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The Development of Flexible Behavior:
Age Differences and Training-Related Changes in Activation,
Connectivity, and Neural Representations During Task Switching

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List of individual papers

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Glossary

aI – anterior insula

CSI – cue stimulus interval

DCCS – Dimensional Change Card Sort Paradigm (Zelazo, 2006); a paradigm to investigate task switching in young childhood

dIPFC – dorsolateral prefrontal cortex

dACC – dorsal anterior cingulate cortex

EEG – electroencephalography

fO – frontal operculum

GLM – general linear model

HDDM – hierarchical drift diffusion models (Wiecki et al., 2013)

IFJ – inferior frontal junction

MRI – magnetic resonance imaging; also fMRI for functional magnetic resonance imaging

MVPA – multivariate pattern analysis (Haynes & Rees, 2006; Kriegeskorte et al., 2006)

PFC – prefrontal cortex; also lPFC for lateral PFC

PPI – psychophysiological interaction; also gPPI for generalized psychophysiological interaction (McLaren et al., 2012)

ROI – (brain) region of interest

RSA – representational similarity analysis (Kriegeskorte et al., 2008)

RT – response time

SPL – superior parietal lobe

Abstract

The ability to flexibly adapt behavior in the light of changing contextual demands is crucial for successful goal pursuit. With age, children become increasingly able to flexibly switch between tasks but show poorer switching performance even in late childhood. Given the crucial role of cognitive flexibility in daily life, such as the ability to shift to a new strategy to solve a problem when the previous one did not work, studies have aimed to improve cognitive flexibility with training in children. A key question for the effectiveness of these interventions is understanding why children show lower cognitive flexibility than adults. In this dissertation, I shed new light on this question, by investigating 8–11-year-old children using behavioral measures in combination with measures of univariate activation, multivariate decoding, and task-related connectivity based on data from functional magnetic resonance imaging (fMRI).

In *Papers 1 & 2*, I first addressed the question of which neural processes support the development of cognitive flexibility. In *Paper 3*, I examined how these neural processes change with training. I have prefaced the three papers with a synopsis in which I outline the theoretical framework of the dissertation and summarize the current empirical findings. Finally, I summarize the results of the empirical part of this dissertation and discuss their contribution to our understanding of the development of cognitive flexibility.

Flexibly switching between tasks comes at a cost, evident in decreased accuracy and increased response times. Specifically, compared to performing single tasks in isolation, task switching poses greater demands on maintaining and managing multiple task sets, thus eliciting so-called mixing costs. Additionally, a switch to a different task compared to a repetition of the same one requires the inhibition of the previously relevant task set and updating the newly relevant one, resulting in so-called switch costs. Previous research has demonstrated that mixing and switch costs show different patterns of age differences with switch costs approaching adult levels earlier. The present dissertation builds on these findings to examine the neurocognitive processes contributing to the presumably protracted development of mixing costs.

In *Paper 1*, comparing children (8–11 years) and adults (20–30 years), I examined how neural processes supporting sustained and transient control processes support age-related decreases in mixing and switch costs, respectively. I showed that while evident for both, age differences were greater for sustained activation and mixing costs than for transient activation and switch costs. Additionally, the results of *Paper 1* outline a potential alternative mechanism via which children can address increased sustained control demands: children that showed a

less adult-like sustained activation pattern but greater increases in connectivity performed better. Taken together, *Paper 1* demonstrated that children managed increased sustained control demands during task switching in at least two ways, (1) increased activation in the brain regions also recruited by adults, or (2) increased connectivity with additional brain regions in the lateral prefrontal cortex (IPFC), thus potentially relying on additional metacontrol processes.

One factor proposed to contribute to age-related improvements in task switching is an increasing ability to represent multiple rules and effectively update these when necessary. Using the same sample of children and adults, *Paper 2* investigated this hypothesis using multivariate pattern analysis to elucidate the role of neural task-set representations on age differences in task switching. Results demonstrated that neural activation patterns on switch trials held less information regarding the currently relevant task than on repeat trials. Intriguingly, this switch-related reduction of task-set distinctiveness did not differ between children and adults, showing a striking level of maturity in the neural representation of task sets and raising the question which other mechanisms contributed to greater switch costs in late childhood.

Building on the insights from *Papers 1* and *2*, *Paper 3* explored how the neural and cognitive processes supporting the development of task switching changed in children that either trained intensive single tasking or intensive task switching over nine weeks. Using drift-diffusion models and fMRI data, I investigated how cognitive and neural processes during task switching changed with training. Faster accumulation of evidence as indicated by increased drift rates, along with decreased activation in the IPFC suggested more efficient rule processing with intensive task-switching training. The accompanying changes in boundary separation further suggested strategy changes, such that children may have allocated cognitive control resources differently, potentially because of improvements in monitoring task demands, enabling them to match their performance accordingly.

Taken together, the empirical findings of this dissertation converge to reveal a consistent picture of increasingly more refined recruitment of frontoparietal brain regions, in particular the IPFC, both with age and with intensive training during childhood. They thus raise questions on the role of hierarchical cognitive control and metacontrol processes for developmental improvements of cognitive flexibility. The novel insights into task switching presented in this dissertation thus further our understanding of development and learning in cognitive control, and cognition more generally.

Zusammenfassung

Die Fähigkeit zur Anpassung unseres Verhaltens an wechselnde kontextuelle Anforderungen bildet eine wichtige Voraussetzung für die flexible und effiziente Verfolgung von Handlungszielen. Mit zunehmendem Alter gelingt es Kindern besser, zwischen verschiedenen Aufgaben zu wechseln. Im Vergleich zu Erwachsenen lassen sich aber auch am Ende der Kindheit noch Effizienzunterschiede im Aufgabenwechsel nachweisen. Angesichts der hohen Bedeutung kognitiver Flexibilität sind Versuche unternommen worden, die kognitive Flexibilität bei Kindern durch Training zu verbessern. Die theoretische Begründung dieser Trainingsstudien war häufig wenig präzise und die Befundlage entsprechend unklar. In meiner Dissertation gehe ich daher einer überwiegend grundlagenwissenschaftlichen und vorgelagerten Fragestellung nach: Ich untersuche auf behavioraler und neuronaler Ebene die Gründe von Altersunterschieden und Trainingszugewinnen in der kognitiven Flexibilität. Zu diesem Zweck untersuche ich 8–11-jährige Kinder mithilfe von Verhaltensdaten sowie von Bildgebungsdaten der funktionellen Magnetresonanztomographie bezüglich der univariaten Aktivierung, der Konnektivität und der multivariaten Dekodierung von Repräsentationen.

In den *Schriften 1* und *2* gehe ich zunächst der Frage nach, welche neuronalen Prozesse die Entwicklung der kognitiven Flexibilität unterstützen. *Schrift 3* untersucht, wie sich Verhalten und neuronale Prozesse trainingsbedingt verändern. Den drei Schriften habe ich eine Synopse vorangestellt, in der ich den theoretischen Rahmen der Dissertation erläutere und die Befundlage zusammenfasse. Abschließend fasse ich die Ergebnisse meiner Dissertation zusammen und erörtere ihren Beitrag zum Stand der Forschung.

Die Kosten eines Aufgabenwechsels zeigen sich in geringerer Genauigkeit und längeren Reaktionszeiten. Dabei stellt der Aufgabenwechsel im Gegensatz zur isolierten Ausführung einzelner Aufgaben höhere Anforderungen an die Aufrechterhaltung und Handhabung mehrerer Aufgabensets (engl. task sets), die mit sogenannten *Mischkosten* einhergehen. Darüber hinaus stellt der Wechsel zu einer anderen Aufgabe im Vergleich zur Wiederholung derselben Aufgabe erhöhte Anforderungen an die Hemmung des zuvor relevanten Aufgabensets und die Aktualisierung des nun relevanten Aufgabensets, die zu sogenannten *Wechselkosten* führen. Vorliegende Befunde zeigen, dass Mischkosten und Wechselkosten unterschiedliche Muster von Altersunterschieden aufweisen; dabei nähern sich die Wechselkosten von Kindern dem Niveau von Erwachsenen früher an als die Mischkosten. Die vorliegende Dissertation baut auf diesen Befunden auf und untersucht die Gründe der

unterschiedlichen Entwicklungsverläufe von Misch- und Wechselkosten auf behavioraler und neuronaler Ebene.

In *Schrift 1* untersuche ich den Beitrag andauernder und vorübergehender Kontrollprozesse zu Altersunterschieden in Misch- und Wechselkosten. Die Ergebnisse zeigen, dass die Altersunterschiede zwischen Kindern und Erwachsenen in Mischkosten und der damit zusammenhängenden andauernden Aktivierung größer sind als bei den Wechselkosten und der vorübergehenden Aktivierung. Darüber lassen die Ergebnisse von *Schrift 1* Rückschlüsse auf einen möglichen alternativen Mechanismus zu, mit dem Kinder erhöhte Anforderungen an die andauernde Kontrolle bewältigen: Kinder, deren andauerndes Aktivierungsmuster weniger dem der Erwachsenen ähnelte, die dafür aber eine stärkere Zunahme der Konnektivität zeigten, wiesen geringere Mischkosten auf. Insgesamt konnte ich in *Schrift 1* meiner Dissertation somit zeigen, dass Kinder erhöhte Anforderungen an andauernde Kontrolle während des Aufgabenwechsels auf mindestens zwei Arten bewältigen: (1) durch die erhöhte Aktivierung von Hirnregionen, die auch bei Erwachsenen rekrutiert werden, oder (2) durch erhöhte Konnektivität mit weiteren Hirnregionen im lateralen präfrontalen Kortex, die möglicherweise auf die Beteiligung zusätzlicher Prozesse der Handlungssteuerung hinweisen.

Die Zunahme der Fähigkeit zur Repräsentation und handlungsdienlichen Aktivierung mehrerer Regeln könnte einen wichtigen Grund für die zunehmende Genauigkeit und Schnelligkeit des Aufgabenwechsels darstellen. In *Schrift 2* habe ich diese Hypothese mit Hilfe einer multivariaten Musteranalyse untersucht, mit der sich der Beitrag der neuronalen Repräsentation von Aufgabenset zu Altersunterschieden im Aufgabenwechsel bestimmen lässt. Die Ergebnisse zeigen, dass die neuronalen Aktivierungsmuster bei Aufgaben, denen ein Wechsel von einem Aufgabenset zu einem anderen vorausgeht, weniger Informationen über die aktuell relevante Aufgabe enthielten als bei Aufgaben, denen kein Wechsel vorausgeht. Interessanterweise ließen sich zwischen Kindern und Erwachsenen keine Unterschiede in der wechselbedingten Verringerung der Repräsentationsgüte nachweisen. Dies lässt auf einen bemerkenswerten Reifegrad der neuronalen Repräsentation von Aufgabensets bei den Kindern schließen und wirft die Frage auf, welche weiteren Mechanismen zu den im Vergleich zum Erwachsenenalter erhöhten Wechselkosten in der späten Kindheit beitragen.

Aufbauend auf den zuvor gewonnenen Erkenntnissen gilt *Schrift 3* meiner Dissertation der detaillierten Untersuchung trainingsbedingter Veränderungen von Aufgabenwechselkosten in der späten Kindheit. Mithilfe von Drift-Diffusionsmodellen habe ich trainingsbedingte Veränderungen in den kognitiven Prozessen des Aufgabenwechsels untersucht. Hier zeigte sich,

dass intensives Training des Aufgabenwechsels zu einer schnelleren Evidenzakkumulation für die korrekte Antwort führt. Ein schnelleres Akkumulieren von Evidenz, zusammen mit einer Reduktion der Aktivierung im lateralen präfrontalen Kortex deutet auf eine effizientere Regelverarbeitung durch Training hin. Diese Veränderungen gingen außerdem mit Strategieänderungen einher, sodass die Kinder ihre kognitiven Kontrollressourcen anders zugewiesen haben könnten, möglicherweise aufgrund von Verbesserungen bei der Überwachung der Anforderungen und der entsprechenden Anpassung ihrer Leistung.

Zusammengenommen ergeben die empirischen Befunde meiner Dissertation das Bild einer zunehmend verfeinerten Beteiligung frontoparietaler Hirnregionen am Aufgabenwechsel. Dabei scheint der laterale präfrontale Kortex eine wichtige Rolle zu spielen, und zwar sowohl in Bezug auf Altersunterschiede zwischen Kindern und Erwachsenen als auch in Bezug auf trainingsbedingte Veränderungen bei den Kindern. Dies unterstreicht die Bedeutung des lateralen präfrontalen Kortex für hierarchische Kontrollprozesse sowie deren Beitrag zur Entwicklung der kognitiven Flexibilität im Kindesalter. Die Ergebnisse meiner Dissertation erweitern das Verständnis des Beitrags kognitiver Kontrollprozesse zur kognitiven Entwicklung. Sie bilden zugleich eine Grundlage für weiterführende Untersuchungen des Zusammenspiels erfahrungsbedingter und reifungsbedingter Einflüsse auf die kognitive Entwicklung im Kindesalter.

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1. Introduction

Flexibly adapting to changing demands of the environment is a challenge individuals face on a daily basis, already at a young age. Children have to switch quickly from their English class to learning about biological concepts, or shift their strategy when trying to solve a problem when the previous one is not working. Over the course of development, children become increasingly proficient in adjusting their behavior to pursue goals even if contexts change, which has been associated with developmental refinement of the neural processes underlying cognitive flexibility (Kupis & Uddin, 2023).

Cognitive flexibility is a key part of cognitive control (E. K. Miller & Cohen, 2001; also referred to as executive functions; Diamond, 2013; Miyake & Friedman, 2012) enabling goal-directed behavior. Cognitive control has commonly been conceived as consisting of three different facets: working memory, inhibition, and cognitive flexibility (Friedman & Miyake, 2017; Miyake & Friedman, 2012). Throughout childhood and adolescence, these processes become increasingly more effective (Tervo-Clemmens et al., 2023), such that cognitive control can be recruited based on the current contextual demands with increased precision (Chevalier, 2015).

Cognitive control abilities during childhood have been shown to predict multiple real-life outcomes, including academic achievement and well being (Best et al., 2011; Denham et al., 2015; Liew, 2012; Moffitt et al., 2011; Titz & Karbach, 2014). These associations have motivated research to understand the underlying neural mechanisms of cognitive flexibility during childhood (Crone & Steinbeis, 2017; Kupis & Uddin, 2023). A parallel line of research has aimed at elucidating how cognitive flexibility is shaped by experiences and practice (Kray & Dörrenbächer, 2020). However, so far, no study has linked these two questions by investigating how neural mechanisms of cognitive flexibility change with practice in children. In the light of mixed evidence of the effectiveness of cognitive training (Gobet & Sala, 2023), investigating training-induced change in neural mechanisms might help to clarify which interventions are effective in increasing cognitive flexibility in children (cf. Frith, 2019; von Bastian et al., 2022). A key consideration for effectively supporting cognitive flexibility in children is understanding why they show lower cognitive flexibility. Thus, in this dissertation, I first address the question of which neural mechanisms support the development of cognitive flexibility. Next, I address the gaps in our understanding of the neural mechanisms of training-induced improvements by exploring how cognitive and neural processes of cognitive flexibility change with task-switching training. Specifically, by using multiple timepoints of

neuroimaging data during task-switching training, I aim to understand how neural activation, connectivity, and task-set representations occurring during task switching differ between children and adults, and how these are influenced by nine weeks of intensive task-switching training. To this end, I specifically focus on the period of late childhood (i.e., 8–11-year-olds), a period in which cognitive control not only develops rapidly (cf. Tervo-Clemmens et al., 2023) but in which behavioral measures capturing different aspects of task-switching ability are starting to show differential age effects.

2. Empirical Background and Theoretical Foundation

The following sections outline the current empirical background on the development of cognitive flexibility (section 2.1), the neural processes associated with it (section 2.2), and our current knowledge of training-related changes in cognitive flexibility (section 2.3). In each of the three sections, I first outline empirical findings in adults that form a basis for the developmental studies described next. Given the lack of task-switching training studies that include neuroimaging, I have adopted a broader view in the section on training-related changes, drawing on training studies targeting other cognitive control facets to derive hypotheses of changes in neural processes with task-switching training.

2.1 Task switching

2.1.1 The costs of switching between tasks

Cognitive flexibility, that is, the ability to flexibly switch between tasks, has been described as a key component of goal-directed behavior (e.g., Diamond, 2013; Miyake & Friedman, 2012). Task-switching studies can broadly be categorized into three main paradigms: predictable or alternating task switching, cued task switching, and voluntary task switching, with cued task switching the most commonly studied of the three (Koch & Kiesel, 2022). While these paradigms mainly focus on the mechanisms that underlie the ability to switch between tasks, they also tap into cognitive control functions of working memory updating and inhibition (cf. Koch & Kiesel, 2022; Miyake & Friedman, 2012). A task in this context is generally conceptualized as consisting of a task set which includes the cue, stimulus, response, and the mappings or rules between these (Rogers & Monsell, 1995; Cragg & Chevalier, 2012; Koch & Kiesel, 2022; Hazeltine et al., 2022; Monsell, 2017). Recent neurophysiological data supports this concept of task-set representations integrating both higher-level representations of rules as well as low-level representations of actions (Kikumoto et al., 2022; Kikumoto & Mayr, 2020). However, these task-set representations still remain flexible and are adjusted with experience and task goals (Badre et al., 2021).

Task-switching paradigms require rapid switches between task sets and elicit two main types of performance declines. The first describes increased error rates and longer response times (RTs) in contexts where tasks are to be performed intermixed (i.e., in *mixed* blocks) compared to contexts where tasks are performed separately (i.e., *single* blocks). Such

performance costs are termed global switch costs when comparing mixed and single blocks (e.g., Kray & Lindenberger, 2000), or mixing costs, when comparing trials in single blocks to task repeat trials in mixed blocks (e.g., Kiesel et al., 2010). Note, however, that these terms are not always clearly distinguished in the literature investigating the factors influencing mixing or global switch costs (Cragg & Chevalier, 2012; Kray & Dörrenbächer, 2020; Marí-Beffa & Kirkham, 2014).

Mixing costs have been shown to be elicited by the demands to keep task sets active and resolve interferences among them during mixed runs. For instance, ambiguous stimuli that increase interference among task sets (Philipp et al., 2008; Rubin & Meiran, 2005) as well as a greater probability of switches within the mixed blocks (Bonnin et al., 2011) have been shown to increase mixing costs. This is further supported by findings of reduced mixing costs when task sequences in mixed blocks are predictable (Poljac et al., 2009) and thus allow for the avoidance or preparatory resolution of interference. Thus, mixing costs reflect sustained control demands such as maintaining, monitoring, and managing multiple task sets, which are required in a continuous fashion during mixed-task blocks (Braver et al., 2003; Pettigrew & Martin, 2016; Rubin & Meiran, 2005).

Second, switch costs describe performance declines within mixed blocks on trials that require a switch to a different task compared to trials where the previous task is repeated (Allport et al., 1994; Mayr & Kliegl, 2000; Monsell, 2003; Rogers & Monsell, 1995; Wylie & Allport, 2000), and are thus thought to reflect transient, trial-specific control processes. There are multiple task parameters that influence the magnitude of the switch costs, such as preparation time and time between stimuli. Longer cue-stimulus intervals (CSI), and thus longer preparation time, reduce switch costs, indicating the crucial role of retrieving and updating the task set that has become newly relevant for successful performance on switch trials (Mayr & Kliegl, 2000; Monsell, 2003; Rogers & Monsell, 1995). However, even with extended preparation time, residual switch costs remain, indicating that task switches might follow a two-step process of first updating the task set as soon as the cue is presented, and second the implementation of this task set into action once the relevant stimulus is presented (see Kiesel et al., 2010; Vandierendonck et al., 2010 for reviews).

Additionally, longer CSIs not only provide more time for preparation, they also allow for the previous task set to passively decay or to be actively inhibited, resulting in reduced switch costs (Meiran et al., 2000). Even without any knowledge of the upcoming task, longer intervals between trials result in reduced switch costs, presumably due to the passive decay of

the previously relevant task set, resulting in less interference between task sets on switch trials (i.e., task-set inertia; Allport et al., 1994; Wylie & Allport, 2000; see also Horoufchin et al., 2011). If the previously relevant task set is still lingering on a switch trial, interference might be reduced by active inhibition as demonstrated by the phenomenon of $n - 2$ repetition costs. Specifically, in a sequence of two task switches, costs are greater for switches to a task that was relevant on the trial before the immediately previous trial (i.e., the $n-2$ trial) and that has presumably been inhibited for successful task execution on the previous trial, as opposed to a third task (Koch et al., 2010; Mayr & Keele, 2000; Schuch & Koch, 2003). In line with this, studies that intermixed more than two tasks and thus allow proactive inhibition of the previous task have shown that the knowledge of an upcoming task switch results in a reduction of switch costs (Aufschnaiter et al., 2021; Dreisbach et al., 2002; Koch, 2008). However, if participants not only knew that they have to perform a task switch but also to which of the tasks they had to switch, switch costs were further reduced, suggesting that task preparation involved activating the new task in addition to inhibiting the previously relevant task (Aufschnaiter et al., 2021; Dreisbach et al., 2002; Koch, 2008).

Taken together, the demand to switch between tasks elicits both mixing and switch costs. Mixing costs reflect the increased demand to maintain and monitor multiple task sets during mixed compared to single-task blocks. Switch costs reflect control processes of preparing the upcoming task by updating the newly relevant task set, actively inhibiting the previous, no-longer-relevant task set, as well as the passive decay of the previous task set.

2.1.2 Age differences in task switching

Across most of child development, children show greater costs of switching between tasks than adults (Cragg & Chevalier, 2012; Gupta et al., 2009; Huizinga et al., 2006; Huizinga & van der Molen, 2007). However, mixing and switch costs show different developmental trajectories: while both improve during middle and late childhood, children approach adult levels of switch costs at around age 9–11 years, but show higher mixing costs than adults until adolescence (13–15 years; Cepeda et al., 2001; Crone, Bunge, et al., 2006; Crone et al., 2004; Huizinga & van der Molen, 2007; Karbach & Kray, 2007; Reimers & Maylor, 2005).

While not as proficient as adults until adolescence, given certain task characteristics, children are able to switch between tasks as early as 3 years of age (Brooks et al., 2003; Diamond, 2013; Kloo et al., 2010; Perner & Lang, 2002; e.g., Zelazo et al., 1996, 2003). Task switching requires overcoming a previously executed or habitual behavior, which is dependent

on the ability to identify the relevant rule for a task (e.g., as instructed by a parent or experimenter), as well as to apply the newly relevant rule and adjust behavior accordingly (Chevalier & Blaye, 2008; Zelazo, 2006; Zelazo et al., 1996). Identifying and applying the new rule has been shown to be easier for young children if the rule-relevant information is separate (cf. Diamond, 2013). For example, 3-year-olds struggle to switch between categorizing a stimulus based on its color to categorizing it based on its shape, as required in the Dimensional Change Card Sort (DCCS) task (Zelazo, 2006). However, if the color is presented as the background of the stimulus, 3-year-olds' performance improves substantially (Brooks et al., 2003; Diamond et al., 2005; Kloo et al., 2010; Perner & Lang, 2002), suggesting that children in that age group can conceptualize the rules but need additional aid to extract the relevant information from the stimuli. Thus, a first key shift in the development of cognitive flexibility is the ability to overcome a habitual behavior when instructed to do so (Munakata et al., 2012)

However, while children are able to perform switches between tasks at a relatively young age, they continue to show greater switch costs compared to adults. For example, children have greater difficulties overcoming the previously relevant task, as suggested by smaller reductions of switch costs with increased inter-trial intervals in children compared to adults (Cepeda et al., 2001; see also Hommel et al., 2011). Witt and Stevens (2012) further showed that task-set inertia affects children's performance to a greater extent than in adolescents and adults. Additionally, children's performance suffers more when task sets overlap, e.g., when tasks require responses with the same hand, suggesting greater difficulty resolving interference between tasks (Crone, Bunge, et al., 2006). Thus, while children are to some extent able to perform switches based on external cues from preschool age onwards, these abilities are continually refined across middle childhood. The refinements of these transient control processes contribute to the reduction in switch costs resulting in adult-like levels of switch costs around middle to late childhood (Crone, Bunge, et al., 2006; Reimers & Maylor, 2005).

A second important shift in the development of cognitive flexibility (cf. Munakata et al., 2012) involves not only reacting to external cues but actively preparing for potential changes in control demands (e.g., in mixed blocks of a task-switching paradigm). First instances of such proactive control can already be observed around the age of 8 (Chatham et al., 2009) but continue to be refined throughout adolescence (Cepeda et al., 2001; Reimers & Maylor, 2005). Proactive control of task sets has been suggested to be a key characteristic of mature flexible cognitive control (Koch & Kiesel, 2022; Monsell, 2003; Vandierendonck et al.,

2010). It heavily relies on the ability to represent (multiple) relevant task sets in a sustained manner (Braver, 2012), and thus the development of active task-set maintenance in working memory (Chevalier & Blaye, 2008; Crone et al., 2004; Lorscheid & Reimer, 2010; Luciana et al., 2005). In addition to maintaining task rules to enable switches between them, the goal of task execution has to be identified and represented continuously throughout the task. Chevalier and colleagues have demonstrated that age differences in the ability to set and maintain goals contribute to greater mixing costs in 7–9-year-olds compared to adults (Chevalier & Blaye, 2009; Cragg & Chevalier, 2012). Thus, an increasing ability to represent task sets and goals throughout late childhood supports the reduction of mixing costs in those developmental periods.

Finally, the ability to engage cognitive control in a self-directed manner, that is, independently of specific task cues but based on internal assessment of one's current performance and the task demands, matures in early adolescence and seems to be continually refined until early adulthood (cf. Munakata et al., 2012). For instance, while 10-year-olds are able to identify the control demands of a task, they are not able to independently adjust their behavior accordingly (Niebaum et al., 2021, see also 2019). The ability to adjust the amount of cognitive control with changing demands of a task (i.e., metacontrol; Chevalier, 2015) is crucial for self-directed flexible behavior and relies on the ability to track information of the current context and use this information for behavioral adjustments (Frick et al., 2022; Frick & Chevalier, 2023; Lorscheid & Reimer, 2008). Thus, mature cognitive control is not exclusively defined by more exertion of control but rather by more flexible deployment of control that is better aligned to the current demands (Chevalier, 2015).

Taken together, developmental studies of task switching demonstrate continual refinement of performance throughout childhood and adolescence. Trial-specific processes underlying switch costs, such as rule updating and inhibiting the no-longer relevant rule, approach adult-levels by middle childhood, whereas sustained processes associated with mixing costs, such as rule and goal maintenance continue to develop until adolescence. The continual refinement of metacontrol abilities may further support flexible employment of cognitive control based on task demands with age.

2.2 Neural mechanisms of task switching

2.2.1 Brain regions associated with task switching in adults

Meta-analyses across multiple different task-switching paradigms have repeatedly identified frontoparietal regions as key regions associated with task switching (Kim et al., 2012; Niendam et al., 2012; Richter & Yeung, 2014; Wager et al., 2004; Worringer et al., 2019; Zhang et al., 2021). Kim and colleagues (2012) have identified the inferior frontal junction (IFJ) and the superior parietal lobe (SPL) as domain-general regions across different types of task-switching paradigms, concluding that these regions are likely involved in task-set representation and updating, processes common to most task-switching paradigms (see also Brass et al., 2005; Brass & von Cramon, 2004; Derrfuss et al., 2005; Gurd et al., 2002; Ruge et al., 2005).

However, the involvement of certain brain regions depends on the specific demands of the switching task. For example, the dorsolateral prefrontal cortex (dlPFC) showed greater involvement for response switches, while context switches were associated with greater activation in anterior prefrontal cortex (PFC; Kim et al., 2012; see also Braver et al., 2003; Ravizza & Carter, 2008; Niendam et al., 2012; Kupis & Uddin, 2023). One approach to distinguishing different roles of brain regions related to mixing and switch costs is by contrasting activation that is sustained throughout mixed compared to single blocks, and transient differences between switch and repeat trials within mixed blocks, respectively. Capitalizing on such an analysis, Braver and colleagues (2003) identified the right anterior PFC to be exclusively involved in sustained control, while the left lateral PFC (lPFC), including the IFJ and the dlPFC, showed transient control activation (see also Dosenbach et al., 2006).

Differences in brain activation associated with specific processes supporting task switching have further been demonstrated by using different experimental manipulations. For instance, the dlPFC showed greater activation for bivalent than univalent rules during task switching, suggesting that it supports the maintenance of multiple rules during rule-based tasks (Crone, Wendelken, Donohue, & Bunge, 2006; see also Johnston et al., 2007). Additionally, the dlPFC showed greater activation with greater incongruency on switch trials, suggesting its involvement in the selection and implementation of task sets in the face of conflicting information (Hyafil et al., 2009; see also Ruge et al., 2013). Specifically, Hyafil and colleagues (2009) proposed that the dlPFC is involved in resolving interference between task sets based on information regarding task priorities provided by the dorsal anterior cingulate cortex (dACC; see also Ridderinkhof et al., 2004). These observations are further in line with the

putative role of the dACC, including the pre-supplementary motor area, in monitoring task relevance during task switching (Brass & von Cramon, 2002, 2004; Crone, Wendelken, Donohue, & Bunge, 2006).

