may broaden the scope of plasticity and induce compensation instead of magnification effects; and second, to provide children with ambiguous (high inhibition load) and un-cued (high memory load) task-switching training variants, while providing older adults with ambiguous (high inhibition load) and cued (low memory load) task-switching training variants. These variants have been shown to induce a suitable intensity of mismatch for the respective age groups;

(2) *considering the sustainment of the training mismatch*, we aimed to provide older participants with variable training to keep the mismatch challenging throughout the training period, but to provide child participants with adaptive instead of variable task-switching training to prevent cognitive overload;

(3) *considering the duration of the training mismatch*, we aimed to apply at least four sessions of task-switching training (or eight sessions in the case when examining neural plasticity, such as in older adults, see further below), spaced over several weeks with at least one day in between to prevent massed practice;

(4) *considering the interface of training mismatch*, we aimed to provide child participants with a high-motivational training setting to enhance their treatment compliance.

2 Empirical studies

The subsequent three articles of this thesis (Paper II – Paper IV) report empirical findings from intervention studies in typically developed children, children suffering from ADHD, and older adults. We first provide a general overview of our research agenda and introduce the main research goals of the empirical part of this thesis for both age groups. We then provide closer details on the theoretical rationale and the main findings from the empirical studies for each age group separately.

2.1 Research agenda

2.1.1 Empirical studies in children: motivational influences on cognitive plasticity

The empirical part on training-induced plasticity in childhood (*Paper II and Paper III*) is focused on the modulation of task-switching training by the motivational enrichment of the training setting. Especially in late middle childhood and preadolescence (i. e., between the approximate ages of 8 and 11 years), there seems to be a disproportionate ratio between cognitive and motivational functioning (Eccles, 1999; Mizuno, Tanaka, Fukuda, Imai-Matsumura, & Watanabe, 2011). Unlike the 'cold' executive-functioning system, the 'hot' energetic socio-emotional system is already mature at this stage of development, which makes children relatively more sensitive to reward incentives and appetitive goals (Casey et al., 2008; Luna & Wright, 2015; Shulman et al., 2016; Steinberg, 2008). In turn, in high-demanding cognitive training, children often do not perform to their full capability on the training task due to insufficient reward. A motivationally enriched training context, such as a video-game setting, could therefore be useful for children to enhance their engagement in meeting the demands of task-switching training, and in turn, to compensate for their maturational imbalance between cognitive and energetic systems.

1) *Firstly, the present thesis aimed at investigating the separate effects of game-based task-switching training on training motivation and on training performance in middle childhood.*

The general idea of executive-control interventions is that training will result in transfer to other cognitive tasks that also partly rely on the same control processes (Karbach & Kray, 2016). Thus, transfer refers to indirect training benefits in structurally similar (i.e., near transfer) or dissimilar task domains (i.e., far transfer) to those performed in the practice sessions, determining whether training had succeeded to expand the latent executive control ability or only facilitated task-specific processes. Aside from reliable gains in training and near-transfer tasks, there are rather mixed effect sizes for far transfer from task-switching training, notably in children in the preadolescent age range (Karbach & Kray, 2009; but see Pereg et al., 2013; Zinke, Einert, Pfennig, & Kliegel, 2012).

2) *It was a second aim of the present thesis to investigate whether a motivationally enriched video-game setting would also promote transfer from task-switching training to dissimilar tasks, such as other tasks of inhibition-control or working memory, in middle childhood.*

Importantly, neuropsychological evidence accumulating over the past decades suggests that dysfunctions of both 'cold' cognitive information processes - particularly of inhibition or working memory (WM) in task switching contexts – and 'hot' motivational mechanisms may drive behavioral symptoms in children diagnosed ADHD, which encompass poor regulation of attention, impulsivity, and physical activity (e.g., Sergeant, 2000; Sonuga-Barke, 2002, 2005). The interaction of disturbances along cognitive and energetic pathways in ADHD children may culminate in an increase of response variability during the performance on challenging cognitive tasks, such as task switching (for a meta-analytic review, see Kofler et al., 2013). Such performance fluctuations over time indicate both a lack of consistent task effort as well as lacking attentional and cognitive resources to meet the task demands (i.e., together indicating a suboptimal regulation of the 'task state', see Nigg, 2005; Sergeant, Oosterlaan, & van der Meere, 1999). However, little is known about the interaction of task switching impairments with state-regulation impairments in ADHD compared to typically developed (TD) children.

3) *Following this line, a third aim of the present thesis was to provide new insights into the relative involvement of process-specific limitations in executive functions (i.e., inhibition and WM during task switching) and state regulation in ADHD children as compared to typically developed children by including information on response variability.*

Unlike in typically developed children, in children suffering from ADHD, motivationally enriched task-switching training could perhaps not only help children regulate the developmental balance between cognitive and motivational systems, but overcome clinical alterations along both pathways.

4) *A fourth aim of the present thesis was to investigate whether specific training can promote impaired task-switching processes in ADHD children, especially when it was embedded into a motivationally enriched video-game setting.*

2.1.2 Empirical study in old age: neurocognitive plasticity depending on spatio-temporal brain-activity dynamics

While a lack of willingness often prevents performance to full capability in children, in older adults it is age-related neural alterations that are a major contributing factor to an impairment of cognitive abilities. Hence, the second empirical part of the thesis (*Paper IV*) is focused on the neural correlates of training-induced plasticity in executive control in old age. Executive-control functioning is intimately linked to the functional interplay of the prefrontal cortex (PFC) with posterior-parietal and striatal circuits. This interplay is inasmuch dynamic as the involved neural hubs release activation on different timescales in order to support different cognitive functions: operations tapping into global maintenance demands are subserved by a sustained mode of brain activation (i.e., enduring, block-related, and changing in the minutes range) in fronto-polar and striatal networks, while operations tapping into local switching or updating demands instead require a mode of transient activation (i.e., brief, trial-related, and changing in the seconds range) in more posterior networks (e.g., Braver et al., 2003). The task-switching paradigm allows us to look closely into separate transient and sustained activity. Older adults do not only show general alterations in this dynamic recruitment of brain activation during task switching (Jimura & Braver, 2009), but the involved fronto-parietal and fronto-striatal circuits are vulnerable to early and disproportionate age-related atrophy and altered task-related activations (Hedden & Gabrieli, 2004). Although it has been shown in older adults that executive control can be enhanced by targeted training, little is known so far about the precise nature and scope of the neural mechanisms that drive such practice-induced plasticity. A number of functional brain imaging studies point to training-induced changes on the spatial distribution of brain activation, with activation decreases or increases across fronto-parietal and fronto-striatal networks (e.g., Heinzel et al., 2016). Yet, previous studies failed to investigate spatio-temporal interactions of brain mechanisms.

5) *It was therefore a further aim of this dissertation project to phenotype practice-induced functional plasticity in old age by applying functional magnetic resonance imaging (fMRI) techniques that were sensitive to track both spatial and temporal features of brain activation.*

One possible outcome of training in older adults is a refinement of neural compensation. Neural compensation can be described as alternative neural recruitment in older adults, when primary resources are compromised (Barulli & Stern, 2013), and is reflected in similar behavioral performance but dissimilar neural processing patterns between younger and older adults. A variety of functional mechanisms have been associated with neural compensation of age-related executive-control impairments, such as a posterior-to-anterior shift of brain activation and increased bilateral recruitment of frontal areas only in older adults (Cabeza, 2002; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008). However, such accounts focus again only on changes in the spatial distribution of brain activation underlying compensation in advanced age. There is little research on temporal aspects of age-related compensation.

6) *Therefore, in the present thesis, we aimed to elucidate whether in older adults, training would induce a dissimilar processing pattern to younger adults considering both spatial and temporal dynamics of brain activity.*

2.2 Empirical studies in childhood: motivational influences on cognitive plasticity

This chapter is based on Paper II and Paper III:

Dörrenbächer, S., Müller, P. M., Tröger, J., & Kray, J. (2014). Dissociable effects of game elements on motivation and cognition in a task-switching training in middle childhood. *Frontiers in Psychology, 5*, 1275.

Dörrenbächer, S. & Kray, J. (submitted). The impact of a game-based task-shifting training on motivation and executive control in children with ADHD.

2.2.1 Theoretical and empirical background (childhood)

2.2.1.1 Relevance of task-switching training

Why target specifically the child age range for training of executive control (for reviews, see Buttelmann & Karbach, 2017; Kray & Ferdinand, 2013)? In childhood and preadolescence, the efficiency of executive control is highly important for several reasons: first, executive skills in childhood predict executive abilities in later life, which also implies that early impairments in executive control may amplify poor control in adulthood (see Kray & Ferdinand, 2013). Hence, early interventions tapping into executive-control functioning can be seen a kind of preventive measure. Second, given the high correlations with other fluid intellectual abilities (Brydges, Reid, Fox, & Anderson, 2012), well trained executive-control functions may, in turn, stimulate general cognitive development. Third, in these age ranges, executive control is closely related to core developmental tasks, such as academic activities (for a review, see Titz & Karbach, 2014). For example, executive-control functions have been documented to predict reading and arithmetic skills (Clark, Pritchard, & Woodward, 2010; van der Sluis, de Jong, & van der Leij, 2007), and or even cross-curricular learning skills (Garner, 2009). Executive-control functions also enable good habits and adequate peer behavior by reducing impulsive behavior and allowing 'thinking before acting' (Diamantopoulou, Rydell, Thorell, & Bohlin, 2007). Fourth, childhood is the sensitive phase for the maturation of critical cortical structures that may underlie executive control, such as the prefrontal lobe (see chapter 1.1.4). Hence, the early lifespan period is by nature a highly plastic and changeable phase, making it prone to environmental and learning input, especially in terms of executive-control interventions (see also the recent review of Buttelmann & Karbach, 2017). Fifth, during childhood, the cognitive system is still poorly differentiated (e.g., Brydges, Fox, Reid, & Anderson, 2014; Brydges et al., 2012; Shing, Lindenberger, Diamond, Li, & Davidson, 2010). Hence, the unity in executive component processes may disproportionately outweigh the diversity of functions, which, however, makes it broadly accessible by training. Specifically, such a poorly differentiated executive system may increase the likelihood to obtain broad transfer from training because tapping into one cognitive process may easily spread over to other processes (although it is therefore indeed more difficult to fine-tune *specific* functions in children).

2.2.1.2 The executive-control ‘supply’ and its trainability

As has been already outlined in the first chapter of this thesis, childhood is a highly sensitive phase for the development of core executive-control functions that may last into late adolescence or even adulthood (Buttelmann & Karbach, 2017; Davidson, Amso, Anderson, & Diamond, 2006; Huizinga, Dolan, & van der Molen, 2006). To recapitulate the core assumptions on the immature processes during early stages of the lifespan:

1) Children still have narrow ranges of behavioral repertoires that they can deploy in a flexible manner. In turn, they need to invest a large amount of metabolic resources to expand these repertoires by plastic changes (Kühn & Lindenberger, 2016; Lövdén et al., 2010).
2) Children show a still poorly differentiated structure of executive control (see Karbach & Unger, 2014).
3) Within these narrow and poorly differentiated repertoires, children already show less effective global executive functions (i.e., set-maintenance abilities) than local executive functions (i.e., set-switching abilities) due to the more protracted maturation of global control (Huizinga & van der Molen, 2007).

Importantly, such an immature cognitive system, that has high potential for plasticity, *‘is likely characterized by both increased vulnerability to risk and enhanced opportunities for intervention’* (Wiebe & Karbach, 2017).[12]

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[12] Given that this e-book doesn’t have page numbers, we omit that part of the reference for this citation throughout the thesis.

Cognitive impairments in ADHD. Regarding the *'increased vulnerability to risk'* (Wiebe & Karbach, 2017), children are indeed often at high risk of suffering from developmental disturbances or even disorders associated with executive control. For instance, accumulating evidence has documented that impairments in executive-control processes lie at the core of behavioral symptoms in children diagnosed with attention-deficit/hyperactivity disorder (Crosbie et al., 2013; Kofler, Rapport, Bolden, Sarver, & Raiker, 2010; Martinussen, Hayden, Hogg-Johnson, & Tannock, 2005; Rapport et al., 2009; Tillman, Eninger, Forssman, & Bohlin, 2011; and Willcutt, Doyle, Nigg, Faraone, & Pennington, 2005). ADHD is a heritable neurodevelopmental disorder with reported rates of prevalence varying between 2.2 and 17.8 % worldwide in school-aged children and adolescence (for a review, see Skounti, Philalithis, & Galanakis, 2007) and associated with chronicity over the lifespan if not treated adequately. The core behavioral symptoms in ADHD are characterized by poor regulation of attention, impulsivity, and physical activity.[13] Such impairment of behavior dramatically increases the risk of negative long-term outcomes across various domains, such as addictive or antisocial behavior, academic underachievement, occupational difficulties, or obesity (for a review, see Young, Fitzgerald, & Postma, 2013). The key driving mechanism of executive control impairments underlying ADHD symptoms in childhood is debated to be a major deficit in inhibition (e.g., Barkley, 1997; Quay, 1988) or in working memory (Kofler, Rapport, Bolden, & Altro, 2008; Martinussen et al., 2005; Rapport et al., 2008), that both are exacerbated in task-switching situations (Cepeda et al., 2000). The latter finding has been attributed to specific performance impairments in ADHD children when several executive components are required to act together in an interactive rather than an additive fashion, such as in an un-cued, alternating-runs variant of task switching (i.e., high memory load) coupled with ambiguous stimuli and response formats (i.e., high inhibition load; e.g., Wu, Anderson, & Castiello, 2006).

Training-induced cognitive plasticity. However, considering the *'enhanced opportunities for intervention'* in childhood (Wiebe & Karbach, 2017),

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[13] In the present study, we focus only on the ADHD-combined subtype showing regulation deficits in all three behavioral domains.

such double demands on WM and inhibition during task switching may provoke the optimal intensity of mismatch to induce plastic changes. Following this line, recent cognitive training studies have shown that specific practice in switching between competing tasks in alternating runs can promote executive-control functioning in typically developed children (Karbach & Kray, 2009) and seems especially beneficial for ADHD children who have more room for improvement (Kray et al., 2012b). For example, Kray et al. (2012b) provided a group of ADHD children (8 - 12 years) with training on an AR task switching variant with bivalent stimuli and overlapping response formats, and contrasted their training-induced improvements against those of an active waiting control group that practiced only low-level single-task blocks in the critical period. Relative to this single-task group, the task-switching training group showed larger practice-induced improvements in task-switching performance on a structurally similar but untrained switching task (i.e., near transfer). The task-switching training group also showed larger far transfer to structurally dissimilar tasks, such as the Stroop task, which captures transfer to inhibitory control, or the Digit Sorting task, which captures transfer to verbal WM. However, in this study, task difficulty was kept constant across all training sessions and not adjusted to individual performance. Referring back to the framework principles of Lövdén et al. (2010), it might be, though, important to apply adaptive training in order to keep the training challenging. Hence, only adaptive training may provide the optimal sustainment of the training-induced mismatch (Holmes et al., 2009). Moreover, training in the study of Kray et al. (2012b) was presented in a low-motivational standard training setting, which might not be the optimal interface for a training mismatch in children (refer to chapter 1.16). Following this line, children, especially when they are diagnosed with ADHD, often do not gain from such lab-based cognitive interventions to their *full* potential due to a lack of willingness (e.g., Luman, Oosterlaan, & Sergeant, 2005). This may be associated with an imbalance between 'cold' cognitive and 'hot' affective-motivational mechanisms in this lifespan period (Zelazo, Li, & Kesek, 2010).

2.2.1.3 Motivational influences on the executive-control ‘supply’ and on its trainability

As has been outlined in the introduction section, from a developmental perspective, the childhood period is characterized by a more progressive development of the subcortically mediated ‘hot’ socio-emotional system compared to the ‘cold’ cognitive system. Dual-system theories (Casey et al., 2008; Luna & Wright, 2015; Shulman et al., 2016; Steinberg, 2008) predict a dominant responsiveness to rewards and motivational, appetitive goals up to adolescence. Hence, increasing the motivational appeal of task-switching training (e.g., by manipulating the interface of training) may be specifically useful in the middle childhood and adolescence age ranges.

Motivational impairments in ADHD. Such an increase in the motivational appeal of training may be particularly important for children diagnosed with ADHD who show clinically relevant anomalies not only in ‘cold’ executive control but also in ‘hot’ energetic mechanisms, as described in dual-pathway etiology models (e.g., Sonuga-Barke, 2002, 2005). Three mechanisms of alterations in the motivational style of ADHD children have been proposed:

First, researchers pointed to a suboptimal arousal level in ADHD children (Leung & Connolly, 1994; Petrescu-Ghenea, Trutesco, Mihailescu, Kobylinska, & Rad, 2013; Sergeant et al., 1999); that is, a lowered or excessive phasic responding to stimulus processing (hypo- or hyper-arousal theory; Pribram & McGuinness, 1975). Arousal, together with behavioral activation (i.e., a tonic readiness for action), may control the allocation of motivational effort that one is willing to invest into cognitive task performance.[14]

A second candidate mechanism is an altered delay of reward gradient in ADHD children (e.g., Sonuga-Barke, 2002), with a preference for small-immediate rewards and a disproportionately high aversion against time-lagged gratification.