Importantly, these frontal and parietal brain regions do not enable task switching individually but as networks (Menon & D'Esposito, 2022), with the frontoparietal and the cingulo-opercular as the most relevant networks for cognitive control (Dosenbach et al., 2007, 2008; Shine & Poldrack, 2018; Wood & Nee, 2023; Yin et al., 2018). The frontoparietal network, including the IFJ, SPL, dlPFC and the precuneus, has been associated with transient control, while the cingulo-opercular network, including the anterior PFC, dACC, and anterior insula/frontal operculum (aI/fO), has been associated with sustained control processes (Dosenbach et al., 2007, 2008). While precise network affiliations are inconsistent, especially regarding sustained and transient control demands (e.g., Menon & Uddin, 2010), frontoparietal and cingulo-opercular regions are consistently associated with networks that closely interact to enable adaptive cognitive control (Shine & Poldrack, 2018; Wood & Nee, 2023; Yin et al., 2018). During task switching specifically, the IFJ seems to play a key role in network coordination, such that connectivity between the IFJ and other regions across control networks has been associated with better task-switching performance (Yin et al., 2018; see also Dajani et al., 2020). Furthermore, the IFJ has been shown to adapt its connections based on task demands: if the task required switches of the response hand, connectivity of the IFJ and motor regions was increased, while rule switches elicited increased IFJ connectivity with more anterior and superior PFC regions (Stelzel et al., 2011).

Taken together, task switching in adults has been associated with increased activation in frontoparietal and cingulo-opercular brain regions, with the IFJ and the SPL playing key roles for task-set representation and updating. Connectivity within and between frontoparietal and cingulo-opercular networks has further been associated with task-switching demands, with the IFJ hypothesized to coordinate the connections among the involved brain regions.

2.2.2 Structural development of frontal and parietal cortices

Frontoparietal and cingulo-opercular brain regions associated with cognitive control show prolonged structural development extending into late adolescence or even early adulthood (Giedd, 2004; Lenroot & Giedd, 2006). Gray matter development has been described as non-linear, such that the overall peak of gray matter volume and cortical thickness (i.e., the volume/thickness of the layer of the brain containing the majority of neuronal cell bodies)

across the whole cortex is reached early in childhood, followed by refinement of circuitry as evident in cortical thinning (Gilmore et al., 2018; Raznahan et al., 2011; Remer et al., 2017; Shaw et al., 2008). However, the trajectory of maturation of gray matter is not uniform across brain regions (Giedd, 2004; Giedd et al., 1999). Specifically, Giedd (2004) showed that frontal gray matter reaches peak volume around 11–12 years of age, while parietal gray matter only peaks around age 16 years (cf. Sydnor et al., 2021). Interestingly, some researchers have suggested that periods of more rapid changes in gray matter in the frontal cortex occur between age 7 and 9 years and again between 11 and 13 years and thus match periods of improvement in executive functions (P. Anderson, 2002).

Not only gray matter in association cortices shows prolonged developmental trajectories but also white matter, presumably reflecting the myelination of axons (Beaulieu, 2002). Regional-specific myelination as well as microstructural development of white-matter tracts has been shown to differ between sensory-motor and association cortices, with the former reaching peak levels earlier around the age of 1 year, and the latter showing extended linear development (Barnea-Goraly et al., 2005; Deoni et al., 2012, 2015; Giedd et al., 1999; Lebel et al., 2008, 2019; Lebel & Beaulieu, 2011; Lebel & Deoni, 2018; Schilling et al., 2023). Importantly, white matter tracts are not only strengthened with development, as suggested by increased myelination, but the configuration of structural networks continually becomes more adult-like (Baum et al., 2017). Specifically, structural connections among regions subserving similar functions (e.g., frontoparietal brain regions supporting cognitive control) are strengthened over development, while structural connections between brain regions associated with different functional networks weakened. The combination of this network integration and segregation leads to a modular organization of structural networks that supports the development of cognitive control (Baum et al., 2017).

Taken together, structural development of frontoparietal association cortices continues throughout childhood and into adolescence. Association between these structural changes and the development of cognitive control, and thus task switching as one of its facets, is likely complex and non-linear (J. Anderson et al., 2023; Goddings et al., 2021; Wendelken et al., 2015). However, studies have also demonstrated that the match between developmental timing of structural changes and the refinement of functional recruitment of brain regions or networks is crucial for effective cognitive control (Baum et al., 2020; Vijayakumar et al., 2021; Wendelken et al., 2017).

2.2.3 Age differences in brain activation during task switching

The development of the neurocognitive mechanisms subserving cognitive control has been characterized by increasingly fine-tuned recruitment of frontoparietal brain regions. While many studies have reported activation increases with development (Crone, Wendelken, Donohue, van Leijenhorst, et al., 2006; Rubia et al., 2006; Satterthwaite et al., 2013; Velanova et al., 2008), some studies also reported decreases in activation with age (Booth et al., 2003; Geier et al., 2009). One proposition reconciling these mixed patterns is that activation becomes more regionally focused with brain maturation (Bunge et al., 2002; Bunge & Wright, 2007; Casey et al., 2000; Chevalier et al., 2019; Durston et al., 2006; Engelhardt et al., 2019; Luna et al., 2010, 2015; Satterthwaite et al., 2013; Scherf et al., 2006). Specifically, younger children show more diffuse activation in response to cognitive control demands than adults (cf. Durston et al., 2006). If the activation at the fringes of these diffuse activation patterns is examined, it would show a decrease with age, while activation at more focal location would show increases with age (cf. Crone & Steinbeis, 2017).

During task switching, children recruit similar frontoparietal and cingulo-opercular brain regions as adults, including the IFJ, SPL, dlPFC, dACC, and aI (see Zhang et al., 2021 for a meta analysis). However, smaller upregulation of activation with increased control demand on switch compared to repeat trials suggests that children cannot adapt activation as flexibly to the task demands as adults (e.g., Chevalier et al., 2019; Church et al., 2017; Crone, Donohue, et al., 2006; Wendelken et al., 2012). As described above, cognitive flexibility requires both the active maintenance of task sets and goals (i.e., sustained control), as well as the adjustment of these with changing context demands (i.e., transient control). In line with the behavioral studies discussed above, Crone and colleagues (2006) have shown different developmental trajectories of processes associated with sustained and transient control such that activation related to task-set inhibition in the pre-supplementary motor area reaches adult levels earlier than activation in the LPFC associated with task-set representation.

Transient control during task switching does not only entail the inhibition of the no-longer relevant task set but also the updating of the newly relevant task set. One study reported age differences in the timecourse of activation in the dlPFC, suggesting that children update rules more slowly than adults, further contributing to greater switch costs in children (Wendelken et al., 2012). Additionally, evidence from electroencephalography (EEG) suggests that children not only update task sets when necessary (i.e., on switch trials) but also when the task set did not change relative to the previous trial (i.e., on repeat trials; Manzi et al., 2011).

These findings are in line with the less effective condition-dependent modulation of activation reported in fMRI studies (Chevalier et al., 2019; Church et al., 2017; e.g., Crone, Donohue, et al., 2006; Wendelken et al., 2012), together suggesting that children struggle to adapt the recruitment of frontoparietal brain regions to task demands. Finally, task-set inertia has been shown to contribute to switch costs (e.g., Allport et al., 1994; Wylie & Allport, 2000). Witt and Stevens (2012) investigated neural processes associated with task-set inertia between late childhood and early adulthood (i.e., between 12 and 31 years). They demonstrated that brain regions associated with overcoming high task-set inertia on rapidly presented trials, including prefrontal and parietal regions, showed increasing activation with age. Thus, less effective recruitment of frontoparietal brain regions to overcome task-set inertia might further contribute to higher switch costs in children (Witt & Stevens, 2012).

Few developmental neuroimaging studies have investigated the development of neural processes associated with mixing costs. Crone and colleagues (2006) showed more widespread activation in 8–12-year-old children relative to adults when demands on task-set representation were higher. This pattern suggests that task-set representation was more effortful in children. In addition to these differences in task-set representations, greater mixing costs in children have also been associated with less proactive control during mixed task performance, as evident from slower anticipatory updating of task sets in children (Manzi et al., 2011).

No study has so far directly compared developmental trajectories of sustained and transient activation associated with task switching. In the context of inhibitory task sets of an antisaccade task, Velanova et al. (2009) have shown that sustained control activation was lower in children (8–12 years) and adolescents (13–17 years) compared to young adults, while transient activation was higher in children than in adolescents and adults, with no differences between the latter two groups. While this is generally in line with the observation that switch costs approach adult levels earlier than mixing costs, it raises the question whether a similar pattern would be observed for sustained and transient control during task switching. While inhibition of the no-longer relevant task set is a key transient process during task switching, switch costs are additionally influenced by updating processes (cf. Vandierendonck et al., 2010) potentially resulting in a different developmental pattern for transient control during task switching.

Finally, some studies suggest that compared to adults, children recruit additional or different brain regions during tasks requiring cognitive flexibility (Crone, Donohue, et al., 2006; Morton et al., 2009). This might indicate the recruitment of a different strategy, raising

the important notion that children and adults do not necessarily solve a task with the same strategies. For example, children might have to exert greater cognitive control for successful performance of a task, while adults might rely on adjustments of lower level cognitive processes such as attention (cf. Kupis & Uddin, 2023).

Taken together, throughout development, children become increasingly better able to adaptively recruit frontoparietal brain regions for cognitive flexibility. This does not necessarily mean monotonic increases of activation with development, but rather more selective activation depending on the task-specific demands, potentially following the hierarchical organization of the PFC from posterior to more anterior regions (cf. Crone & Steinbeis, 2017). However, it is unclear how age differences in sustained and transient control processes might underlie the different developmental trajectories of mixing and switch costs. I address this gap in the literature in Paper 1 of this dissertation, by specifically investigating activation associated with sustained and transient control processes during task switching.

2.2.3 Age differences in connectivity during task switching

In addition to adaptive changes in activation, developmental changes in connectivity between brain regions have also been associated with improvements in cognitive flexibility (Kupis & Uddin, 2023). Accordingly, developmental studies have investigated age differences in how the interaction of brain regions at rest (i.e., resting-state functional connectivity) is associated with task-switching performance, or how their interaction is modulated by switch demands (i.e., task-based functional connectivity).

Studies comparing developmental differences in resting-state network organization have shown that by late childhood, networks are similarly organized as in adults. However, the strength of connections within as well as between these networks continues to change until adolescence and early adulthood (Bassett et al., 2018; Cui et al., 2020; Grayson & Fair, 2017; Gu et al., 2020; Kupis et al., 2021; Marek et al., 2015; Pines et al., 2022; Tooley, Park, et al., 2022). For instance, Kupis and colleagues (2021) identified multiple patterns of dynamic resting-state connectivity among frontoparietal and cingulo-opercular networks, which differed in the time they were present during a scan. A greater number of switches between these connectivity patterns was associated with better cognitive flexibility across age groups. However, children generally showed a smaller number of these switches, suggesting that their functional network architecture may limit the flexible adaptation of network recruitment with changing demand during task-switching paradigms (Kupis et al., 2021). Large-scale network

studies have further provided a fine grained view of network development, showing that network organization in sensory and motor areas reaches adult levels earlier than association networks including the frontoparietal control network (Tooley, Bassett, et al., 2022; Tooley, Park, et al., 2022).

Task-based functional connectivity provides a further perspective on how children recruit brain networks for cognitive control and task-switching performance. Investigating frontoparietal connectivity during task switching, Ezekiel and colleagues (2013) found lower connectivity in children compared to adults. However, children integrated the anterior PFC into the frontoparietal network to a greater extent, suggesting that, when faced with greater task-switching demands, children might rely on connections to regions not as commonly recruited for task switching. However, as the study applied principal and independent component analyses, it did not directly compare how connectivity patterns dynamically change with increases in control demand across conditions. It thus remains unclear whether networks associated with cognitive control become overall more efficient and adult-like with development or whether children become more effective at adaptively matching connectivity strength to task demands. To this end, psychophysiological interactions (PPI; Friston et al., 1997; or generalized PPI (gPPI); McLaren et al., 2012) could be leveraged as it allows one to test how connectivity between regions varies as a result of task demands or conditions, instead of relying on correlational measures.

Taken together, functional networks associated with cognitive control become increasingly refined throughout childhood. However, age differences in how children adaptively recruit these networks based on task-switching demands are still unclear and require further studies. In Paper 1 of this dissertation, I address this gap in the literature by leveraging gPPIs to investigate how child-specific adaptations in connectivity might be an alternative mechanism to support task switching when activation in frontoparietal brain regions is not recruited at an adult level.

2.2.4 The role of neural representations for task switching

The demand to update the task-set representation when a task changes on a switch trial has been suggested to result in less stable task sets on switch than repeat trials, which in turn is thought to contribute to increased switch costs (Mayr & Kliegl, 2000; Meiran, 1996). Additionally, the previously relevant task set is thought to linger (task-set inertia) and thus dilute the currently relevant task set and have a negative impact on task performance (Rangel

et al., 2023; Rogers & Monsell, 1995; Wylie & Allport, 2000). Recent evidence has demonstrated the potential of multivariate analyses for understanding how task rules are represented and applied. Specifically Kikumoto and colleagues (Kikumoto et al., 2022; Kikumoto & Mayr, 2020) demonstrated that tasks are represented in a conjunct manner, such that cues, stimuli, responses, and all relevant mappings among them are represented together (see also Rangel et al., 2023). However, while it is clear that multivariate analyses such as multivariate pattern analysis (MVPA; Haynes & Rees, 2006; Kriegeskorte et al., 2006) are crucial for conclusions about the role of representations for cognitive control (Badre et al., 2021; Brass & De Baene, 2022; Coutanche, 2013; Ruge et al., 2019), studies applying this methodology to task switching are limited in adults (Loose et al., 2017; Qiao et al., 2017; Tsumura et al., 2021) and non-existent in developmental populations.

Furthermore, the existing studies investigating neural representations of task sets during task switching in adults so far provide inconclusive evidence about the contribution of the distinctiveness of task-set representations to task-switching performance. Leveraging MVPA, these studies investigated how well the currently relevant task in a task-switching paradigm can be predicted by multivariate patterns of brain activation. In line with the hypothesis based on behavioral data, one study could show that decoding accuracy of such multivariate patterns was higher on repeat than on switch trials (Qiao et al., 2017). However, other studies do not support this pattern (Loose et al., 2017; Tsumura et al., 2021), suggesting that the effect of switching demand on task-set representations might depend on the specific task-switching paradigm and type of switches it requires (cf. Brass & De Baene, 2022). Specifically, switches between arbitrary rules may be more likely to modulate the distinctiveness of representations, as suggested by differences in decoding accuracy between repeat and switch trials (Qiao et al., 2017; see also Woolgar et al., 2011). In contrast, if the relevant rule conceptually remains the same but the response switches between trials, neural task-set representations might be less impacted as suggested by comparable (above-chance) decoding for both switch and repeat trials (Loose et al., 2017).

Multivariate approaches have further been used to investigate the role of task-set inertia for task switching. Specifically, Qiao et al. (2017) investigated the similarity of multivariate patterns of neural activation between subsequent trials using representational similarity analysis (RSA; Kriegeskorte et al., 2008). The authors showed that on switch trials, the lingering information of the previous trial, measured by greater similarity of the current neural activation pattern to the previous neural activation pattern, negatively impacted performance

(Qiao et al., 2017). However, the paradigm of Qiao and colleagues only involved two tasks between which participants had to switch. It thus did not allow the comparison of the amount of information that lingered from the previous task to the amount of information present just because the task is part of the mixed-task block. In other words, information about the previous task in the neural activation pattern might not solely be present because it was just performed previously but rather because it has to be maintained to switch to the task once it becomes relevant again. A task-switching paradigm including three tasks would allow one to distinguish between these two options by comparing the strength of the representation of the task relevant on the previous trial to the strength of the representation of the task that was neither relevant on the previous nor on the current trial.

The lack of multivariate task switching studies during development is intriguing, given that children's difficulties to switch between tasks have been associated with their difficulty to represent multiple task sets, especially when these representations overlap (Crone, Bunge, et al., 2006; Crone, Donohue, et al., 2006; Lorscheid & Reimer, 2008; Zelazo, 2004). Additionally, increasingly distinct representations in temporo-occipital regions with age have been suggested to scaffold the development of cognitive control (Amso & Scerif, 2015). This raises the question whether representations in temporo-occipital compared to frontoparietal brain regions differ in their importance for behavior during development (cf. Fandakova et al., 2019). For instance, Jung and colleagues (2023) have recently demonstrated that attention biases task representation in prefrontal and visual cortices of children (7–9-year-olds) and young adults differently. Specifically, both task-relevant and task-irrelevant information could be decoded during a one-back working memory task in children, while only task-relevant information was present in adults. This study demonstrates the potential of multivariate analyses to extend our understanding of developmental differences in goal-directed behavior and also suggests that children might indeed have difficulties during task switching because task-relevant information is represented less distinctly.

While conclusions based on decoders cannot reveal processes, they can provide information on the results of these processes (Kriegeskorte & Douglas, 2018). Thus, applying MVPA to fMRI data acquired during task switching can inform how task-set representations are affected by switch demand and how age differences in these representations contribute to children's difficulties in cognitive flexibility. In Paper 2 of this dissertation, I leverage these methods to extend our understanding of the role of task-set representations during task switching in children. I further explore how switch demand impacts neural representations in

brain regions showing different developmental trajectories (Sydnor et al., 2021). Here I focus on frontoparietal and cingulo-opercular regions associated with cognitive control, as well as temporo-occipital regions that scaffold control development (Amso & Scerif, 2015; Rosen et al., 2019).

2.3 Cognitive control and task-switching training

Given the importance of childhood cognitive control for real-life outcomes (e.g., Moffitt et al., 2011), many studies have aimed to improve cognitive control in children of different ages. However, success in improving cognitive control, especially beyond immediate improvements in the trained task has been mixed (see Diamond & Ling, 2019, for an extensive review). These training studies have either focused on one of the three main facets of cognitive control: working memory (Holmes et al., 2009; Jolles et al., 2012, 2013; Klingberg et al., 2002), inhibition (Cañigüeral et al., 2023; Ganesan, Smid, et al., 2023; Ganesan, Thompson, et al., 2023), and task switching (Dörrenbächer et al., 2014; Karbach & Kray, 2009; Kray et al., 2013; Kray, Karbach, Haenig, et al., 2012; Zinke et al., 2012; for a review, see Buttelmann & Karbach, 2017); or a combination of these facets (e.g., Kubota et al., 2023; Zuber et al., 2023).

In a recent meta-analysis, Kassai and colleagues (2019) showed that cognitive training in children was generally successful in improving the targeted ability and often showed transfer to untrained tasks that tap into the same ability (e.g., a different task-switching paradigm after task-switching training). However, training-related improvements rarely transferred to other cognitive control facets or real-life outcomes (Kassai et al., 2019). This is critical, as the improvement of real-life outcomes including academic achievement and wellbeing is often stated as a motivation for training studies in children (see also Blair, 2017; Diamond & Lee, 2011; Diamond & Ling, 2019; Simons et al., 2016). These results have recently raised the question how training paradigms can be improved to elicit not only training effects but also long-lasting transfer (Gobet & Sala, 2023; Green et al., 2019; Smid et al., 2020).

Systematically addressing *how* cognitive training improves performance could help to disentangle the processes underlying these improvements and potentially inform how they can be transferred to different tasks (Gobet & Sala, 2023; Smid et al., 2020). In this section, I will present the current state of the field of cognitive training, focussing on task-switching training and training studies in developmental populations, and outline which questions have so far remained unanswered.

2.3.1 Task-switching training in adults

A multitude of studies demonstrate that task-switching performance can be improved, with training across different training paradigms as well as different age groups (for a review, see Kray & Dörrenbächer, 2020). Generally, these studies compare a group that intensively trained switching between two or more tasks to a group that trained on the same tasks in a single-task manner (Minear & Shah, 2008), often referred to as an active control group. Comparing the experimental training group and the active control group thus allows one to isolate performance improvements specific to task-switching training. Any changes that become evident only in comparison to a passive control group (that performed no training) may be due to the experience with the task rules or structure, limiting the attribution of training-related changes to the practice of switching between tasks.

Using such training designs, studies have demonstrated training-induced improvements in task-switching performance across different populations (Berryhill & Hughes, 2009; Cepeda et al., 2001; Dörrenbächer et al., 2014; Kray & Lindenberger, 2000; Minear & Shah, 2008; Strobach et al., 2012; von Bastian & Oberauer, 2013). Specifically, task-switching training studies can drastically reduce or eliminate mixing costs (e.g., Berryhill & Hughes, 2009; Strobach et al., 2012), suggesting that cognitive processes associated with mixing costs, including task-set maintenance and management (cf. Pettigrew & Martin, 2016; Rubin & Meiran, 2005), can be improved with training to a level of efficiency similar to single-task performance. Switch costs are often reduced by task-switching training but continue to be present (e.g., Cepeda et al., 2001; Kray & Lindenberger, 2000; Strobach et al., 2012) (e.g. Cepeda et al., 2001; Kray and Lindenberger, 2000; Strobach et al., 2012), suggesting that while task-set updating and inhibition processes allow for some room for improvement, they continue to pose demands on control processes even after extensive training.

Training-induced changes in dual-task performance have been associated with more efficient activation of task-sets after training (*Efficient Task Instantiation* model; Schubert & Strobach, 2018; Strobach et al., 2014). Dual-tasking requires the execution of two tasks simultaneously and taps into similar cognitive processes as task switching, including maintenance of multiple task sets, the resolution of interference between task sets, and the selection of the relevant task set (Koch et al., 2018). Thus, the *Efficient Task Instantiation* model suggests that training increases the efficiency of processing task sets in contexts that require such management of multiple task sets. A recent study by Reinhartz and colleagues (2023) further suggests processing speed as a potential mechanism underlying cognitive control

improvements with training. Specifically, the authors showed that increases in the speed of extracting relevant information from the stimuli of a processing-speed task (i.e., drift rates or evidence accumulation parameters in a drift diffusion model; Ratcliff, 1978) supported faster performance at the end of training (Reinhartz et al., 2023; see also Schmiedek et al., 2023).

Studies including both a passive control group and a (single-task) active control group have demonstrated that task-switching performance increases even in the single-task group that only practiced the component tasks, although not as substantially as though task-switching training (e.g., Karbach & Kray, 2009; Minear & Shah, 2008). While such changes are not the effect of practicing switches between tasks but potentially due to increased familiarity with the rules, they raise multiple questions as to the mechanisms that underlie performance improvements in task switching. For example, are differences between single-task and task-switching training due to the task-switching training being more demanding and thus creating a greater supply–demand mismatch (cf. Lövdén et al., 2020)? Or is the process of switching itself crucial for training-related improvements (cf. Karbach & Kray, 2009)? In other words, would a more demanding single-task condition (e.g., due to a greater number of rules or shorter stimulus presentation) also induce improvements? Is there a certain dosage or ratio of switching training that is necessary for improved task-switching once the rules have been learned well? This latter question is especially relevant given the variability in the duration of training interventions, which has yet to be investigated systematically. For example, participants in the study of von Bastian and Oberauer (2013) trained for about 700 minutes, while participants in the study of Karbach and Kray (2009) trained for about 140 minutes, with both studies showing training-related improvements in performance as well as transfer to other tasks tapping into cognitive control processes.

2.3.2 Task-switching training in children

As discussed above, the costs of task-switching can be reduced with training. These training-related reductions, especially in mixing costs, have been reported to be greater in children than in adults (Cepeda et al., 2001; Karbach et al., 2017; Karbach & Kray, 2009). For instance, children benefitted to a greater extent from training than adults, resulting in diminished age differences post-training (Karbach et al., 2017). These findings suggest greater malleability of cognitive control while it is still developing in childhood (cf. Wass et al., 2012). Given that children show greater difficulties with task switching (Buttelmann & Karbach, 2017; Kupis & Uddin, 2023), the same training will elicit a greater mismatch between training demands and

current ability in children than in adults which may, additionally or alternatively, contribute to greater training effects in children (cf. Kühn & Lindenberger, 2016). This is in line with further observations by Karbach and colleagues (2017) that across age groups, individuals with lower baseline performance, and thus presumably greater mismatch between current capacity and training demands, benefited more from task-switching training.

However, greater mismatches between capacity and demands are not always beneficial: if the mismatch is too large, it might even limit the effectiveness of training. For instance, Karbach and Kray (2009) trained children, young, and older adults in task switching, such that some participants practiced on one specific task-switching paradigm during training, and others on varying task-switching paradigms. Specifically, the variable training consisted of task-switching paradigms of identical structure but different stimuli, while the regular training consisted of the identical task-switching paradigm at each training session. In young adults, varying task-switching paradigms during training led to greater performance improvements and greater transfer to other task-switching paradigms, but not in children. In older adults, variable training neither improved nor hampered training success. This pattern suggests that the higher cognitive load elicited by varying training tasks might have prevented children from constructing a representation of the task structure, thereby restricting the transfer of the learned structure to other task-switching paradigms (Karbach & Kray, 2009).

A further study by Kray and colleagues (2013) corroborated these findings by showing that verbalization of task rules, a strategy previously demonstrated to support task switching in children (Kray et al., 2008), only increased their performance if they were already familiar with the task rules. In other words, children only benefitted from supportive strategies for the application of task rules if they had previously formed representations of the rules, but not if they had to learn the rules and apply the strategy at the same time. Thus, given the smaller processing capacities of children, training paradigms may be especially effective if they combine less demanding training setups (e.g., single-task blocks) to establish the necessary representations of rule structure with more demanding parts (e.g., mixed-task blocks) to practice the effective application of these rules.

Taken together, children's task-switching performance can be improved with training, potentially even to a greater extent than adults. However, given the different starting points of children and adults, demands with regard to the cognitive processes during task switching that children particularly struggle with have to be considered when designing a training.

2.3.3 Training-induced neural plasticity and flexibility

Intensive training aims to improve performance in various skills and cognitive abilities. As proposed by Lövdén and colleagues (2010), the success of such training-induced changes depends on the capacity of an individual's brain for cognitive flexibility and plasticity. Specifically, the brain can achieve long-lasting changes in behavior by adapting the way a task can be solved within the range of the brain's structure, thus relying on flexibility. Plasticity, on the other hand, describes the process in which the brain's structure is altered by a prolonged mismatch between the current resources and the demands of the task or skill. Thus, plastic changes in brain structure can only happen if environmental (task) demands are sufficiently high. Lövdén, Lindenberger, and colleagues have formalized the process of brain plasticity in the *Expansion, Exploration, Selection, and Refinement model* (Lövdén et al., 2020; see also Lindenberger & Lövdén, 2019).

While demands within the current capacity of the brain can be quickly responded to by flexible adaptations of behavior, plastic changes require prolonged periods of sustained demand (Wenger, Kühn, et al., 2017). Specifically, in the initial step of expansion and exploration, multiple different behavioral solutions are explored, which is accompanied by the expansion of microcircuits to support these solutions (Lindenberger & Lövdén, 2019; Lövdén et al., 2020; Wenger, Brozzoli, et al., 2017). Subsequently, the most efficient solution is selected and refined. The expansion and exploration step becomes evident in larger cortical maps (e.g., Kleim et al., 2002). These have been associated with neuroanatomical changes, including increased numbers of dendritic spines in rodent models (e.g., Xu et al., 2009; Yang et al., 2009) that are hypothesized to underlie increased gray matter thickness in human neuroimaging (e.g., Draganski et al., 2006; Ilg et al., 2008; Wenger et al., 2012; Wenger, Kühn, et al., 2017). The selection and refinement steps manifest in decreased gray matter thickness and a reduced number of dendritic spines, while performance remains high or even improves further (cf. Lövdén et al., 2020). To capture this pattern of dynamic change in brain and behavior with intensive practice, cognitive and neural processes should not only be measured pre and post training intervention, but also throughout the training. Importantly, as noted by Lindenberger and Lövdén (2019), these theoretical considerations rely heavily on studies of motor skill learning, raising the scientific challenge to test whether similar mechanisms underlie plasticity in cognitive control processes (see also Buschkuehl et al., 2012).

Childhood and adolescence may pose a unique phase of enhanced plasticity in the context of cognitive control. For instance, children generally show lower cognitive control

abilities than young adults (Tervo-Clemmens et al., 2023), which makes a mismatch between the brain's current capacity and the task demands during training particularly likely. Additionally, the potential for plastic change has been proposed to be greater in childhood than in adulthood (Ismail et al., 2017; Kühn & Lindenberger, 2016; Laube et al., 2020; Sauce et al., 2021). Thus, cognitive control training might be particularly effective in children.

2.3.4 Neural changes associated with cognitive-control training in adults

The mechanisms underlying training-induced behavioral changes are complex and likely diverse, thus requiring a range of methods to uncover them (cf. Frith, 2019). Neuroimaging can be used as part of this methodology and thus provide a better understanding of how cognitive processes change with training to address the current lack of mechanistic understanding of cognitive training (Gobet & Sala, 2023; Smid et al., 2020; von Bastian et al., 2022). Studies investigating how neural processes change with task-switching training are scarce across both adult and child populations. Thus, the following sections outline previous research on changes in neural processes across different types of cognitive control training to form an empirical basis on potential trajectories of change with task-switching training in children.