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[14] It should be noted that while earlier unidimensional views emphasized one unique arousal reservoir underlying the regulation of the motivational state (Kahneman, 1973), more recent multidimensional accounts speak in favor of several energy supply systems controlling the mental effort invested into a task (Hockey, 1993; Humphreys & Revelle, 1984; Sanders, 1983; Sanders, 1981).

This gradient may bias the attentional focus selectively away from cognitively demanding situations where reward is delayed.

Third, ADHD children may demonstrate a shifted reward threshold, implying that these children need a higher degree of stimulation to obtain motivational levels comparable to typically developed children, especially in the face of high task demands (Haenlein & Caul, 1987).

State-regulation impairments in ADHD. The interaction of disturbances along cognitive and energetic pathways in ADHD children has been shown to induce first, a shift in regulating the speed-accuracy trade-off, with rapid responding relative to the baseline rate but also a higher tolerance to errors (Mulder et al., 2010; Wu et al., 2006). Second and more importantly, this cognitive-motivational double deficit fosters an increase of overall response inconsistency during the performance on challenging cognitive tasks (Epstein et al., 2011; Kofler et al., 2013; Wu et al., 2006). The increased performance variability indicates a lack of consistent task effort as well as an insufficient allocation of general attentional and cognitive resources to meet the task demands. This phenomenon has been referred to as a suboptimal regulation of the 'task state' (e.g., Sergeant et al., 1999; see also Wu et al., 2006). Hence, one behavioral indicator to measure the current task state might be overall performance as expressed in mean performance and especially performance variability (Scheres, Oosterlaan, & Sergeant, 2001; Sergeant, Geurts, Huijbregts, Scheres, & Oosterlaan, 2003; Sergeant et al., 1999; van der Meere & Stemerdink, 1999).[15] Higher mean performance levels may represent higher state regulation, whereby large performance fluctuations over time may indicate lower state regulation.

Stimulation or fine-tuning of training motivation should allow ADHD children to regulate their task state und, in turn, to allocate more motivational effort to show their latent performance potential. Hence, incorporating arousing,

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[15] It should be noted that state regulation has been traditionally investigated in the context of manipulations of the stimulus event rate (Sonuga-Barke, Wiersema, van der Meere, & Roeyers, 2010). In the present dissertation project, we measured state regulation in terms of overall performance in an executive-control task (i.e., independent of the executive demands of different trial conditions), while executive control itself is measured as performance difference between trial conditions of differing executive demands.

immediately rewarding, or highly stimulating motivational features into an executive-control training regime could not only help these children regulate the developmental imbalance between energetic and cognitive factors but to overcome clinical alterations along both pathways (see also Prins, Dovis, Ponsioen, Ten Brink, & van der Oord, 2011).

General motivational influences on executive control. But what are the assumed mechanisms through which a high-motivational state, such as in an enriched task setting, may enhance executive-control performance in experimental or intervention contexts? A high-motivational state may trigger the following effects:

First, a high-motivational state may allow for the alignment of goal-directed behavior as reflected by an increased voluntary allocation of general processing resources or attentional effort that can be invested into higher-order task control (Sarter, Gehring, & Kozak, 2006). Accordingly, a number of event-related brain potential studies have shown that motivationally salient stimuli engage higher cognitive processing resources than neutral stimuli (Bradley, Greenwald, Petry, & Lang, 1992; Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Diedrich, Naumann, Maier, Becker, & Bartussek, 1997; Dolcos & Cabeza, 2002; Naumann, Bartussek, Diedrich, & Laufer, 1992; Schupp et al., 2000; Schupp et al., 2004).

Second, a high-motivational state may take 'a prioritization function in biasing the selection, the activation, and the intensity level of (…) task goals' (Braver, 2016, p. 3). This prioritization function of motivation may be particularly useful in a task-switching context, where there is a constant need for dynamically switching between different task-rule priorities.

Third, a high-motivational state may aid the proactive maintenance of goal-relevant information, thus sharpening WM-related processes. For example, Nieuwenhuis and Monsell (2002) found that adding reward incentives to a task-switching paradigm led to a reduction of task-switching costs by increasing the likelihood to engage in advanced preparation.

Fourth, a high-motivational state may help to control the aversive significance of conflicting information: there is evidence for an aversive quality of conflicting information, such as incompatible trials in a task-switching paradigm with bivalent stimuli (for a review, see Pessoa, 2009). Hence, one may need high inhibition control to resolve trial incompatibility, but at the same time high motivational control to overcome the intrinsic aversiveness of such conflict trials.

Taken together, high motivation seems to complement and support executive functioning at multiple levels, and may especially sharpen WM and inhibition control during task switching in experimental or intervention contexts (Kleinsorge & Rinkenauer, 2012). Hence, a 'hot' training setting should provide additional support for children, and even more so when they are diagnosed with ADHD, to deal with the challenging cognitive demands of task-switching training.

2.2.1.4 The implementation of motivational training settings

An increasing amount of motivational manipulations of cognitive training for children have been proposed in recent years (for recent reviews, see Deveau, Jaeggi, Zordan, Phung, & Seitz, 2015; Farcas & Szamosközi, 2016). These include cover stories, monetary or illustrative incentives and - belonging to the latter class - video-game manipulations to enhance and maintain training motivation throughout the training intervention (e.g., Bioulac et al., 2014; Dovis, van der Oord, Wiers, & Prins, 2012; Goldin et al., 2014; Klingberg et al., 2005; Prins et al., 2011; Prins et al., 2013). By way of example, Prins et al. (2011) investigated the influence of a setting manipulation on training-induced working memory improvements in middle-aged ADHD children (7 – 12 years). In this study, the authors varied between a low-motivational (without video-game setting) and a high-motivational (with video-game setting) variant of WM training. Comparing performance improvements between both training groups revealed that the high-motivational group indeed outperformed the low-motivational group throughout all practice sessions and demonstrated significantly larger near transfer to an untrained working memory situation. It is important to note that Prins et al. (2011) provided their child participants with an adaptive training regime as recommended by Lövdén et al. (2010), by adjusting the trial difficulty to the children's individual performance. However, a severe limitation was that such adaptive training was only presented to the low-motivational group and not to the high-motivational group. The researchers argued that an adaptive trial difficulty may interfere with a high-motivational context by causing larger mood fluctuations. However, the difference in the training procedures may have strongly limited the validity of the setting manipulation.

General design principles. Some further important design principles have often been neglected in previous research on the interaction of motivation and cognition in trainings in childhood:

First, many previous game trainings have designed their game environments somewhat arbitrarily. Yet, it is essential to prevent 'overheating' of the task context (Zelazo et al., 2010), especially when one challenges sensible functions, such as executive-control functions in children (with ADHD). Hence, one requirement for the implementation of a game environment should be its *appropriateness in the light of a sophisticated theoretical rationale*. The well-established self-determination theory (SDT, Ryan, Rigby, & Przybylski, 2006) provides a suitable candidate rationale for designing effective game settings. The SDT has been applied across a number of studies to isolate the fundamental constituents that drive the 'motivational pull' of video-games. Results revealed that enjoyment and future game play were predicted by three basic needs, namely (1) *autonomy*, reflecting the need for free choices, informational feedback, and non-controlling instructions; (2) *relatedness*, reflecting the need for identification with a game's cover story, virtual world, actors and game characters; and (3) *competence*, reflecting the need for upgrading options and gaming success, such as feedback that leads to virtual rewards. Hence, these three basic psychological needs may in sum foster the amount of intrinsic interest in a given 'gamified' task: By systematically manipulating these three subcomponents of intrinsic interest in a training environment, one might adequately stimulate the interaction of 'hot' motivational factors with 'cold' executive-control performance (Sergeant, 2000; Zelazo, 2000).

Second, almost all previous training studies in typically developed or ADHD children have focused on the influence of 'serious game' settings on training of pure working memory (Klingberg et al., 2005; Prins et al., 2011). In contrast, *training that taps into multiple executive processes at once*, such as task-switching training, has not yet been thoroughly tested in a 'gamified' context (but see Dovis, van der Oord, Wiers, & Prins, 2015b).

Third, previous training studies have investigated only performance differences between different motivational settings without having carefully tested for the manipulation success: that is, by first investigating how such motivational manipulations of the setting contribute to gains in training motivation itself before probing incremental performance benefits (e.g., Egeland, Aarlien, & Saunes, 2013; but see Prins et al., 2011).

2.2.1.5 The measurement of the effects of a motivational setting on outcome motivation and performance

Independent measurement of motivation and performance. One of the first studies that did systematically investigated the separate effects on motivational and cognitive benefits from a low- versus high-motivational variant of executive-control training (albeit still in a pure WM training regime) was again the study of Prins et al. (2011). In their schedule, at a certain point during the training session, the researchers offered children the possibility to train in more task sequences before they left the observation room. Willingness was measured as the number of additionally chosen sequences during the experimenter's absence time. Motivational results of this study suggested that the high-motivational training group performed significantly more voluntary training sequences, hence demonstrating higher willingness. However, in this study, the measurement of training willingness might have been a confounder of training experience, because choosing additional sequences had automatically increased the amount of training. This potential confound was controlled for statistically in post-hoc analyses but might have still limited the experimental validity of the training variation.

Multifaceted measurement of training motivation in ADHD. Unlike typically developed children, children suffering from ADHD show specific impairments across different facets of motivation (see chapter 2.2.1.3), and in turn, may also require a multifaceted measurement of the motivational training results. An important distinction, especially in an intervention context, is made between voluntary mechanisms of motivational control, such as effort allocation, willingness, or treatment compliance, and involuntary driving mechanisms, such as arousal, motor activation, or behavioral inappropriateness (for a review, see Audiffren, 2009). Voluntary motivational mechanisms support controlled behavior, while involuntary energy sources may in part hinder adaptive responding and instead induce behavioral inappropriateness. A variety of indices of overt behavior (e.g., voluntary: reported feelings of enjoyment; amount of voluntary training; involuntary: symptom ratings of inappropriate behaviors, response impulsivity) have been proposed to measure the various energetic pools in ADHD children (Audiffren, 2009). The product of both voluntary and involuntary motivational mechanisms may determine the 'task state' in a given cognitive situation as expressed in the overall mode of responding (including overall mean performance and especially performance variability).

2.2.2 Intermediate summary and implications for the present studies in childhood

To summarize, childhood is a sensitive phase for the development and training of executive control. Yet, given the immature status of cognitive development, children are at high risk for the manifestation of developmental disorders such as ADHD. ADHD impairments center on working memory and inhibition-control functions and are pronounced in task contexts, where different executive components are required to act together (e.g., un-cued AR task switching between competing task sets). However, most of the recent training studies in children have focused only on working memory, while task-switching training, that taps into several executive-control processes at once, has been administered less frequently.

Children have a still poorly differentiated cognitive system, which may, however, increase the likelihood for broad transfer gains from training. Yet, far-transfer effects after cognitive training have been seldom investigated in children and have produced rather mixed results. One possible moderator of the training success might be the training willingness. Children, especially when they suffer from ADHD, show a reduced training motivation during repetitive practice on a challenging cognitive task, and in turn, often do not deploy their full potential for training-induced plasticity. At the same time, children are highly susceptible to rewarding stimulation, such as by game elements. Hence, such game elements can be harnessed as an advantage for the enrichment of training settings in order to enhance children's training willingness.

When following this line and creating a 'serious game' environment for cognitive training, it is imperative, first, to rely on a sophisticated rationale to limit arbitrariness in the variation of facets; and second, to measure the separate effects of this setting manipulation on motivation and performance benefits independently. Both concerns have been neglected in previous research. One previous study did systematically dissociate between outcome motivation and performance, but their motivation indicator confounded the amount of training.

In the specific case of ADHD children, it seems mandatory to measure training motivation at multiple levels given that these children not only show reduced motivational control, such as willingness, but also altered involuntary motivational impulses, such as shifted arousal levels and behavioral inappropriateness. The impairments along voluntary and involuntary motivational energies may together induce a sub-optimal regulation of the 'task state' (i.e., large performance variability) in ADHD children, which, in turn, hinders adequate executive-control performance.

Hence, in the first two studies of the present dissertation project, we aimed to evaluate the impact of game-based task-switching training in typically developed and ADHD children with slightly different research foci. Yet, two superordinate goals of these studies were first, to create a game setting according to the suggestions of a theoretical rationale, such as the self-determination theory; and second, to avoid the confound of the training experience when measuring the separate effects on training motivation.

2.2.3 Summary of studies

In two empirical training studies, we investigated the interaction of cognitive and motivational mechanisms underlying training-induced plasticity in healthy (*Paper II*) and attention-deficit/ hyperactivity (ADHD)-diagnosed children (*Paper III*) in middle childhood.

Paper II

Dörrenbächer, S., Müller, P. M., Tröger, J., & Kray, J. (2014). Dissociable effects of game elements on motivation and cognition in a task-switching training in middle childhood. *Frontiers in Psychology, 5*, 1275.

Theoretical background and design. Although reinforcing settings, such as with added video-game elements, have been often used to enhance the attractiveness of cognitive interventions in children, little is known about how such manipulations of the setting contribute to separate gains in motivation (as a manipulation check) and cognitive performance. While previous research has mainly focused on 'gamified' versions of pure WM training (e.g., Egeland et al., 2013; Klingberg et al., 2005; Prins et al., 2011), we were interested in the incremental impact of a motivational setting in a task-switching regime. Therefore, an empirically testable framework was developed for investigating the separate impact of a motivational video-game setting on training willingness, task performance, and transfer success in a task-switching training regime in 54 children between the ages of 8 and 11 years. Children were assigned to one of four training conditions that all underwent a pretest-training-posttest regime, including four training sessions of different practice: two conditions received low-demanding single-task training (active control), while two conditions received high-demanding task-switching training (un-cued, alternating-runs task switching between competing task sets). Within each training type, training was either embedded into a low-motivational setting variant without video-game elements or a high-motivational setting variant with video-game elements. Regarding the motivational setting manipulation, we varied cover story, layout, type of feedback presentation, and upgrade options to nurture the three theorized basic needs of self determination that may together induce the 'motivational pull of video games' (i.e., autonomy, presence, competence; Ryan et al., 2006, p. 344; for details on the manipulation, refer to Paper III, Table 1).

Unlike in Kray et al. (2012b); Prins et al. (2011), all groups were provided with adaptive feedback to keep the task challenging throughout the training regime (Holmes et al., 2009; Lövdén et al., 2010). Importantly, we wanted to avoid the case that children who would demonstrate more willingness by choosing more optional training blocks would subsequently receive more task-switching training overall (Prins et al., 2011). Therefore, we incorporated a novel willingness indicator: this indicator counted the number of training blocks that participants were willing to perform in addition, while in fact kept the overall amount of presented training blocks constant. To make sure that children would not become aware that they did not actually perform any blocks in addition, we presented the willingness question at random positions (after each 4+- 1 block) during each training session based on a jitter algorithm (see Figure 4).

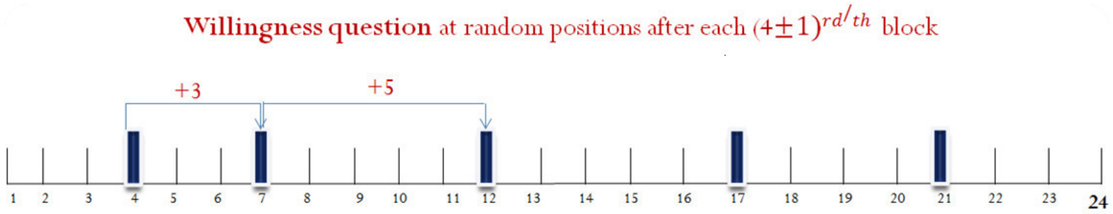

Figure 4. **Visualization of the jittering algorithm.**

To summarize our realized design principles in respect of the overarching framework of this thesis (Lövdén et al., 2010): First, regarding the *nature of the training mismatch*, we applied process-based training because it may enhance the likelihood for broad transfer. Second, we provoked a larger *mismatch intensity* in the task-switching training groups (i.e., switching in alternating runs) than in the single-task training groups (i.e., performing on single blocks). Third, regarding the *sustainment of the training mismatch*, we applied adaptive training in all groups to keep the training challenging throughout the intervention phase; fourth, regarding the *duration of the training mismatch*, we applied a short-term intervention (i.e., 4 sessions) that may balance the trade-off between training economy and power. And fifth and most importantly for the purpose of the present study, regarding the *interface of the training mismatch*, we manipulated the motivational enrichment of the training setting between groups by video-game elements.

Research predictions. We predicted that adding game elements to task-switching training would have an incremental impact on (1) the willingness to train (motivational manipulation check); (2) training performance (i.e., lower local switching costs in the training task); (3) near transfer (i.e., lower local switching and global mixing costs in an untrained switching task); as well as (4) far transfer to other executive task domains, namely to working memory (i.e., larger span sizes in prototypical memory span tasks) or inhibition (i.e., i.e., smaller incompatibility costs in a Stroop and a continuous-performance task).

Main results and conclusion. Results suggested on the level of motivation, that the addition of game elements to the training setting indeed enhanced training motivation independently of the training type as measured based on our willingness indicator. However, with increasing practice, the willingness declined in all setting groups.

On the level of cognitive performance, within the two task-switching training groups, the high-motivational training setting enabled an incremental benefit on local task-switching performance (i.e., a larger reduction of switching costs) in both the training task and in an untrained task switching paradigm. This incremental benefit of the high-motivational training setting on near transfer was only found for response latencies, while not for response accuracy, and the effects were confined to local executive control (i.e., no larger reduction of mixing costs). In contrast to our assumptions, we found no incremental benefit of our high-motivational setting on transfer to other measures of executive control. Hence, the motivational setting clearly had a positive impact on training willingness (at least in early learning stages) and on the specifically trained local executive-control abilities, but did not generalize to broad cognitive functioning.

It seems plausible that our motivational setting had boosted specifically response latencies given that motivation is, by definition, an energizing force that may preferentially drive response dynamics and speed of processing (Sergeant, 2000). A reason why we found the motivational benefits on near transfer to be confined to local task-switching abilities might be that local executive processes (i.e., set-switching abilities) mature critically in the investigated age range (i.e., between 8 - 11 years of age), while global process development (i.e., set-maintenance abilities) is somewhat delayed in adolescence (up to 15 years of age; see Huizinga & van der Molen, 2007). Hence, in childhood, the motivational setting may have stimulated mutual synergies with current developmental changes in local processes.

Paper III

Dörrenbächer, S. & Kray, J. (submitted). The impact of a game-based task-shifting training on motivation and executive control in children with ADHD.

Theoretical background and design. In a second step, we were interested in how this game setting, empirically tested in typically developed children, would benefit task-switching training in children suffering from ADHD. Importantly, recent cognitive training studies, including *Paper II* of the present dissertation, have suggested that practice in switching between competing tasks (i.e., high inhibition load) in alternating runs (i.e., high memory load) can promote executive control in TD children (Karbach & Kray, 2009). Such training may be especially beneficial for ADHD children (Kray et al., 2012b) who have more room for improvement due to their clinical impairment in working memory, inhibition, and switching functions. In addition, ADHD children show a number of motivational deficits that may, in turn, induce a highly impulsive and variable mode of responding during cognitive tasks (Haenlein & Caul, 1987; Sergeant, 2000; Sonuga-Barke, 2002). The nature of such 'state-regulation' impairments has rarely been investigated in the context of task switching. Hence, a first goal of this study was to provide new insights into the baseline interaction of state-regulation and task-switching deficits in ADHD children compared to typically developed (TD) children. To that end, we aimed to include not only information of mean performance, but also of performance variability in our analyses (Epstein et al., 2011). Baseline performance (including performance variability) as well as training-induced changes of 26 children diagnosed with combined-type ADHD between the ages of 8 and 13 years were compared against the performance of 26 age- and IQ-matched, untrained TD children.[16]

State-regulation impairments in ADHD children may worsen with repetitive training on a challenging cognitive task in a low-motivational training setting. By a high-motivational game training setting, ADHD children should be enabled to align their task state, and in turn, to achieve greater practice-induced

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[16] As a reference group of TD children, we included a subsample from the previous study that was presented in *Paper I*. Because this group was not a priori matched to the ADHD group of the current study, they were matched post hoc based on the propensity score matching method of (Austin, 2011).

changes on task-switching performance. One important antecedent for a regulated task state is the alignment of voluntary (i.e., training willingness) and involuntary motivational energies (i.e., behavioral inappropriateness; see also Audiffren, 2009). Therefore, training motivation should be measured at multiple levels in ADHD children. Hence, the second goal of this study was to examine the benefits of task-switching training on motivation and executive-control performance in children with ADHD, where a multifaceted measurement of motivation was provided, including the measurement of: (1) training willingness based on our novel willingness indicator (see *Paper II*; see Figure 5, first row, left upper panel); (2) interest in the training task based on a self-report measure (see Figure 5, first row, left lower panel); (3) behavioral inappropriateness during training (i.e., higher inattention, impulsivity, hyperactivity) based on a behavioral log (see Figure 5, first row, right panel). On the level of performance, we measured (1) regulation of the task state based on overall performance (especially performance variability, see Figure 5, second row); and (2) proper task-switching performance. To answer the second research goal, we trained only ADHD children in a task-switching training regime and applied the same setting manipulation as in *Paper II*. Hence, we varied between task-switching training that was embedded into a low-motivational setting without video-game elements or a high-motivational setting with video-game elements.[17]

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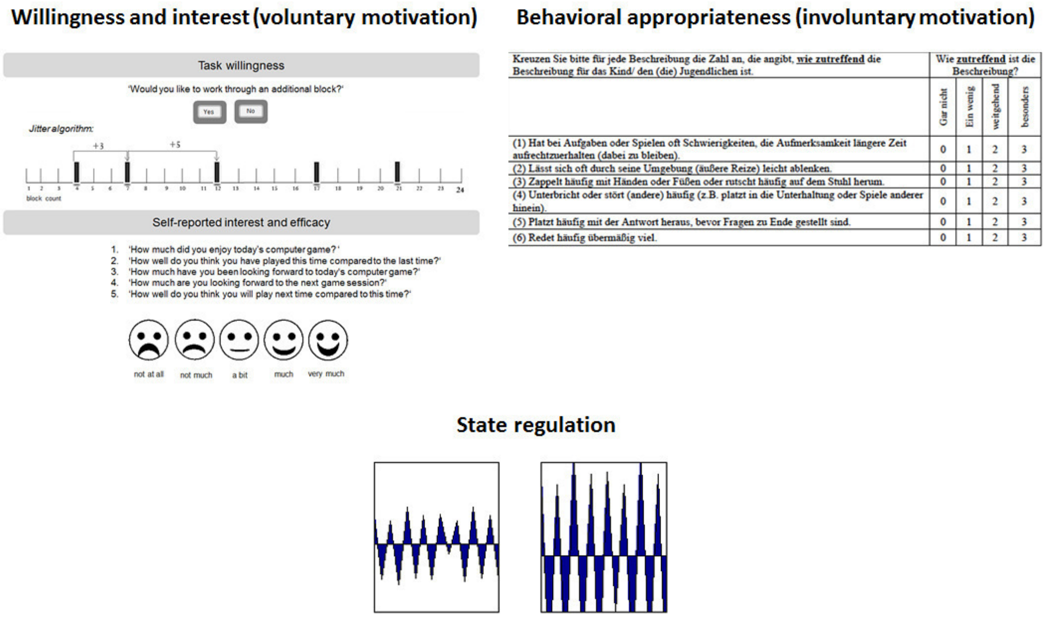
[17] It should be noted that we did not manipulate the training type (i.e., task switching vs single task training) in this study.



'Would you like to work through an additional block?'

1. 'How much did you enjoy today's computer game?'
2. 'How well do you think you have played this time compared to the last time?'
3. 'How much have you been looking forward to today's computer game?'
4. 'How much are you looking forward to the next game session?'
5. 'How well do you think you will play next time compared to this time?'

Kreuzen Sie bitte für jede Beschreibung die Zahl an, die angibt, **wie zutreffend** die Beschreibung für das Kind/ den (die) Jugendlichen ist.	Wie **zutreffend** ist die Beschreibung?			
	Gar nicht	Ein wenig	weitgehend	besonders
(1) Hat bei Aufgaben oder Spielen oft Schwierigkeiten, die Aufmerksamkeit längere Zeit aufrechtzuerhalten (dabei zu bleiben).	0	1	2	3
(2) Lässt sich oft durch seine Umgebung (äußere Reize) leicht ablenken.	0	1	2	3
(3) Zappelt häufig mit Händen oder Füßen oder rutscht häufig auf dem Stuhl herum.	0	1	2	3
(4) Unterbricht oder stört (andere) häufig (z.B. platzt in die Unterhaltung oder Spiele anderer hinein).	0	1	2	3
(5) Platzt häufig mit der Antwort heraus, bevor Fragen zu Ende gestellt sind.	0	1	2	3
(6) Redet häufig übermäßig viel.	0	1	2	3

Figure 5. Multifaceted measurement of training motivation in children with ADHD. First row: left, upper panel: task-willingness indicator with jittering algorithm (see also Figure 4); left, lower panel: 5-item self-report questionnaire; right panel: 6-item behavioral log (German rating version); second row: visualization of performance variability, left panel: low variability, right panel: high variability

In respect of the Lövdén et al. (2010) framework, in this study, we took heed of the same design principles as in the previous study (*Paper II*), except that we did not directly vary the *intensity of the training mismatch* by the training type (see footnote 14) but only the *interface of the training mismatch* to investigate the *incremental* value of a motivational setting.

Research predictions. Regarding the first part on baseline impairments in ADHD children compared to TD children, we predicted (1) in the case of a major state-regulation impairment: worse overall mean performance and larger overall performance variability in ADHD children than in TD children (i.e., independent of the executive demands); and (2) in the case of a major executive impairment: larger mixing costs, indicating WM impairment, and/ or larger inhibition costs, indicating impairments in inhibition control in ADHD children than in TD children (either on the level of mean-performance or on the level of performance variability).

Regarding the second part on training plasticity in ADHD children, we predicted that adding game elements to task-switching training would have an incremental impact on (1) the willingness to train (motivational manipulation check); (2) self-reported interest in the training; (3) the alignment of involuntary motivational tendencies, such as inappropriate behavior; (4) training performance (i.e., lower local switching costs in the training task); and (5) near transfer to an untrained task-switching situation (i.e., lower global mixing costs and/ or lower inhibition costs).

Specific analysis considerations in ADHD children..

1. *Accounting for speed-accuracy bias (i.e., impulsive behavior).* Unlike raw latencies and error rates, our task-switching analyses were based on rates of correct responses per second as described in Hughes, Linck, Bowles, Koeth, and Bunting (2014), which incorporate both error and reaction time data into one single score. Such composite scores have the advantage that they directly take potential trade-offs between speed and accuracy into account (see Kofler et al., 2013).
2. *Accounting for performance variability (i.e., inconsistent behavior)*. For each participant, we additionally calculated an intra-individual response variability index; that is, the relative standard deviation of correct-response rates (Bellgrove, Hawi, Kirley, Gill, & Robertson, 2005; but see also Kofler et al., 2013, for a debate on other metrics).
3. *Accounting for small sample bias in sub-clinical samples.* In the presence of small sample sizes, as quite often is the case in (sub-)clinical samples, p-values may vary widely, which has been also called the ‘dance of the p-value’ (Cumming, 2011). Given our small sample of ADHD children, we decided to apply not only classical statistical approaches but to confirm them with Bayesian evidence. Hence, the main analyses were performed based on traditional analyses of variance (ANOVAs) and in addition, for each outcome effect, we calculated Bayes factors based on default priors (Love et al., 2015;

Morey & Rouder, 2015; Rouder, Morey, Speckman, & Province, 2012).[18]

Main results and conclusion. ADHD-diagnosed children showed specific alterations in performance variability during task switching at baseline, both overall (indicating disturbances in state regulation) and conditionally on WM demands (indicating a major WM deficit).

Moreover, within the ADHD training groups, the high-motivational setting compared to the low-motivational setting led to relatively *higher voluntary motivational control* (i.e., demonstrated more willingness and self-reported interest in the training task). However, at the same time, the high-motivational setting condition induced relatively more severe behavioral inappropriateness, thus *lower control of involuntary motivational tendencies*. In turn, given this discrepancy in the effects on voluntary and involuntary motivational tendencies, the high-motivational training setting did not enable larger performance improvements than the low-motivational setting on the cognitive level (i.e., on performance in the training task or in an untrained switching task).

In contrast, the low-motivational setting induced *relatively lower voluntary motivational control* but also fewer ADHD symptoms (i.e., *better control of involuntary motivation*) compared to the high-motivational condition. In turn, the low-motivational training also did not enable larger performance improvements on the cognitive level.

However, at least, after the intervention, both ADHD training groups recovered from their initial WM alterations and achieved a more similar performance pattern to TD children.

The results obtained from Bayesian analyses were mainly consistent with those of traditional variance-analytical procedures, which allowed us to draw more firm conclusions. The lacking incremental benefit from a high-motivational training setting on cognitive training and transfer performance was attributed to a suboptimal arousal-performance relationship in either of our setting conditions: That is, in the low-motivational group, we were still facing the

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[18] The Bayes factor refers to the relative strength of evidence for two alternative theories (Dienes, 2014), such as the ratio between the likelihood of data under an alternative hypothesis (H1) relative to the null hypothesis (H0). If the data is more likely to arise under H1 than under H0, this provides evidence in the data for H1 (for details, see Dienes, 2014).

habitual unwillingness of ADHD children to train in a ‘boring’, low-rewarding task environment (Haenlein & Caul, 1987). In contrast, in the high-motivational group, we may have presented too many enriching elements that may have led to distraction and over-arousal (Katz, Jaeggi, Buschkuehl, Stegman, & Shah, 2014). However, this null effect of our motivational setting manipulation in ADHD children also conforms to a growing body of evidence (for a recent meta-analysic review, see Farcas & Szamosközi, 2016) claiming that ‘game-like features might not improve data’ (Hawkins, Rae, Nesbitt, & Brown, 2013, p. 1).

2.3 Empirical studies in older adults: spatio-temporal brain-activity dynamics underlying neurocognitive plasticity

This chapter is based on Paper IV:

Dörrenbächer, S., Wu, C., Zimmer, H., & Kray, J. (submitted). Compensation in brain activity dynamics after cognitive-control training in older adults.

2.3.1 Theoretical end empirical background (old adulthood)

2.3.1.1 Relevance of task-switching training

Why target specifically the old age range for training of executive control? It is well documented that culturally transmitted components of intelligent behavior, also termed the 'pragmatics' of cognition or 'crystallized' cognitive abilities, (gc; e.g., verbal or wisdom-related knowledge; Cattell, 1971; Horn, 1989), are largely preserved or even increase 'up to the sixth or seventh decades of life' (Kühn & Lindenberger, 2016, p. 116). In contrast, the biological component of intelligent behavior, also termed the 'mechanics' of cognition or 'fluid' cognitive abilities (gf; Cattell, 1971; Horn, 1989), that are invested into the culturally solidified bodies of knowledge, shows substantial decrements with advanced age (Baltes et al., 1999; Kühn & Lindenberger, 2016; Li et al., 2004). Such fluid abilities encompass basic mechanisms like perceptual speed, attention, spatial orientation, or reasoning (Kühn & Lindenberger, 2016). Of particular importance for the present dissertation is that the latter age-sensitive fluid mechanisms are intimately linked to executive-control functions (for reviews, see Kray & Lindenberger, 2007; Lindenberger & Kray, 2005), so that executive functions show similar age-related reductions. Vice versa, enhancing executive control in old age by 'compensatory or remedial' training approaches (Willis & Belleville, 2016, p. 221) may then also serve to slow down the general cognitive decline in the fluid domain of intelligence. From an applied perspective, intact executive control might support the effective management of instrumental activities of daily and independent living into old age (for a review, see Kelly et al., 2014), such as telephone use, shopping, cooking, housework, and management of finances (e.g., Cahn-Weiner, Boyle, & Malloy, 2002; Royall, Palmer, Chiodo, & Polk, 2004, 2005). In turn, preserved executive functions may maintain health status, delay social dependence, and prolong independent living (Dodge, Du, Saxton, & Ganguli, 2006; Johnson, Lui, & Yaffe, 2007; Schmiedek, Bauer, Lövdén, Brose, & Lindenberger, 2010). This seems especially important considering that individuals in modern societies are expected to live to an increasingly older age and that the relative proportion of elderly people will dramatically increase in the next decades.

2.3.1.2 The executive-control 'supply' and its trainability in older adults

As already outlined in the introduction section, old adulthood is a phase susceptible to pronounced decline in executive-control functioning (for a review, see Kray & Ferdinand, 2014). To summarize again the general changes late in lifespan:

1) In contrast to children, yet similar to younger adults, older adults have accumulated larger behavioral repertoires over the lifespan that they can deploy in a flexible manner (Lövdén et al., 2010). In turn, they are less in need of metabolically costly plastic changes, however there is also less potential for plasticity to occur at this age range. Instead, older adults may show strategically alternative deployment of given behavioral repertoires in support of compensation.
2) While children show an increasing differentiation in executive functions, older adults show a successive de-differentiation in fluid abilities (Baltes, Cornelius, Spiro, Nesselroade, & Willis, 1980; Lindenberger & von Oertzen, 2006).
3) Similar to children, older adults show less effective global executive functions (i.e., set-maintenance abilities) than local executive functions (i.e., set-shifting abilities) due to the disproportionately larger age-related decline in global control (Kray & Lindenberger, 2000).

Similarly to children, the changing cognitive system in older adults is also *'characterized by both increased vulnerability (...) and enhanced opportunities for intervention'* (Wiebe & Karbach, 2017).