Overall, cognitive control training induces quantitative changes in brain networks already showing task involvement before training (Constantinidis & Klingberg, 2016). However, the trajectory and direction of these quantitative changes remain unclear: cognitive training studies do not necessarily lead to monotonic increases in activation (Landau et al., 2004; Kelly & Gravan, 2005; Buschkuhl et al., 2012; Constantinidis & Klingberg, 2016). Indeed, both non-human primate and human neuroimaging studies show differential patterns of change. Specifically, some primate studies investigating training-induced changes in neuronal firing rate have demonstrated increased involvement in the PFC with training (Qi et al., 2011; Constantinidis & Klingberg, 2016), while others have shown that activity of PFC neurons both increased and decreased with training (Asaad et al., 1998; Chen & Wise, 1995).

Studies in humans show a similarly inconsistent pattern: while some studies have shown increased task-related activation with cognitive training (Buschkuhl et al., 2014; Erickson et al., 2007; Jolles et al., 2010; Olesen et al., 2004; Schweizer et al., 2013; Westerberg & Klingberg, 2007), others have demonstrated decreased task-related activation (Dux et al., 2009; Jimura et al., 2014; Landau et al., 2004, 2007; Schneiders et al., 2011). Training-induced increases in activation have been interpreted to reflect stronger recruitment of the corresponding brain regions for task execution, while decreases are thought to reflect more

efficient processing of task-related information with training (Kelly et al., 2006; Kelly & Garavan, 2005; Poldrack, 2000). These different patterns of change with training may reflect differences in specific features across training studies, such as task difficulty, training length, and the timing of the image acquisition, which can impact how neural mechanisms change with training (Belleville et al., 2014; Buschkuhl et al., 2012; Erickson et al., 2007; Hempel et al., 2004; Kelly & Garavan, 2005; Klingberg, 2010; Schweizer et al., 2013). For instance, Belleville and colleagues (2014) have proposed that in general, repeated practice of a task results in activation decreases, while training the ability to adapt control allocation to task demands (i.e., metacognitive training) would result in activation increases specifically in cognitive control networks. However, while this is a first helpful taxonomy, a systematic investigation of how certain training features impact changes in neural mechanisms is still lacking. This further stresses the importance of not only investigating activation and connectivity pre and post training but also throughout training to elucidate the trajectories of changes (cf. Hempel et al., 2004).

Quantitative changes, that is, increases and decreases in activation of brain regions recruited for task performance pre training, have generally been interpreted as a redistribution of demands (cf. Kelly & Garavan, 2005). One framework for understanding how the brain responds to cognitive training is the *scaffolding-storage framework* (Petersen et al., 1998). This framework suggests that with practice rules and processes required for task performance are more efficiently stored and thus require less resources to be accessed, reducing activation in frontoparietal control regions. However, training-induced decreases and increases in activation might also be part of a reorganization of neurocognitive processes with training, especially when strategy shifts underlie performance changes (cf. Poldrack, 2000).

One process proposed to underlie decreases in activation are changes in neural representations of task sets. Specifically, with training, representations might become more precise and thus activation might spread over a smaller area resulting in less voxels showing above-threshold activation (cf. Poldrack, 2000). Garner and Dux (2015) have provided first evidence for this based on multivariate activation patterns: with dual-task training, task-set representations became more distinct and this increased distinctiveness supported improved performance. The authors concluded that such increased precision of task-set representation aids their processing in prefrontal brain regions during dual-tasking and thus enables increased efficiency evident in reduced activation of these prefrontal regions (Dux et al., 2009; Garner &

Dux, 2015) in line with the Efficient Task Instantiation model (Schubert & Strobach, 2018; Strobach et al., 2014).

Furthermore, cognitive training has been associated not only with activation changes within brain regions associated with task switching changes but also the connections among these regions. Studies using resting-state connectivity suggest that cognitive training leads to increased connectivity among frontal and parietal brain regions (Jolles et al., 2013; Mackey et al., 2013; Takeuchi et al., 2013). These studies demonstrate the importance of investigating training-induced changes in neural activation in the context of a region's affiliation with a brain network (Guerra-Carrillo et al., 2014). Additionally, task-based connectivity among frontoparietal regions of interest (ROIs) has been shown to increase with working memory training (Kundu et al., 2013; Thompson et al., 2016), but has rarely been examined in other types of cognitive training.

Taken together, training studies leveraging different measures of neural processes have implied three potential changes in these processes with cognitive training. First, activation in frontoparietal regions recruited for cognitive control might increase, suggesting that greater involvement of these regions supports training-related increases in cognitive control. Second, frontoparietal activation might decrease with training suggesting more efficient processing of task demands or reduced control demands due to automatization of the task. Increasingly distinct task-set representations might support more efficient processing and thus activation decreases (Garner & Dux, 2015; Poldrack, 2000). Finally, increased task performance might further be supported by stronger and thus more efficient connections among frontoparietal brain regions. Note that these changes could happen at different trajectories during training and are not mutually exclusive, such that with the same training, neural activation could increase in some brain regions and decrease in others, with concurrent changes in connectivity.

2.3.5 Neural mechanisms of cognitive control training in children

Research on how changes in neural mechanisms might support training-related performance improvements of cognitive control in children is very limited and nonexistent for task-switching training. Based on the studies in adults described above, one could hypothesize that children also show decreased activation with training subserving more efficient processing. Rueda and colleagues (2012) provided first evidence of such a pattern using EEG to investigate the timecourse of network recruitment and thus showed that with attention training, children

recruited the attention network faster. However, further studies are needed to extend these findings to other cognitive domains.

Another hypothesis proposed by Jolles and Crone (2012) is that cognitive training affects brain function in a similar manner as age-dependent maturation (see also Klingberg, 2014). In line with this hypothesis, studies have shown more adult-like activation in children after working memory training (Jolles et al., 2012) and executive attention training (Rueda et al., 2005). Evidence from studies investigating changes in connectivity with training in children is so far inconclusive: while some studies showed stronger, more adult-like resting-state connectivity after cognitive control training (Astle et al., 2015; Lee et al., 2022) others did not observe any changes with training (Jolles et al., 2013). Note that children generally show less upregulation of activation with increased cognitive control demand. Thus, if the second key pattern observed in adults – activation increases with cognitive control training – holds for children as well, the resulting activation increases would also be greater for more difficult conditions and thus not different from what we would expect when activation becomes more adult-like.

Finally, training-related changes in neural processes might be fundamentally different in children than adults (Galván, 2010). Thus, rather than the quantitative changes commonly observed in adults, children might show qualitative changes in brain activation with training. Such changes might be particularly likely in children, given the greater potential for experience-dependent plasticity in this developmental period (Kühn & Lindenberger, 2016; Sauce et al., 2021).

Taken together, studies investigating changes in neural processes with cognitive control training are scarce and do not provide a clear pattern of training-related changes. In particular, no study has yet investigated how neural processes during task switching change with task-switching training in children. However, there are three main hypotheses that can be derived based on research of cognitive control training in adults and the initial developmental training studies of cognitive control outlined above. First, cognitive training in children might affect neural processes of task switching similar to age-dependent maturation, resulting in selective activation and connectivity increases, especially for more difficult conditions. Second, children might show decreased activation in frontoparietal control regions, suggesting more efficient task processing with training. Finally, changes in neural processes with task-switching training in children might be qualitative as opposed to quantitative, such that children recruit additional or different brain regions for task performance after training. In Paper 3 of this dissertation, I

test these three hypotheses in a task-switching training study of 8–11-year-old children. Using activation and connectivity measures, I thus shed light on the training-related changes in neural processes associated with task-switching performance.

3. Summary and Research Objectives

The overarching goal of this dissertation is to expand our understanding of the development of cognitive flexibility by examining age differences and training-related changes in the neural mechanisms of task switching in childhood. To this end, I investigate three research questions:

1. How do children differ from adults in task-switching behavior and the sustained and transient neural processes underlying it?

The ability to flexibly switch between tasks is key for goal-directed behavior and continually improves over the course of development (cf. Munakata et al., 2012). These improvements have been associated with more adaptive recruitment of frontoparietal brain regions (e.g., Chevalier et al., 2019; Church et al., 2017; Crone, Donohue, et al., 2006; Wendelken et al., 2012). While processes supporting task switching can be differentiated into transient and sustained processes (cf. Braver et al., 2003), developmental neuroimaging research has so far not systematically investigated how the neural mechanisms underlying these processes differ in children compared to adults. Additionally, while the development of task switching has been associated with increased connectivity among frontoparietal brain regions (Kupis et al., 2021), it is still unclear how children and adults differ in the adaptive recruitment of these networks based on variations in task-switching demand.

I address these gaps in the literature in the first paper of this dissertation by investigating age differences and individual individual differences in the neural underpinnings of sustained and transient cognitive control using task-based activation and connectivity analyses. The combination of task-based activation and connectivity analyses allows me to investigate how these processes enable task-switching performance interactively, in line with the idea that there might be multiple different pathways to successful task performance within and across individuals (Edelman, 1987; Lautrey, 2003; Li & Lindenberger, 2002).

2. How do children and adults differ in their neural representations of task sets and how do these representations contribute to age differences in task-switching performance?

Furthermore, less distinct task-set representations on switch than repeat trials have been suggested to contribute to switch costs (e.g., Mayr & Kliegl, 2000; Rangel et al., 2023; Rogers & Monsell, 1995). However, multivariate studies of neural representations in adults have so far been inconclusive (Loose et al., 2017; Qiao et al., 2017; Tsumura et al., 2021). From a developmental perspective, the lack of studies investigating neural representations during task

switching is surprising, as children's task-switching difficulties have been linked to their difficulties in representing multiple task sets (Crone, Bunge, et al., 2006; Crone, Donohue, et al., 2006; Lorscheid & Reimer, 2008; Zelazo, 2004). In the second paper of this dissertation, I thus investigate how age differences in neural representations contribute to age differences in task switching by leveraging MVPA (Haynes & Rees, 2006). I further explore how these age differences might vary between brain regions that show different developmental trajectories (Sydnor et al., 2021) and have been suggested to scaffold the development of the PFC and thus cognitive control (Amsos & Scerif, 2015).

3. How does task-switching performance change with training and how is this supported by changes in neural activation and connectivity?

Task switching can be improved with training, in children potentially to a greater extent than in adults (Cepeda et al., 2001; Karbach et al., 2017; Karbach & Kray, 2009). However, the neural mechanisms of these improvements are still poorly understood. Previous research in adults as well as in other domains of cognitive control training raises three main hypotheses of how neural processes associated with task switching might change with training in children. Specifically, with training, children might (1) show decreased frontoparietal activation suggesting more efficient rule processing, (2) show adaptive increases in activation and connectivity, suggesting similarities between training effects and age-dependent maturation, and/or (3) recruit additional or different brain regions with training, suggesting differences in the mechanisms supporting training effects in children and adults.

Therefore, the third paper of this dissertation aims to examine these hypotheses in a task-switching training study in children. To this end, I leverage the combination of drift diffusion models to investigate changes in cognitive processes underlying training-related improvements in task switching and analyses of task-based brain activation and connectivity. Additionally, to shed light on the trajectories of change beyond pre- and post-training measures (cf. Lövdén et al., 2020), the study included two additional measurement occasions throughout training, such that neural and cognitive processes of task switching were assessed four times in total. This paper thus builds on the first two papers and contributes to our understanding of how mechanisms of task switching change with training in childhood.

In this dissertation, I address these research questions in a neuroimaging study of task-switching performance and training in children between 8 and 11 years, an age range in which

cognitive control abilities are still developing (cf. Tervo-Clemmens et al., 2023), and neither mixing nor switch costs have reached adult levels but might be starting to dissociate (cf. Reimers & Maylor, 2005). Thus, both age differences in neural activation, connectivity, and representations, as well as their training-related changes are of particular interest in this age group to explain performance differences. To this end, Paper 1 and 2 focus on behavioral and neural patterns of the children's group before training, comparing them to a group of adults (20–30-years-old) that performed the identical task-switching paradigm. Paper 3 then explores how these neural processes change with different doses of task-switching training in the child group.

4. Overview of Individual Papers

Paper 1: Does prefrontal connectivity during task switching help or hinder children's performance?

Schwarze, S. A., Laube, C., Khosravani, N., Lindenberger, U., Bunge, S. A., & Fandakova, Y. (2023). Does prefrontal connectivity during task switching help or hinder children's performance? *Developmental Cognitive Neuroscience*, *60*, 101217. <https://doi.org/10.1016/j.dcn.2023.101217>. This article is licensed under a [Creative Commons Attribution 4.0 license](#).

Objective. This study aimed to understand how age differences and individual differences in the neural underpinnings of sustained and transient cognitive control contribute to age differences in task-switching performance using task-based activation and connectivity analyses. By elucidating how the neural mechanisms of sustained and transient control contribute to task switching it extends our understanding of developmental improvements in the ability to flexibly switch between tasks.

Theoretical background. Flexibly switching between tasks elicits mixing (mixed- vs. single-task blocks) and switch costs (switch vs. repeat costs) which have been shown to be greater in children than adults (e.g., Huizinga & van der Molen, 2007). Furthermore, mixing costs have been shown to reach adult levels later than switch costs (e.g., Reimers & Maylor, 2005). Developmental neuroimaging studies investigating age differences in the neural basis of task switching have shown that children recruit similar frontoparietal brain regions during task switching as adults, but showed less specific upregulation of activation with increasing switching demands (e.g., on switch compared to repeat trials; Crone, Donohue, et al., 2006; Wendelken et al., 2012; Zhang et al., 2021). Similarly, by middle to late childhood, network organization is comparable to adults, while connection strength within and between networks continues to change until adolescence (Engelhardt et al., 2019; Ezeziel et al., 2013). Finally, inter-individual differences among children during task switching (Dauvier et al., 2012) might further be associated with differences in the neural processes of task switching.

Methods. Children (8–11 years; $N = 89$, mean age = 10.06 years, $SD = 0.7$; 50 girls) and young adults (20–30 years; $n = 53$; mean age = 24.7 years, $SD = 2.6$; 28 women) performed a task-switching paradigm in the fMRI scanner. The paradigm included both single and mixed blocks. The mixed blocks were made up of 50% trials that repeated the previous task (repeat trials) and 50% that required switches to a different task (switch trials). I investigated age differences in mixing and switch costs (in accuracy and RTs) as well as in activation associated with sustained control (i.e., differences between mixed and single blocks) and with transient control (i.e., differences between switch and repeat trials). Furthermore, I explored task-based connectivity of the IFJ with the rest of the brain using seed-based generalized psychophysiological interaction models (gPPI; McLaren et al., 2012).

Main results. Both age groups showed mixing and switch costs in accuracy and RTs, with mixing and switch costs in accuracy being greater in children than adults. Children recruited similar frontoparietal brain regions for sustained and transient control demands during task switching as adults, including the dlPFC, IFJ, SPL, dACC, and precuneus. However, with increasing sustained and transient control demand children showed less pronounced increases in activation compared to adults. In line with previously proposed developmental trajectories, I observed greater age differences in mixing costs and sustained control activation (cf. Bunge & Wright, 2007). These findings suggest that sustained control processes of task-set maintenance and monitoring (Braver et al., 2003) may be associated with protracted developmental trajectories. Connectivity related to sustained control demand was increased between the IFJ and the IPFC with greater demand in children but less so in adults. The relation of these changes in connectivity to performance depended on how similar a child's sustained activation pattern was to the average adult activation: for children with less adult-like sustained activation, greater increases in IFJ-IPFC were associated with better performance, while the opposite pattern emerged for children with more adult-like activation. These results suggest that there are multiple ways in which children can handle switch demands, either by recruiting activation in frontoparietal brain regions in an adult-like manner or by adaptively increasing connections with additional prefrontal brain regions. The prominent role of the IPFC in this second pattern may indicate an increased reliance on metacontrol to allocate the limited frontoparietal resources.

Paper 2: Task-switch related reductions in neural distinctiveness in children and adults: Commonalities and differences

Schwarze, S. A., Bonati, S., Cichy, R. M., Lindenberger, U., Bunge, S. A., & Fandakova, Y. (2023). *Task-switch related reductions in neural distinctiveness in children and adults: Commonalities and differences*. Manuscript submitted for publication.

Objective. Recently updated and thus less distinct task-set representations on switch trials are thought to contribute to switch costs. Neural representations are especially relevant to understanding the development of task switching, as children's difficulty to switch between tasks has been associated with overall less distinct representations and less efficient updating of the relevant task-set representation. This study thus uses MVPA of neuroimaging data to investigate how neural task-set representations are impacted by task switching.

Theoretical background. Compared to adults, children show greater costs of switching between tasks (e.g., Huizinga & van der Molen, 2007). Based on lower univariate activation in frontoparietal brain regions on switch than repeat trials, this has been linked to less effective updating of the newly relevant and inhibition of the no-longer relevant task set in children (Crone, Bunge, et al., 2006; Wendelken et al., 2012). These behavioral and univariate neuroimaging results leave open the question whether children's difficulties during switching are related to less distinct neural representations during task switching, especially on switch trials. Furthermore, while such differences in neural representations are relevant in frontoparietal brain regions due to their prominent role in task switching, representations in temporo-occipital brain regions might be particularly important during development. Specifically, representations in temporo-occipital brain regions play an important role in scaffolding cognitive control development (Amso & Scerif, 2015) and show a different developmental trajectory compared to frontoparietal regions (Sydnor et al., 2023). Thus, we expected age differences in neural representation during task switching to differ between temporo-occipital, frontoparietal, and cingulo-opercular brain regions.

Methods. Eighty-eight children (8–11 years; mean age = 10.07 years, SD = 0.69; 49 girls) and 53 adults (20–30 years; mean age = 24.69 years, SD = 2.6; 28 women) performed a task-switching paradigm with three different tasks in the fMRI scanner. Note that this is the same

sample as included in Paper 1 (Schwarze et al., 2023). We conducted MVPA in three sets of ROIs: frontoparietal and cingulo-opercular ROIs showing activation during task performance compared to rest, and temporo-occipital ROIs associated with the task-relevant stimuli (i.e., faces, scenes, and objects) based on automatic meta-analysis tools (Dockès et al., 2020; Yarkoni et al., 2011). We tested whether decoding accuracy, that is, the percentage of the linear classifier correctly predicting the currently relevant task, differed between switch and repeat trials, and between age groups. Additionally, we tested for task-set inertia by investigating whether for false predictions, the classifier was more likely to predict the previously relevant task as opposed to the third task that was neither relevant on the previous nor on the current trial.

Main results. Across age groups and all three sets of ROIs (i.e., frontoparietal, cingulo-opercular, and temporo-occipital ROIs), decoding accuracy was higher on repeat than switch trials, suggesting that task-set representations were less distinct when they had recently been updated on switch trials. The difference in decoding accuracy between switch and repeat trials did not differ between children and adults. We did not observe any evidence of task-set inertia in neural representations, that is, for false predictions, the classifier was as likely to predict the previously relevant task as to predict the third task. Finally, in children, the demand to switch to a different task seemed to affect representations in frontoparietal and cingulo-opercular ROIs similarly, as evident in higher correlations in decoding accuracy costs (i.e., the difference in decoding accuracy between switch and repeat trials) between frontoparietal and cingulo-opercular ROIs. These results raise the question of which mechanisms beyond the strength of representations contribute to age differences in switch costs. Potential mechanisms include age differences in the application of task sets (cf. Kriegeskorte & Douglas, 2018) or continued specialization of representations within different brain regions (cf. Vaidya & Badre, 2022).

Paper 3: Intensive task-switching training and single-task training differentially affect behavioral and neural manifestations of cognitive control in children

Schwarze, S. A., Laube, C., Khosravani, N., Lindenberger, U., Bunge, S. A., & Fandakova, Y. (2023). *Intensive task-switching training and single-task training differentially affect behavioral and neural manifestations of cognitive control in children*. Manuscript submitted for publication.

Objective. Switching between tasks comes with performance costs. While studies have shown that these costs can be reduced with training, the cognitive and neural processes subserving these performance improvements, especially in children, are still unclear. This study addresses this gap by leveraging a combination of computational models of cognitive processes underlying task switching and task-based activation and connectivity measures to investigate training-related changes in task-switching performance in children.

Theoretical background. Children's task-switching performance can be improved with training (cf. Buttelmann & Karbach, 2017). While age-related improvements in task switching have been associated with faster accumulation of evidence for the correct response, less cautious response strategies, and reductions in preparation times as captured by drift diffusion modeling (Weeda et al., 2014), it is unclear how these cognitive processes change with training in childhood. Additionally, training-related performance improvements in adults have been associated with reduced activation in prefrontal brain regions, suggesting increased processing efficiency in the regions with training (Dux et al., 2009). However, it remains unclear whether children show similar changes in neural mechanisms with training or whether their activation and connectivity might become more adult-like with training (Jolles & Crone, 2012).

Methods. A sample of 181 children (8–11 years; mean age = 9.96 years, SD = 0.71) either intensively trained task switching (SW; N = 70) or single tasking (SI; N = 72) at home over the course of nine weeks, or were part of a passive control group (PC; N = 41). Children in the SI group mainly practiced single tasking (83% of each training session) and only a small percentage of task switching, while the SW group mainly practiced task switching (83%). Task-switching performance and functional MRI was assessed at the beginning and the end of the study in all three groups, and additionally on two timepoints during training for the SI and SW

group. We used hierarchical drift diffusion models (Wiecki et al., 2013) to investigate changes in cognitive processes associated with task switching. We investigated changes in task-based activation in, and connectivity among brain regions associated with mixing demands (i.e., between repeat and single trials) and switch demands (i.e., between switch and repeat trials).

Main results. At the end of training, children in the SW group but not the SI group showed improvements in accuracy and RTs. After the first three weeks of training, both training groups showed faster response accumulation (i.e., higher drift rates), more cautious responses (i.e., greater boundary separation). These changes were more pronounced for the SW group, which also maintained the changes in drift rate and boundary separation. In contrast, these parameters returned to pre-training levels in the SI group. This pattern of change suggests that intensively practicing switches between tasks as opposed to primarily practicing the task rules separately led to more substantial and sustained performance improvements in task switching. These changes in performance were accompanied by activation decreases in frontoparietal activation. While activation in the dlPFC decreased across repeat and single trials specifically in the SW group, activation in the superior parietal lobe decreased specifically for trials in the mixed blocks (i.e., repeat and switch trials) as opposed to single-task trials across both training groups as well as the PC group. Taken together, these results suggest that improved task-switching performance is supported by changes in response strategies as well as more efficient processing of task information in dlPFC. Connectivity among frontoparietal brain regions was greater on repeat than single trials with these differences decreasing in both training groups, with larger decreases in the SI group at the end of training. Importantly, group differences between the SI and SW group demonstrate that while a small amount of task-switching training already led to improved task switching, more intensive training of switching between rules is crucial for more efficient rule processing and the maintenance of changes over time.

5. Discussion

In this dissertation, I have used a combination of complementary approaches to integrate different perspectives and shed new light on the question how neural processes subserve the development of flexible behavior in children between 8 and 11 years. The first paper demonstrated that children recruited sustained and transient control activation less effectively than adults. However, focusing on individual differences, I demonstrated that particularly children with adult-like activation could counteract the resulting negative consequences for behavior by selectively increasing connectivity to additional prefrontal control regions with increased mixing demands. In Paper 2, I showed that the distinctiveness of task-set representations was lower on switch than on repeat trials in both children and adults, in line with the expectation that the recent updating of task sets renders representations less distinct. However, children neither showed less distinct representations than adults, nor were their representations more severely impacted by the demand to switch, suggesting that difficulties representing the currently relevant task contribute less to age differences in switch costs than so far assumed. The third paper showed that task switching can be improved in 8–11-year-olds by promoting faster accumulation of evidence for the correct response while following a more cautious response strategy. Alongside these changes in cognitive processes, training-related decreased activation in dlPFC suggested more efficient processing of task-relevant information, especially upon higher doses of task switching during training.

In the following, I will integrate the findings of the three papers, position them in the existing literature on cognitive control development, and outline open questions for future work. I first address how the presented results inform our understanding of different developmental trajectories of sustained and transient control processes, especially in the context of refined recruitment of frontal and parietal brain regions. Second, I discuss the role of neural representations for our understanding of cognitive control development. Next, I outline the importance of considering individual differences, both in a developmental perspective as well as for effective training of cognitive control. Fourth, I consider the training-related changes in brain function presented in this dissertation in light of training-induced neural flexibility and plasticity and how they can form a basis for addressing neural plasticity of higher cognitive functions in childhood. Finally, I discuss methodological issues and limitations of the present dissertation.

5.1 The development of sustained and transient control processes

Cognitive control during task switching can be separated into sustained control processes, the demands on which become evident in mixing costs, and transient control processes evident in switch costs (Braver et al., 2003). As outlined in this dissertation, sustained and transient control and the associated neural processes approach adult levels on different trajectories and are differentially impacted by intensive training in children. In this section, I discuss these results, outlining how the increasingly specific recruitment of frontal and parietal brain regions supports the development of sustained and transient control and in turn improved cognitive flexibility.

The neuroimaging findings of this dissertation corroborate the previously reported patterns of age difference showing that children rely on similar frontoparietal brain regions during task switching as adults but recruit these regions less efficiently as cognitive control demands increase (e.g., Chevalier et al., 2019; Church et al., 2017; Crone, Donohue, et al., 2006; Wendelken et al., 2012). However, the neuroimaging results of Paper 1, which were in close alignment with the behavioral results, demonstrated that age differences were more pronounced for sustained than for transient control, suggesting that sustained control processes including task-set maintenance and monitoring (Braver et al., 2003; Pettigrew and Martin, 2016; Rubin and Meiran, 2005) as well as selection (Chevalier et al., 2018; Chevalier and Blaye, 2009; Emerson and Miyake, 2003) follow an extended maturational path. Conversely, transient control processes, as measured with switch costs and activation differences between switch and repeat trials, already approached adult levels at the investigated age range of 8–11 years. Paper 2 extended the findings of similarities in transient control between children and adults by showing that the impact of switch demand on neural task-set representations did not differ between the age groups. Finally, Paper 3 showed greater and more continuous effects of task-switching training on sustained processes, indicating that sustained cognitive control processes are more malleable than transient processes, potentially because they are still developing.

I propose two potential mechanisms underlying the relatively more prolonged developmental trajectory of sustained processes during task switching: (1) the development of hierarchical cognitive control in IPFC (cf. Badre & Nee, 2018), which describes cognitive control on different levels of abstraction, and (2) the development of metacontrol (cf. Chevalier, 2015), which enables the adaptive adjustment of cognitive control based on current performance and task demands.

5.1.1 Hierarchical cognitive control

Our daily life is structured by rules. Some of these rules are explicit, such as a road sign instructing your driving speed, others are implicit, such as knowing that one should greet the people present when joining a meeting. Many of these rules are also interdependent, making it necessary that we follow a sequence of rules to achieve our goals (cf. Bunge & Wallis, 2008). For instance, if one is late to a formal meeting it might be more appropriate to quietly take one's place instead of vocally greeting the group, while a greeting would be appropriate if it is an informal gathering of friends. Such embedded rules can be described as hierarchical rules, where higher-level rules (e.g., the context) guide how or which lower-level rules are applied, for example by defining in which contexts a lower-level rule is appropriate (cf. Collins & Frank, 2013).

The framework of hierarchical cognitive control proposes that rule-based tasks require control on different hierarchical levels (Botvinick, 2008; G. A. Miller et al., 1960; Schneider & Logan, 2006). In a common conceptualization of these hierarchies, the lowest level describes control demands related to the encoding of stimuli and the execution of responses. The intermediate level consists of contextual control, that is, behavioral and cognitive adjustments based on changing context, while the highest level is temporal or episodic control, that is, control processes adjusting behavior and cognition in line with previous performance and events (Badre, 2008). Cognitive flexibility, as a facet of cognitive control, can be conceptualized in such a hierarchical framework (cf. Schneider & Logan, 2006). Specifically, switch costs can be viewed as resulting from greater demands of sensory-motor control on switch than repeat trials, given their dependence on stimuli and response processing. Mixing costs can be viewed as resulting from greater contextual control demands on mixed- compared to single-task blocks.

The framework of hierarchical cognitive control further proposes that the LPFC (and potentially the parietal cortex; Nee, 2021) subserving cognitive control is similarly organized in a hierarchical fashion (Badre, 2008; Badre & D'Esposito, 2007; Badre & Nee, 2018; Botvinick, 2008; Christoff et al., 2009; Duverne & Koechlin, 2017; Fuster, 2000; Koechlin & Summerfield, 2007; Nee & D'Esposito, 2016; O'Reilly, 2010). Specifically, more posterior LPFC regions (i.e., the premotor area) are recruited for lower levels of control demand such as sensory-motor or stimulus-specific control, followed by more central LPFC regions (i.e., dlPFC) associated with intermediate levels of cognitive control such as contextual control, while the most anterior LPFC regions are recruited for higher levels such as temporal or episodic control

(Badre & D'Esposito, 2007; Koechlin et al., 2003; Nee, 2021; Nee & Brown, 2012; Nee & D'Esposito, 2016). This organization is further thought to enable the neural representation of hierarchical rule structures and thus the ability to perform tasks in a goal-directed manner (Nee & Brown, 2012). To date, research regarding regional brain differences of hierarchical representations using multivariate methods is scarce and has provided no consistent results (Pischedda et al., 2017).