Cognitive aging theories. Regarding the *'increased vulnerability'* (Wiebe & Karbach, 2017) in old adulthood, several prominent hypotheses have been formulated to explain the senescent changes in the mechanics of cognition (for recent reviews, see Reuter-Lorenz, Festini, & Jantz, 2016; Verhaeghen, 2014). The key driving mechanism is debated to be impairments (1) in a general domain-general processing resource, such as perceptual speed, as proposed in the *general* *slowing hypothesis* (Salthouse, Fristoe, McGuthry, & Hambrick, 1998); (2) in domain-specific elementary processes of executive control, such as an elementary *inhibition deficit* (Hasher, Stoltzfus, Zacks, & Rypma, 1991; Hasher & Zacks, 1988), *working-memory deficit* (see Basak & Verhaeghen, 2003) or *goal-maintenance deficit* (Braver & West, 2008), whereby the latter also refers to a neurobiological framework on cognitive aging (see next point); and (3) in specific brain structures and mechanisms associated with executive control, as proposed in *neural theories on aging*, such as the *frontal lobe hypothesis of aging* (West, 1996) or the more recent *context-processing* or *goal-maintenance framework*[19] (Braver et al., 2001; Braver & West, 2008).

Regarding the first class of aging theories, the *general slowing hypothesis* (Salthouse et al., 1998) predicts age-related impairments across a wide array of perceptual, motor, and cognitive operations at different complexity levels, such as local and global functions, that may all be attributed to one fundamental mechanism; that is, a general slowing in processing speed by a proportional factor of 1.5 to 2 in older adults compared to younger adults (Brinley, 1965). Although this account has been very influential in aging research, it seems not so biologically plausible and cannot explain age differences in performance markers of executive control that remain stable after accounting for differences in speed, such as mixing costs in the task-switching paradigm (Kramer & Kray, 2006; Verhaeghen & Cerella, 2002). Hence, this theory has been ‘clearly falsified’ in the meantime (Verhaeghen, 2014).

Regarding the second class of aging theories, the *inhibition deficit account* (Hasher et al., 1991; Hasher & Zacks, 1988) suggests that age-related impairments primarily pertain to the reduced ability to suppress irrelevant information at different processing stages. That is, in hindering irrelevant information from the entrance into WM; in clearing information that is no longer relevant from the current workspace in WM; and in preventing prepotent, yet

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[19] In their former framework, the authors referred to ‘context processing’ instead of ‘goal maintenance’, but they use the terms more or less interchangeably (Paxton, Barch, Racine, & Braver, 2007). By ‘context’, they mean all ‘task-relevant information represented in such a form so as to bias selection oft he appropriate task response‘ (Chiew & Braver, 2017; p. 143).

inappropriate, information from dominating WM (Friedman & Miyake, 2004; Hasher et al., 2007). This theory points to mutual relationships between inhibition and working-memory impairments, thus bridging the *working-memory deficit account*. Basak and Verhaeghen (2003) proposed that deficits in WM capacity may mediate general slowing in older adults because a smaller capacity increases the latency for moving 'items in and out of the attentional focus' (Basak & Zelinski, 2013, p. 87). Moreover, deficits in WM may also account for impairments in the maintenance of multiple task sets, which produces robust age differences in global mixing costs in task switching (Basak & Zelinski, 2013). Basak and Zelinski (2013) further propose that it is possible that this 'set of supervisory processes of managing multiple goals, which are not easily differentiated from WM, is the underlying primitive' of cognitive aging (Basak & Zelinski, 2013, p. 88). Hence, such assumptions propose an elementary deficit in global executive-control processes (i.e., maintenance and scheduling). This idea fits to the *goal-maintenance deficit* hypothesis (Braver & West, 2008; for an early similar account, see also Miller & Cohen, 2001). The goal-maintenance account also proposes that age deficits in various cognitive operations are attributable to a fundamental decline in the ability to actively maintain multiple goal representations in WM. Such goal-maintenance deficits are assumed to originate from specific *neural* alterations in advanced age, especially in the prefrontal lobe and the DA system (Chiew & Braver, 2017; see also section 1.1.4).

***Training-induced cognitive plasticity*.** Assuming elementary impairments in executive-control functions as a likely candidate for causing the general age-related cognitive decline, one may at the same time consider the *'enhanced opportunities for intervention'* (Wiebe & Karbach, 2017) in exactly these fragile executive-control functions in older adults (e.g., Anguera et al., 2013; Karbach & Kray, 2009; Kray & Fehér, 2017). The above-described executive-deficit theories of aging have proposed major impairments in inhibition and working memory in advanced age. Hence, similarly to children, it would again seem useful to apply a task-switching training regime that places double demands on WM (i.e., AR variant) and inhibition (i.e., ambiguous stimuli and overlapping response formats) to induce an optimal intensity of the training mismatch. However, in a recent behavioral task-switching training study, Kray and Fehér (2017) systematically manipulated the memory and inhibition demands during training in younger and older participants, by providing task switching either in a variant with univalent or bivalent stimuli (inhibition load manipulation) and in a cued or an un-cued version (memory load manipulation). The researchers found that for older adults, the largest reduction of global mixing costs from pre- to posttest was obtained after training with high inhibition load but low memory requirements. Similarly, Anguera et al. (2013) applied dual-tasking training to determine cognitive plasticity in older age. They revealed considerable transfer gains of training and argued that especially the practice in resolving task interference required in multitasking situations is critical for inducing plasticity in the elderly. Hence, training in dual-tasking or task-switching situations with a high degree of task-set competition has been proven a suitable tool to induce compensation in impaired (global) executive-control in older adults (Anguera et al., 2013; Bherer et al., 2005; Bherer et al., 2008; Karbach & Kray, 2009; Kray & Fehér, 2017).

Importantly, the study of Anguera et al. (2013) did not only report behavioral transfer of dual-tasking training. The authors were among the first to provide evidence for training-inducible changes in age-impaired neural resources of executive control (here, training empowered oscillatory theta brain activity in older adults), which points to the third and most important class of aging theories, namely *neural aging theories*.

2.3.1.3 The neural 'supply' of executive control and its trainability

At the neural level, age effects in executive control are primarily linked to the structural and functional status of the prefrontal cortex (West, 1996; see also chapter 1.1.4). This *frontal lobe hypothesis of aging* is grounded in earlier neuropsychological lesion studies that found high similarity between executive deficits in patients with frontal-lobe lesions and in older adults (see Stuss & Alexander, 2000; Stuss & Knight, 2002). The frontal-lobe hypothesis may have the broadest reach among current executive theories of cognitive aging (Reuter-Lorenz et al., 2016) but was in its original version too general. Hence, this theory has been thoroughly refined in the last decade, especially based on findings from more sophisticated neuroimaging techniques, such as (functional) magnetic resonance imaging.[20]

More specifically, recent neural aging theories emphasized the additional contribution of *cortical and subcortical networks beyond the PFC* (Braver et al., 2001) and made an attempt to clarify the neurobiological *mechanisms* underlying age impairments in executive control in more detail.

Basically, the 'neural supply' of executive control is nowadays assumed to be an interplay of distributed fronto-striatal and fronto-parietal networks (for meta-analyses, see Kim, Cilles, Johnson, & Gold, 2012; Nee et al., 2013). Indeed, the PFC still plays a key role among these networks due to its unique ability to integrate multiple pieces of internal and external information into coherent representations that streamline controlled behavior. However, this general, integrative function of the PFC is enabled by specific contributions of many involved sub-regions serving distinct functions that are hierarchically organized along a rostral-caudal abstraction gradient (Badre & D'Esposito, 2009; Bunge & Zelazo, 2006; O'Reilly, 2010; see also chapter 1.1.2). Anatomically, more rostral PFC portions, such as the frontal pole (FP) and the anterior part of the cingulate cortex (ACC) have been associated with the processing of global executive control (i.e., task-set maintenance and selection), such as being in a mixed-task situation during task switching (Braver et al., 2003; Jimura & Braver, 2009; Nee & Brown, 2013). In contrast, the processing of local executive control, e.g., switching back and forth between different tasks, has been linked to more posterior PFC portions (Montojo & Courtney, 2008; Nee & Brown, 2013), especially to the lateral PFC (i.e., dorsolateral and ventrolateral, dlPFC and vlPFC) and the inferior frontal junction (IFJ; Derrfuss, Brass, Neumann, & von Cramon, 2005; Muhle-Karbe et al., 2015). Importantly, the study of Nee and Brown (2013) revealed that this hierarchical organization within the PFC is differentially modulated by the basal ganglia (BG), including the putamen and the caudate head, and the

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[20] Functional magnetic resonance imaging is a non-invasive technique that allows us to indirectly measure neural activity via the blood oxygenation level dependent (BOLD) effect. To provide a simplified explanation of this BOLD effect: The BOLD effect is based on the assumption that increased neural activation in a brain region leads to an increased amount of blood flow through this region (due to the larger metabolic needs of the active cells). However, there is a relative surplus in the local blood oxygen concentration, because the amount of blood that is sent to this region exceeds its demands for replenishing the oxygen consumed by the activity of cells. Due to the different magnetic properties of oxygenated and deoxygenated hemoglobin, this local change in blood oxygenation causes magnetic changes that are measurable (Poldrack, Mumford, & Nichols, 2011).

posterior parietal cortex (PPC), including the superior (SPL) and inferior parietal lobules (IPL). More specifically, the fronto-striatal circuitry selectively supported global control and the fronto-parietal circuitry selectively supported local executive control (Nee & Brown, 2013). Figure 8 provides an overview of the canonical executive-control regions.

Neural aging theories. These distributed fronto-striatal and fronto-parietal circuits are the most vulnerable to early and disproportionate structural atrophy (Hedden & Gabrieli, 2004) and have shown large alterations in task-related activations in advanced age (for reviews, see Grady, 2008; Schneider-Garces et al., 2010). Several fMRI studies examining age differences in the neural correlates of cognitive functioning found specific reproducible patterns of age-related changes in the spatial distribution of brain activation across these networks:

First, a *hemispheric asymmetry reduction in older adults* (HAROLD; Cabeza, Anderson, Locantore, & McIntosh, 2002): this pattern refers to the additional recruitment of the homologous region in the contralateral hemisphere in older adults, resulting in bilateral activation (especially in frontal areas) where younger adults show a more lateralized pattern of activation (see also the STAC – Scaffolding Theory of Aging and Cognition account proposed by Park and Reuter-Lorenz (2009).

Second, a *posterior-to-anterior shift in aging* (PASA; Davis et al., 2008) indicates a pattern with an over-recruitment of prefrontal areas and an under-recruitment of posterior parietal and occipital regions in older adults as compared to younger adults.

Third, the *compensation-related utilization of neural circuits hypothesis* (CRUNCH; Cappell, Gmeindl, & Reuter-Lorenz, 2010) suggests a pattern of neural activation that depends on task demands. Specifically, relative to younger adults, older adults show an over-recruitment of brain activation in low-demanding task conditions, possibly pointing to more needed effort, while an under-recruitment of brain activation in high-demanding task conditions, possibly pointing to capacity limitations.

Fourth, in contrast to the latter CRUNCH assumption, older adults also show sometimes a *non-selectivity or de-differentiation* in activation levels, meaning that they recruit similar activation levels across different task conditions, irrespectively of the task demand, where younger adults show differing brain responses contingent to the demand level of the task (e.g., DiGirolamo et al., 2001).

Neural compensation. Such reliable neural activation patterns have been claimed to reflect neural compensation in age. Neural compensation in old age is defined as additional or alternative neural recruitment, when primary resources are compromised (Barulli & Stern, 2013). Comparing behavioral performance between younger and older adults helps to determine whether such alternative neural patterns in older adults reflect only ‘attempted compensation’ or serve ‘successful compensation’ (Reuter-Lorenz & Park, 2014).

Specifically, if these alternative neural patterns in older adults go along with increased behavioral age differences, they point to ‘attempted’ or ‘unsuccessful’ compensation (i.e., the alternative pattern may here indeed reflect more needed effort, limitations in capacity, or reduced abilities to differentiate between relevant and irrelevant brain processes in old age).

In contrast, if these alternative neural patterns in older adults go along with reduced behavioral age differences, they point to ‘successful’ compensation in older adults (i.e., the alternative pattern may here reflect an over-recruitment of the still preserved processes to help offset other losses in old age).

Spatio-temporal interactions. However, such hypotheses have only been formed based on age-related changes in the amplitude and distribution of brain activation in spatially separated networks. A recent theory called the *temporal hypothesis for compensation* (THC; alternatively termed as 'early to late shift in aging' (ELSA)/ ; see Dew, Buchler, Dobbins, & Cabeza, 2012) instead emphasized not only “WHICH regions of the brain show increased activation, but [also] WHEN (…) [or HOW LONG] these regions [are] activated” (Martins, Joanette, & Monchi, 2015, p. 10-11). Hence, successful neural compensation in older adults may critically depend on both spatial and temporal features of brain activation. This may especially hold for age differences in global and local executive-control processes given their neural reflection in transient versus sustained time scales of brain signals (Koechlin et al., 2003; see also chapter 1.1.2). To recapitulate, transient timescales underlie processes that span a short-lasting temporal episode, such as a task trial, while sustained timescales underlie temporally extended processes that endure over a longer time interval, such as a task block.

Neurobiological mechanisms: the goal-maintenance framework. A recent neurobiological framework, namely the *context-processing* or *goal-maintenance framework* (Braver et al., 2001; Braver & Barch, 2002), takes these interactions between spatial and temporal dynamics of brain activation into account (for a recent review, see Chiew & Braver, 2017). In this framework, activation peaks of the sustained processing stream are related to (1) anterior and fronto-lateral PFC regions serving the stable maintenance of global task context; (2) the ACC reflecting supervisory monitoring processes and the detection of an ongoing conflict (see also Botvinick, Braver, Barch, Carter, & Cohen, 2001); and (3) the BG, where an interplay between sustained and transient DA[21] gates the access of information relevant for global task representations into the PFC under appropriate conditions (Gruber, Dayan, Gutkin, & Solla, 2006). The recent extension of this framework, namely the *dual-mechanisms of control (DMC)* theory (Braver, 2012), further specifies the functional role of this sustained activation: it may subserve an early top-down bias of ongoing processes, reflecting a *proactive, preparatory control mode* (Braver, 2012). Such a proactive mode is mainly required in the case of demands on global executive control (Chiew & Braver, 2017).

In contrast, transient signals in the PFC-PPC loop (Braver et al., 2003; Jimura & Braver, 2009), especially in the lateral PFC and the SPL (Richter & Yeung, 2014), can be flexibly utilized for both task preparation and conflict resolution, depending on whether they are recruited at cue or probe onset. The latter *probe-related, reactive control mode* refers to correction mechanisms that are implemented late and in a 'just-in-time-manner' (Braver, 2012, p. 106) and that depend on the bottom-up information from encountered stimuli (Braver,

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[21] It should be noted that the blood-oxygen-level-dependent (BOLD) response in the striatum has often been directly linked to DA release (Schott et al., 2008). Furthermore, it is worth noting that DA release is more typically described in terms of 'phasic' and 'tonic' release. However, for the sake of consistency, we adopted the terms of 'transient' and 'sustained' DA release for the present dissertation.

2012). Such a reactive mode is mainly required in the case of demands on local executive control (Chiew & Braver, 2017).

More important for the dissertation project is that even in the absence of behavioral age differences, older adults show reduced amplitudes of sustained activation in the FP and ACC during task switching (Jimura & Braver, 2009), as well as generally reduced sustained DA in the striatum (Braver, Satpute, Rush, Racine, & Barch, 2005). Such alterations have been attributed to losses in sustained activation resources (Dennis, Daselaar, & Cabeza, 2007). Regarding specifically the DA system, older adults face a number of issues, including alterations in DA concentration, synthesis, receptor density or transporter availability (Bäckman et al., 2006; Hedden & Gabrieli, 2004). These impairments may fundamentally impair the homeostasis between sustained and transient activation levels in fronto-striatal loops.[22] In contrast, transient activation mechanisms, such as within the PFC-PPC circuitry, appear largely preserved in age when performing cognitive control tasks like task switching (Jimura & Braver, 2009). Hence, it could be an important avenue for older adults to more heavily rely on the still-preserved neural mechanisms (i.e., transient activation) as a means to successful compensation (Jimura & Braver, 2009; Madden et al., 2010).

Training-induced neural plasticity. Regarding training in older adults, taking such compensatory brain imaging patterns as 'surrogate biomarkers' of training efficacy (Willis & Belleville, 2016; p .233) may help to elucidate the underlying processes of training-induced plasticity in old adulthood. Hence, trainings in older adults might aim for a boost of successful compensation, which would be reflected in behavioral improvement associated with (a) amplitude changes in spatially separated networks reflecting typical compensatory age patterns, such as HAROLD, PASA, CRUNCH, or de-differentiation, and/ or (b)

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[22] The BG system exerts its gating function by transient DA modulations above and beyond an average sustained DA level: transient DA modulations facilitate or inhibit the entrance of relevant information into the prefrontal 'work space', while sustained DA serves to adjust the general responsivity threshold (Frank & O'Reilly, 2006). Cohen et al. (2002) argued that higher sustained DA levels in the BG are likely to be associated with relatively lower transient release, and vice versa, which they call 'homeostasis'.

changes in temporal processing by a larger recruitment of transient at the expense of sustained brain processes.