Developmental research suggests that children are able to identify and apply hierarchical rules from a very young age, e.g., within the first year (Werchan et al., 2015, 2016), but hierarchical rule use is refined throughout childhood and adolescence (Kray, Karbach, & Blaye, 2012; Unger et al., 2016). Age differences in hierarchical rule use have been taken to suggest that hierarchies in the IPFC are not as clearly established in childhood and thus children might recruit more anterior brain regions for lower levels of cognitive control (cf. Crone & Steinbeis, 2017). Intriguingly, recent evidence suggests that hierarchical cognitive control is orchestrated by mid IPFC (i.e., the dIPFC; Nee, 2021; Nee & D'Esposito, 2016; Pitts & Nee, 2022), a region that is among the regions that show the most protracted trajectory of structural development into early adulthood (Giedd, 2004; Sowell et al., 1999; Sydnor et al., 2021; but see Fuhrmann et al., 2022). Additionally, evidence from large-scale network analyses support a hierarchical development of functional networks (Keller et al., 2022) such that the degree of segregation and integration among networks depend on the networks' respective hierarchical level. However, studies directly testing the association between the development of specific recruitment of the IPFC and of the ability for hierarchical cognitive control are still lacking.

While task switching in the paradigm implemented in the studies of this dissertation did not directly manipulate all levels of control hierarchies, it required both sensory-motor and contextual control. Thus, from the perspective of hierarchical cognitive control, the findings of Paper 1 suggest that lower levels of control (i.e., switch costs) approach adult levels earlier than intermediate levels do (i.e., mixing costs). Additionally, the connectivity findings of Paper 1 further indicate that control hierarchies in the IPFC are less clearly established in children than in adults (Bunge & Zelazo, 2006; Unger et al., 2016). Specifically, with increasing contextual control demands on mixed- compared to single-task blocks, children increased connectivity between the IFJ and a cluster stretching from posterior to anterior IPFC. Thus, children potentially not only involved the part of the IPFC associated with contextual control (i.e., the dIPFC) but also higher-order control regions.

Taken together, in the framework of hierarchical cognitive control, the larger age differences in sustained control shown in Paper 1 might be due to less clearly defined cognitive control hierarchies in the developing LPFC. Indeed, Bunge and Zelazo (2006) have proposed that the ability to flexibly apply rules, as necessary during task switching, depends on the development of the LPFC (see also Crone et al., 2009; Lynn & Amso, 2023; Munakata et al., 2013). Future studies should experimentally manipulate the hierarchy of cognitive control demands to test how children selectively recruit the LPFC to represent hierarchical rules and explore how hierarchical patterns of activation are related to flexible behavior.

Such studies are especially important to understand cognitive flexibility given the role of abstract representations for flexible behavior. For instance, Snyder and Munakata (2010) demonstrated that 4–5-year-olds who showed higher abilities of abstract representations showed better self-directed switching, that is, a greater ability to switch to a different task based on internal goals. These results suggest that abstract representations of rules aided more flexible transitions between tasks, potentially due to their hierarchical nature reducing selection demand. Specifically, abstract hierarchical rules restrict the number of lower-level options, so that higher-level information (e.g., context) informs which lower-level rules are even applicable, so that not all rules have to be considered for selection (Munakata et al., 2013).

Paper 3 showed greater effects of task-switching training on brain activation associated with mixing costs, suggesting that sustained cognitive control may be more malleable than transient cognitive control in the investigated age range. Importantly, the more pronounced changes in boundary separation parameters in children who trained intensive task switching (as opposed to intensive single tasking) suggest that children in this group might have implemented different task-switching strategies than their peers in the intensive single task group. Specifically, children mainly practicing the task rules separately as single tasks might have represented the mappings between stimuli and responses separately from the task cue, as the cue was less relevant during single tasking, except on the first trial of a block. While single tasking may become more efficient via such flat rule structures, hierarchical representations are potentially more efficient during mixed task performance, where the cue is relevant on each trial (cf. Verbeke & Verguts, 2023). While these considerations cannot be directly tested within this study as hierarchical rule structure was not systematically manipulated in the training tasks, they raise the important notion that 8–11-year-old children are able to construct and apply hierarchical rules upon training, especially if the training encourages the hierarchical representation of rules. Future research should test this hypothesis directly by designing task-

switching training paradigms whose tasks differ in rule structures, for example, comparing flat to hierarchical rule structures and testing how these rule structures impact training outcomes and potentially even transfer to new, untrained tasks.

Taken together, the development of the IPFC and the resulting ability to recruit it along a hierarchy from posterior to anterior in support of cognitive control provides a fruitful framework for conceptualizing the different patterns of age and training-related differences in sustained and transient control. Future research exploring the development of hierarchical cognitive control is necessary to understand how and when children become increasingly able to behave flexibly based on hierarchical rule representations. Importantly, testing the hierarchical cognitive control framework from a developmental perspective is crucial for the concepts proposed in the framework itself, as understanding the function of brain regions or networks requires the understanding of how such a brain circuit has developed (cf. Astle et al., 2023).

5.1.2 Metacontrol development

The previous section focused on the notion that maturation of frontoparietal brain regions is associated with an increasingly fine-grained recruitment of specific control processes. However, flexible behavior requires that the recruited control processes correspond to the demands of the current task or situation, an ability referred to as *metacontrol* (Eppinger et al., 2021; Ruel et al., 2021). From middle childhood to adolescence, metacontrol abilities increase, such that children become increasingly able to adjust control allocation based on current demands (Chevalier, 2015; Chevalier et al., 2019).

With age, children become increasingly successful at judging the demands of the tasks and whether their current performance meets them (Chevalier, 2015; Fleur et al., 2021; Niebaum & Munakata, 2020), which forms the basis for adequate allocation of control. For instance, Niebaum and colleagues (2019) showed that 11-year-old children and adults were able to select the less effortful task when choosing between two tasks differing in difficulty, while 6-year-olds were not. Additionally, 6-year-olds could not indicate which task was the more demanding one, presumably because unlike older children and adults, they did not monitor task demands (see also Niebaum et al., 2021). These findings suggest that between the ages of 6 and 11 years children become better at correctly judging the demands of a task and at adjusting their behavior accordingly, thereby demonstrating increasingly efficient metacontrol. Given that the studies in this dissertation examined children in this age range (i.e.,

8–11-year-olds), age differences in metacontrol have to be considered as a potential contributing factor to the age differences observed in task-switching performance and associated brain activation and connectivity. For instance, the pattern of connectivity results of Paper 1 indicated the potential relevance of metacontrol for age differences in task switching. Specifically, on the neural level, metacontrol has been associated with the IPFC, especially more anterior regions of the IPFC (Eppinger et al., 2021; Ruel et al., 2021). Thus, the results of Paper 1 suggest that the increased involvement of metacontrol, as evident in increased connectivity between the IFJ and the IPFC on the more demanding mixed blocks, may support task switching in children. Increased metacontrol might have been especially helpful in children that showed less adult-like sustained activation, such that it aided the effective allocation of these limited control resources. Note that these individual differences described in Paper 1 are consistent with the reliance on metacontrol as well as the hierarchical cognitive control account given in the previous section. However, these accounts cannot be distinguished in the studies of this dissertation, thus requiring future studies to elucidate their respective contributions to the development of flexible behavior.

Another aspect of metacontrol involves the ability to track changes in the context and adjust performance accordingly (Doebel, 2020; Frick & Chevalier, 2023). Effective context tracking continues to develop in late childhood (Frick et al., 2022; Frick & Chevalier, 2023; Waskom et al., 2014), which is particularly relevant for the training-related findings of this dissertation. More specifically, the task-switching training in Paper 3 required children to practice switches between different rules as well as tracking the context of the presented stimuli, as it indicated which of the stimuli was relevant. Thus, greater performance improvements with higher doses of switching during training may also be related to improvements in context tracking. These improvements might in turn have supported a more adaptive allocation of control during more demanding mixed-task blocks indicated by changes in response strategy (i.e., boundary separation parameters).

Adequate control allocation also means that cognitive control is allocated proportionally to the expected outcome. The consideration of whether or not the exertion of (certain amounts of) cognitive control is worthwhile based on the expected reward or goal outcome has been formalized in the *Expected Value of Control* (EVC) framework (Shenhav et al., 2013, 2017). It postulates that the amount of cognitive control allocated to perform a task depends on the expected value of the exertion of this control. Considering the continuous development of cognitive control throughout childhood, one would expect the performance of

a cognitive control task to pose greater demands on cognitive control in children. If estimated outcome values of control are comparable in both age groups, control allocation would be estimated as being more costly in children, as they would have to exert more control to reach identical outcomes. Thus, children may allocate less control, resulting in lower performance (Ganesan & Steinbeis, 2022; Ruel et al., 2021; Steinbeis, 2023). Recent studies investigating the EVC framework in children suggest that 8–12-year-old children do indeed select tasks by matching control demands and task outcomes (Chevalier, 2018), indicating the importance of considering the value of outcomes for cognitive control development in late childhood.

Taken together, first studies have started to demonstrate that children in the investigated age range improve their metacontrol substantially and that they begin to include estimations of the value of cognitive control exertion into their allocation of control. While the design of the studies presented in this dissertation did not allow me to directly test the role of expected outcomes on control allocation during task switching or on training-related changes, the EVC provides a fruitful lens for future investigation of task-switching and cognitive control training in childhood (cf. Ganesan & Steinbeis, 2022). Specifically, interventions may become more efficient by directly training metacontrol abilities (Kubota et al., 2023), and may also improve from focussing on training children’s abilities to match their control allocation efforts to task demands based on expected outcomes (cf. Lieder et al., 2018).

5.2 Representations for flexible behavior

Previous behavioral and univariate activation studies have suggested that children might especially struggle during task switching due to less distinct task-set representations as well as less efficient updating of these representations (e.g., Crone, Donohue, et al., 2006; Wendelken et al., 2012). However, the results of Paper 2 indicated that neural representations of task sets showed similar distinctiveness and were similarly affected by switch demands in children and adults. These results thus suggest that switch costs in 8–11-year-olds are less affected by the distinctiveness of representations than previously assumed. However, given the age differences in switch costs observed in Paper 2, some aspects regarding neural representations for control should be considered.

First, decoding methods, as applied in Paper 2, can only reveal the content of an activation pattern, but not how this representation came to be and how it influences behavior (cf. Kriegeskorte & Douglas, 2018). This is especially relevant in the context of development, as previous studies have suggested that age differences between children and adults are

especially prominent in activation associated with manipulation of working memory representations, while age differences were smaller if mere maintenance was required (Crone, Wendelken, Donohue, van Leijenhorst, et al., 2006). This latter study suggests that children manipulated working representations differently than adults, raising the possibility that even though distinctiveness of representations did not differ between children and adults (Paper 2), children might have had difficulties in modulating task-set representations for implementation. Similarly, the results of Paper 1 of this dissertation demonstrated that children upregulated frontoparietal activation with increasing switch demands to a smaller extent than adults did, raising the possibility that it was the less effective implementation of the relevant task set in children that negatively affected their performance on switch trials.

A second aspect to be considered is that even if the content of neural representations as decoded via MVPA is similarly affected by switch demands across age groups, neural representations of task sets may still differ in their representational structure (Badre et al., 2021; Kikumoto et al., 2022). For instance, they may differ regarding the level of abstraction, which in the present task-switching paradigm would be whether the cue was represented as a higher-level rule determining the mapping of stimulus to response in a hierarchical manner, or whether stimulus-response mappings were represented independent of the cue. Importantly, the analysis of individual differences in Paper 2 suggested that in children, representations across brain regions are more similarly affected by switch demand than in adults. In light of recent considerations that representational structures differ substantially between brain regions in adults (Vaidya & Badre, 2022), these results invite the speculation that regional differences in representational structure could be less distinct in children than in adults and thus might contribute to age differences in (task-switching) performance.

Such regional differences in representational structure have, for instance, been demonstrated in a recent study examining how representational structure in adults changes during protracted learning of task rules (Mill & Cole, 2023). Specifically, early in learning, subcortical regions represented information in a conjunct, that is, task-specific manner, while cortical regions exhibited compositional representations that were task-general. Importantly, with learning, representations across cortical regions changed into conjunct representations (Mill & Cole, 2023). Other studies have shown that rule representations during learning differ between various cortical regions (Eichenbaum et al., 2020; Park et al., 2023; Theves et al., 2021; Vaidya et al., 2021). For instance, Theves and colleagues (2021) showed that evidence is accumulated and integrated by medial PFC regions and hippocampus in a trial-by-trial

manner, whereas the hierarchical general concepts resulting from this integration are represented in the anterior IPFC. Taken together, these findings can be conceptualized such that medial temporal regions and orbito-medial PFC represent task information in a flexible map, while hierarchically represented rules or task structures in IPFC, and potentially parietal regions, prepare rule-based actions (Vaidya & Badre, 2022).

Thus, while age differences in regional heterogeneity of abstract representations could provide one potential explanation for the results of Paper 2, indicating that neural representations in children – but not adults – were more similarly affected by switch demand across regions, future studies explicitly testing this hypothesis in developmental populations are necessary. Given the importance of refinement of representations in temporal-occipital brain regions for the development of representations in frontoparietal brain regions (Amso & Scerif, 2015) the exploration of functional and effective connectivity among these brain regions (cf. Qiao et al., 2020; Tsumura et al., 2021) would provide a valuable insight into the development of such neural representations for cognitive control.

5.3 Inter-individual differences in the development of cognitive flexibility

Generally, performance on cognitive control tasks increases steeply throughout childhood, leveling off in adolescence, and stabilizing around late adolescence or early adulthood (Tervo-Clemmens et al., 2023). Thus, across the age range investigated in this dissertation, children should still show substantial increases in cognitive control abilities. However, some studies also point out substantial inter-individual differences in cognitive control development (e.g., Brydges et al., 2014; Fields et al., 2021; Friedman et al., 2016; Friedman & Miyake, 2017; Miyake & Friedman, 2012; Rodehake et al., 2014). The studies in this dissertation further underline the importance of considering individual differences both in the investigation of the neural processes associated with task switching (Papers 1 & 2) and in studying training-related changes (Paper 3; see also Könen & Karbach, 2015, 2021).

Paper 1 demonstrated that while sustained control showed protracted development, there might be child-specific, potentially developmentally earlier mechanisms in place that enable children to reach a certain level of task performance. Specifically, children whose activation pattern associated with sustained control was less adult-like but who showed increased connectivity between the IFJ and the IPFC, performed better. However, the transition from such child-specific mechanisms to the presumably more efficient mature mechanisms of adaptive activation of the core frontoparietal control regions associated with task switching

harbors room for selecting inefficient or inappropriate strategies. While longitudinal studies are needed to inform the trajectory of this transition from child-specific to adult-like neural mechanisms, the complex pattern of brain-behavior relationship outlined in Paper 1 demonstrates that children can meet increased control demands in different ways (cf. Lautrey, 2003; Li & Lindenberger, 2002).

Inter-individual differences are especially crucial in the context of cognitive training: multiple studies have demonstrated that pre-training performance is associated with training trajectories and outcomes across age groups (Dong et al., 2024; Karbach et al., 2017; Könen & Karbach, 2015; Lövdén et al., 2012; see Karbach & Unger, 2014; Kray & Dörrenbächer, 2020, for reviews). Considering the starting point might be especially important when investigating training effects in children (cf. Frith, 2019), given the interactive nature of brain development. Specifically, models such as the *interactive specialization* theory by Johnson (2001, see also 2011) outline the importance of interactions of brain regions for development as well as the importance of the child's interaction with their environment. Bayesian frameworks of learning further extend these considerations of how experience-dependent change depends on an individual's current representation of the world around them (Stamps & Frankenhuis, 2016) by proposing that experiences result in updated posterior distributions of these representations of the world. From a training perspective, this means that information received during training will be integrated into existing representations of the environment, but the extent to which this happens, depends on the relevance of the information received during training (Smid et al., 2020). Beyond these theoretical considerations, as Smid and colleagues (2020) outlined, these models additionally provide a helpful computation framework to model how individual differences shape training outcomes.

While training studies have started to investigate how individual differences in pre-training performance impact training outcomes and trajectories (e.g., Karbach et al., 2017; Könen & Karbach, 2015; Lövdén et al., 2012; Nemmi et al., 2016; for a recent review see Katz et al., 2021), it is important to further consider interventions adapted to individuals' performance during training, so that the optimal training outcomes can be achieved for each individual (e.g., Holmes et al., 2009; Karbach et al., 2015; Karbach & Unger, 2014). Kuchinsky and Haarman (2019) further stress the importance of adaptive training to elicit lasting changes in the neural mechanisms that support the trained task and increase the likelihood of transfer to untrained tasks. The differences between training groups presented in Paper 3 of this dissertation invite a similar conclusion. Specifically, lower doses of task-switching training

might have shown less extensive and more short-lived changes in performance and dlPFC activation as it posed less demands on the task-switching network (cf. Lövdén et al., 2010). As the aim of Paper 3 was to uncover general changes in neural processes with task-switching training, however, the sample size makes it difficult to investigate individual differences. Nevertheless, it stresses the importance of training demands for sustained changes in neural processes and provides important starting points for future research of how individual differences impact outcomes and mechanisms of training.

Taken together, both the investigation of neural mechanisms and of training-related improvements of cognitive control benefit from investigating the role of individual differences. Importantly, the investigation of individual differences requires re-examination of the current methodology commonly applied in developmental cognitive neuroscience. This includes adequate sample sizes (Marek et al., 2022), the refinement of current measures, and the development of novel ones to better capture individual differences (Gratton et al., 2022; Pezzoli et al., 2023; Rosenberg & Finn, 2022).

5.4 Plasticity of cognitive control in childhood

One aim of this dissertation was to provide mechanistic understanding of training-related changes in cognitive control (Gobet & Sala, 2023). Paper 3 suggests that training-related improvements in task-switching performance are supported by an increased efficiency of task processing, as indicated by changes in drift rate and frontoparietal brain activation, and by strategy changes, as indicated by changes in boundary separation.

To further elucidate how such changes in brain function are supported by neural plasticity and flexibility, studies investigating how brain structure changes with task-switching in relation to other types of cognitive control training are needed. As Lindenberger and Lövdén (2019; see also Lövdén et al., 2020) have proposed, plastic changes in brain structure with skill learning follow a trajectory of expansion, exploration, selection, and refinement of neural circuits that support a skill. However, the authors also outline that it is so far unclear how these observations would transfer to training-induced plasticity of higher cognitive functions, such as task switching. Not only is research regarding the question of structural changes with cognitive training lacking in humans, but also research on this question in animal models (Kolb et al., 2012; Kolb & Gibb, 2015). One rare example is a study by Kolb and colleagues (2003) that indicated that experience-related changes in rodent brains differed in PFC compared to other brain regions. Specifically, after housing rats in complex environments, their PFC

neurons showed increased spine density, while neurons in parietal and occipital cortices showed increased dendritic length (Kolb et al., 2003). As outlined in Paper 3, functional changes with task-switching training were associated with functional changes in LPFC, suggesting these regions as potential sites of training-induced structural changes. Thus, potential differences of plasticity mechanisms in these LPFC regions compared to sensory-motor regions commonly investigated in plasticity research have to be taken into consideration when setting out to investigate mechanisms of plasticity in association with training-related changes in cognitive control.

A further consideration when studying plasticity of cognitive control in childhood is the fact that brain structure continues to develop throughout childhood and adolescence so that these developmental changes in structure might happen alongside any training-induced changes in structure (Laube et al., 2020; Tymofiyeva & Gaschler, 2021). Specifically, while studies in adults suggest training-induced increases in gray matter, at least initially (Lindenberger & Lövdén, 2019; Lövdén et al., 2020; Wenger, Kühn, et al., 2017), gray matter volume decreases throughout child development (e.g., Giedd, 2004; Giedd et al., 1999) making the interpretation of potential training-induced changes in structure more complex. While research on training-induced changes in brain structure in children is scarce, some preliminary evidence of inhibitory control training suggests that it might be characterized by decreases rather than increases (Delalande et al., 2020). However, it also indicates that plastic changes with cognitive training may be more complex in the developing brain (Delalande et al., 2020; see also Omont-Lescieux et al., 2023). Thus, while results of Paper 3 demonstrate that children show a similar pattern of decreased prefrontal activation with task-switching training as previously shown in adults, the potential structural changes that support these functional changes likely differ between children and adults.

Trajectories of change in behavior and brain activation discovered in Paper 3 further outline the importance of creating a sustained mismatch between demand and current capacity. Specifically, the lower doses of task switching may not have posed enough demands to evoke sustained challenges to the task-switching networks to maintain initial activation and performance changes (cf. Lövdén et al., 2010). Eliciting such a mismatch may generally be easier in children, given their still developing cognitive control ability, but may also harbor a greater risk of making training too demanding so that it does not lead to the expected improvements (cf. Karbach & Kray, 2009). This further stresses the importance of individual-based adaptive training for plastic changes discussed above, especially when training

populations showing greater inter-individual differences in both performance and activation, such as children do (Kuchinsky & Haarmann, 2019).

Additionally, given that cognitive control is supported by a network of brain regions (Menon & D'Esposito, 2022), changes in structural connectivity may be especially relevant for investigating plasticity of cognitive control. With increasingly precise methods to image white matter structure, studies of white matter plasticity are starting to emerge. Studies in developmental populations have so far focused on education-related interventions (Huber et al., 2018, 2021; Jolles et al., 2016). For instance, Huber et al. (2018) showed that reading training improved the targeted skill and elicited changes in white matter structure in 7–12-year-old children. Although it is unclear of yet whether myelination or other neurobiological mechanisms are driving these changes (cf. Huber et al., 2021), these studies suggest that training higher cognitive functions leads to rapid changes in the structural connectome of the developing brain. Constantinidis and Klingberg (2016) further suggested that changes in structural connectivity might be especially likely in pathways that are specifically recruited with greater task demands, again underlining the importance of an adequate mismatch between current capacity and training demands outlined above. In light of this, the findings presented in Paper 1 suggest the hypothesis that training-induced changes in structural connectivity are especially relevant when training task switching in children. Specifically, the alternative mechanism of upregulated connectivity between the IFJ and the IPFC may well be structurally strengthened with training.

Taken together, future research is needed to understand how plastic changes in gray and white matter support training-related changes in brain function and thus performance improvements. The research presented in this dissertation provides a valuable starting point for these studies by highlighting the importance of IPFC functions and the crucial role of additional connections in the IPFC for task performance in children.

5.5 Methodological considerations and limitations

In this section, I would like to acknowledge limitations and discuss methodological considerations of the studies presented in this dissertation.

As any study based on cross-sectional comparisons of age groups, age differences in Papers 1 and 2 can provide evidence on how processes might differ between children and adults and thus a starting point for future research. However, such designs do not allow conclusions of how these processes change over the course of development, and how individuals differ in

the trajectories of these changes (Lindenberger et al., 2011; Louis et al., 1986). Thus, the patterns of results presented in Paper 1 should be seen as a starting point for investigating how sustained and transient control develop in a longitudinal sample from middle childhood to adolescence to track how their neural mechanisms differentiate. This is especially crucial for understanding the inter-individual differences reported in Paper 1 to address the question whether the transition from a child-specific to an adult-like neural processing strategy is gradual. Additionally, longitudinal studies are vital for understanding the complex, interacting trajectories of brain structure, activation, and connectivity, that may exhibit non-linear and non-monotonic relationships to behavior, which potentially further differs between individuals (Lautrey, 2003; Li & Lindenberger, 2002; Wendelken et al., 2017).

Similarly, investigating neural task-set representations like in Paper 2 in a longitudinal manner may further inform when in the course of ontogeny children show comparably distinct task-set representations. It may further be crucial to investigate how neural task-set representations change during rule learning. In Paper 2, participants learned and practiced the rules prior to scanning such that the reported results were based on the application of the already learned rules during task switching. Recent evidence suggests that it is crucial *when* during learning representations are investigated because the representational structure changes with learning, with these changes differing between brain regions (Mill & Cole, 2023). Given the importance of representational structure for effective cognitive control in adults (Badre et al., 2021; Kikumoto et al., 2022; Vaidya & Badre, 2022), studies addressing how representations are built during learning could inform how the ability to represent different features contribute to the development of flexible behavior.

Additionally, the present task design did not allow me to explore the propositions regarding hierarchical representations outlined above. Specifically, limited trial numbers and limitations in testing differences in decoding accuracy on higher levels of the rule hierarchy (i.e., single vs. mixed), prevented the exploration of this possibility within the scope of this dissertation. However, the recent findings discussed above encourage the exploration of these hypotheses in future studies specifically designed to test the development of the representation of hierarchical rule structures and the role of regional heterogeneity in these representations.

In this dissertation, I addressed the question of the development of flexible behavior using multiple methods to understand cognitive and neural processes underlying task switching. While I applied both univariate and multivariate analyses of neuroimaging data, our understanding of cognitive flexibility may further benefit from combining these methods into

multimodal approaches (cf. Baykara et al., 2021; Elliott et al., 2020; Hu et al., 2022). It may thus be fruitful to extend the findings presented in this dissertation by combining different analysis methods and data not only at a ROI-based level but also at a whole-brain level. This could unveil patterns of individual differences that do not become evident in analyses of the separate modalities and could thus clarify how these individual differences contribute to cognitive control development and training outcomes (Hu et al., 2022).

Regarding the training-related changes in neural processes associated with task switching reported in Paper 3, it is important to acknowledge that task-based activation and connectivity measures are inherently dependent on performance, and are thus always limited in that the interpretation of training-related changes in activation or connectivity are confounded by performance changes rather than being their driver (Kelly & Garavan, 2005; Poldrack, 2000; Sanes & Donoghue, 2000). Additionally, changes in fMRI activation need to be interpreted with caution, especially when inferring increased efficiency based on decreased activation, as commonly done in the training studies on which Paper 3 also builds. While Paper 3 analyzes within-subject change in activation and thus partly mitigates this problem, future studies need to investigate how decreasing activation with training is associated with changes in brain metabolism to support the claim of increased efficiency (cf. Poldrack, 2015). Furthermore, as Constantinidis and Klingberg (2016) have discussed, the mapping between training-induced changes in fMRI activation and neuronal firing rate is not yet completely understood. Thus, we cannot draw firm conclusions as to how cellular mechanisms change with training and thus support behavioral improvements.

Finally, Smid and colleagues (2020) have outlined the importance of computational models for understanding the effect of cognitive training and designing interventions that lead to transferable performance improvements (see also von Bastian et al., 2022). In Paper 3, I therefore use hierarchical drift diffusion models to elucidate how the cognitive processes of task switching change with training. However, these models in themselves do not account for inter-individual differences in pre-training performance, which might be especially crucial to understand training mechanisms in children (Smid et al., 2020). Specifically, as discussed above, previous learning experiences drastically affect how the demands posed on cognitive control due to an intervention are met by the cognitive system of a child and thus shape the extent of experience-related change (Fawcett & Frankenhuis, 2015; Stamps & Frankenhuis, 2016). Thus, Bayesian learning models could contribute substantially to understanding the

cognitive and neural mechanisms of training-induced changes, especially during childhood development.

5.6 Conclusion

In this dissertation, I have examined brain activation, connectivity, and neural representations associated with cognitive flexibility to elucidate how the developing brain supports increasingly flexible behavior during late childhood. Taken together, this dissertation demonstrates that while 8–11-year-old children do not quite reach adult-levels of cognitive flexibility, they show recruitment of additional neural mechanisms to support still developing frontoparietal regions supporting cognitive control, show surprisingly adult-like levels of distinctiveness of task-set representation, and an increased efficiency of rule processing in frontoparietal brain regions with task-switching training.

Investigating both age differences as well as training-related changes, the empirical work in this dissertation showed that the sustained and transient neural processes supporting mixing and switching, respectively, do not approach adult-levels at the same time. Specifically, Paper 1 showed different extents of age differences in neural processes and adaptive recruitment of additional neural mechanisms for sustained control. The pattern of results suggests that these changes are closely related to more specific recruitment of the IPFC in line with hierarchical control demands of the task, as well as the development of metacontrol abilities that adaptively support control allocation in line with current demands.

Furthermore, Paper 3 showed that the potential to train task switching depends on these developmental trajectories and how the demands of the intervention are matched with them. In particular, changes in neural activation and connectivity associated with mixing costs showed greater and more continuous change with task-switching training. As sustained cognitive control abilities show protracted development, the mixing demands of the training may have elicited a greater mismatch with current sustained control abilities, than the switch demands with current transient control abilities. Additionally, training-related changes in task-switching performance were more prominent in children that had trained higher doses of task switching. This pattern of results further implies that task-switching training might be particularly effective if hierarchical rule structures were made more explicit. Analyses of the cognitive processes of task switching further suggest that response strategies changed with training, underlining the role of metacontrol for performance improvements. The work in this dissertation thus extends previous theoretical considerations of the importance of considering

metacontrol for cognitive control development, and provides starting points for further investigation.

Investigating neural task-set representations (Paper 2), this dissertation further demonstrated that the neural processes supporting representations during task switching are more mature in late childhood than previously assumed. It thus warrants the reassessment of how representations contribute to switch and mixing costs.

I have further outlined how future research into developmental differences in the hierarchical representation and implementation of task sets, the structure of representations, and regional heterogeneity in representations can contribute to our understanding of why children struggle with cognitive flexibility. Specifically, studies could investigate how representational structure changes with learning and how this might support the development of flexible behavior. Crucially, such studies should also adopt longitudinal approaches to elucidate how the role of hierarchical representations changes during child development. Additionally, future studies mapping training-related changes in brain function to changes in brain structure are necessary to clarify how mechanisms of plasticity support training-related improvements in performance.

Taken together, this dissertation sheds new light on age differences and training-related changes in neural activation, connectivity, and representations of task switching and has thus helped to gain a more mechanistic understanding of the neurocognitive development of flexible behavior.