However, previous studies on the neural correlates of training in executive control have mainly addressed younger adults (Erickson et al., 2007b; Hempel et al., 2004; Jolles, van Buchem, Rombouts, & Crone, 2012; Salminen, Kühn, Frensch, & Schubert, 2016). Empirical evidence for training-induced functional brain changes from executive-control training in support of compensation in older adults is scarce so far. One finding from a small number of studies is a *change in the spatial distribution* of brain activation across canonical control networks in older adults (Erickson et al., 2007a; Heinzel et al., 2016). For example, in the study of Erickson et al. (2007a), younger and older adults practiced dual-tasking on two visual-manual tasks and the authors found training-induced spatial brain changes in both age groups, with a combined pattern of increases and decreases of brain activation across canonical executive-control networks (e.g., the left and right ventral and dorsal PFC). However, it should be noted that this training study had only included a passive control group, which might limit general conclusions about training-induced neural changes. In the second study of Heinzel et al. (2016), older adults practiced working memory on an adaptive n-back training task. The authors revealed a selective decrease of neural activation in the right caudal superior frontal sulcus (cSFS) during the n-back task for the older adult training group as compared to controls, which was interpreted in terms of a training-related boost in processing efficiency in canonical WM networks. However, also in this study, the authors had only included a passive control group.

Spatio-temporal dynamics in training-induced neural plasticity. More importantly, both studies (Erickson et al., 2007a; Heinzel et al., 2016) only investigated spatial changes in brain activation levels across canonical networks but did not examine changes in temporal dynamics, in such a way that transient brain processes could be promoted at the expense of sustained brain processes in older adults.

Only one study so far did measure changes in such spatio-temporal dynamics after training in older adults (Braver, Paxton, Locke, & Barch, 2009). However, this study applied a directed strategy training instead of a process-based training regime. Nevertheless, the authors found a temporal shift in older adults within a number of lateral PFC regions (i.e., increased cue-related transient activation and decreased probe-related transient activation; but no change in sustained activation in older adults). Hence, the investigation of temporal dynamics seems essential in older adults, especially for the dissociation of training-induced changes in local and global executive control processes. However, such an analysis of both spatial and temporal dynamics of brain activation requires a particular, complex fMRI design, which will be introduced in chapter 3.1.4.

2.3.1.4 The analysis of spatio-temporal interactions of brain activation: the mixed block-/ event-related fMRI design

How can we separate the temporal dynamics of brain activation underlying executive control based on fMRI techniques? One possibility to dissociate sustained and transient timescales of brain processes is the mixed block-/ event-related fMRI design (Visscher et al., 2003). In this kind of design, task blocks are presented in alternation with rest periods. Within each task block, different trial events are presented in a randomized, temporally jittered manner. As can be seen from Figure 6, the logic of such a mixed design is that event-related amplitudes of the neural signal from single trial events will decay back to baseline during each inter-trial interval, while the amplitudes of sustained neural responses remain relatively stable throughout a task block. At the analysis stage, these effects can be implemented in a traditional general-linear model (GLM) analysis approach. The basic idea is to estimate parameters for both event-related (transient) and block-related (sustained) effects simultaneously but to enter them as independent regressors within the same analysis design. This approach has been validated well through both empirical and simulation studies in experimental contexts (Braver et al., 2003; Braver et al., 2009; Dennis et al., 2007; Jimura & Braver, 2009; Madden et al., 2010; Visscher et al., 2003) but has rarely been implemented in intervention contexts (Braver et al., 2009).

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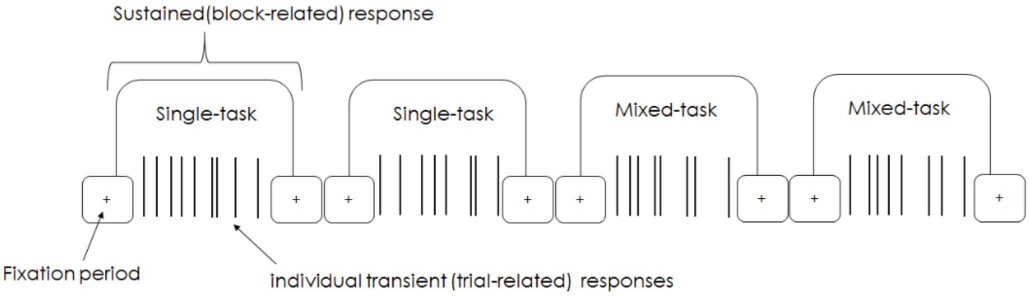

Figure 6. Schematic of the mixed block-/ event-related design.

2.3.2 Intermediate summary and implications for the present studies in old adulthood

To summarize, old adulthood is a phase susceptible to decline in executive control. Older adults have a preference to deploy their, albeit richer, behavioral repertoires in a flexible manner, because they have less potential for plasticity. Older adults show a general de-differentiation in fluid abilities, yet a steeper decline in global than in local executive control. Such senescent changes have been explained in terms of (cross-domain) general slowing or of fundamental deficits in distinct components of executive control (i.e., inhibition, working memory/ goal maintenance). Training procedures that specifically tap into such impaired 'executive primitives' (e.g., task-switching training) have been proven useful to induce behavioral compensation.

The ideal mismatch in older adults may be evoked by a high demand on the ability to resolve interference. Such training may allow for profound neural changes in the senescent brain. This is highly relevant in the light of findings from neuroimaging studies on age differences in task activation: older adults show large functional alterations across networks underlying executive control, such as fronto-striatal and fronto-parietal circuits. These functional alterations have been identified as patterns of changes in the spatial distribution of brain activation (i.e., HAROLD, PASA, CRUNCH, or de-differentiation). Such patterns can reflect unsuccessful or successful spatial compensation, depending on whether they promote or hamper the task behavior in older adults.

However, the recent THC account raised awareness for the high importance of temporal features of brain activation for neural compensation in advanced age. Especially, when one aims to separate age differences in global (sustained) versus local (transient) executive control, one may require temporal information. Neural aging may preferentially concern sustained and preparatory (proactive) brain activation, while transient and reactive brain activation is retained. Hence, a higher reliance on preserved transient resources may provide a useful strategy for temporal compensation in older adults. Importantly, such successful neural compensation may be target outcome for training in older adults. However, the few previous studies on the neural correlates of training and transfer in older adults focused exclusively on changes in the spatial distribution of brain activation. Besides, the investigation of spatio-temporal interactions requires particular design and analysis considerations. The recent mixed block-/ event-related fMRI design has proven a valuable tool to capture both the spatial and temporal dynamics of brain activation, but has rarely been applied in intervention studies.

2.3.3 Summary of studies

In the course of an empirical training study in older adults, we investigated training-induced neural changes (*Paper IV*) in older adults as a function of spatio-temporal dynamics of the underlying brain mechanisms.

Paper IV

Dörrenbächer, S., Wu, C., Zimmer, H., & Kray, J. (submitted). Compensation in brain activity dynamics after cognitive-control training in older adults.

Theoretical background and design. To recapitulate, task switching is neurally subserved by specific spatio-temporal interactions of brain mechanisms; that is, by a dynamic interplay of transient brain activation that shows activation peaks in fronto-parietal networks, and enduring or sustained brain activation that shows activation peaks in fronto-striatal networks (Braver et al., 2003). Older adults are impaired in the coordinated recruitment of brain activation from different timescales. Specifically, they are affected in the recruitment of sustained and preparatory activation while less impaired in the recruitment of transient activation (Dennis et al., 2007; Jimura & Braver, 2009). A few fMRI studies provide the first evidence that practice in dual tasking and working memory may enable older adults to change the spatial distribution of brain activation across cortical and subcortical networks, which in turn can provide compensation for behavioral impairments (Erickson et al., 2007a; Heinzel et al., 2016). A different way for neural compensation might be the reliance on transient activation resources (in fronto-parietal networks) at the expense of sustained resources (in fronto-striatal networks) that are less flexibly modifiable in old age. Yet, no study so far has investigated changes in the spatial distribution of brain activation depending on the timescale of brain signals (i.e., spatio-temporal interactions). Therefore, in *Paper IV*, we analyzed training-related functional plasticity of task activation in old age by applying a hybrid epoch-/event-related functional magnetic resonance imaging (fMRI) design coupled with a region-of-interest (ROI) based analysis approach that together sensitively track both spatial and temporal features of brain activation. We manipulated the training demands on executive control (low-demanding/ single-task training vs. high-demanding/ task-switching training) between fifty healthy seniors (61 to 79 years of age) and compared their pretest/posttest activation-change maps against 25 untrained younger controls (18 to 28 years of age). Regarding the comparison with younger adults, we were specifically interested in signatures of successful neural compensation; that is, a more dissimilar post-intervention pattern in older adults as compared to younger adults coupled with a more similar behavioral performance.

To summarize our realized design principles in respect of the overarching framework of this thesis (Lövdén et al., 2010): First, regarding the *nature of the training mismatch*, we applied process-based training because it may enhance the likelihood for broad transfer. Second, we provoked larger *mismatch intensity* in the task-switching training groups (i.e., switching) than in the single-task training groups (i.e., performing on single blocks). In line with the suggestions from a previous task-switching training study in older adults (Kray & Fehér, 2017), the requirements on the resolution of interference were kept high (i.e., ambiguous stimuli and overlapping response formats), while the memory requirements were kept low (i.e., cued paradigm variant) for both groups. Third, regarding the *sustainment of the training mismatch*, we applied variable training in all groups to keep the training challenging throughout the intervention phase (see Figure 7). Fourth, regarding the *duration of the training mismatch*, given that we were interested in profound neural changes, we set, in line with the recommendation of Klingberg (2010), eight hours of practice that were spaced over eight sessions. Fifth and most importantly for the purpose of the present study, regarding the *scope of the training mismatch*, we measured the neural correlates of training (and more specifically, the underlying spatio-temporal dynamics of brain activation) by applying neuroimaging techniques.

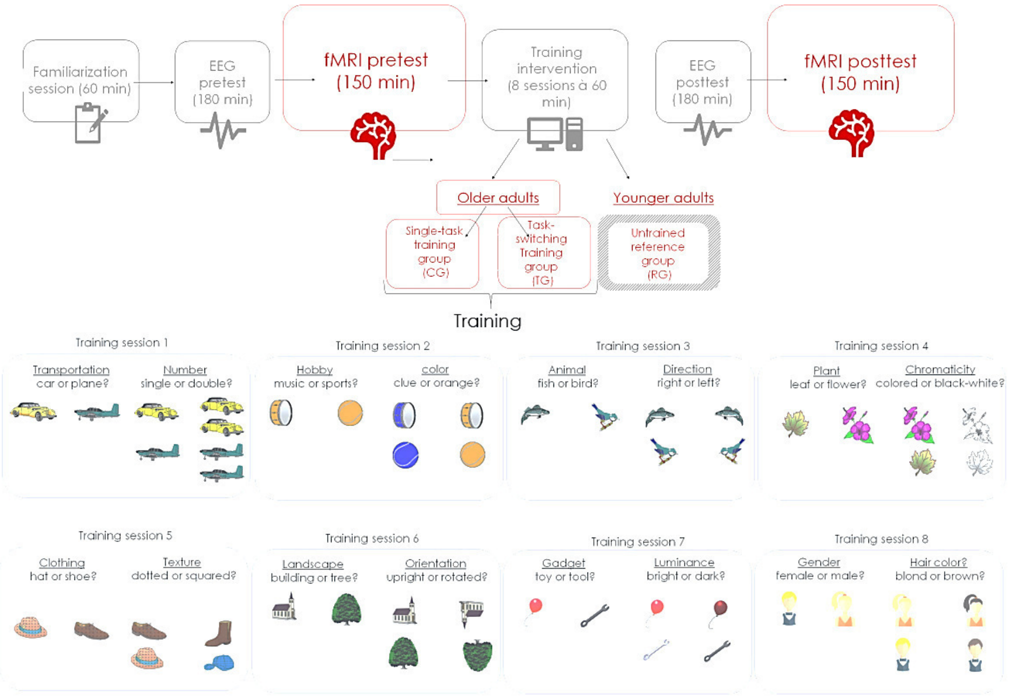

Figure 7. **Study Design.** First row: pretest-training-posttest design; relevant sessions are marked in red ink (i.e., fMRI pretest, posttest). Second row: Variable training with different training tasks and stimuli in each session (for details, refer to *Paper IV*, methods section).

Research predictions. We predicted that, as compared to single-task training, task-switching training in older adults would promote training-induced changes towards a pattern of successful compensation, implying (1) a similar behavioral performance in older and younger adults; (2) at the neural level, a fine-tuning of transient brain activation in fronto-parietal networks that is largely retained in older adults. It was an open question whether such changes in transient brain activation would be more pronounced for probe-related activation than for cue-related activation, because proactive resources, perhaps even on a transient timescale, might be less modifiable in old age (Braver et al., 2009; but see Paxton, Barch, Storandt, & Braver, 2006); (3) a reduction of sustained activation levels in the fronto-striatal circuitry (Jimura & Braver, 2009; Madden et al., 2010); and (3) a different pattern of neural activity in older adults than in younger adults, which would point to proper compensation.

Specific analysis considerations in older adults.

(1) *Applying age-unbiased multi-session templates.* We implemented a customized longitudinal preprocessing and analysis pipeline. First, we calculated mid-point average functional and structural output images from the pretest and posttest measurement of our sample and took it as a basis for several preprocessing steps. Second, for spatial normalization, we registered the segmented mid-point average image via a high-dimensional fast diffeomorphic registration (DARTEL; Ashburner & Friston, 2011) to the default template of the computation anatomy toolbox extension (CAT12, http://dbm.neuro.uni-jena.de/cat12/) that is generated based on the structural images of nearly 600 healthy adults of ages ranging from 19.98 to 86.32 years (averaged across similar numbers of old and young adult brains), thus providing a good basis for age-unbiased registration.

(2) *Accounting for time-on-task effects*. Time-on-task effects in fMRI may be especially problematic in samples of older adults due to age-related general slowing effects. To exclude such effects that were of no interest for the present study, we entered parametric regressors in our statistical model that were defined by the same onsets as the primary regressors but by a duration varying according to response times. These parametric modulators were orthogonalized with respect to the primary regressor within event type (Poldrack et al., 2011).

(3) *Calculating regions of interest based on relevant prior knowledge.* In the present study, we restricted our analyses to regions of interest that were carefully selected based on prior knowledge regarding the following criteria: the region of interest (a) should belong to canonical executive-control regions; (b) should have produced activation in task designs comparable to the task-switching paradigm; (c) should have proven

sensitive to the modulation of sustained or transient activation dynamics; (d) should have proven sensitive to age effects. To create the ROI masks, we combined anatomical hypotheses with functional findings from meta-analyses and applied the literature-based probabilistic ROI generation approach a described in Schubert et al. (2008).

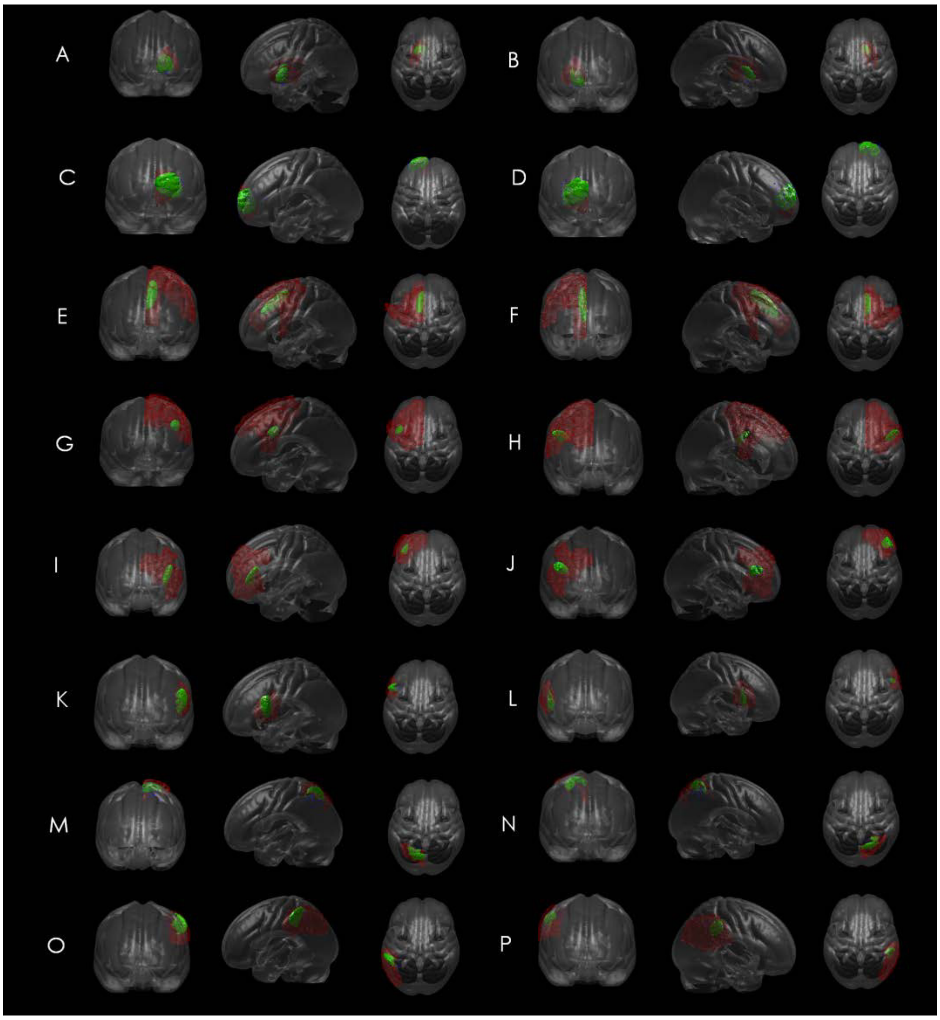

Figure 8. Literature-based probabilistic regions of interest. Red area reflects atlas-based anatomical borders; blue dots reflect coordinates retrieved from the literature; green area reflects the computed probabilistic region of interest. **A.** = Frontal pole (FP) left. **B.** = Frontal pole (FP) right. **C.** =Anterior cingulate cortex (ACC) left. **D.** = Anterior cingulate cortex (ACC) right. **E.** = Basal ganglia (BG) left. **F.** = Basal ganglia (BG) right. **G.** = Inferior frontal junction (IFJ) left. **H.** = Inferior frontal junction (IFJ) right. **I.** = Dorsolateral prefrontal cortex (dlPFC) left. **J.** = dorsolateral prefrontal cortex (dlPFC) right. **K.** = Ventrolateral prefrontal cortex (vlPFC) left. **L.** = Ventrolateral prefrontal cortex (vlPFC) right. **M.** = Superior parietal lobule (SPL) left. **N.** = Superior parietal lobule (SPL) right. **O.** = Inferior parietal lobule (IPL) left. **P.** = Inferior parietal lobule (IPL) right.

Main results and conclusion. Results revealed that task-switching training compared to active-control single-task training in older adults induced somewhat larger improvements on behavioral task-switching performance. Second and more importantly, we found that only after task-switching training, older adults showed a reduction of the transient mixing-cost contrast in brain activation within the bilateral mid-vlPFC and the left IFJ (i.e., only in prefrontal regions). Third, in the right IFJ and the left SPL (i.e., in fronto-parietal regions), we further obtained a group-selective reduction of the transient switching-cost contrast in brain activation. It was important that the selective reductions of both the mixing-cost and switching-cost activation contrast in the task-switching training group were driven by a *de-differentiation* or convergence of activation levels in the different trial conditions, meaning that older adults recruited similar transient activation for the different task conditions. Only in the task-switching training group, these changes in transient brain activation in prefrontal areas were related to fewer behavioral mixing costs (i.e., better global executive control) at posttest, and in fronto-parietal areas to fewer behavioral switching costs (i.e., better local executive control) at posttest. A further finding was that high-demanding task-switching training led to an overall down-regulation of sustained resources in fronto-striatal circuits (i.e., in the FP and the BG). At the same time, this type of training induced a larger crossover change of sustained and transient brain activation dynamics within the BG. Finally, we found that the selective training-induced changes after task-switching training led to more dissimilar neural processing compared to younger adults, indicating that this type of training may have boosted neural compensation. The main results of this study are summarized in Figure 9.

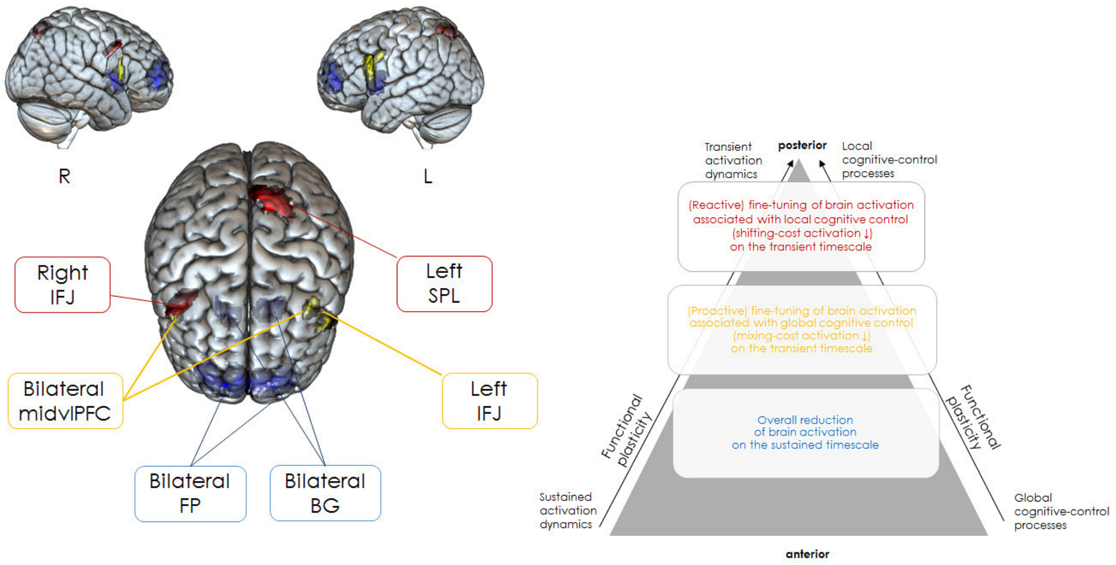

Figure 9. Summary of main results. Left panel: Regions sensitive to training-induced functional plasticity. The color indicates which results have been obtained in these regions as summarized in the right panel. For visualization purposes, sensitive regions are rendered onto 3D surface of a standard template as provided by MRICroGl (Rorden & Brett, 2000). Right panel: Summary of results obtained across the different regions of interest. *From the bottom to the top*: from anterior to posterior regions; from sustained to transient brain activation dynamics; from proactive to reactive resources; from global processing to local processing. Overall reductions of sustained activation were found in the bilateral FP and the bilateral BG (shaded blue). Specific reductions of transient activation were found in the bilateral midvlPFC and the left IFJ on the mixing-cost activation (shaded yellow). Specific reductions of transient activation were found in the right IFJ and the left SPL in the shifting-cost activation (shaded red). R = right hemisphere; L = left hemisphere; FP = frontal pole; BG = basal ganglia; midvlPFC = mid-ventrolateral prefrontal cortex; IFJ = inferior frontal junction; SPL = superior parietal lobule.

Our findings indicated that the training-induced fine-tuning of transient brain activation served a better coordination of local and global executive-control functions. Global executive control has been often associated with sustained activation (Braver et al., 2003). The present study showed that specific training may enable older adults to use an alternative route: namely, the proactive (preparatory) modulation of global control (i.e., mixing-cost activation) on the transient rather than on the sustained timescale. This improvement in global functions is especially notable given that global executive-control abilities are fragile in old age (Kray & Lindenberger, 2000). The sustained resources were down-regulated, which might be useful in advanced age to save already less efficient resources. The finding of reductions in mixing- and switching-cost activation were due to a convergence of activation levels in the different trial conditions, hence our training enabled a neural de-differentiation coupled with better behavioral performance (DiGirolamo et al., 2001; Karayanidis et al., 2010; Schmitt, Wolff, Ferdinand, & Kray, 2014b; Whitson et al., 2013). However, this compensation in activation amplitudes depended on the (transient) timescale of brain activation. Hence, the results clearly emphasize the importance of spatio-temporal interactions of brain activation supporting training-induced neural plasticity in older adults.

3 General discussion

The aim of the present dissertation was to determine different mechanisms underlying and modulating plasticity in response to training of executive control in childhood and in old age.

Paper II and *III* focused on task-switching plasticity in childhood. It has been well documented that children often do not sufficiently benefit from cognitive training, merely due to a lack of training willingness (Luman et al., 2005). This has been associated with a disproportionately high reward sensitivity in childhood or adolescence, which is due to the earlier maturation of the appetitive socio-emotional compared to the rational cognitive system (Casey et al., 2008; Luna et al., 2010; Shulman et al., 2016; Somerville, Hare, & Casey, 2011; Steinberg, 2008). In challenging cognitive tasks, children's longing for reward may, however, not be satisfied. Children suffering from specific developmental disorders, such as ADHD, face a particularly large imbalance between motivational and cognitive factors (Haenlein & Caul, 1987; Sergeant, 2000; Sonuga-Barke, 2003). As a consequence, ADHD children show not only a reduced willingness to train but also a fundamentally altered response behavior in cognitive tasks, such as a general increase in inconsistent responding (Epstein et al., 2011). Implementing a motivationally enriched training setting by adding video-game elements may be a helpful manipulation to enhance the engagement in meeting the task demands of cognitive training and to align the response behavior in children, especially in case when they suffer from ADHD (Luman et al., 2005; Prins et al., 2011). Therefore, in the course of two intervention studies, we empirically investigated the interaction of cognitive and motivational mechanisms underlying training-induced plasticity in healthy (*Paper II*) and ADHD-diagnosed children (*Paper III*).

Paper IV aimed to determine task-switching plasticity at the other end of the lifespan. Regarding the use of task-switching training in old adulthood, senescent changes in the brain appear to be a major contributor to deficient performance. These changes include a disproportionately large volume shrinkage in the prefrontal lobe and associated cortical and sub-cortical structures (Hedden & Gabrieli, 2004). At the same time, several fMRI studies examining the neural correlates of age differences in executive control have determined a specific compensatory pattern of task activation in older adults; that is, a lesser recruitment of sustained brain activation in fronto-polar networks but partly an increased recruitment of transient brain activation in fronto-parietal networks (Dennis et al., 2007; Jimura & Braver, 2009). Hence, the authors showed that neural age effects were dependent on both spatial as well as temporal features of the involved brain mechanisms. Therefore, in older adults, we focused on an empirical investigation of training-induced neural changes as a function of spatio-temporal interactions of brain activity dynamics (Braver et al., 2003; Dennis et al., 2007; Jimura & Braver, 2009).

3.1 Motivational influences on cognitive plasticity in childhood

The first two empirical studies aimed to examine the impact of a motivational video-game setting on the training and transfer success from executive-control training in typically developed children or children suffering from ADHD, respectively. To address this issue, we designed a ‘motivationally pulling’ game variant of task-switching training resting on the assumptions of the self-determination theory (Ryan et al., 2006). We measured the effects of this game variant against a standard variant of task-switching training (and active control groups) on outcome training willingness and performance. Critically, our willingness indicator was independent of the amount of training as we made sure that the willingness decisions did not actually change the overall number of the presented training blocks. The main findings and their implications are discussed in the following.

The dissociable influence of a game-based training setting on motivation and executive control in typically developed children. The results of *Paper II* suggested that in typically developed children, adding video-game elements to a task-switching training setting boosted first the willingness to train, which was in line with our assumptions and in accordance with similar game training studies (e.g., Prins et al., 2011). This finding may have validated our motivational setting manipulation. However, irrespective of the setting condition, training willingness declined over time, pointing to a general fatigue with an increasing amount of practice on the same task (e.g., Mitchell & Jolley, 2009). Hence, our setting manipulation seemed not rewarding enough to attenuate motivational losses over time in typically developed children. Future studies should investigate first, whether other motivational variables, such as material incentives and prices, may induce a more persisting boost of willingness (but see Katz et al., 2014, who found no differentially rewarding quality of different motivational features); and second, whether inter-individual differences in motivation at the trait level, such as achievement goal orientations (Pintrich, 2000; Wolters, 2004), self-efficacy beliefs (Bandura, 1993; Chiaburu & Lindsay, 2008; Zimmerman, 2000) or need for cognition (Cacioppo, Petty, Feinstein, & Jarvis, 1996; Furnham & Thorne, 2013), that are relatively invariant across situations, may modulate the motivational loss over time in the different setting groups.

More importantly, our video-game setting clearly boosted local task-switching performance. Specifically, we obtained a larger reduction of switching costs in the training task and in an untrained task switching situation in the high-motivational setting group compared to the low-motivational setting group, suggesting that game elements were suited to foster cognitive development on top of training willingness. Yet, this incremental benefit from the game setting was limited to local switch costs and did not generalize to global task-switching abilities (i.e., to the mixing-cost level) or to different task domains of executive control (i.e., to different inhibition or working memory tasks). Thus, as far as domain-general executive control was concerned, a high-motivational game setting appeared not to be more effective than a standard setting. This was an unexpected finding given that global mixing costs show usually the more reliable transfer gains in the training literature than local switching costs and, in turn, should be more malleable by training manipulations (Karbach & Kray, 2009; Minear & Shah, 2008).

One reason why only local but not global task-switching processes were boosted in our game training setting might be that local set-switching abilities mature critically in the investigated age range in children between 8 and 11 years of age (for a review on the development of cognitive flexibility in childhood, see Buttelmann & Karbach, 2017; Huizinga et al., 2006). In contrast, global set-maintenance abilities show a more delayed maturation into adolescence (i.e., up to approximately 15 years; see Huizinga & van der Molen, 2007). Hence, our motivational setting may have specifically encouraged mutual synergies with the current developmental changes in local processes in childhood.

The lacking finding of setting modulations on broad transfer to other executive task domains seems striking from a developmental perspective. The poorly differentiated cognitive system in childhood should have increased the likelihood for a generalization of effects from incoming manipulations. However, recently, it has been documented that the single-factor structure in executive functions may best fit to data from children of preschool and early middle age ranges (until approximately 7 to 9 years of age), while in school age and adolescence, there might be a drastic increase in the differentiation of separable EF components above and beyond the common EF factor (Brydges et al., 2014; for a review, see also Karbach & Unger, 2014). In turn, in these age ranges, a fine-tuning of specific functions may start to take priority over domain-general processes.

The influence of a game-based training setting on voluntary and involuntary motivational tendencies in children with ADHD. The results of *Paper III* indicated that in children suffering from ADHD, adding video-game elements to a training setting also clearly enhanced the willingness to train, and had an even more persisting drive than in healthy children (i.e., the willingness did not decline with increasing practice). Hence, in ADHD children, who have more room for improvement, our setting might have been sufficiently rewarding to set a stable level of training motivation. Similarly, Dovis et al. (2012) revealed that as compared to typically developed controls, only ADHD children showed gains on task persistence from a high-motivational WM training variant.

However, at the same time, the high-motivational game setting condition also established a more severe level of behavioral inappropriateness, thus may have fueled an unintentional motivational drive. This unexpected finding indicated that our game setting may have been too arousing for ADHD children according to the early Yerkes-Dodson law (1908). Specifically, this law proposes an inverted U-shaped relationship between arousal and performance: performance may increase with mental arousal but only up to a certain maximum level. If arousal levels exceed this maximum, the performance will drop off. This may especially concern ADHD children that suffer from a shifted arousal level already at the beginning (Leung & Connolly, 1994; Petrescu-Ghenea et al., 2013; Sergeant, 2000). In the present study, we might have manipulated too many motivational features at once (i.e., cover story, stimulus material, task labels, instructions, upgrades, feedback presentation). This fits to the findings of Katz et al. (2014) who made an attempt to disentangle the separate contributions of different kinds of monetary or illustrative rewards, such as scores, prices, or scene-changes, to performance and revealed considerable differences among the impact of these features on the training outcomes. Importantly, they determined adverse effects of certain illustrative rewards on task performance (see also next section).

In turn, on the cognitive level, the high-motivational training setting did not enable larger performance improvements than a standard setting in ADHD children. This was the case for both local and global task-switching processes, both on mean-level performance and performance variability.

Vice versa, our standard setting induced behavioral inappropriateness to a lesser extent, but at the same time enabled only a lower willingness to train and a lower self-reported enjoyment in the training task. Thus, this setting condition might have better balanced involuntary motivational tendencies, but had a strongly limited level of voluntary motivational control.

The apparently unsuccessful alignment of voluntary and involuntary motivational tendencies may have caused a suboptimally biased ‘task state’ in either setting condition. Therefore, it was a logical consequence that executive-control performance was not better promoted in any of these settings. Future training studies should strive for a better alignment of such different sources of motivational energy in ADHD children by a more carefully designed game environment. This could, in turn, allow the children to better meet the double demands arising from the combination of cognitive task content with an arousing task setting.