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Appendix

The appendix of this dissertation includes the following documents

A: Paper 1 – Schwarze, S. A., Laube, C., Khosravani, N., Lindenberger, U., Bunge, S. A., & Fandakova, Y. (2023). Does prefrontal connectivity during task switching help or hinder children's performance? *Developmental Cognitive Neuroscience* 60:101217.

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B: Paper 2 – Schwarze, S. A., Bonati, S., Cichy, R. M., Lindenberger, U., Bunge, S. A., & Fandakova, Y. (2023). *Task-switch related reductions in neural distinctiveness in children and adults: Commonalities and differences*. Manuscript submitted for publication.

C: Paper 3 – Schwarze, S. A., Laube, C., Khosravani, N., Lindenberger, U., Bunge, S. A., & Fandakova, Y. (2023). *Intensive task-switching training and single-task training differentially affect behavioral and neural manifestations of cognitive control in children*. Manuscript submitted for publication.

A: Paper 1

Schwarze, S. A., Laube, C., Khosravani, N., Lindenberger, U., Bunge, S. A., & Fandakova, Y. (2023). Does prefrontal connectivity during task switching help or hinder children's performance? *Developmental Cognitive Neuroscience* 60:101217.

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Does prefrontal connectivity during task switching help or hinder children's performance?

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ABSTRACT

The ability to flexibly switch between tasks is key for goal-directed behavior and continues to improve across childhood. Children's task switching difficulties are thought to reflect less efficient engagement of sustained and transient control processes, resulting in lower performance on blocks that intermix tasks (sustained demand) and trials that require a task switch (transient demand). Sustained and transient control processes are associated with frontoparietal regions, which develop throughout childhood and may contribute to task switching development. We examined age differences in the modulation of frontoparietal regions by sustained and transient control demands in children (8–11 years) and adults. Children showed greater performance costs than adults, especially under sustained demand, along with less upregulation of sustained and transient control activation in frontoparietal regions. Compared to adults, children showed increased connectivity between the inferior frontal junction (IFJ) and lateral prefrontal cortex (IPFC) from single to mixed blocks. For children whose sustained activation was less adult-like, increased IFJ-IPFC connectivity was associated with better performance. Children with more adult-like sustained activation showed the inverse effect. These results suggest that individual differences in task switching in later childhood at least partly depend on the recruitment of frontoparietal regions in an adult-like manner.

1. Introduction

The ability to switch flexibly between tasks enables individuals to adapt their behavior to changing environments and is a key component of cognitive control (Miyake et al., 2000; Miyake and Friedman, 2012). However, this flexibility comes at a cost. When faced with the demand to switch rapidly between tasks, individuals exhibit two types of performance decline. First, they show greater error rates and longer response times (RTs) on blocks of intermixed tasks (*mixed blocks*) compared to *single blocks* in which they perform only one task. These *mixing costs* are assumed to reflect sustained control demands, including the selection of the relevant goal (Chevalier et al., 2018; Chevalier and Blaye, 2009; Emerson and Miyake, 2003), and the maintenance and monitoring of multiple sets of rules associated with each task – so-called task sets

(Braver et al., 2003; Pettigrew and Martin, 2016; Rubin and Meiran, 2005). Within the mixed blocks, performance declines further on trials that require a different task than the previous trial (i.e., *switch trials*) compared to trials repeating the previous task (i.e., *repeat trials*). These *switch costs* are thought to reflect transient control processes of inhibiting the no-longer-relevant task set (Allport et al., 1994; Meiran, 1996; Wylie and Allport, 2000) and retrieving and updating the newly relevant task set (Mayr and Kliegl, 2000; Rogers and Monsell, 1995).

Functional magnetic resonance imaging (fMRI) studies have highlighted the left inferior frontal junction (IFJ) and the left superior parietal lobe (SPL) as key regions involved in task switching (Derrfuss et al., 2005; Kim et al., 2012; Niendam et al., 2012; Richter and Yeung, 2014; Worringer et al., 2019; Zhang et al., 2021), particularly for transient processes including task-set updating and attentional shifts (Brass

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et al., 2005; Brass and von Cramon, 2004; Braver et al., 2003; Gurd et al., 2002). Sustained control processes, including task-set maintenance and monitoring, have been associated with the anterior and dorsolateral prefrontal cortex (aPFC and dlPFC, respectively; Badre, 2008; Braver et al., 2003; Gold et al., 2010) and the SPL (Brass and von Cramon, 2004; Bunge et al., 2003). Functional connectivity analyses have associated a frontoparietal network (FPN) of similar regions (i.e., the IFJ, SPL, dlPFC, and the precuneus) with transient control, and a cingulo-opercular network including the anterior insula/frontal operculum (al/fo), the dorsal anterior cingulate cortex (dACC), and the aPFC with sustained control (Dosenbach et al., 2008, 2007, 2006).

Flexibly switching between tasks entails larger costs in children than adults (Cragg and Chevalier, 2012; Gupta et al., 2009; Huizinga et al., 2006; Huizinga and van der Molen, 2007). While children show similar switch costs to adults by 9–11 years, mixing costs only approach adult levels during adolescence (13–15 years; Cepeda et al., 2001; Crone et al., 2004, 2006a; Reimers and Maylor, 2005). The age differences reported previously suggest that sustained and transient control follow different developmental paths, with a more protracted development for sustained control, presumably reflecting the later maturation of relevant frontal brain regions and their connectivity.

The majority of developmental neuroimaging studies of task switching support a view of quantitative age differences, with children recruiting the same set of regions as adults, albeit in a less specific manner (Bunge and Wright, 2007; Engelhardt et al., 2019; Velanova et al., 2008; Wendelken et al., 2012; Zhang et al., 2021; but see Crone et al., 2006b; Morton et al., 2009). According to this view, the neural underpinnings of task switching typically observed in adulthood are in place by middle childhood and are subsequently fine-tuned, showing more differential activation between task conditions (Durstun et al., 2006; Luna et al., 2015; Satterthwaite et al., 2013).

Similarly, by the age of around 10 years, children show network organizations that are similar to those of adults, but with continuing changes in connectivity strengths within and between networks (Engelhardt et al., 2019; Grayson and Fair, 2017; Marek et al., 2015). To date, only one study has examined age differences in network connectivity during task switching (Ezekieli et al., 2013). Children showed lower connectivity within the FPN than adults along with greater integration of the aPFC into the FPN, as reflected in ICA-based voxel-wise factor loadings, suggesting that children might configure brain networks in different ways than adults to meet increased control demands during task switching. However, this study did not examine age differences in connectivity change with increased control demand. Thus, it is unclear whether developmental changes in connectivity in response to increased control demands consist in the gradual evolution of the adult pattern, or whether one can observe a shift from a child pattern to an adult pattern. Conceptually, the brain typically provides more than one pathway to implement a task, both within and across individuals (Edelman, 1987; Lautrey, 2003; Li and Lindenberger, 2002). In the course of brain maturation, one way of implementing cognitive control may gradually become more effective than another, such that children eventually shift from one configuration to another (e.g., Van der Maas and Molenaar, 1992).

Of note, children differ considerably in task-switching development (Dauvier et al., 2012; Fields et al., 2021) and the pace of brain maturation (e.g., Mills et al., 2021). Church et al. (2017) reported that children who showed more adult-like (i.e., greater) frontoparietal activation during the preparatory period of task switching showed less activation in other regions during the target stimulus. Thus, age-related changes in brain-behavior mappings during task switching may not be uniform but follow different routes in different groups of children (e.g., Lautrey, 2003), creating an additional source of heterogeneity in the neural implementation of task-switching demands among children.

We examined the neural correlates of sustained and transient control during task switching in children aged 8–11 years and adults aged 20–30 years. We expected greater mixing and switch costs in children,

reflecting the continued development of task-switching. We predicted that children would recruit similar frontal and parietal regions as adults but that they would show less upregulation of activation and connectivity in these regions with increased control demands. Further, we predicted that age differences in behavior and task-related activation would be more pronounced for sustained than transient control, consistent with the proposition that children reach mature levels of sustained control, operationally defined as task-set maintenance and monitoring, at a later age than mature levels of transient control, defined as task-set retrieval and updating. Finally, we explored whether individual differences in sustained activation and connectivity are associated with individual differences in task-switching performance. In particular, we were interested in the degree to which the link between connectivity and task-switching performance was modulated by the maturational status of individual children. We hypothesized that children with less mature sustained activation in the core task-switching network might show heightened connectivity with other brain regions, as a vicarious neural implementation of task-switching behavior.

2. Methods

2.1. Research participants

Children between 8 and 11 years of age ($n = 117$; mean age = 10.0, $SD = 0.71$; 59 girls) and adults between 20 and 30 years of age ($n = 53$; mean age = 24.7, $SD = 2.6$; 28 women) were recruited from the internal participant database of the Max Planck Institute for Human Development. Participants were screened for MRI suitability, had no history of psychological or neurological diseases, and German was their primary language. All participants were right-handed. Adult participants and the participating children's parents provided informed consent; the participating children additionally provided written assent. All participants were reimbursed with 10 € per hour spent at the MRI laboratory. The study was approved by the ethics committee of the Freie Universität Berlin and conducted in line with the Declaration of Helsinki.

Based on previous research on the developmental trajectories of sustained processes (measured by mixing costs) and transient processes (measured by switch costs) during task-switching (e.g., Cepeda et al., 2001; Crone et al., 2006a, 2004; Reimers and Maylor, 2005), we were particularly interested in the neural mechanisms supporting task switching between 8 and 11 years. This age group represents a period in childhood when both sustained and transient processes are still developing but are starting to dissociate, with transient control beginning to plateau and sustained control continuing to improve.

Participants were included in analyses if they performed the task in accordance with the task rules and had good fMRI data quality. Accuracy below 50% in the run of single blocks (run 1, see below for more details on the paradigm) or accuracy below 35% in either of the two runs of mixed blocks (run 2 and 3) was defined as poor performance. We defined a threshold well above chance (33%) in the single runs to make sure participants knew and could successfully apply the rules when no additional demand on switching among them was present. fMRI volumes with framewise displacement (Power et al., 2012) above 0.4 mm were marked as low-quality (see Dosenbach et al., 2017). If any of the fMRI runs exceeded 50% of low-quality volumes, the participant was excluded from further analysis. Twenty children were excluded because of excessive motion, four children due to poor performance, and four children due to both excessive motion and poor performance. Thus, a total of 89 children (mean age = 10.06, $SD = 0.7$, 50 girls) and 53 adults were retained in the analyses reported below.

2.2. Experimental design

Participants performed a task-switching paradigm consisting of three different categorization rules (Fig. 1A). In every trial, a face, a scene, and an object were presented, and participants were cued by the shape of the

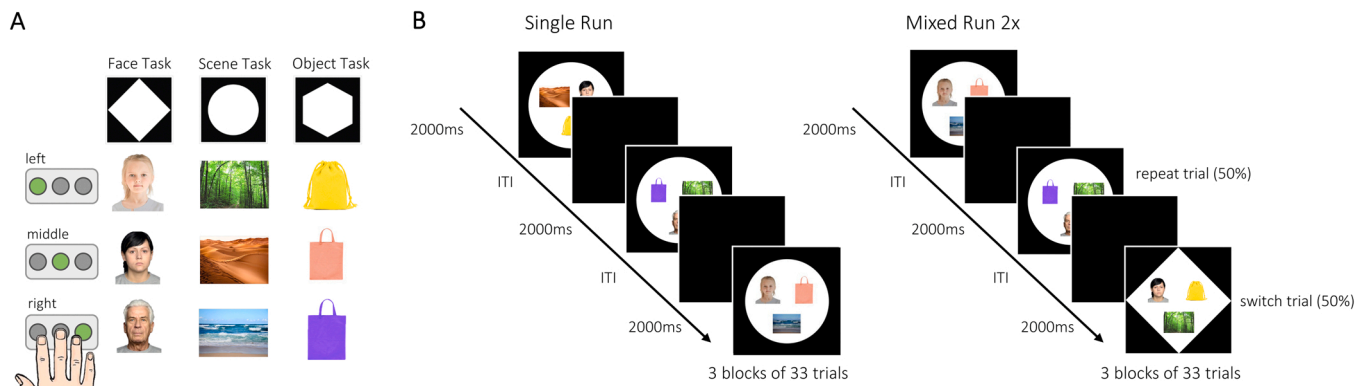


Fig. 1. *Experimental Design.* (A) The task-switching paradigm consisted of three tasks, the face task, the scene task, and the object task. Participants had to perform the task indicated by the shape of the background. Depending on the stimulus presented, one of three buttons had to be pressed in response (here indicated by the green button). There were two different stimuli for each of the three levels of the three categorization rules (e.g., two different scenes of a desert). (B) Participants performed one single run, where the three tasks were presented in blocks of 33 trials and two mixed runs, where the tasks were intermixed. Each run consisted of 99 trials presented for 2 s with a jittered inter-trial interval (ITI). For a full description of the task, see text. Image credits: Young and old adult faces were taken from the FACES collection (Ebner et al., 2010).

background (diamond, circle, or hexagon) as to whether to perform the face task, scene task, or object task. If the stimuli were presented in a diamond-shaped background, the face image had to be classified according to the age of the face (child vs. young adult vs. older adult). If the stimuli were presented in a circle, the image of the scene had to be classified according to the depicted scenery (forest vs. desert vs. sea). For stimuli presented in a hexagon, the image of the object had to be classified according to its color (yellow vs. red vs. purple). All stimuli and the task cue appeared at the same time. The arrangement of images on the screen varied randomly independent of the categorization rule. For each of the three tasks, participants had to respond via button press using their right index, middle, and ring finger. The assignment of finger to response option was held constant across participants. There were two different stimuli for each of the three levels of each of the three categorization rules, e.g., two faces of children, two yellow bags, two forest scenes, etc., resulting in a total of 18 different stimuli.

Participants performed three runs of 99 trials each (Fig. 1B). Each trial lasted 2000 ms, followed by a fixation cross for a jittered time period (1000–6000 ms). After every 33 trials, there was an extended fixation period (20 s), resulting in three blocks of 33 trials per run. Each of the three runs lasted ca. 7 min. In the first run (i.e., *single blocks*), each block contained trials of a single task (i.e., the first 33 trials were of the face task, followed by 33 trials of the scene task, and 33 trials of the object task). Across runs two and three (i.e., *mixed blocks*), the three tasks were intermixed, so that participants needed to repeat a task in 50% of the trials (*repeat trial*) and switch to a different task in the other 50% of the trials (*switch trial*). The switches between task rules were not predictable, such that participants did not know in advance which task had to be performed next. In run two, 50 trials required a task switch and 48 a task repetition; in run three, 48 trials were switch trials and 50 were repeat trials. As the first trial of each run could not be categorized as a switch or repeat trial, it was excluded from all analyses.

The data analyzed here are part of a larger training study, during which participants were scanned multiple times. The present data were acquired during the second session of the training study. The first session of the study included a computerized assessment of general cognitive functioning not analyzed here, as well as a shortened version of the MRI task to ensure that participants were familiar with the rules. Prior to scanning, participants were shown the instructions again and practiced the task in a mock MRI scanner. The mock scanner looked identical to a regular MRI scanner, with MR scanning sounds being mimicked via speakers so that participants could get accustomed to the scanning environment. The three runs of the MRI task were performed in the scanner after an initial T1-weighted scan during which participants

watched a muted cartoon.

2.3. Behavioral analysis

Trials with response times (RT) below 200 ms and above 3000 ms were excluded from all analyses. Median RTs and mean accuracies were analyzed for effects of task rule condition (single block trials vs. repeat trials in mixed blocks vs. switch trials in mixed blocks), effects of age group (adults vs. children), and their interaction using separate linear mixed-effects models with a random intercept for subject. Only correct trials were considered for the RT analysis. Accuracy was calculated as the percentage of correct responses across all responses for a given condition. Outliers were defined as mean accuracy or median RTs that deviated by 3.5 standard deviations or more from the age-group mean, and were removed from analyses of accuracy and RT separately (Tabachnick and Fidell, 2013).

Main effects of condition were followed up by pairwise comparisons, with p-values FDR-corrected for multiple comparisons (Benjamini and Hochberg, 1995). Analyses were performed in R 4.0.3 (R Core Team, 2018) with the tidyverse (Wickham et al., 2019), ggpubr (Kassambara, 2020a), rstatix (Kassambara, 2020b), rmisc (Hope, 2013), sjPlot (Lüdtke et al., 2021), lme4 (Bates et al., 2022), lmerTest (Kuznetsova et al., 2017), and emmeans (Lenth et al., 2022) packages.

2.4. fMRI data acquisition and preprocessing

Anatomical and functional MR images were collected on a 3-Tesla Siemens Tim Trio MRI scanner with a 32-channel head coil at the Max Planck Institute for Human Development. A high-resolution T1-weighted structural image was acquired (220 slices; 1 mm isotropic voxels; TE = 2.35 ms; FoV = 160 × 198 × 220). Functional runs consisted of 230 whole-brain echo-planar images of 36 interleaved slices (TR = 2000 ms; TE = 30 ms; flip angle = 80°; slice thickness = 3 mm; in-plane resolution (matrix) = 3 × 3 mm (72 × 72); FoV = 216 × 216 × 129.6). During the acquisition of functional images, the task was projected on a screen behind the participant's head that they could see via a mirror mounted on the head coil. During task execution participant motion was monitored using Framewise Integrated Real-time MRI Monitoring (FIRMM; Dosenbach et al., 2017). Participants were provided feedback on their movement after each run and were encouraged to try to move less if they exceeded the threshold of 0.4 mm of movement for at least 10% of frames of the previous run.

Preprocessing was performed using fMRIprep (Version 20.2.0; Esteban et al., 2019). For a detailed description, see the fMRIprep

documentation (link). Briefly, BOLD images were co-registered to individual anatomical templates using FreeSurfer, which implements boundary-based registration (Greve and Fischl, 2009). Additionally, they were slice-time corrected (using AFNI; Cox and Hyde, 1997), and realigned (using FSL 5.0.9; Jenkinson et al., 2002). Finally, images were resampled into MNI152Nlin6Asym standard space with a voxel size of 2 mm × 2 mm × 2 mm and spatially smoothed with an 8 mm FWHM isotropic Gaussian kernel using SPM12 (Functional Imaging Laboratory, UCL, UK).

2.5. fMRI data analysis

2.5.1. General linear model

GLM analyses were performed using SPM12 software. For each subject, we estimated two general linear models (GLM). The first GLM modeled sustained control demands in a blocked design (*sustained* GLM). Condition regressors included *single task*, consisting of three blocks of 127 s each within the first run, and *mixed task*, consisting of six blocks of 127 s each, evenly split over the second and third run. Data were high-pass filtered at 172 s

A second GLM modeled transient control demands in an event-related design (*transient* GLM). Here, each stimulus presentation was coded as an event with zero duration, and convolved with a canonical hemodynamic response function (HRF). Separate regressors were included for correct *switch trials* and *repeat trials*. Incorrect trials, trials with extreme RTs (below 200 ms or above 3000 ms), trials with missed responses, and the first trial of each run were modeled as nuisance regressors. Data were high-pass filtered at 128 s

To minimize head motion artifacts, both GLMs included the amount of frame displacement per volume, in mm (Power et al., 2012), realignment parameters (three translation and three rotation parameters), and the first six anatomical CompCor components (as provided by fMRIPrep; Behzadi et al., 2007) as regressors of no interest. The first five volumes of each run were discarded to allow for stabilization of the magnetic field and temporal autocorrelations were estimated using first-order autoregression.

Sustained control activation was defined as higher activation in mixed compared to single blocks (mixed > single) in the sustained GLM. Transient control activation was defined as higher activation on switch trials compared to repeat trials (switch > repeat) within the mixed runs of the transient GLM. The sustained GLM modeled control in a continuous manner, such that mixed blocks included both switch and repeat trials (e.g., Braver et al., 2003). With these separate models, it is not possible to directly compare single and repeat trials; thus, we also constructed an event-related GLM that included correct single, repeat, and switch trials as separate regressors of interest (*control* GLM). All nuisance regressors and additional parameters were identical to the transient GLM.

2.5.2. Region-of-interest definition and analysis

First, we identified regions of interest (ROIs) involved in sustained and transient control over all subjects (whole-brain analyses; $p < .05$ family-wise-error (FWE) corrected). For sustained control, we selected voxels that showed greater activation in mixed blocks than in single blocks in the sustained GLM. We identified regions involved in transient control by selecting voxels showing greater activation on switch than on repeat trials in the transient GLM. Second, to identify ROIs that showed modulation by sustained and transient control demand, which we referred to as *overlap* ROIs, we applied inclusive masking which identified common voxels for sustained and transient activation. Finally, to define regions that showed modulation by either sustained or transient control demand, we applied the map of the overlap as an exclusive mask to the sustained control contrast—which we termed *sustained* ROIs—and the transient control contrast, termed *transient* ROIs. Only clusters of at least 50 voxels were considered for ROI definition. If clusters were stretched across multiple anatomical areas, they were additionally

masked using anatomical regions of the Harvard-Oxford atlas (Makris et al., 2006) thresholded at 30%. No anatomical mask is available for the IFJ; therefore this ROI was created by splitting the cluster based on a meta-analysis (Derrfuss et al., 2005). Hemisphere masks were applied to restrict clusters that extended beyond one hemisphere. Finally, ROIs were binarized and used as masks for beta-parameter extraction using MarsBar (Brett et al., 2002).

With these ROI analyses, we sought to test whether children and adults differed in the extent of upregulation of sustained and transient control activation with increased control demand. Upregulation of sustained control was computed as the difference between parameters of mixed and single blocks, and upregulation of transient control was computed as the difference between parameters of switch and repeat trials. We then compared the extent of upregulation between age groups for each ROI using t-tests in R, reporting Cohen's d as effect size (Cohen, 1988) and p -values FDR-corrected for multiple comparisons.

To examine age differences in regions involved in task switching that were not defined in the present task, we conducted additional analyses in ROIs based on a meta-analysis in children and adults (Zhang et al., 2021). Specifically, we constructed 6 mm spheres around the activation peaks for task switching across both age groups (see Supplementary Table 2). Subsequently we extracted activation parameters from the *sustained* and *transient* GLMs and tested for age differences using t-tests as described above.

To investigate whether children or adults recruited additional brain regions beyond the ones we identified over both age groups, we computed exploratory whole-brain age comparisons of the mixed > single and switch > repeat contrasts in the sustained and transient GLM, respectively ($p < .05$, FWE-corrected).

2.5.3. Psychophysiological interaction analysis

Generalized psychophysiological interactions (gPPI; McLaren et al., 2012) were analyzed using the CONN toolbox (Version 20b; Whitfield-Gabrieli and Nieto-Castanon, 2012). Unlike correlational measures of functional connectivity, PPI models how the strength of coupling between a seed region and a voxel elsewhere in the brain differs across conditions. To this end, a GLM predicting the time series of the target voxel by the interaction regressor is constructed. The interaction regressor is created by multiplying the time series of the seed region with the task regressor for each condition (i.e., the condition onset times convolved with the HRF). The PPI analysis focused on effects of sustained control, as we had predicted greater age differences here.

The main effects of the two sustained control conditions (single and mixed blocks) and the effect of the nuisance regressors previously applied to the sustained GLM were regressed from the BOLD signal time series before estimating the interaction factor. Importantly, voxel-level time series were estimated using the smoothed data, while ROI level (i.e., seed) time series were estimated using unsmoothed data to prevent a “spillage” of the BOLD signal of voxels outside the ROI into the ROI time series. Interaction parameters were estimated separately for each condition, i.e., single and mixed blocks (McLaren et al., 2012).

Based on the prominent role of the left IFJ in task switching (Derrfuss et al., 2005; Kim et al., 2012; Richter and Yeung, 2014) and the fact that it showed activation in our univariate analysis, we selected it as a seed region for the PPI analysis. More specifically, a sphere of 6 mm radius was placed around the group peak coordinates of the mixed > single contrast of the sustained GLM.

We compared the difference in seed-to-whole brain connectivity for the IFJ for mixed vs. single blocks between children and adults. Analyses were performed on a gray-matter mask of the whole brain and corrected for multiple comparisons at the cluster level ($p < .05$ FDR-corrected, voxel threshold at $p < .001$ uncorrected). Beta estimates were extracted from clusters showing age differences in connectivity for the mixed > single contrast to visualize the results and to relate connectivity patterns to performance in the task. Additionally, the large cluster in the prefrontal cortex (PFC) was split into a medial and lateral part, as these

have been associated with different aspects during task switching (Koechlin et al., 2000). More specifically, the medial PFC (mPFC) was defined by the superior frontal and paracingulate gyrus and the lateral PFC (lPFC) by the frontal pole and middle frontal gyrus of the Harvard-Oxford Atlas (Makris et al., 2006), thresholded at a probability of 30%.

2.5.4. Functional activation deviation scores

To take individual differences among children in sustained activation into consideration, we computed functional activation deviation scores (cf. Düzel et al., 2011; Fandakova et al., 2015). The deviation scores reflect the similarity of task-related activation of an individual child to the adult mean. To this end, we created a mask including all clusters that showed sustained activation across adults ($p < .05$, FWE-corrected). The deviation score for each child was then calculated as the difference between the average T-value of the sustained control contrast (mixed > single) of all voxels inside this adult mask and outside it. Thus, a negative score represented more adult-like activation patterns, and a more positive score represented less adult-like patterns.

To examine relations between deviation scores, connectivity, and performance, we used the adjusted accuracy mixing costs. Adjusted mixing costs were calculated based on a measure of task-switching efficiency (Brüning and Manzey, 2018) by dividing the difference between single- and mixed-block accuracy by the single-block accuracy, and thus allowed us to adjust mixing costs to differences in overall performance. The adjustment to the mixing costs was applied because children varied considerably in their single-block performance, with about 12% of children showing single-task accuracy below 80%. We focused on individual differences in accuracy rather than RT, as we only observed age group differences in mixing and switch costs in accuracy. We posit that this study yielded lower accuracy because the task was more challenging than in prior studies, in that it required switches between three tasks with three stimulus-response mappings each, as opposed to, for example, two tasks with two arbitrary mappings each (e.g., Crone et al., 2006a; Reimers and Maylor, 2005). As a measure of connectivity, we used the difference in PPI beta parameters between mixed and single blocks of the connections between the IFJ and the lateral and medial PFC clusters separately, to investigate whether they showed different influences on performance.

3. Results

3.1. Greater costs of task switching in children

Accuracy results are shown in Fig. 2A. We fit a linear mixed-effects model with accuracy as the dependent variable and the factors age group (children vs. adults) and condition (single vs. repeat vs. switch), the interaction between these two factors and a random intercept for subject using log-likelihood optimization. To enable comparisons of mixing costs (i.e., performance differences between repeat and single trials) and switch costs (i.e., performance differences between switch and repeat trials), the condition repeat was used as the reference condition in the model. The model revealed a significant effect of age group ($\beta = -0.068$, $p < .001$) and the switch condition (vs. repeat; $\beta = -0.031$, $p = .01$). The effect for the single condition (vs. repeat) was at trend level ($\beta = -0.024$; $p = .06$). Thus, children showed overall lower accuracy ($M = 0.81$, $SD = 0.16$) than adults ($M = 0.96$, $SD = 0.04$) and across age groups that accuracy was highest on single trials ($M = 0.94$, $SD = 0.08$), followed by repeat trials ($M = 0.87$, $SD = 0.13$), and then switch trials ($M = 0.80$, $SD = 0.17$). There were significant interactions of age group with both conditions (single: $\beta = -0.089$, $p < .001$; switch: $\beta = -0.054$, $p < .001$) indicating that children showed greater differences between the conditions than adults, especially with respect to the difference between single and repeat conditions. Taken together, while both age groups demonstrated reliable mixing and switch costs, the age differences for mixing costs (i.e., the interaction of age group and single condition) were more pronounced than the age differences for switch cost (i.e., the interaction of age group and switch condition).

RT results are shown in Fig. 2B. The mixed-effects model of RT, set up with the same fixed and random effects as the model of accuracy, revealed significant effects of age group ($\beta = 0.28$, $p < .001$) and both conditions (single: $\beta = -0.27$, $p < .001$; switch: $\beta = 0.24$, $p < .001$; both compared to repeat as reference). There was no significant age-group-by-condition interaction, neither with the single condition ($\beta = 0.0047$, $p = .83$) nor with the switch condition ($\beta = 0.013$, $p = .54$). Overall, children ($M = 1.45$ s, $SD = 0.26$) responded more slowly than adults ($M = 1.17$ s, $SD = 0.26$). Across both groups, responses to single trials ($M = 1.08$ s, $SD = 0.19$) were fastest, followed by repeat (M = 1.35 s, SD = 0.20) and switch trials (M = 1.60 s, SD = 0.22).

Taken together, children and adults demonstrated reliable declines in performance both in terms of lower accuracy and slower RTs going

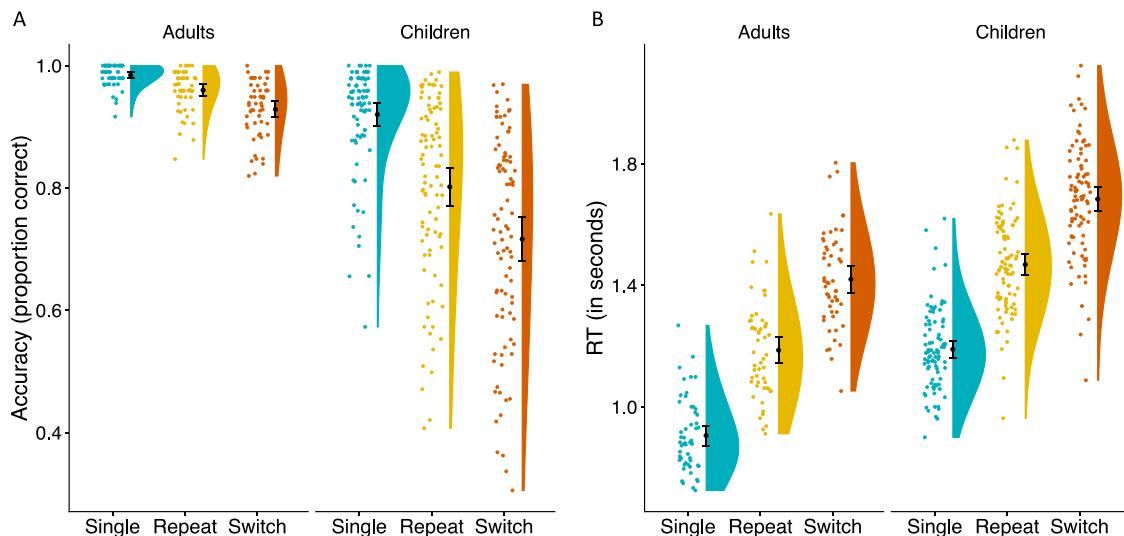


Fig. 2. Behavioral results. (A) Proportion of correct responses for single, repeat, and switch trials. Across age groups accuracy was highest for single trials, followed by repeat and switch trials. Children showed greater mixing (single vs. mixed trials) and switch (repeat vs. switch trials) costs, while age differences were more pronounced for mixing costs. (B) Response time for single, repeat, and switch trials. Across age groups, responses to single trials were fastest, followed by repeat and switch trials. Mixing and switch costs in response times (RT) were similar across age groups.

from single blocks to mixed blocks, and from repeat trials to switch trials. Critically, children showed greater declines in accuracy than adults with increasing task switching demands, with age differences being particularly pronounced for mixing costs.

3.2. Frontal and parietal brain regions associated with sustained and transient control

Analyses of whole-brain activation associated with sustained control (mixed > single blocks) across children and adults indicated enhanced activation in multiple bilateral prefrontal and parietal regions (see [Supplementary Table 1](#)), including the IFJ, SPL, dACC, and dlPFC (see [Fig. 3](#), green color). A whole-brain analysis of transient control (switch > repeat trials) across children and adults revealed enhanced activation in left lateral and medial parietal and prefrontal regions as well as bilateral occipital regions, including the left IFJ, left SPL, left dACC, and the bilateral precuneus ([Fig. 3](#), red color; [Supplementary Table 1](#)).

Activation patterns of sustained and transient control partially overlapped. Inclusive masking revealed several regions activated by both sustained and transient control demands, including the left IFJ, left SPL, left dACC, left inferior lateral occipital cortex (iLOC), left anterior insular (aI), and left middle frontal gyrus (MFG). On the other hand, regions exclusively showing modulation of activation with sustained control demand included the bilateral dlPFC, right IFJ, right SPL, right aI, and right MFG. Activation in the bilateral precuneus and a region in the bilateral premotor cortex (preMC) was exclusively modulated with transient control demand.

Thus, across age groups, we found frontal and parietal regions to be associated with sustained and/or transient control, including regions—the IFJ, SPL, dACC, dlPFC, and precuneus—that have been associated with task switching in previous research in adults ([Kim et al., 2012](#); [Richter and Yeung, 2014](#)). Of these regions, the left IFJ, SPL, and dACC showed modulation of activation for both sustained and transient control demand, bilateral dlPFC exclusively for sustained control demand, and bilateral precuneus exclusively for transient control demand.

To test whether sustained control effects were driven by switch trials during mixed blocks or were also present when comparing single and repeat trials only, we performed a control GLM that included single, repeat, and switch trials in an event-related design. Univariate results of the repeat > single contrast of this control GLM were comparable to the mixed > single contrast of the sustained GLM (see [Supplementary Figure 1](#)), suggesting that sustained control effects were jointly driven by switch and repeat trials within the mixed blocks.

3.3. Less upregulation of sustained and transient control activation in children

Having identified regions across the whole sample that are involved in one or both types of control across both age groups, we next sought to

examine age differences in the modulation of activation by sustained and transient control demands within these regions. We tested for age differences in the upregulation of sustained control activation by performing t-tests on the difference between mixed and single parameter estimates. As shown in [Fig. 4A](#), the overlap ROIs, including left IFJ, SPL, and dACC, showed a significant age difference in the degree of increase in activation from single to mixed blocks (IFJ: $t(118.66) = -3.86$, $p_{\text{corrected}} < .001$, Cohen's $d = 0.66$; SPL: $t(125.71) = -4.02$, $p_{\text{corrected}} < .001$, $d = 0.68$; dACC: $t(121.59) = -5.57$, $p_{\text{corrected}} < .001$, $d = 0.72$; FDR-corrected), such that, across all ROIs examined, children showed less upregulation of activation from single to mixed blocks.

Similarly, we found significant age differences in the extent of upregulation of activation by sustained control demands in the bilateral dlPFC, right IFJ, and right SPL, ROIs that were exclusively associated with sustained control (dlPFC: $t(127.31) = -4.49$, $p_{\text{corrected}} < .001$, $d = 0.76$; IFJ: $t(107.1) = -3.12$, $p_{\text{corrected}} = .003$, $d = 0.54$; SPL: $t(122.58) = -2.96$, $p_{\text{corrected}} = .004$, $d = 0.5$; FDR-corrected, see [Fig. 4A](#) and [Supplementary Figure 3](#)), indicating that children showed less upregulation of task-related activation in the mixed blocks than adults. Taken together, these results suggest that even though children upregulated brain activity in regions that have been identified as key task-switching regions across both age groups with increasing demands on sustained control, they did so to a lesser extent than adults, both for overlap and sustained ROIs.

Next, we tested for age differences in the upregulation of transient control activation by performing t-tests on the difference between switch and repeat parameter estimates (see [Fig. 4B](#)). The overlap ROIs in left IFJ, SPL, and dACC showed significant age differences in upregulation of transient control activation (IFJ: $t(130.14) = -2.25$, $p_{\text{corrected}} = .045$, $d = 0.38$; SPL: $t(138.61) = -2.30$, $p_{\text{corrected}} = .045$, $d = 0.37$; dACC: $t(135.53) = -3.74$, $p_{\text{corrected}} = .002$, $d = 0.62$; FDR-corrected). The bilateral precuneus, exclusively associated with transient control, also showed greater upregulation of transient control activation in adults than in children ($t(134.18) = -2.32$, $p_{\text{corrected}} = .045$, $d = 0.39$, FDR-corrected). Taken together, children upregulated activation due to transient control demand to a lesser extent than adults did across the key regions implicated in task-switching.

The preceding ROI-based analyses revealed age differences in activated regions common to adults and children. However, it is possible that children or adults showed different activation in additional regions. Thus, we also conducted an exploratory analysis investigating age differences in sustained and transient activation on the whole-brain level. Consistent with the results of the ROI analysis, the whole-brain analysis of sustained control showed greater upregulation of activation (mixed > single) for adults than children in the left SPL, left IFJ/dlPFC, and left superior lateral occipital cortex ($p < .05$ FWE-corrected; [Supplementary Figure 4a](#)). No regions showed greater upregulation of sustained control activation in children. Further, no regions showed age differences in upregulation of activation due to transient control demand (switch >

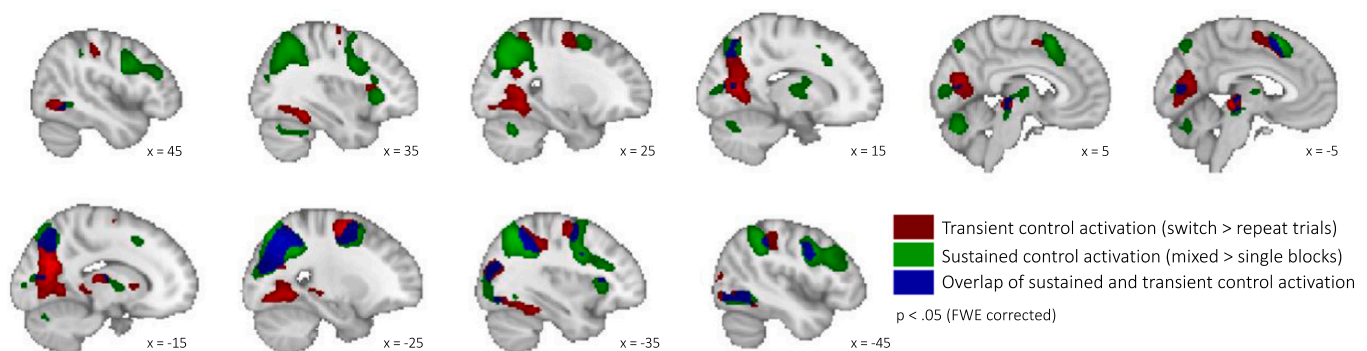


Fig. 3. Univariate activation across age groups. Transient control activation (switch > repeat trials) depicted in red, sustained control activation (mixed > single blocks) in green, and overlap (voxels showing transient and sustained activation) in blue. $N = 142$ (53 adults, 89 children), $p < .05$ FWE-corrected, $k = 50$.

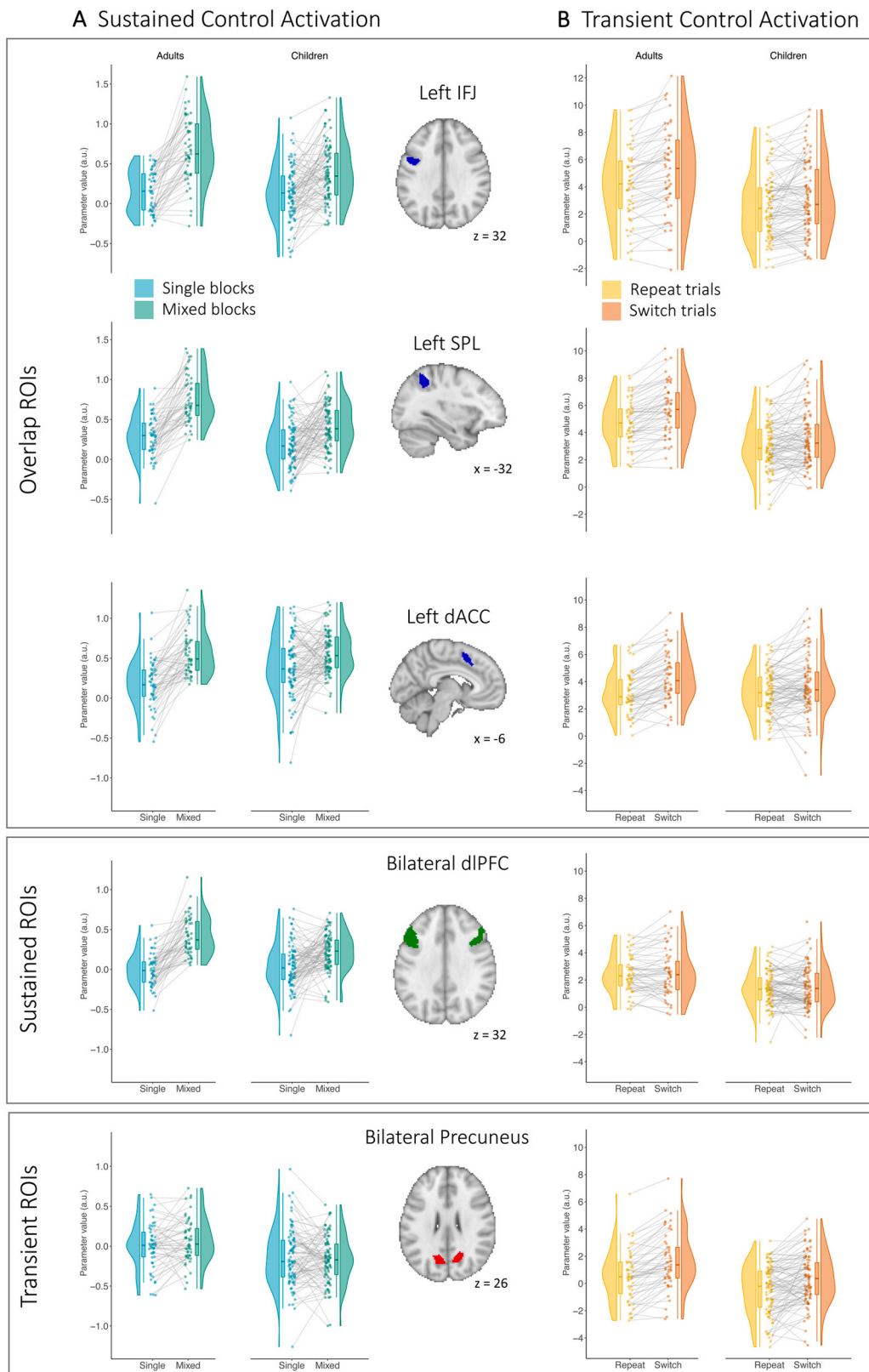


Fig. 4. Age differences in activation due to sustained and transient control demands by ROI. (A) Extracted parameter estimates for single blocks (blue) and for mixed blocks (green). Children showed less upregulation of activation due to sustained control demand in the left IFJ, SPL, and dACC, and the bilateral dlPFC. Neither age group showed upregulation of sustained control activation in the Precuneus. (B) Extracted parameter estimates for repeat trials (yellow) and for switch trials (orange). Children showed less upregulation of activation due to transient control demands in the left IFJ, SPL, dACC, and the bilateral precuneus. Neither age group showed upregulation of transient control activation in the dlPFC.

repeat); for further details, see the [Supplementary Material](#).

Finally, we conducted additional analyses in ROIs based on a recent meta-analysis of task switching across adolescents and adults (Zhang et al., 2021) in order to examine age differences in regions that were not specifically defined in the context of the present task. These additional analyses revealed a similar pattern as reported above. More specifically, we found significant age differences in activation associated with sustained control in multiple frontoparietal regions, including bilateral SPL, bilateral middle frontal gyrus, and precentral gyrus (see [Supplementary Table 2](#) and [Supplementary Figure 5](#)). With regards to transient control, fewer regions showed age differences in activation, including two ROIs in the left and right middle frontal gyrus (see [Supplementary Table 2](#) and [Supplementary Figure 5](#)). The remaining regions (i.e., SPL, precentral gyrus, superior frontal gyrus) showed no significant differences between children and adults.

3.4. Greater increases in connectivity under increased sustained control demand in children

Based on previous research (e.g., Cepeda et al., 2001) showing that differences between adults and children in the age range investigated here are more pronounced during sustained control, and the fact that

our results showed more pronounced age differences for mixing costs, we focused on connectivity associated with sustained control. More specifically, we were interested in the regions showing age differences in connectivity with the IFJ under increased sustained control demands. The left IFJ was selected as a seed, as it has been identified as a key brain region during task switching (Derrfuss et al., 2005; Kim et al., 2012; Richter and Yeung, 2014).

A whole-brain PPI analysis revealed that children showed a more pronounced increase in connectivity with the IFJ from single to mixed blocks in the bilateral angular gyrus (AG), and the medial and lateral prefrontal cortex (mPFC and lPFC, respectively) ($p < .001$, FDR cluster corrected $p < .05$). Neither of these regions overlapped substantially with the regions showing greater sustained control activation across age groups (see [Supplementary Figure 6](#)). The PFC cluster was split to account for possible differences between lateral and medial regions (Koechlin et al., 2000). The lPFC cluster was localized anteriorly adjacent to the bilateral dlPFC that showed sustained activation, and the mPFC cluster was localized anterior to the dACC showing transient and sustained activation. [Fig. 5](#) shows extracted connectivity parameters of the clusters that showed age differences in the comparison of mixed and single blocks. Specifically, age differences were driven by the fact that children showed higher IFJ–mPFC, IFJ–lPFC, and IFJ–AG connectivity

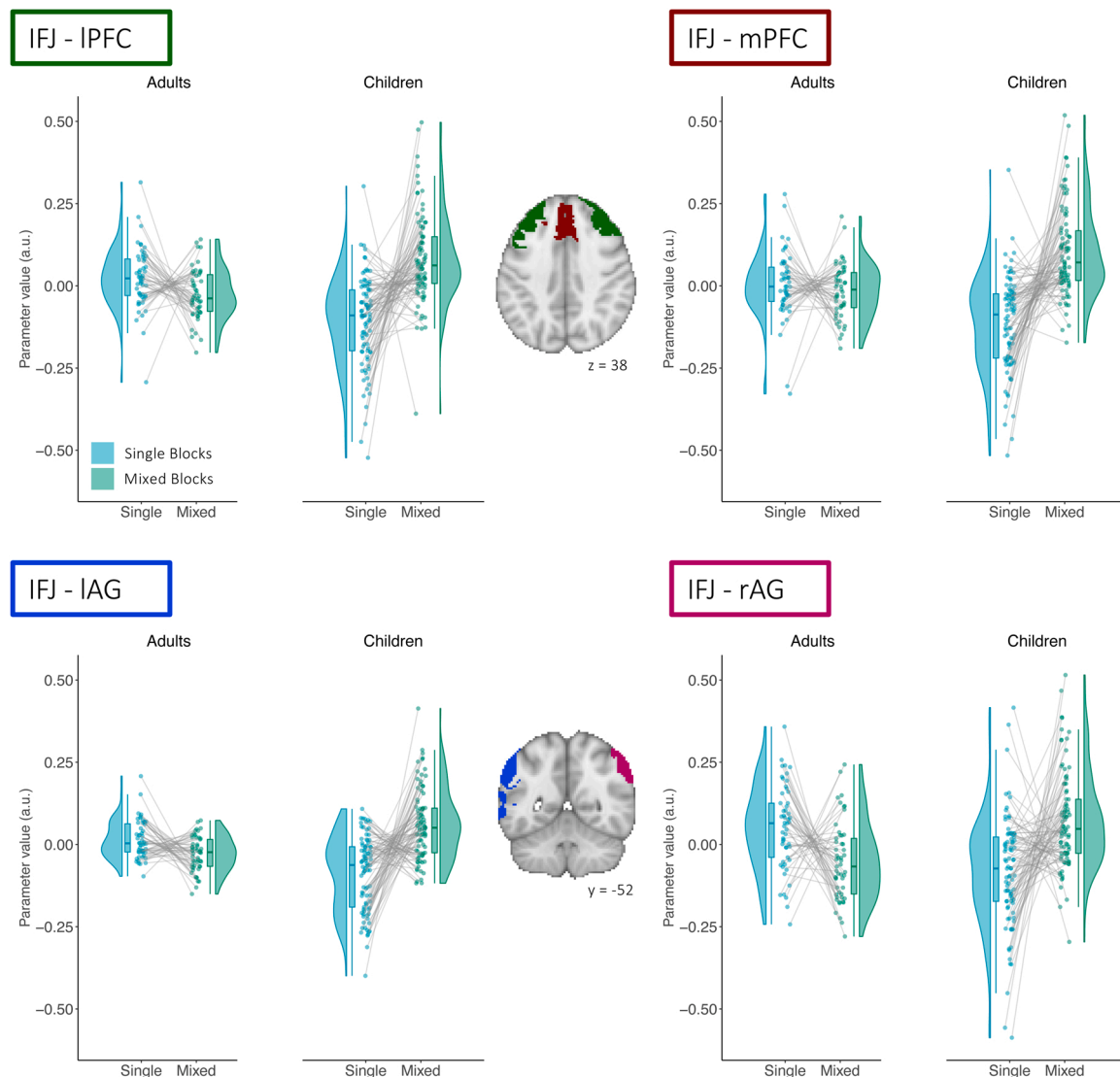


Fig. 5. Age differences in connectivity increases under greater sustained control demands. PPI parameter estimates for clusters showing greater connectivity with the IFJ during mixed blocks (green) than during single blocks (blue) in children compared to adults identified in a whole-brain analysis with the left IFJ as a seed.

in mixed than in single blocks, whereas adults did not show differences in connectivity for these regions between conditions. Additionally, Fig. 5 illustrates the variation in the increase of connectivity from single to mixed blocks among children, such that some showed very steep increases, while others showed rather shallow increases or even decreases. Thus, these data suggest that many, but not all children showed a greater control demand-related increase in connectivity to broad swaths of prefrontal and parietal cortices outside the core areas implicated in task-switching. Note, however, that while these age group differences were identified in the aggregated group comparison, the individual estimates presented in Fig. 5 suggested large interindividual differences, such that some children showed more pronounced increases in connectivity, while others showed smaller increases.

3.5. Connectivity effects on performance depend on adult-like activation in frontal and parietal regions

Children showed less upregulation of activation in sustained control regions, but a greater increase in IFJ connectivity with additional regions as a function of increased demands on sustained control, including regions in lateral and medial PFC that have been implicated in cognitive control processes (e.g. Braver et al., 2003). This pattern of results raises the important question whether the broader connectivity pattern observed in children represents an alternative, presumably developmentally earlier way to support task performance specifically in those children whose frontoparietal activation patterns differ more markedly from those observed among adults. If so, the relation of connectivity increases and accuracy may vary across children, and may depend on the extent to which an individual child showed a mature pattern of sustained control activation.

To test this hypothesis, we computed deviation scores indicating how similar each child's sustained control activation was to that of the average adult. For every individual child, this score was calculated by subtracting the average T-value of the mixed > single contrast of all voxels *inside* the clusters that showed sustained control activation in adults from the average T-value of the mixed > single contrast of all voxels *outside* of the clusters that showed such activation in adults (cf. Düzel et al., 2011; Fandakova et al., 2015). Thus, a more negative score indicates less deviation from the average adult activation pattern, while a more positive score indicates greater deviation and therefore a less adult-like activation pattern. This approach allowed us to take two previously observed aspects of age differences in brain activation into account. First, age differences have been found in the strength of task-related activation within the same regions, such that children show overall weaker activation than adults (e.g., Wendelken et al., 2012). Second, children have been shown to have less specific task-related activation than adults (e.g., Durston et al., 2006). Both of these aspects would result in more positive scores, indicating a greater difference to the average adult pattern. The deviation scores were not correlated with children's age ($r = -.088$, $p = .41$). However, our sample was not evenly distributed across the age range (see Supplementary Figure 7), limiting our ability to adequately test for this association.

We performed a linear regression on the accuracy mixing costs with deviation scores, increases in IFJ-PFC connectivity (in response to increased sustained control demands), and the deviation score by connectivity interaction as predictors. The goal of these analyses was to examine whether the association between connectivity and performance depended on the maturity of activation under sustained control demands. Regressions were performed separately for connectivity with the IPFC and mPFC clusters.

We found significant main effects of deviation score ($\beta = 0.07$, $p = .009$) and of increased IFJ-IPFC connectivity ($\beta = -0.18$, $p = .026$) on mixing costs. However, these effects were qualified by a significant interaction between deviation score and connectivity ($\beta = -0.22$, $p = .03$). Thus, the association between connectivity increases and performance was modulated by the extent to which children showed an

adult-like pattern of sustained control activation (Fig. 6). Specifically, for children with a more adult-like activation pattern (i.e., more negative deviation scores), a greater increase in connectivity for mixed blocks was associated with greater mixing costs, or lower performance. Thus, for children with more adult-like activation patterns, the inclusion of the IPFC in the control network due to greater sustained control demands was associated with poorer performance.

In contrast, for children who showed less adult-like sustained control activation (i.e., more positive deviation scores), accuracy mixing costs and connectivity increases were *negatively* correlated. Thus, for children who deviated more from the expected sustained activation pattern, stronger incorporation of the IPFC into the control network—as evidenced by heightened connectivity with IFJ in response to an increase in the need for sustained control—was related to better performance. Similar results were obtained regarding IFJ-mPFC connectivity, albeit with the interaction of deviation scores and connectivity increases at a trend level ($\beta = -0.15$, $p = .1$). Neither the connectivity between the IFJ and the left AG nor the right AG showed such a relationship with performance.

Taken together, these results suggest that greater IPFC involvement represents an adaptive alternative to implement task-switching affordances among children whose FPN activation patterns deviate more from the adult pattern.

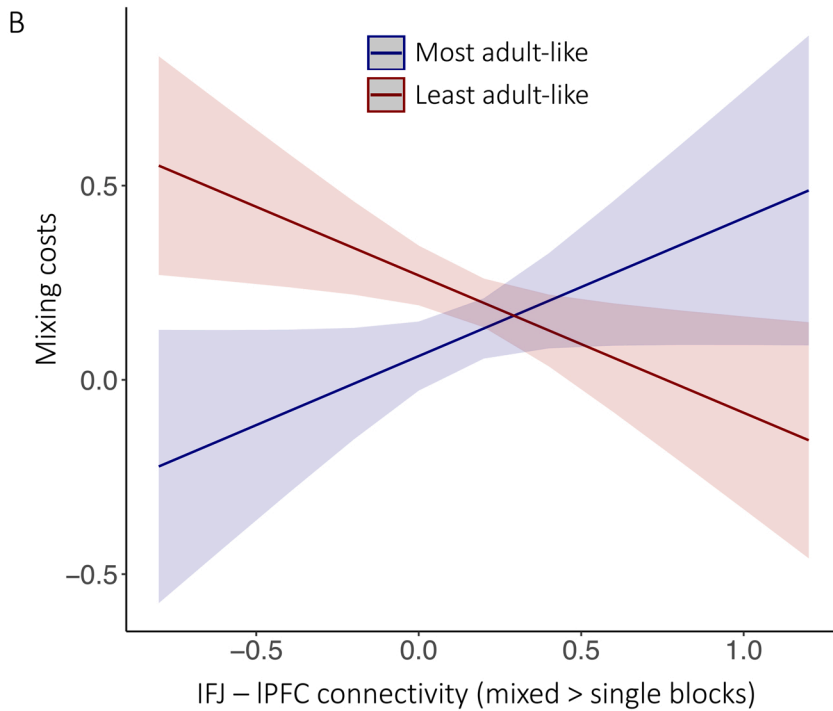
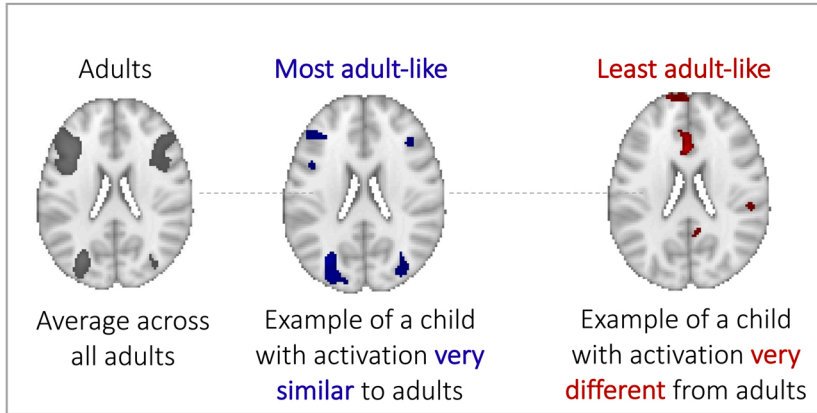
4. Discussion

In the present study, we sought to shed light on the development of sustained and transient control processes by taking a closer look at (a) age group differences between children aged 8–11 years and adults in performance, brain activation, and connectivity related to transient and sustained task-switching demands; and (b) individual differences in the association between task-switching proficiency, neural activation, and connectivity among children. Our results indicated that children showed greater mixing and switch costs than adults. While children engaged the same frontal and parietal regions during task switching, they upregulated brain activation in these areas to a lesser extent than adults. Age differences were more pronounced for mixing costs and sustained control activation, in line with the notion that brain areas and circuits associated with sustained control mature more slowly than those associated with transient control (Bunge and Wright, 2007; Cepeda et al., 2001; Crone et al., 2006a, 2004; Reimers and Maylor, 2005). Task-based connectivity analyses revealed that connectivity between the IFJ and the IPFC increased with greater sustained control demands in children. Critically, the association between task-related connectivity and task-switching performance was linked to how dissimilar the activation pattern of an individual child was to the typical adult pattern: Children who showed less adult-like activation in response to sustained control demands showed better performance with greater IFJ-IPFC connectivity increases, whereas children with a more adult-like activation pattern showed the opposite association, that is, lower performance with greater IFJ-IPFC connectivity increases. This finding suggests that children whose FPN is less mature make adaptive use of an alternative neural implementation of cognitive control to cope with increases in sustained switching demands.

4.1. Age differences in task-related activation and modulation by switching demand

Age differences were more pronounced in sustained control processes than in transient control processes, at both behavioral and neural levels. These results suggest that sustained control processes such as task-set selection (Chevalier et al., 2018; Chevalier and Blaye, 2009; Emerson and Miyake, 2003), maintenance, and monitoring (Braver et al., 2003; Pettigrew and Martin, 2016; Rubin and Meiran, 2005) follow an extended maturational path, potentially continuing into adolescence (Cepeda et al., 2001; Crone et al., 2006a, 2004; Huizinga

A Sustained Control Activation (mixed > single blocks)



and van der Molen, 2007; Reimers and Maylor, 2005). Of note, successful task selection depends on the ability to process relevant task cues in the environment. A recent study using eye tracking during task switching revealed that adults and older children (8.5–12 years) first focused on the cue indicating the currently relevant task, whereas younger children (3–8 years) were more likely to first focus on the target (Chevalier et al., 2018). While these findings suggest that the children in the present study were old enough to process and select the goal-relevant task cue, the targets (face, scene, object) in our paradigm were presented at a different location on every trial. This trial-by-trial spatial reconfiguration requiring that participants search for the relevant stimulus on every trial may have drawn focus away from successful cue identification and undermined the successful engagement of sustained control.