The benefits and costs of a game-based training setting in childhood. The lacking finding of clear incremental benefits from a high-motivational game setting on cognitive performance in both typically developed children (*Paper II*) and children with ADHD (*Paper III*) is not entirely surprising, but conforms to research placing the value of game environments into question (Hawkins et al., 2013). Indeed, it is an ongoing debate whether game-based modifications of the training setting may or may not benefit cognitive trainings (for a review, see Deveau et al., 2015). Many recent attempts to train cognitive (particularly WM) abilities in ADHD children within a game-based environment have revealed larger training gains than training variants with the same tasks provided in a low-motivational training setting (Dovis et al., 2012; Goldin et al., 2014; Prins et al., 2011). However, quite a number of studies did not obtain this incremental benefit of a high-motivational setting condition. For example, Shaw and Lewis (2005) provided ADHD children with a WM task (albeit not in an intervention context) that was either enriched by game animations or not. The authors obtained a worsening of working-memory performance in ADHD children in the high-motivational compared to the standard task context. Children reported that they had suffered from distraction by the task animations in the game variant. Similarly, Katz et al. (2014) reported a lesser average learning gain after training in a condition with different motivational features than in a condition without any motivational features. Several reasons might explain why gamified cognitive trainings sometimes hamper the learning process: First, changing the surface level can be seen as a second, independent learning event, which ties up cognitive processing resources from the main task and, in turn, may create a dual-task like situation in a high-motivational setting as compared to a low-motivational setting. Second, a wrong dose of motivational enrichment may lead the trainees to miss the turning point of the arousal-performance curve. Third, a suboptimal arrangement of task elements in space and time, such as sudden onsets of motivational features (e.g., animated elements) or an incongruence between cognitive stimuli and motivational elements, can provoke greater distraction

(Deveau et al., 2015; Shaw & Lewis, 2005). Fourth and conversely, game-like features can also be not sufficiently salient to capture attention as discussed in Hawkins et al. (2013). Either way, these arguments clearly show that a good training approach needs to align the directions of both reinforcement and attention to promote learning (Deveau et al., 2015), which may be especially important for children with attention disorder. In many existing forms of game variants, also including ours, this optimal balance has not been achieved. Therefore, the relative costs of game settings may so far still outweigh their benefits (see also Farcas & Szamosközi, 2016).

Recommendations for future training studies. The present dissertation project provided new insights into baseline impairments in state regulation and executive-control abilities in children with ADHD compared to typically developed children that might be of diagnostic value. Importantly, it seems mandatory to include information on performance variability when trying to phenotype alterations in cognitive performance.

Furthermore, the dissertation project made contributions to current research on the complex interactions of motivational training settings and performance outcomes in ADHD children. Given the high prevalence of this disorder (Skounti et al., 2007) and the wide array of negative long-term outcomes (Young et al., 2013), it is imperative to find out effective ways how to promote those children's cognitive development beyond medication treatment. Based on our findings, we recommend:

1) to enrich learning environments for ADHD children only with moderate doses of motivational features in order to avoid an 'overheating' of their motivational status;
2) to rest the implementation of self-designed game environments on an established theoretical rationale (in our case the self-determination theory) in order to limit arbitrariness in the variation of motivational features, and, relating to the first, to carefully manipulate only single features within this rationale;
3) to measure the effects of a setting manipulation on outcome motivation and performance separately by avoiding a

mutual confounding effect (see our innovative willingness indicator);

4) to present ADHD children with a multifaceted measurement of training motivation in order to sensitively capture not only intentional but also unintentional motivational tendencies.

Altogether, finding the right balance between reinforcement and attention should be a main focus of future research (Deveau et al., 2015). Another point of concern is the lacking ecological validity of current game settings. It could be an important avenue for future research to implement more naturalistic settings to increase the likelihood for transfer to everyday behavior. However, from a clinical perspective, a limitation of our empirical study was that we focused only on combined-type ADHD children although the different ADHD subtypes may differ widely in their neuropsychological weaknesses (Dovis, van der Oord, Wiers, & Prins, 2015a; Egeland, Ueland, & Johansen, 2012). Furthermore, future research should address the impact of comorbid disorders on motivational and executive-control functioning in intervention contexts in ADHD children (Demurie, Roeyers, Baeyens, & Sonuga-Barke, 2012).

3.2 Neurocognitive plasticity in old adulthood

Our empirical study in older adults aimed to determine the neural correlates of training in task switching and its transfer to neural processing during executive tasks from different task domains. To address this issue, we measured selective neural changes after task-switching training compared to single-task training (active control group). Specifically, we were interested in training-induced plasticity as a function of spatio-temporal dynamics of the underlying brain activation. To this end, we applied a mixed block-/ event-related design that allows for the dissociation of transient and sustained brain activation within the same paradigm (Petersen & Dubis, 2012; Visscher et al., 2003).

Training-induced neural changes as a function of spatio-temporal dynamics in brain activity in old adulthood. The results of *Paper IV* revealed that training-induced neural changes are dependent on both spatial and temporal characteristics of brain activation: Only on the transient timescale, task-switching training (as compared to single-task active control training) promoted a fine-tuning of brain activation in fronto-parietal circuits. More specifically, participants in this training group showed a reduction of the transient mixing-cost activation in prefrontal areas (i.e., in the bilateral mid-vlPFC and the left IFJ) that was associated with a reduction of behavioral mixing costs. These group differences were pronounced for cue-related instead of probe-related activation. In contrast, in more posterior fronto-lateral and parietal regions (i.e., in the right IFJ and the left SPL), older adults showed a reduction of the transient switching-cost activation that was associated with a reduction of behavioral switching costs. These group differences were pronounced for probe-related instead of cue-related activation. The obtained changes on the mixing-cost activation may indicate that after task-switching training, older adults needed less recruitment of specific prefrontal regions for the advance preparation of global executive-control demands (such as in a mixed-task situation). Conversely, the obtained changes on the switching-cost activation suggest that after task-switching training, older adults needed less recruitment of fronto-lateral and parietal regions for the reactive management of local task demands (such as in switch trials).

The critical point was that this neural fine-tuning of global and local brain processes was limited to the transient timescale of brain activation. In contrast, on the sustained timescale, we found after task-switching training an overall reduction of activation levels that did not aid the precise fine-tuning of global or local executive demands. This down-regulation may have served the release of (sustained) resources that are already less flexibly usable in old age in order to enable a more strengthened use of preserved (transient) activation..

Spatio-temporal neural compensation in old adulthood. In younger adults, global mixing costs in the task-switching paradigm have been primarily linked to modulations of sustained activation in fronto-polar brain regions (Braver et al., 2003). However, sustained activation is less flexibly usable in older adults (Dennis et al., 2007; Jimura & Braver, 2009). In contrast, brain mechanisms from the transient timescale are largely preserved even into very old age (Dennis et al., 2007; Jimura & Braver, 2009), but are often not used to their full potential. Prior brain imaging and event-related brain potential studies suggest that only high-performing older adults rely more heavily on transient and reactive control mechanisms (e.g., Jimura & Braver, 2009; Karayanidis et al., 2010; Schmitt et al., 2014b; Whitson et al., 2013). In contrast, low-performing older adults often try to continue applying the same routines as younger adults, which can in turn lead to behavioral failure. Given that in our study in older adults, the mixing-cost activation was selectively fine-tuned on the transient rather than on the sustained timescale after task-switching training (see *Paper IV*) may indicate that these elder participants had been enabled to use an alternative route for the proactive modulation of global executive control. Hence, our result pattern may reflect training-induced spatio-temporal compensation in old age; that is, a replacement of less flexible sustained proactive control in frontopolar regions by a refined transient proactive control in lateral prefrontal regions. This idea was also confirmed by the crossover change in sustained and transient activation dynamics that we were able to detect within the basal ganglia in the task-switching training group. Sustained DA release in the striatum has been primarily associated with WM maintenance and general responsivity, while transient DA release has been related to gating and updating mechanisms (Braver et al., 2005; Cohen et al., 2002; Murty et al., 2011). Hence, the shift from a sustained to a transient timescale in brain activation in the BG – whereby brain activation in the BG has been linked to dopamine release (see Footnote 21) – may again reflect the reduction of age-impaired proactive (sustained) maintenance in favor of enhanced reactive, transient updating mechanisms (Jimura & Braver, 2009).

How do the current findings fit into the more traditional hypotheses on age-related neural compensation, such as HAROLD, PASA, CRUNCH or non-selectivity (see chapter 2.3.1.3)? Although we did not explicitly test these accounts in the present dissertation project (as we were mainly interested in traces of temporal compensation), some of our results were clearly in line with these assumptions.

Importantly, the results of *Paper IV* also demonstrated that the reductions in the mixing- and switching-cost activation after task-switching training in older adults were due to a convergence of activation levels in the different trial conditions. This fits to the assumption of a neural *de-differentiation* in advanced age (DiGirolamo et al., 2001; Karayanidis et al., 2010; Schmitt et al., 2014b; Whitson et al., 2013). This neural processing pattern was more dissimilar to the processing pattern of untrained younger adults. As we had previously carried out (see chapter 2.3.1.3), successful compensation is reflected in increased neural age differences coupled with reduced behavioral age differences. Given that the training-induced pattern of a neural de-differentiation in older adults was in our study coupled with a more similar behavioral performance to younger adults thus pointed clearly to successful compensation (Reuter-Lorenz & Park, 2014).

Another result was that after task-switching training, older adults showed less recruitment of neural resources, thus higher processing efficiency, in mixed-task trials. A similar result was obtained by Heinzel et al. (2016) after WM training in older adults. The authors revealed a selective decrease of BOLD signals in the superior frontal sulcus in the n-back task for their older adult training group compared to a passive control group, which they attributed to a training-related boost of processing efficiency in canonical WM networks. However, in that study, the activation decreases were limited to task activation during 1-back and 2-back (low and medium task demand) levels, and not obtained for activation during 3-back (high task demand) levels. To interpret this pattern, the researchers referred to the CRUNCH account (Cappell et al., 2010). The CRUNCH account suggests that older adults may improve in neural efficiency in lower-demanding task conditions but not in higher-demanding task conditions that may exceed their capacity limit. In contrast, in our study, we found the activation decrease in the high-demanding mixed-task condition (compared to a slight increase in the low-demanding single-task condition) in trained older adults, which might at first sight contradict the CRUNCH hypothesis. However, this finding might be explainable as follows: The demand level of an experimental task is defined in relative rather than in absolute terms. For example, if one compares only 1- and 2-back conditions in an n-back task, the 2-back condition will be framed as the high-demand condition (i.e., placing relatively higher demands than the 1-back condition). If one, however, compares 1-, 2-, and 3-back conditions, the 2-back condition will be reframed as the medium-demand condition. Similarly, in our task-switching paradigm, we compared global single- and mixed-task demands (or local switch and repeat demands, respectively). While we can clearly state that the mixed-task condition will place relatively higher demands on executive control than the single-task condition, we cannot determine whether the mixed task was (in absolute terms) of medium or high difficulty according to CRUNCH. Either way, we found that transient activation associated with the relatively more difficult mixed-task (or switch trials, respectively) was reduced in older adults after task-switching training. Vice versa, the relatively easier conditions (i.e., single-task trials or repeat trials, respectively) showed instead an increase of brain activation after task-switching training. Importantly, the single-task training group showed the reverse pattern, namely a decrease of brain activation for the relatively easier single trials (or for repeat trials, respectively). Hence, each training group seemed to enhance neural efficiency specifically for the practiced task condition. This implies that in intervention contexts, it would be advisable to reframe the distinction between 'more and less *difficult*' conditions (such as according to the CRUNCH hypothesis) by a distinction between 'more or less *practiced*' conditions when trying to predict the direction of brain activation changes.

A number of fMRI studies examining age differences in cognitive functioning, such as in memory performance, found that older adults additionally recruited the homologous region of the opposite hemisphere (i.e., the HAROLD account by Cabeza, 2002), while younger adults showed a more lateralized pattern of activation. In the present dissertation project, we did not systematically compare uni- versus bilateral recruitment between younger and older adults after the intervention.

Moreover, we did not distinguish between training-induced spatial redistribution and reorganization effects (Kelly & Garavan, 2004): a redistribution refers to activation increases or a decreases in already previously activated brain regions, while a reorganization refers to activation changes in brain regions that have not been activated before the training. Both patterns have been identified in younger as well as in older adults and, in turn, may interact differently with temporal dynamics (Erickson et al., 2007a; Erickson et al., 2007b). Hence, future studies should further specify neural age differences depending on the hemispheric laterality and on redistribution versus reorganization effects and try to relate them to our findings on temporal compensation.

3.3 Modulations of flexible and plastic changes in local and global executive control across the lifespan

In terms of the overarching framework on cognitive plasticity of Lövdén et al. (2010), our findings in childhood may imply that our manipulation of the *interface of the training mismatch* (i.e., a high-motivational game setting versus a low-motivational standard setting) had specifically promoted flexibility (i.e., a better deployment of already mature local cognitive processes). It had less an impact on profound plastic changes in global cognitive functioning. This seems, however, reasonable from the viewpoint that a game setting with multiple feature manipulations can also tie up processing resources from the main task, thus leaving fewer resources that could be invested into such metabolically costly changes.

Our findings in old adulthood may imply that our manipulation of the *intensity of the training mismatch* (i.e., task-switching training versus single-task training) had also promoted flexibility; that is, a better deployment of still retained transient brain processes at the expense of sustained processes. In the introduction chapter of this dissertation, we had outlined that older adults may engage preferentially flexible changes for two reasons: first, because they are less in need of metabolically costly plastic changes as they have already accumulated richer flexibility ranges over a lifetime; and second, because their biologically altered brain status may no longer allow them to engage too expensive changes (Kühn & Lindenberger, 2016). Hence, unlike in younger adults, their 'secondary' response (i.e., after primary immediate adaptions) is often not plastic but flexible in nature: specifically, a 'fine-tuned' flexible deployment of resources. Our findings were well in line with this assumption: We found after task-switching training in older adults a fine-tuned, flexible utilization of preserved *transient* brain processes to compensate for the less efficient *sustained* resources.

3.4 Limitations

Although this dissertation project provided important new insights into the nature and scope of training-induced changes in executive control over the lifespan, several further limitations should be addressed in future research:

Regarding training interventions in childhood, from a methodical perspective, we recommend first, to account for baseline differences in the general susceptibility to motivational input; for example, by measuring inter-individual differences in motivational dispositions (Cacioppo et al., 1996; Pintrich, 2000) and especially in markers of initial voluntary and involuntary motivation. To this end, one may also combine measures of overt behavior with physiological indices (e.g., pupil dilation, cardiac responses, skin conductance levels, evoked brain potentials, or hormonal excretions) to get more valid proxies for arousal or behavioral activation (Audiffren, 2009). This may be particularly important in ADHD children due to their impairments at multiple motivational levels.

Second, unlike the training task in the high-motivational group, the transfer measurement in our study had been presented in a standard setting. This may entail the following risks: First, the interface of the transfer battery was more similar to the training setting of the low-motivational setting group. The early ‘identical elements theory’ of Thorndike (1903) posits that the greater is the number of shared elements between training and transfer tasks, the greater is the likelihood for transfer to occur. Applying this idea to the ‘elements’ of the task setting, our low-motivational standard setting group may have had the higher likelihood for transfer to occur because their training and transfer settings had shared more features. Hence, this might have counteracted our setting manipulation at the posttest. Second, the contrast between the highly encouraging training sessions and the low-rewarding transfer posttest session may have induced a large motivational gap in the video-game setting group. In turn, children in this group might have been driven at posttest to a drop in task engagement even below their baseline level.

Regarding training interventions in older adults, from a methodological perspective, it might be criticized that we relied exclusively on an ROI-based approach. ROI-based approaches have the advantage that they have more statistical power than whole-brain analyses because the number of statistical comparisons is greatly reduced. This limits the need for multiple-comparisons correction (Poldrack et al., 2011). However, such an approach may also prevent one from discovering other regions outside the ROI-mask that could be involved in the mechanisms of interest. Nevertheless, we still applied the more powerful ROI given our strict criteria for ROI selection. Besides, the applied mixed block-/event-related design already forfeits power due to the loss of degrees of freedom by the large number of sustained and transient regressors involved, which we believed made a ROI-based approach a suitable compromise in our study. However, future replications of the present results could combine whole-brain and ROI-based approaches to obtain a more comprehensive picture.

A second major concern is that neural plasticity cannot be phenotyped exhaustively by considering only changes in brain functioning (i.e., the 'software' of the brain), but requires also the investigation of structural adaptations of brain tissue, such as grey and white matter (i.e., the 'hardware' of the brain). Recent reviews on the cognitive neuroscience of aging have attested a bulk of changes in the neuroanatomical substrate, with an approximately linear macro-level decline in brain weight and volume of 2% per decade, going along with an expansion of cerebral ventricles and sulci (Reuter-Lorenz & Mikels, 2006). These macro-structual alterations become apparent in changes at the micro level, such as shrinkage of neuronal cell bodies, loss of synaptic density, debranching of dendritic arbors, depletion of dopamine receptors, and especially damage to connecting white matter fibers. Although we know about limited potential to plasticity in later stages of the lifespan, the extent to which executive-control training can boost such structural changes in older adults' brain morphometry has not been thoroughly examined yet. Hence, future research should explore the potentials and constraints of structural plasticity (i.e., changes on different tissue classes, such as grey and white matter) in the aging brain.

Regarding general issues concerning both age groups, it was the aim of the present study to measure different executive control processes, such as switching, inhibition and WM processes, when they are required to act together. However, using the same paradigm to measure different executive processes at once, might not guarantee an equally reliable assessment of the separate involved processes. Therefore, we opt for a direct comparison of our findings to findings from 'process-purer' paradigms. However, executive-control tasks are rarely process-pure (Reuter-Lorenz et al., 2016). Therefore, Reuter-Lorenz et al. (2016) further propose that 'a latent variable approach can be used to address the impurity problem with statistical methods that extract common variance across multiple tasks targeting the same putative EF' (Reuter-Lorenz et al., 2016p. 246-247).