At the same time, age differences in transient control were less

Fig. 6. Interaction effect of deviation score and connectivity on accuracy mixing costs in children. (A) Sustained control activation (mixed > single) across adults ($p < .05$, FWE-corrected) used as reference for estimating how similar an individual child's activation pattern was to this adult pattern. An example of a child showing more adult-like activation for the contrast shown in blue ($p < .001$, uncorrected). An example of a child showing less adult-like activation for the contrast shown in red ($p < .001$, uncorrected). (B) Interaction effect. Children who showed less adult-like activation patterns (red line) showed a negative association between connectivity increases from single to mixed block and mixing costs, such that greater increases in connectivity were associated with lower costs (i.e., better performance). Children showing more adult-like activation patterns (blue line) showed a positive association between connectivity increases and mixing costs, such that greater increases in connectivity were associated with greater mixing costs (i.e., worse performance).

pronounced than those in sustained control (behaviorally and in ROI analyses), or even absent in some analyses (whole-brain and meta-analysis ROIs). It is worth noting that previous findings regarding age differences in behavioral switch costs are inconsistent, with some studies reporting comparable switch costs in children and adults (Anderson et al., 2001; Luca et al., 2003; Reimers and Maylor, 2005) and others showing higher switch costs in children (Crone et al., 2006a; Huizinga et al., 2006). These discrepancies may be related to different facets of task switching, such as the ability to apply hierarchical rules beyond increased demands on working memory capacity (Unger et al., 2016) or the number of response options, even under low working memory demands (Bauer et al., 2017). While each of these facets is crucial to successful task switching, they may be targeted to different degrees across task-switching paradigms, thereby showing diverging developmental trajectories and different patterns of age differences in switch costs.

One potential explanation for the dissociation of age differences patterns between sustained and transient control is the concomitant difference in the developmental pace of brain regions activated for sustained or transient control demands. In our task, several frontal and parietal regions (i.e., the IFJ, SPL, and dACC) were recruited for both sustained and transient control; however, the dlPFC was exclusively modulated by sustained control demands. Previous research has shown that the dlPFC is among the latest brain areas to mature during childhood and adolescence (Sowell et al., 1999; Sydnor et al., 2021; but see Fuhrmann et al., 2022). Critically, an entire network's efficiency can be hindered by a specific node, such that connectivity within a network is lower if a node of the network is lesioned, while networks that do not include this lesioned node are not affected in their efficiency (Nomura et al., 2010). Thus, while the regions associated with both transient and sustained control processes may be relatively more functional during transient control, they might be more strongly limited by the insufficient activation in the co-recruited dlPFC region during sustained control.

4.2. Age differences in task-based connectivity during task switching

Based on previous research demonstrating that connections within and between control networks continue to develop into adolescence (Fair et al., 2009, 2007; Luna et al., 2015; Marek et al., 2015), we expected children to show smaller increases in connectivity with greater sustained control demands, reflecting the ongoing development of these task-related networks. To the contrary, we found that children showed increased connectivity of the IFJ to regions that did not show reliable activation increases across children and adults in our task. One of these regions was a large PFC cluster with a lateral portion of the PFC, including the frontal pole/aPFC and middle frontal gyrus, and a medial portion, including the superior frontal gyrus and paracingulate gyrus. These results are consistent with a previous developmental connectivity study that also showed greater integration of the aPFC in a frontoparietal control network during task switching in children compared to adults (Ezekieli et al., 2013).

The IPFC has been suggested to follow a hierarchical organization, such that more posterior IPFC regions are associated with sensory-motor control, dorsolateral regions with contextual control, and the anterior regions with temporal control (Badre, 2008; Badre and D'Esposito, 2007; Badre and Nee, 2018; Nee and D'Esposito, 2016). The present results showing increased connectivity between the IFJ and a cluster stretching from posterior to anterior IPFC raises the question whether control hierarchies in the IPFC are less clearly established in children than in adults (Bunge and Zelazo, 2006; Unger et al., 2016), such that children might recruit higher-order control regions for lower-order demands (cf. Crone and Steinbeis, 2017). This idea is consistent with the protracted behavioral differentiation of cognitive control process in development (e.g., Akshoomoff et al., 2018; Best and Miller, 2010; Brydges et al., 2014; Shing et al., 2010) and the less flexible recruitment of control strategies based on current control demands in younger children (e.g., Chevalier et al., 2019; Chevalier, 2015).

The maturity of children's pattern of activation in response to sustained control demands moderated the relation between IFJ-IPFC connectivity and performance. More precisely, in children showing less adult-like activation, increased IFJ-IPFC connectivity had a positive effect on performance, suggesting that upregulating IPFC involvement with increased sustained control demands functioned as a performance-enhancing alternate neural strategy in this group of children.

IPFC activation and connectivity supports the management (Lara and Wallis, 2015; Miller et al., 2018; Sala and Courtney, 2007) and selection (Badre, 2012; Chatham and Badre, 2015; D'Ardenne et al., 2012) of multiple task-sets in adults. In this context, our findings indicate that additional recruitment of a region supporting task selection and management is more likely to lead to reduced mixing costs in children, for whom core task switching regions are not yet sufficiently mature to be flexibly activated. This idea is in line with recent discussions of

meta-control, broadly defined as control processes that monitor and regulate other control processes (Eppinger et al., 2021) and determine when, how much, and what type of control to exert (Lieder et al., 2018). Children's meta-control improves considerably in middle childhood (Chevalier, 2015; Chevalier and Blaye, 2016; Niebaum et al., 2021; Schuch and Konrad, 2017). The IPFC has been suggested to play a key role in meta-control (Eppinger et al., 2021; Ruel et al., 2021), suggesting that children who showed less mature patterns of task-specific neural activation may have achieved successful task-switching performance by increased reliance on meta-control monitoring and/or regulation.

Alternatively or additionally, children struggle particularly with the management of multiple task-set representations (Crone et al., 2006a, 2004), a key component of sustained control during task switching (Braver et al., 2003; Pettigrew and Martin, 2016; Rubin and Meiran, 2005). Especially when task-set representations are less distinct or unavailable, as might be expected of children showing less adult-like activation patterns, they might benefit from additional resources to accomplish this management process. The IPFC is ideally suited to provide this additional support due to its role in managing attention between internal information (e.g., maintained task-set representations) and external (stimulus) information (Burgess et al., 2007).

In contrast, in children showing more adult-like sustained activation, increased IFJ-IPFC connectivity in mixed blocks was negatively associated with task performance. Interestingly, adults showed a similar brain-behavior relationship (albeit not statistically significant), such that greater increases in connectivity were associated with greater mixing costs. We surmise that once the core regions involved in task switching are relatively more mature, involving additional peripheral regions may make their operation less efficient. Indeed, under certain circumstances, increased control and IPFC involvement can hinder learning and task performance, in particular during stimulus-driven responses and sequence learning (Galea et al., 2010; Kruschke, 2003; Thompson-Schill et al., 2009). Increasingly specific and efficient networks (Chevalier et al., 2019; Dreher and Berman, 2002; Fair et al., 2009, 2007; Zhang et al., 2021) and more flexible adjustments of strategies (Chevalier, 2015; Chevalier et al., 2015) can give rise to more adult-like performance. However, as our results suggest, they also harbor room for selecting inappropriate or inefficient strategies due to ongoing fine-tuning of brain networks and the neurocognitive processes they support. Critically, developmental changes in brain activation and connectivity might show non-linear and possibly non-monotonic relations to behavior that differ between and vary within individuals (Lautrey, 2003; Li and Lindenberger, 2002; Wendelken et al., 2017), further contributing to the complexity of developmental transitions in the neural machinery supporting task switching behavior. Longitudinal studies are needed to understand how brain structure, activation, and connectivity develop interactively with behavior to enable efficient task switching in the course of development. Such studies need to investigate how neural activation at one timepoint is related to connectivity at another, and importantly, how these longitudinal lead-lag relations, and individual differences therein, correlate with, and possibly predict changes in behavior.

4.3. Conclusion

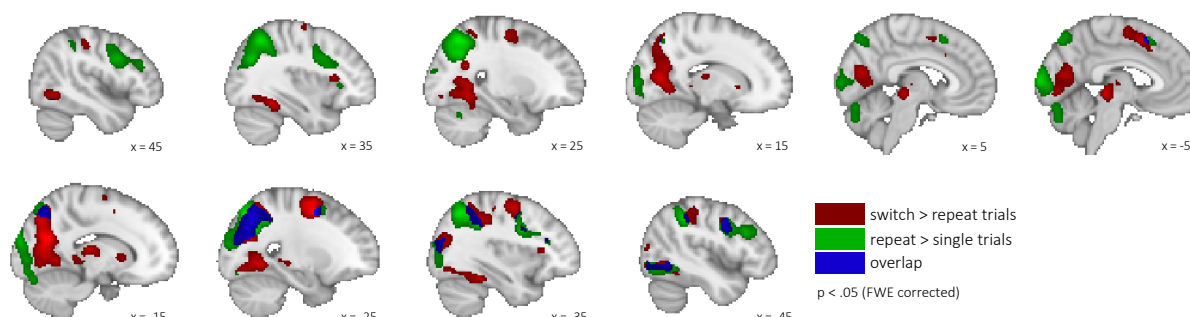
Taken together, the presented data suggest that sustained and transient control processes during task switching follow different developmental trajectories, such that transient processes approximate adult levels relatively earlier than sustained processes do. A potential mechanism giving rise to children's task-switching difficulties might be inefficient upregulation of activation in response to increased control demands, especially for sustained control. However, increased connectivity between the IFJ and the IPFC with greater sustained control demands might offer an alternative, and possibly developmentally earlier mechanism to manage these demands, at least in some children. These findings point to a complex pattern of brain-behavior relationships

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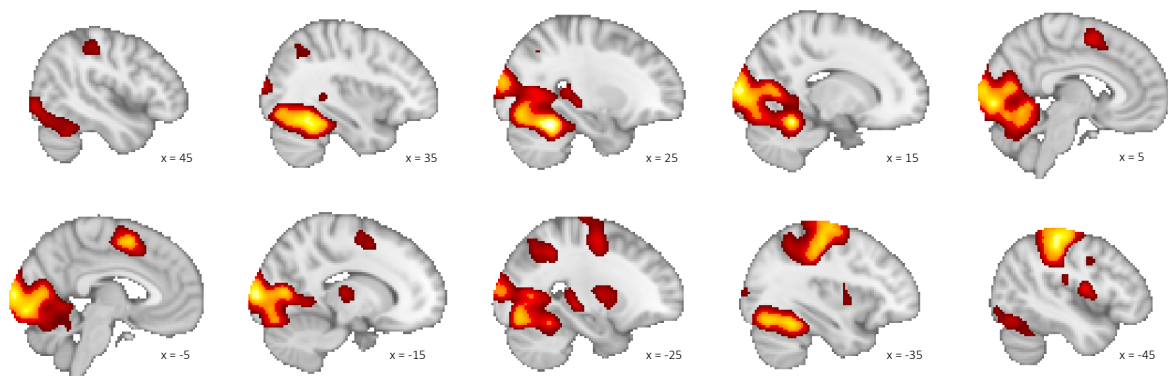
Supplementary Material

	Hemisphere	Region	Mixed > Single Peak	Switch > Repeat Peak	Size (Voxels)
Overlap	left	IFJ	-40 2 32	-40 0 40	240
		SPL	-28 -58 46	-28 -50 44	303
		dACC	-4 14 52	-8 8 52	173
Sustained	left	dIPFC	-48 22 32		952
	right	dIPFC	50 32 24		534
		IFJ	42 4 30		352
		SPL	30 -56 48		299
Transient	left	Precuneus		-16 -68 24	489
	right	Precuneus		22 -58 26	390

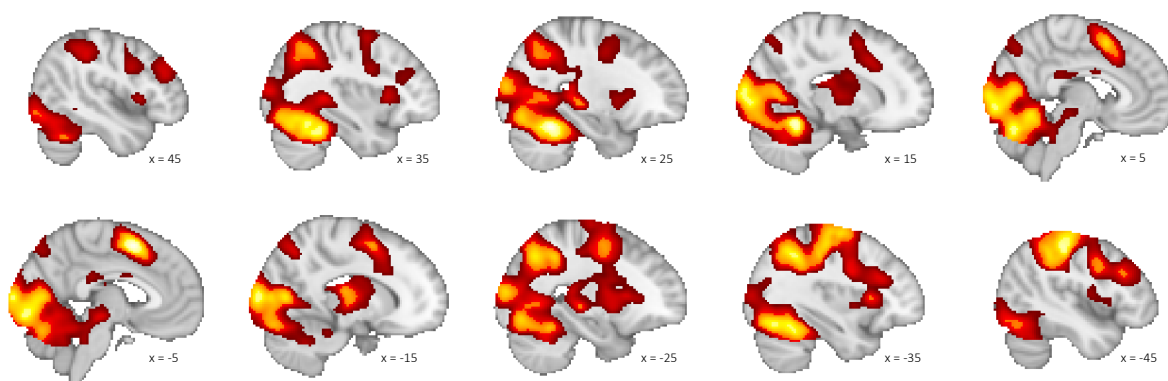
Supplementary Table 1: Regions of interest (ROIs) showing activation under sustained (mixed > single blocks) and transient (switch > repeat trials) control demand (Overlap), exclusively under sustained control demand and exclusively under transient control demand, respectively. Coordinates (X Y Z) in Montreal Neurological Institute space. Size in voxels (2 mm x 2 mm x 2 mm). Abbreviations: IFJ: inferior frontal junction, SPL: superior parietal lobe, dACC: dorsal anterior cingulate cortex, dIPFC: dorsolateral prefrontal cortex.



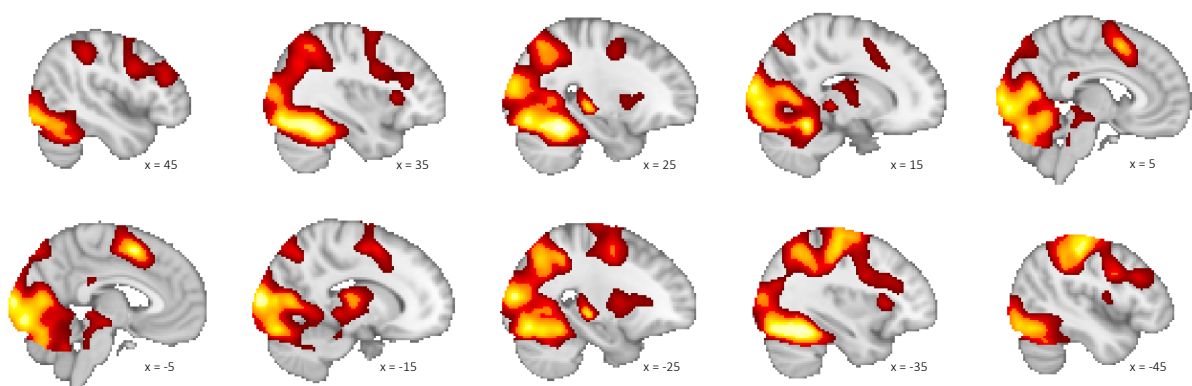
Supplementary Figure 1: Univariate activation across age groups in control GLM. Switch > repeat trials depicted in red, repeat > single trials in green, and overlap in blue. N = 142 (53 adults, 89 children), $p < .05$ FWE-corrected, $k = 50$.



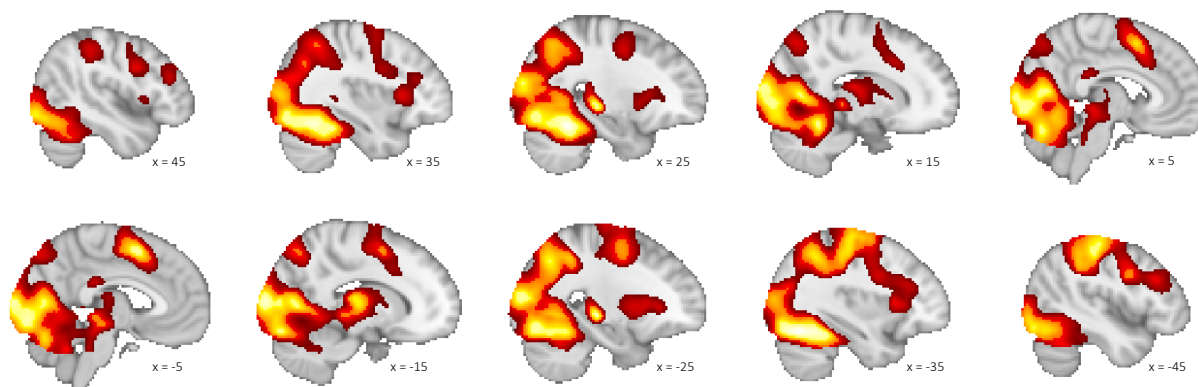
Supplementary Figure 2a: Univariate activation in single blocks. Activation in single blocks (vs. baseline), N = 142 (53 adults, 89 children), $p < .05$ FWE-corrected, $k = 50$.



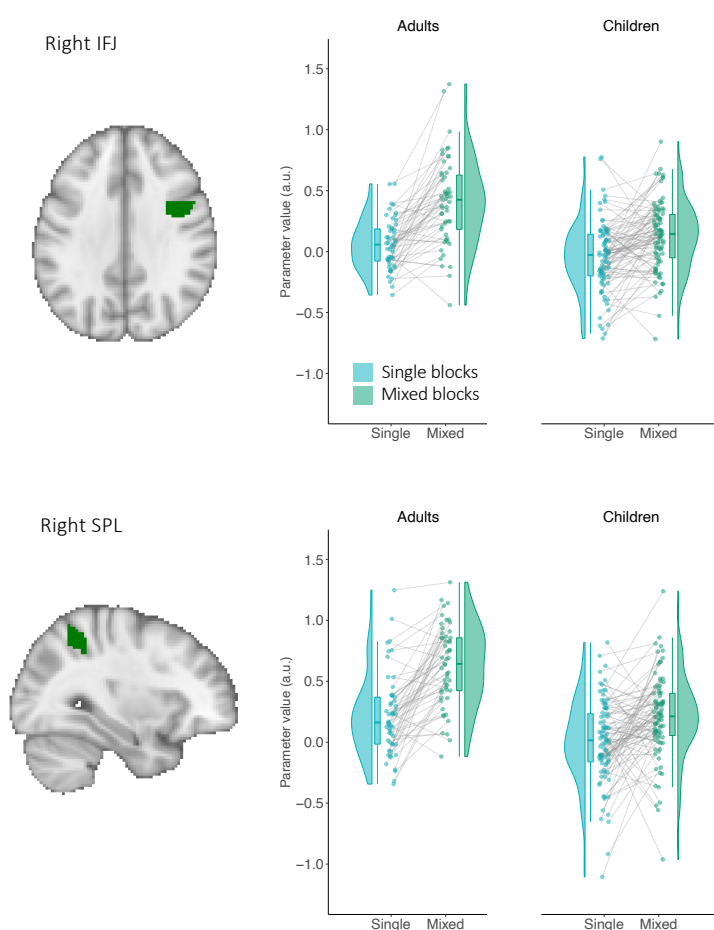
Supplementary Figure 2b: Univariate activation in mixed blocks. Activation in mixed blocks (vs. baseline), N = 142 (53 adults, 89 children), $p < .05$ FWE-corrected, $k = 50$.



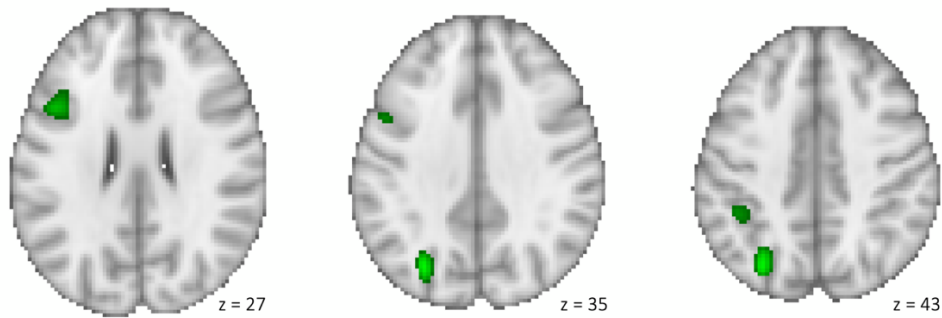
Supplementary Figure 2c: Univariate activation on repeat trials. Activation on repeat trials (vs. baseline), N = 142 (53 adults, 89 children), $p < .05$ FWE-corrected, $k = 50$.



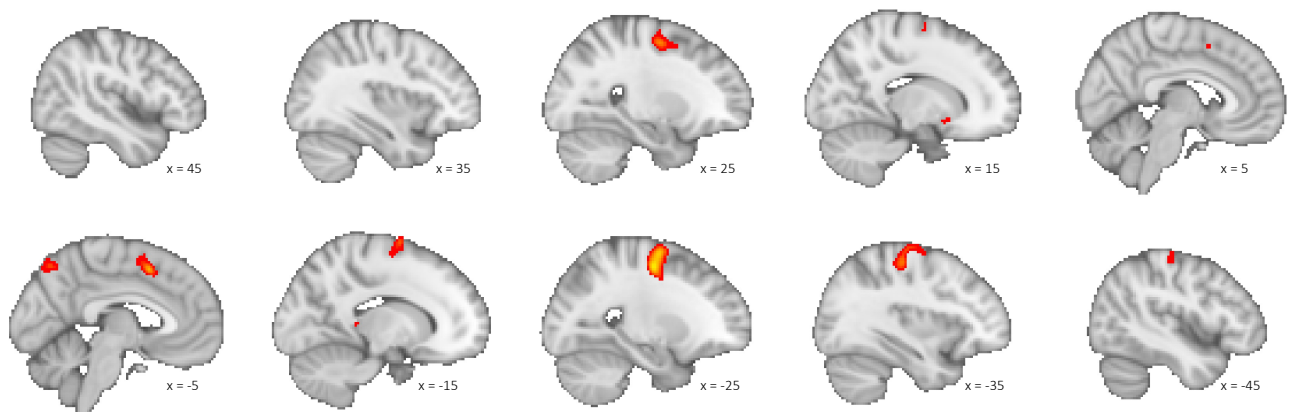
Supplementary Figure 2d: Univariate activation on switch trials. Activation on switch trials (vs. baseline), $N = 142$ (53 adults, 89 children), $p < .05$ FWE-corrected, $k = 50$.



Supplementary Figure 3: Age differences in activation due to sustained control demand by ROI. Extracted parameter estimates for single blocks (blue) and for mixed blocks (green). Children showed less upregulation of sustained activation in the right IFJ and SPL.



Supplementary Figure 4a: Whole brain age differences. Clusters showing greater sustained control activation (mixed > single contrast) in adults than in children ($p < .05$ FWE-corrected, $k=50$).

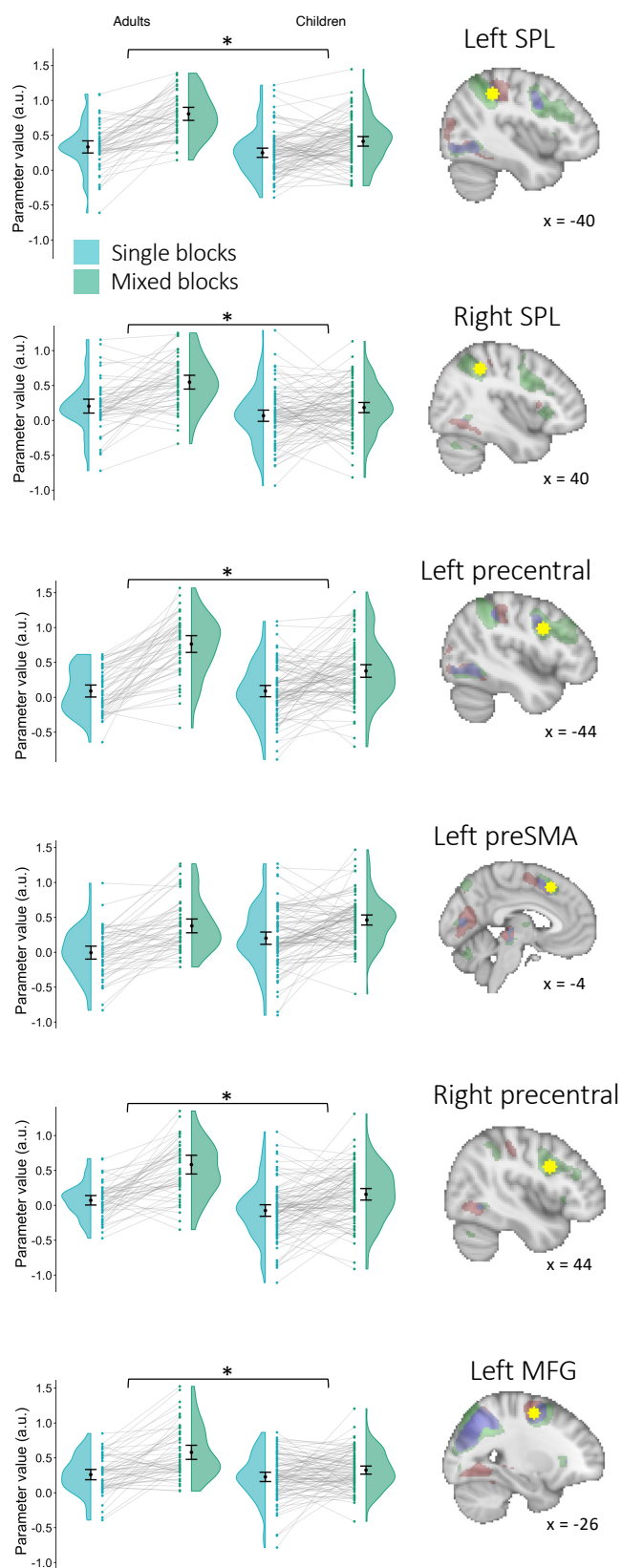


Supplementary Figure 4b: Whole brain age differences. Clusters showing greater transient control activation (switch > repeat trials) in adults than in children ($p < .001$ uncorrected, $k=50$). No clusters survived correction for multiple comparisons with $p < .05$ FWE-corrected.