Beyond the reliable average benefit, there is accumulating evidence for large inter-individual heterogeneity in the initial supply as well as in practice-induced cognitive changes (Karbach & Kray, 2016). Lövdén et al. (2010) designate the amount of practice-induced plasticity a function of the discrepancy between the demands of the training and individual baseline potentials. Comparisons at the group level can clearly not inform about these individual baseline strengths and difficulties interacting with the environmental training demands (Karbach & Kray, 2016). Especially older adults start with very different ability profiles because their learning histories have diverged over a lifetime. The investigation of plasticity in advanced age therefore makes the consideration of pre-existing inter-individual differences indispensable. Hence, future research should analyze practice-induced cognitive and neural plasticity in children and old age as a function of inter-individual differences in baseline capacities and other reserve variables.

3.5 Outlook project: the investigation of neural transfer depending on spatio-temporal activity dynamics in old age.

We are currently in the process of analyzing the neural transfer data of our study in older adults (see *Paper IV*) as a function of spatio-temporal dynamics of the underlying mechanisms. The preliminary results raise even more attention to the importance of temporal brain dynamics. As an outlook, we aim to shortly summarize the background and the preliminary results of this study to emphasize the findings of this dissertation.

Theoretical background and design. In *Paper IV*, we provided evidence for spatio-temporal interactions of neural plasticity associated with improvements in the task-switching task. More specifically, we revealed selective changes in block-related brain activation in fronto-polar regions and in the basal ganglia, while in trial-related brain activation in fronto-lateral and parietal regions after task-switching training. Based on these findings, in a next step, we try to determine whether such spatio-temporal interactions also modulate the neural transfer of training to structurally dissimilar cognitive tasks. In general, neural transfer has been assumed to occur if activation changes associated with the training and transfer tasks rely on the same cognitive processes and on spatially overlapping brain regions (Dahlin, Neely, Larsson, Bäckman, & Nyberg, 2009). However, it has not yet been examined whether the amount of transfer also depends on temporal overlap, that is, on overlapping sustained or transient timescales of the involved neural processes. Therefore, in the current project, we aim to dissolve interactions between spatial and temporal dynamics of brain mechanisms supporting transfer. In our study in older adults, we had also administered two transfer paradigms, either sensitive to capture sustained dynamics of task-switching behavior (i.e., a delayed-recognition working-memory task, adapted from Clapp, Rubens, & Gazzaley, 2010) or to capture transient dynamics (i.e., a context-updating task, adapted from Schmitt, Ferdinand, & Kray, 2014a). These were approached by the appropriate block-related or event-related fMRI design. Neural transfer is here defined as selective changes in task activation during the delayed-recognition or context-updating transfer task after task-switching training compared to single-task control training. *In respect of the Lövdén et al. (2010) framework*, the same design principles as in Paper IV may apply here, except that we tested a broader *scope of the mismatch*, namely transfer to neural processing in other executive tasks than the task-switching training task.

Research predictions. To systematically investigate spatial and temporal overlap of activation changes during the training and transfer tasks, we currently test one of three likely outcomes, again based on a region-of-interest (ROI) analysis approach:

(1) Spatial overlap (same ROIs, different timescale); that is, overlap in ROIs that had proven sensitive to the other timescale in the task-switching training task. Given this overlap criterion, the sustained-sensitive delayed-recognition task would show transfer in exactly those ROIs that had been sensitive to changes in transient activation in the task-switching task (i.e., fronto-lateral, parietal networks; vice versa for the context-updating task in frontal pole, basal ganglia).

(2) Temporal overlap (same timescale, different ROIs); that is, overlap in changes on sustained or transient activation in ROIs outside those obtained for the task-switching task.

(3) Spatio-temporal overlap (same ROIs, same timescale); that is, an exact reproduction of patterns found for the task-switching task. Given this overlap criterion, the sustained-sensitive delayed-recognition task would show transfer in exactly those regions that had also been sensitive to changes in sustained activation in the task-switching task (i.e., frontal pole, basal ganglia; vice versa for the context-updating task in fronto-lateral, parietal networks).

Preliminary results and conclusions. Results of our preliminary analyses suggest that neural transfer was also supported by spatio-temporal interactions. More specifically, for the sustained-sensitive delayed-recognition task, we obtained group-selective changes in sustained activation in exactly the same region where we had previously found training-induced changes in the task-switching task (i.e., in the bilateral basal ganglia). Hence, transfer to the sustained-sensitive task might be clearly overlapping in both spatial and temporal features of brain activation with the training task (i.e., *spatial and temporal overlap of transfer effects*). However, for the transient-sensitive context-updating task, we obtained so far, albeit on a lenient threshold, selective changes in transient activation in different fronto-parietal regions than those where we had previously found training-induced changes in the task-switching task (i.e., in the right dorsolateral PFC and in the inferior parietal lobule). Hence, these transfer effects cannot be simply traced back to overlapping spatial features of brain activation in the training and transfer task (Dahlin et al., 2009) but potentially to temporal overlap *(i.e., only temporal overlap of transfer effects)*.

These results suggest that neural transfer may indeed presume an overlap in 'neural resources' (Karbach & Kray, 2016) but these neural resources can also be defined temporally, especially in the context of executive-control training tapping into global, sustained and local, transient control mechanisms. These first results of an ongoing analysis project point to further evidence for the temporal hypothesis of compensation in age (Dew et al., 2012; see also Martins et al., 2015).

Synopsis and general conclusion

Altogether, the present thesis contributes to a more comprehensive understanding of the complex mechanisms underlying and modulating training-induced plasticity in executive control across the lifespan.

The results of *Paper II* revealed that in typically developed children, a high-motivational training setting could well enhance training willingness in children, although this video-game setting was not sufficient to attenuate the motivational decline over the training sessions. Moreover, the motivational game setting boosted behavioral performance, at least in training-specific, local executive processes. The results of *Paper III* indicated that in children suffering from specific developmental disorders, the addition of video-game elements to a training setting also clearly enhanced the willingness to train, and had an even more sustaining effect than in healthy children as the willingness to practice did not decline over time. This finding may imply successful compensation of impaired motivational resources in ADHD children. However, at the same time, this setting condition also established more behavioral ADHD symptoms. In turn, the high-motivational training setting did not better promote cognitive performance than a standard setting.

Hence, for task-switching training interventions during periods early in the lifespan, we endorse the consideration of an appealing motivational training setting in typically developed children. This may enhance training willingness (at least in early learning stages) and boost their cognitive development (at least in training-specific, local executive processes). However, in subclinical samples that become easily distracted, such as in children diagnosed with ADHD, one should only carefully manipulate the training setting to avoid an 'over-heating' by the task layout. Therefore, similarly to the early Yerkes-Dodson law (1908), the relationship between motivational enrichment of the training setting and executive control might follow a bell-shaped dose-response function in childhood; that is, a motivational enrichment may enhance the development of executive control up to a certain point. However, too much enrichment may cause these functions to decay back to or even beyond baseline– an insight that should be taken into account when trying to design adequate training interventions for children in the future.

Regarding the use of cognitive interventions in old age, the present thesis provided important new insights into the neural mechanisms underlying training-induced behavioral improvement in executive-control functioning. To uncover the latent potentials of the aging brain, one needs to consider interactions between spatial and temporal dynamics of brain activation. Another noteworthy finding is that training in older adults may not simply remediate the neural processing pattern of younger adults. In contrast, training may help older adults establish an alternative, compensatory processing pattern that enables them to deal with executive control demands even at an advanced age. Hence, our findings imply that task-switching training late in the lifespan can serve a powerful fine-tuning and boosting of still preserved mechanisms – which clearly emphasizes the viewpoint of modern lifespan theory (Baltes et al., 1999): … *that the ability to adapt 'is far from set in its trajectory (…) at the completion of [adulthood]' (Nelson & Bloom, 1997) but does continue to unfold into very old age.*

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Appendix

The appendix of this dissertation (i.e., the four original articles included in the publication list) will be provided upon request.

Eigenständigkeitserklärung

Hiermit versichere ich, die vorliegende Arbeit selbständig verfasst zu haben, keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt und die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen kenntlich gemacht zu haben.
Ich habe bei der Auswahl und Auswertung von Material und bei der inhaltlich-materiellen Anfertigung der Arbeit nur von den genannten Personen in der jeweils angegebenen Weise Hilfe erfahren und insbesondere nicht die entgeltliche Hilfe von Vermittlungs- und Beratungsdiensten in Anspruch genommen.

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AUSZEICHNUNGEN UND FÖRDERUNGEN

2014

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„Beste Seminarveranstaltung im Fachbereich Psychologie im akademischen Jahr 2013/2014“

- Einführung in die Psychologie Kurs A - 1. Platz
- Einführung in die Psychologie Kurs C - 2. Platz

Verliehen durch die Fachschaft Psychologie (ermittelt auf Basis der Evaluations-Ergebnisse des Evaluationsprojektes Qualis/ Qualität der Lehre im Studium, Lehrstuhl für Differentielle Psychologie und Psychologische Diagnostik der UdS)

2013

Auszeichnung Masterabschluss

Bestes Abschlussergebnis

Ermittelt anhand des Gesamtnotenspiegels der M. sc.-Kohorte 2013 Psychologie an der UdS

2012 - 2013

Förderung

Deutschlandstipendium für besondere Begabung und Leistungsfähigkeit

Verliehen durch die UdS im Rahmen eines Förderprogramms des Bundesministeriums für Bildung und Forschung

2011

Auszeichnung Bachelorabschluss

Bestes Abschlussergebnis

Ermittelt anhand des Gesamtnotenspiegels der B. sc.-Kohorte 2011 Psychologie an der UdS

MITGLIEDSCHAFTEN

seit Oktober 2014

Mitglied des Netzwerks „Neurowissenschaftliche Methoden in der Entwicklungspsychologie“

(*Network Neuroscientific Methods in Developmental Psychology* FE1247/3-1, Antragssteller: Dr. Nicola Ferdinand/ Universität des Saarlandes, Prof. Dr. Markus Paulus/ LMU München)

seit September 2012

Assoziiertes Mitglied der Deutschen Gesellschaft für Psychologie (DGPs)

Fachgruppen: Entwicklungspsychologie, Allgemeine Psychologie, Psychobiologie und Neuropsychologie, Methoden und Evaluation

AUßERUNIVERSITÄRE TÄTIGKEITEN

2010 - 2011

Co-Supervision der Kindergruppe „Kinder aus suchtbelasteten Familien“, Caritasverband, Neunkirchen (Honorartätigkeit)

September 2010 - Oktober 2010

Praktikum im Caritasverband, Neunkirchen

Juli 2010 - August 2010

Praktikum im Sozialpädiatrischen Zentrum (SPZ), Pädiatrische Kinderklinik, Neunkirchen/Kohlhof

2008 - 2011

Nachhilfe im Campus Lernstudio, Neunkirchen

(Fächer: Deutsch, Englisch, Französisch, Latein, Mathematik, Chemie u. a.)

Juli 2007

Praktikum in der Klinik für Schmerzen und Palliativversorgung, Caritasklinik St. Theresia, Saarbrücken

KENNTNISSE UND FÄHIGKEITEN

Fremdsprachen

Französisch (7 Schuljahre), Englisch (3 Schuljahre), Latein (9 Schuljahre, Großes Latinum)

PC-Kenntnisse

MS Office: sehr gute Kenntnisse
SPSS Statistics: sehr gute Kenntnisse
Deltagraph: gute Kenntnisse
Mplus: gute Kenntnisse
SPM: gute Kenntnisse
E-Prime: gute Kenntnisse
Matlab: Basiskenntnisse
Python: Basiskenntnisse
Adobe InDesign: Basiskenntnisse

PUBLIKATIONEN

JOURNAL ARTICLES

Dörrenbächer, S., Wu, C., Zimmer, H., & Kray, J. (eingereicht). *Compensation in brain activity dynamics after cognitive-control training in older adults.*

Dörrenbächer, S. & Kray, J. (eingereicht). *The impact of a game-based task-shifting training on motivation and executive control in children with ADHD.*

Dörrenbächer, S., Müller., P. M., Tröger, J. & Kray, J. (2014). Dissociable effects of game elements on motivation and cognition in a task-switching training in middle childhood. *Frontiers in Psychology, 5*:1275.

Wagner, D., **Dörrenbächer, S.** & Perels, F. (2014). A framework for designing training programs to foster self-regulated learning and text analysis skills. *Education Research International*, *vol. 2014*, Article ID 510342.

BUCHKAPITEL UND MONOGRAFIEN

Kray, J. & **Dörrenbächer, S.** (im Druck). The effectiveness of training in task switching: New insights and open issues from a lifespan view. In M. Bunting & J. Novick, *Cognitive Training*. Oxford: Oxford University Press.

Dörrenbächer, S. (2013). *Evaluation eines selbstregulationsstrategischen Interventionsansatzes zur Förderung analytischer Sprachfähigkeiten am Beispiel der Struktursprache Latein.* (unveröffentlichte Masterthesis)

Dörrenbächer, S. (2011). *Zum Zusammenhang zwischen selbstreguliertem Lernverhalten und akademischer Fremdsprachenkompetenz.* (unveröffentlichte Bachelorthesis)

ABSTRACTS UND KONFERENZBEITRÄGE

Dörrenbächer, S. & Kray, J. (2017). *The influence of a game-based task-shifting training on cognitive-control and state-regulation impairments in children with ADHD.* ESCOP2017 (Potsdam).

Dörrenbächer, S., Kray, J. & Zimmer, H. (2017). *Temporally dissociable signatures of functional plasticity after taskshifting training in older adults.* ESCOP2017 (Potsdam).

Dörrenbächer, S. & Kray, J. (2017). *How a game setting may or may not benefit a task-shifting training with cross-task competition in children with ADHD*. DGPS PaEPSY 2016: Gemeinsame Tagung der Fachgruppen Entwicklungspsychologie und Pädagogische Psychologie 2017 (Münster).

Dörrenbächer, S. , Kray, J. & Zimmer, H. (2017). *Neural signatures of practice-induced changes after a task-switching training in old age.* DGPS PaEPSY 2016: Gemeinsame Tagung der Fachgruppen Entwicklungspsychologie und Pädagogische Psychologie 2017 (Münster).

Dörrenbächer, S. (2016). Differential effects of a game-based task-switching training on motivation and interference control in children with ADHD. In J. Funke, J. Rummel & A. Voß (Hrsg.), *TeaP 2016: Abstracts of the 58th Conference of Experimental Psychologists* (S. 59). Lengerich: Pabst Science Publishers.

Dörrenbächer, S. (2015). Neuronale Aktivierungskorrelate übungsinduzierter Veränderungen in kognitiver Kontrolle in Abhängigkeit von Lebensalter und interindividuellen Unterschieden. In C. Bermeitinger, A. Mojzisch & W. Greve (Hrsg.), *TeaP 2015: Abstracts of the 57th Conference of Experimental Psychologists* (S. 68). Lengerich: Pabst Science Publishers.

Dörrenbächer, S., Müller., P. M., Tröger, J. & Kray, J. (2015). The influence of a motivational game setting on a task-switching training in middle childhood. In C. Bermeitinger, A. Mojzisch & W. Greve (Hrsg.), *TeaP 2015: Abstracts of the 57th Conference of Experimental Psychologists* (S. 68). Lengerich: Pabst Science Publishers.

TALKS UND POSTER

Dörrenbächer, S. (2016). *Gauging cognitive and neural plasticity in response to task-switching training in old age: an individual-differences approach.* Talk, Berichtskolloquium des IRTG "Adaptive Minds: Neural and Environmental Constraints on Learning and Memory", Weiskirchen, Dezember 2016.

Dörrenbächer, S. (2015). *Is task-switching performance and its dynamic neural signatures modulated by interindividual differences in interference-control abilities?* Posterpräsentation, Deutsch-Chinesische Fallschool des IRTG "Adaptive Minds: Neural and Environmental Constraints on Learning and Memory", Bosen, Oktober 2015.

Dörrenbächer, S., Stenger, K. & Kray, J. (2014). *Neural correlates of age-related changes after practice in task switching: an individual differences approach.* Posterpräsentation, Workshop "The Interplay between Structural Brain Maturation and the Development of Cognitive Functions", LMU München, Dezember 2014.

Dörrenbächer, S. (2014). *Neurocognitive Plasticity in Old Age - Practice-Induced Changes on the Neural Signatures of a Task-Switching Training.* Talk, Brain Imaging Meeting, Saarland University Medical Center, Homburg, November 2014.

Dörrenbächer, S. (2014). *Age-related changes in practice-induced neuronal changes after task-switching training: An individual differences approach.* Talk, Berichtskolloquium des IRTG "Adaptive Minds: Neural and Environmental Constraints on Learning and Memory", Bildungszentrum Kirkel, November 2014.