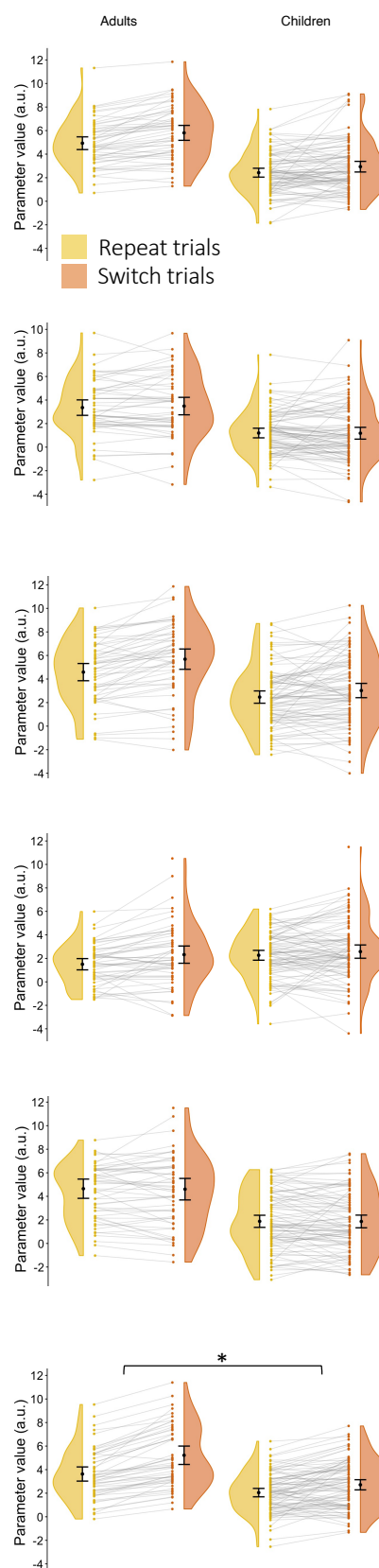
whole sample (adults & adolescents)		MNI coordinates			Age comparison analysis (t-values)	
Hemisphere	Brain region	X	Y	Z	sustained activation	transient activation
left	Inferior parietal lobule/superior parietal lobule/precuneus	-40	-42	44	-5.03*	-1.77
right	Inferior parietal lobule/superior parietal lobule/precuneus	40	-42	44	-3.04*	-0.63
L	Precentral gyrus/middle frontal gyrus	-44	6	32	-4.74*	-2.08
L	Pre-supplementary motor area/superior frontal gyrus	-4	20	48	-1.73	-1.64
R	Precentral gyrus/middle frontal gyrus	44	8	30	-3.31*	-0.099
L	Middle frontal gyrus/precentral gyrus	-26	-6	54	-3.43*	-3.96*
L	Thalamus/putamen/caudate	-10	-16	10	-1.53	-1.49
R	Middle frontal gyrus	30	0	58	-1.95	-2.93*
R	Insula	34	24	-2	-2.55*	-1.52
L	Insula	-32	22	2	-3.27*	-0.91

*Supplementary Table 2: Age comparison analysis results of spherical ROIs (6mm radius) based on regions showing switching related activation across studies with adults and adolescents in Zhang et al., 2021. T-tests were conducted separately for the difference between adults and children in sustained activation (i.e., difference in activation between single and mixed blocks) and transient activation (i.e., difference in activation between repeat and switch trials). Higher t-values represent a greater difference between condition (i.e., greater upregulation of activation) in adults. Note: * denote FDR-corrected $p < .05$*

A Sustained Control Activation

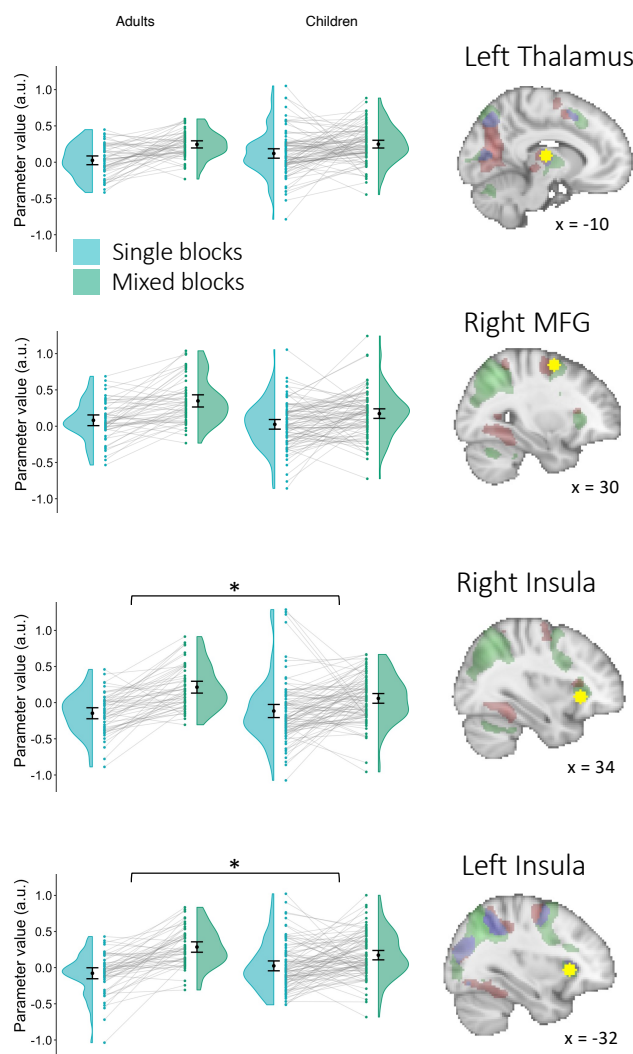


B Transient Control Activation

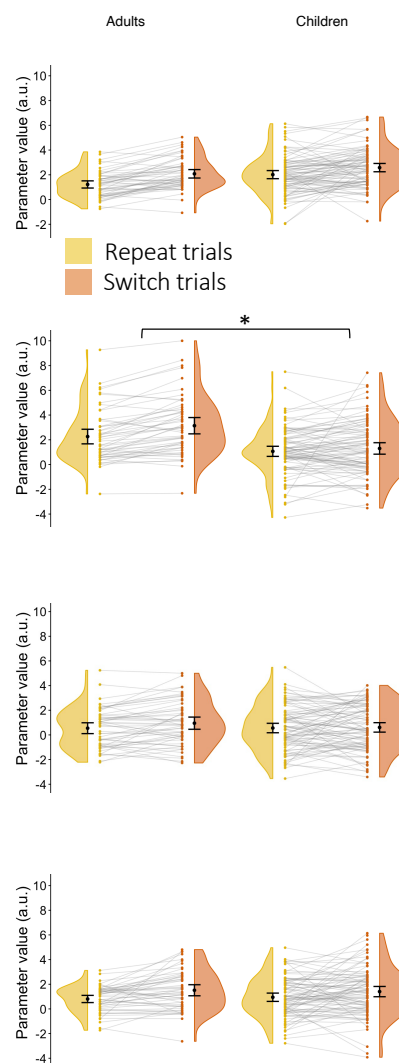


Supplementary Figure 5: Age differences in activation due to sustained and transient control demands in meta-analysis ROIs (Zhang et al. 2021). Figure description on next page.

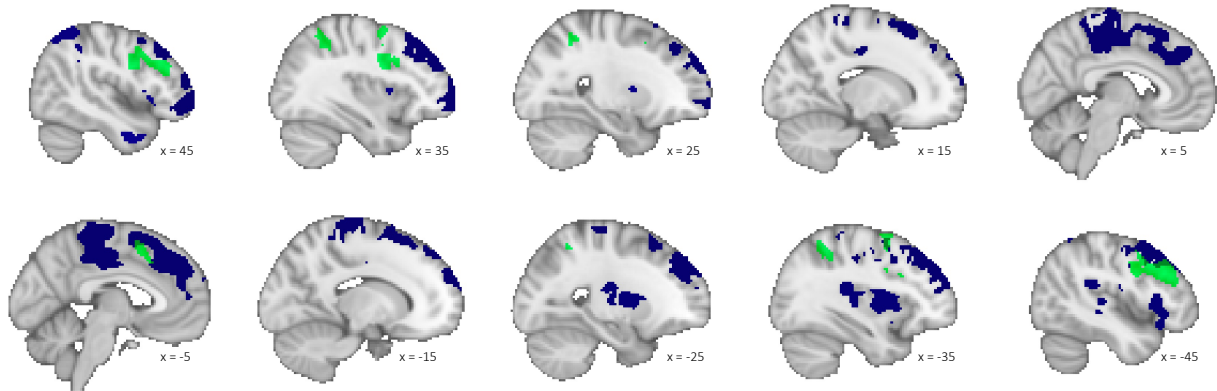
A Sustained Control Activation



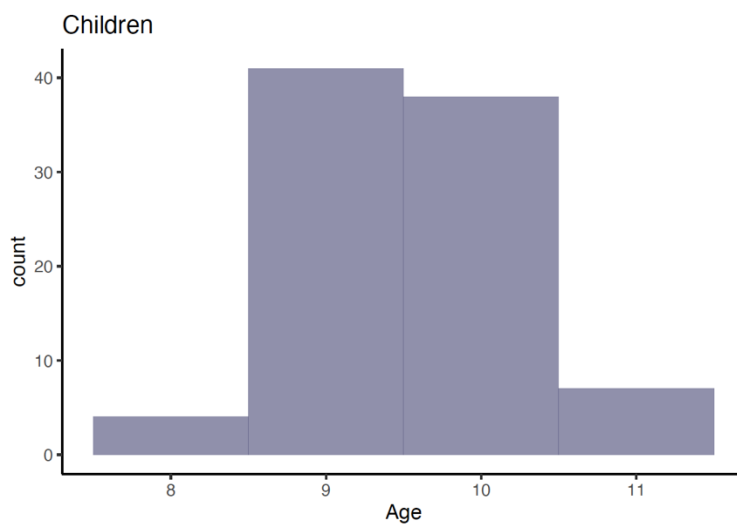
B Transient Control Activation



Supplementary Figure 5 (continued): Age differences in activation due to sustained and transient control demands in meta-analysis ROIs (Zhang et al. 2021).). Extracted parameter estimates from ROIs 6mm spheres around the peaks found by the meta-analysis across adults and adolescents for (A) single blocks (blue) and for mixed blocks (green) and (B) for repeat trials (yellow) and for switch trials (orange). Spheres are displayed in yellow overlain on the sustained/transient/ overlap activation across adults and children in the present study in green, red, and blue, respectively. * denote FDR-corrected $p < .05$



Supplementary Figure 6: Sustained and Overlap ROIs (green) and clusters showing greater connectivity difference (mixed > single blocks) in children than adults (blue). The connectivity clusters do not substantially overlap with the ROIs based on task-related activation.



Supplementary Figure 7: Distribution of age across the age span of children included in the present manuscript.

B: Paper 2

Schwarze, S. A., Bonati, S., Cichy, R. M., Lindenberger, U., Bunge, S. A., & Fandakova, Y. (2023). *Task-switch related reductions in neural distinctiveness in children and adults: Commonalities and differences*. Manuscript submitted for publication.

Task-Switch Related Reductions in Neural Distinctiveness in Children and Adults: Commonalities and Differences

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Abstract

Goal-directed behavior requires the ability to flexibly switch between task sets with changing environmental demands. Switching between tasks generally comes at the cost of slower and less accurate responses. Compared to adults, children show greater switch costs, presumably reflecting the protracted development of the ability to flexibly update task-set representations. To examine whether the distinctiveness of neural task-set representations is more strongly affected by a task switch in children compared to adults, we examined multi-voxel patterns of fMRI activation in 88 children (8–11 years, 49 girls) and 53 adults (20–30 years, 28 women) during a task-switching paradigm. Using multivariate pattern analysis (MVPA), we investigated whether task-set representations were less distinct on switch than on repeat trials across frontoparietal, cingulo-opercular, and temporo-occipital regions. Children and adults showed lower accuracy and longer response times on switch than on repeat trials, with higher accuracy costs in children. Decoding accuracy across regions was lower on switch than repeat trials, consistent with the notion that switching reduces the distinctiveness of task-set representations. Reliable age differences in switch-related representational distinctiveness reductions were absent, pointing to a remarkable degree of maturity of neural representations of task-relevant information in late childhood. However, we also observed that switch-related reductions in distinctiveness were more highly correlated across frontoparietal and cingulo-opercular regions in children than in adults, potentially reflecting the ongoing specialization of different control networks with respect to the representation of task features.

Significance statement

The ability to flexibly switch between tasks enables goal-directed behavior, but is particularly challenging for children, potentially due to protracted development in the ability to represent multiple and overlapping task rules that link stimuli to appropriate responses. We tested this hypothesis by using neuroimaging to measure brain activity during task switching in 8–11-year-olds and adults. Activation patterns in frontal, parietal, and temporal regions could tell us with above-chance accuracy which task a person was performing when the task remained the same, but not when it had switched. Adults showed greater differentiation across regions in terms of

switch-related reductions in distinctiveness than children, suggesting that the relevant functional circuitry is present but has not yet fully matured by late childhood.

1. Introduction

The ability to flexibly switch between tasks, thoughts, or actions when circumstances change is critical for goal-directed behavior (Miyake and Friedman, 2012; Diamond, 2013). However, switching between tasks entails a cost compared to repeating previously executed tasks, such that responses are slower, less accurate, or both. A task switch requires updating the task set, which amounts to retrieving the task set for the newly relevant task and inhibiting the no-longer relevant task set (Rogers and Monsell, 1995; Meiran, 1996; Mayr and Kliegl, 2000; Wylie and Allport, 2000; for a review, see Vandierendonck et al., 2010). Both of these processes are thought to contribute to the switch costs observed in performance.

Behaviorally, switch costs are more pronounced in children compared to adults (Crone et al., 2006a; Huizinga et al., 2006; Huizinga and van der Molen, 2007; Gupta et al., 2009; Cragg and Chevalier, 2012; Church et al., 2017; but see Luca et al., 2003; Reimers and Maylor, 2005). Age-related differences in switch costs have been attributed to children's difficulties to inhibit the no-longer relevant task set and to update the relevant task set when rules switch (Crone et al., 2004, 2006a; Gupta et al., 2009; Wendelken et al., 2012). Moreover, children's representations of goal-relevant task sets have been suggested to be less distinct from one another (Zelazo, 2004; Crone et al., 2006b; Lorscheid and Reimer, 2008; Jung et al., 2023), especially when task sets are partially overlapping (e.g., due to same responses; cf. Crone et al., 2006a).

Children's task-switching difficulties have been associated with smaller increases in activation for switch compared to repeat trials in frontoparietal (FP) brain regions, including the inferior frontal junction (IFJ), the superior parietal lobe (SPL), and the dorsolateral prefrontal cortex (dlPFC), compared to adults (Crone et al., 2006b; Bunge and Wright, 2007; Velanova et al., 2008; Wendelken et al., 2012; Engelhardt et al., 2019; Zhang et al., 2021; Schwarze et al., 2023; but see Morton et al., 2009). The previous studies did not examine differences in multivariate patterns of neural activations between repeat and switch trials, and therefore do not address whether age differences therein are a possible source of age-related differences in switch costs.

Research in adults (Loose et al., 2017; Qiao et al., 2017) has started to feature multivariate pattern analysis (MVPA; Haynes and Rees, 2006) to examine

the distinctiveness of neural representations of task sets in task-switching paradigms. Because task-set representations on switch trials have just been updated, they are hypothesized to be less distinct on switch compared to repeat trials (Meiran, 1996; Mayr and Kliegl, 2000), resulting in lower decoding accuracy. Decoding accuracy describes how well the currently relevant task can be predicted from the pattern of neural activation. Beyond this updating process, the lingering representation of the previously relevant task set (i.e., task-set inertia) might dilute the current task-set representation, further contributing to less distinct representations on switch compared to repeat trials (Rogers and Monsell, 1995; Wylie and Allport, 2000; Rangel et al., 2023). Studies investigating this hypothesis in adults have reported contradictory results. While one study showed greater decoding accuracy on repeat than on switch trials (Qiao et al., 2017), other studies showed the opposite pattern (Tsumura et al., 2021) or no differences between conditions (Loose et al., 2017). To date, neural task-set representations have not been examined in children to provide a direct test of representational accounts of children's difficulties in task switching.

We used MVPA to assess the distinctiveness of task-set representations in children (N = 88, 8–11 years) and adults (N = 53, 20–30 years) who performed a task-switching paradigm during neuroimaging. We expected that, children would show overall lower decoding accuracy and would be disproportionately affected by the demand to switch, resulting in lower decoding accuracy on switch trials compared to adults. To explore whether age differences in task switching were related to stronger task-set inertia in children than in adults (Gupta et al., 2009; Hommel et al., 2011; Wendelken et al., 2012; Witt and Stevens, 2012; but see Crone et al., 2006a), we used three different task sets. As opposed to switches among two task sets, this design allowed us to test whether decoding accuracy for the previously relevant task on switch trials was higher compared to the third task (that was neither relevant on the current nor on the previous trial), which would indicate task-set inertia.

While adult studies of neural representations during task switching have focused on FP regions, the distinctiveness of task-set representations in temporo-occipital (TO) regions (i.e., fusiform gyrus, parahippocampal gyrus, and lateral occipital cortex) may be particularly important for task switching in children. These regions mature earlier than FP regions do (Sydnor et al., 2021) and may contribute to the development of more distinct FP representations during rule-based tasks

(Amso and Scerif, 2015; Rosen et al., 2019). Furthermore, regions of the cingulo-opercular (CO) network, including the dorsal anterior cingulate cortex (dACC) and the anterior insula (ai), have been associated with task-set maintenance during switching (Braver et al., 2003; Dosenbach et al., 2008; Gratton et al., 2018). Due to the relatively more sustained nature of maintenance processes (Braver et al., 2003), representations in CO regions may not be updated in a trial-specific fashion, resulting in smaller differences in decoding accuracy between switch and repeat trials. Thus, we explored how the distinctiveness of task-set representations in brain regions associated with different roles during task switching (i.e., FP vs. CO) and with different developmental trajectories (i.e., FP/CO vs. TO regions) differed with respect to age differences.

2. Materials and Methods

The hypotheses and the analysis plan were preregistered before the start of analysis (<https://osf.io/8mfqx/>). We explicitly note deviations from the preregistered analysis plan below. The behavioral performance and univariate analysis of functional neuroimaging data of this sample are described in detail in Schwarze et al. (2023), and are only briefly summarized below.

2.1 Participants

Children (N = 117) and adults (N = 53) completed the task-switching paradigm in the MR scanner, as reported previously (Schwarze et al., 2023). All participants were right-handed. Prior to running the analyses of interest, participants were excluded if they showed low accuracy (i.e., below 50% in the fMRI run of single tasking or below 35% in either of the two runs that presented tasks intermixed, see details below; N = 8 children excluded), excessive in-scanner motion (more than 50% of fMRI volumes with framewise displacement (Power et al., 2012) above 0.4 mm; N = 24 children, 4 of whom also showed poor performance), or fewer than 5 trials for each class, i.e., each combination of condition (switch vs. repeat) and task (face vs. scene vs. object, see below), in the MVPA analyses (N = 1 child; included in the previous study [Schwarze et al., 2023]). The final sample included 88 children (8–11 years; mean age = 10.07 years, SD = 0.69; 49 girls) and 53 adults (20–30 years; mean age = 24.69 years, SD = 2.6; 28 women). Adult participants, parents, and children provided informed written consent and the study was approved by the ethics committee of the Freie Universität Berlin and conducted in line with the Declaration of Helsinki.

2.2 Experimental design

In the task-switching paradigm performed in the MR scanner, participants had to respond to one of three simultaneously presented stimuli (a face, a scene, and an object) each relevant to a different task (i.e., the face task, the scene task, and the object task). The relevant task was indicated by a simultaneously presented shape in the background, such that, for instance, a diamond-shaped background indicated the face task, which required the classification of the face according to its age (see Figure 1A). On each trial, the spatial arrangement of stimuli varied pseudo-randomly

independent of the currently relevant stimulus. Participants responded via button press.

The fMRI session consisted of three runs: one single run in which the tasks were presented in separate blocks, followed by two mixed runs in which the three tasks were pseudo-randomly intermixed. Each run had 99 trials each lasting 2s, followed by a fixation cross for a jittered time period (1–6 s). In the single run, tasks were presented in three separate blocks of 33 trials, interspersed with blocked fixation cross periods (20 s). In the mixed runs, the three tasks were pseudo-randomly intermixed, with 50% repeat and 50% switch trials, again across blocks of 33 trials with blocked fixation cross periods (20 s) to match the single run. Switches were unpredictable, such that participants did not know which task had to be performed on the upcoming trial. The first trial of each run was excluded from all analyses as it could not be classified as a switch or repeat trial in the mixed runs. The main MVPA determining representational changes during task switching focused on the two mixed runs. Data from all three runs were used to define regions of interest (ROIs) that were representative of the task-related univariate activation.

2.3 Behavioral measures and analysis

Behavioral results were previously reported for essentially the same sample across all three task runs (89 as opposed to 88 children, cf. Schwarze et al., 2023), whereas the present analysis focused on the two mixed runs and thus only on repeat and on switch trials. Individual trials with response times (RT) below 0.2 s or above 3 s were excluded from all analyses, so that responses during stimulus presentation and within the first second of the inter-trial interval were accepted. Only correct trials were considered for the calculation of median RTs per condition. Accuracy was calculated as the percentage of correct responses across all given responses for each condition. No datapoints of individual participants had to be removed based on the predefined outlier criterion of mean accuracy or median RTs that deviated 3.5 standard deviations ($p < .001$) or more from the age group-specific mean (Tabachnick and Fidell, 2013). We used Bayesian linear mixed models, using brms (version 2.19.0; Bürkner, 2017) in R (version 4.3.1; R Core Team, 2018), with flat priors to predict proportions of correct responses or median correct RT from condition, age group, and their interaction, including random intercepts for subject. For all models, reported effects are based on 95% credible intervals (CI) such that

the described effects have a 95% probability in the present data (Bürkner, 2017; see also Morey et al., 2016).

2.4 fMRI data acquisition and preprocessing

Functional MR images were collected on a 3-Tesla Siemens Tim Trio MRI scanner using whole-brain echo-planar images (TR = 2000ms; TE = 30ms; 3 mm isotropic voxels). The first five acquired volumes of each run were discarded before analysis to allow for scanner stabilization.

Preprocessing was performed using fMRIPrep (Version 20.2.0; Esteban et al., 2019; for a detailed description of procedures, see <https://fmriprep.org/en/stable/>). BOLD images were co-registered to individual anatomical templates using FreeSurfer, which implements boundary-based registration (Greve and Fischl, 2009). Additionally, they were slice-time corrected (using AFNI; Cox and Hyde, 1997), and realigned (using FSL 5.0.9; Jenkinson et al., 2002). For the definition of ROIs based on group-level univariate activation, BOLD images were normalized into MNI152NLin6Asym standard space. All multivariate analyses were conducted in individual-specific anatomical space. ROIs defined in MNI space were transformed into individual-specific anatomical space using Advanced Normalization Tools (ANTs; Avants et al., 2009) and FSL (Version 5.0.9; Jenkinson et al., 2002).

2.5 ROI definition

Frontoparietal (FP) and cingulo-opercular (CO) regions. Previous research has demonstrated that lateral FP regions, including the IFJ, the SPL, and dIPFC, show enhanced univariate activation during task switching (Kim et al., 2012; Niendam et al., 2012; Richter and Yeung, 2014; Worringer et al., 2019) and represent the currently relevant task in adult studies (Loose et al., 2017; Qiao et al., 2017). Thus, we focused on these areas as our main ROIs (see preregistration: <https://osf.io/8mfqx/>). Along with the expected FP regions, the univariate activation analyses (see Figure 2) also revealed enhanced activation in the dACC and the al during task switching. Thus, for exploratory analyses, we defined ROIs of the CO network, including the al and dACC (Dosenbach et al., 2007, 2008).

The ROI definition procedure was as follows. ROIs were initially defined based on task activation across all three runs relative to baseline and subsequently

restricted by anatomical location. To this end, we constructed a general linear model (GLM) of correct single, correct repeat, and correct switch trials as separate regressors. Missed trials, error trials, and the first trial of each run were included in a separate regressor of no interest. Framewise displacement per volume (in mm; Power et al., 2012), realignment parameters (three translation and three rotation parameters), and the first six anatomical CompCor components as provided by fMRIPrep were added as regressors of no interest. CompCor identifies patterns of noise using a principle-component analysis approach and the inclusion of the components aids in the removal of noise from fMRI data (Behzadi et al., 2007). We derived a contrast, comparing task (correct single, repeat, and switch trials) with baseline collapsed across age groups. The resulting whole-brain contrast map was thresholded at family-wise error (FWE) corrected $p < .05$, cluster size > 50 voxels.

Multiple brain regions in the frontal and parietal cortices showed greater activation for tasks compared to baseline, including bilateral IFJ, dlPFC, SPL, dACC, and al. Functional activations as determined above were anatomically restricted using the Harvard-Oxford atlas (Makris et al., 2006), thresholded at 30%. The inclusive anatomical masks we used to restrict univariate activation to pre-defined ROIs were the middle frontal gyrus for the dlPFC, the superior parietal lobe for the SPL, insular cortex for the al, and the paracingulate gyrus for the dACC. Because no anatomical mask for the restriction of the IFJ is available, we defined it based on coordinates from a meta-analysis of task-switching studies focusing on the IFJ (Derrfuss et al., 2005). See Figure 2 A–B for task-based FP and CO ROIs, respectively.

Temporo-occipital (TO) ROIs. ROIs in TO were defined on activation maps provided by the Neuroquery (Dockès et al., 2020) and Neurosynth (Yarkoni et al., 2011) platforms, using the search terms “face” “object”, and “place”. A probability map was downloaded for each of the search terms from each platform on November 22nd, 2021. Neuroquery maps were thresholded with a z-score of 3 as recommended by the developers (Dockès et al., 2020); Neurosynth maps were thresholded at $p < .01$ (FDR-corrected; Yarkoni et al., 2011). All negative value voxels were set to zero to keep only positive activation associated with each search term. Next, the Neurosynth and Neuroquery masks for each search term were multiplied with each other to only include voxels identified across both platforms. Note that for the “place” search term

only the Neuroquery mask was used in ROI definition, as the map provided by Neurosynth did not include the parahippocampal gyrus, which has consistently been associated with place/scene perception across age groups (Golarai et al., 2007; Scherf et al., 2007).

Finally, following the same approach as for the FP and CO ROIs, the resulting maps were anatomically masked using the Harvard-Oxford atlas (Makris et al., 2006), thresholded at 30%. The temporal occipital fusiform gyrus was used as an anatomical mask for the face-selective ROI, the inferior lateral occipital cortex for the object-selective ROI, and the anterior and posterior parahippocampal gyrus for the scene/place-selective ROI. The resulting TO ROIs overlapped with activation in temporo-occipital regions of the task > baseline contrast described above. Figure 2C shows the resulting TO ROIs.

Note that we had originally preregistered to define ROIs based on a searchlight MVPA decoding the three tasks (face vs. scene vs. object) across all runs, but we changed our approach due to updated methods for applying corrections of unequal class counts (see below).

2.6 Multivariate pattern analysis

We constructed subject-specific GLMs of the task-switching paradigm using the Nipype (version 1.6.0; Gorgolewski et al., 2011) interface to FSL FEAT (using FSL 5.0.9; Jenkinson et al., 2002), focusing on the mixed runs and more specifically, on the differences between switch and repeat trials therein. GLMs included the combination of task and condition as separate regressors (i.e., face switch, face repeat, scene switch, scene repeat, object switch, object repeat) and the same nuisance regressors of no interest as in the GLM for ROI definition. Activation patterns for individual trials in the two mixed runs were extracted using a least squares separate approach, in which a trial-specific design matrix is used to obtain the activation estimate for that trial (LSS; Mumford et al., 2012).

Next, we conducted MVPA for each participant in each condition separately, using Nilearn (version 0.8.0; see Abraham et al., 2014) and scikit-learn (version 0.24.2; Pedregosa et al., 2011). We used a support vector classifier (LinearSVC, initialized with regularization parameter $C = 1$ and one-vs-rest multiclass strategy) trained to predict the currently relevant task (scene, object, face), given trial

activation patterns in each ROI. We applied leave-one-run-out cross-validation during the analysis, so that at each validation fold, a classifier was fitted on data from one run and tested on data of the other run. Participants with fewer than five trials of each task in a condition were excluded from analysis. To ensure balanced numbers of trials across classes, we undersampled the majority class(es) without replacement. We adopted this approach as opposed to the preregistered method of the scikit-learn “balanced” option (Pedregosa et al., 2011) as it eliminates possible bias rather than correcting for it post-hoc. We repeated model training and testing with leave-one-group-out cross-validation 100 times for each participant in each condition and averaged across iterations. We did not have to remove any participant’s decoding accuracy data based on the predefined outlier criterion of 3.5 standard deviations ($p < .001$) above or below the group-specific mean.

2.7 Analysis of age differences in decoding accuracy

2.7.1 Age and condition differences within ROI sets. To test whether decoding accuracy differed between switch and repeat trials and between the two age groups, analyses in the three sets of ROIs (FP regions: dlPFC, IFJ, SPL; CO regions: dACC, al; TO regions: fusiform gyrus [face-selective], parahippocampal gyrus [scene-selective], and lateral occipital cortex [object-selective]) proceeded in three steps: (1) For each ROI, we tested whether it would be appropriate to combine data across hemispheres: that is, we tested whether decoding accuracy differed between hemispheres, and whether hemisphere interacted with age group or condition. We did not find main effects or interactions involving hemisphere in any of the ROIs and thus averaged across the two hemispheres for all subsequent analyses. (2) Within each ROI set (FP, CO, TO), we tested a Bayesian linear mixed model across all regions in the corresponding set. Decoding accuracy was predicted by condition (repeat vs. switch), ROI, age group (adults vs. children), and their interactions. All linear mixed models included a random intercept for participant. If an effect of region or any interaction of region with another effect of interest (condition or age group) became evident with 95% probability (i.e., the 95% CI did not include zero), we proceeded to test for the main effects and interactions of condition and age group in each ROI separately. (3) Using t-tests, we tested whether decoding accuracy for each condition in each age group and ROI differed from chance (i.e., 0.33). In

addition to comparing decoding accuracy between switch and repeat trials across all three tasks, we tested whether each of the TO ROIs showed selectivity for the theoretically preferred task on repeat trials. To this end, we compared repeat decoding accuracy of the preferred task (i.e., the face task for the fusiform gyrus) to the two non-preferred tasks (i.e., the scene and object task for the fusiform gyrus), and whether this effect differed between age groups.

2.7.2 Age and condition differences between ROI sets. To examine whether age group and condition effects differed between the three sets of ROIs, we first modeled decoding accuracy including all ROIs. Specifically, models included fixed effects of condition, age group, and set of ROIs (FP vs. CON vs. TO), and their interactions, along with random slopes for set of ROI and random intercepts for participant. The model including all interactions fit slightly better than a model without any interactions of condition.

2.7.3 Task-set inertia. In a set of exploratory analyses, we explored if the lingering representation of the previously relevant task set contributed to lower decoding accuracy on switch trials. Specifically, we tested whether incorrect predictions of the classifier on switch trials were more likely to predict the previously relevant task. As described above, the classifier predicted one of the three tasks for each trial. This prediction could either be correct and thus count towards the decoding accuracy measure, or incorrect if the prediction indicated one of the other two tasks not relevant on that specific trial. To test the task-set inertia hypothesis within each set of ROIs, we tested whether the classifier was more likely to predict the previously relevant task over the task that was neither relevant on the previous nor current trial; further, we tested whether this differed between age groups. To this end, we modelled percentage of false predictions as the dependent variable and the type of false prediction (previous vs. third task) and age group as the fixed effects, additionally including fixed effects of region and random intercepts of participant.

2.7.4 Individual differences in the impact of switch demand on representations across ROI sets. While analyses up to this point tested whether the effect of switch demand on neural task-set representations differed between children and adults, they did not shed light on the question whether switch demand affected different

brain regions similarly within an individual. Thus, to further understand these individual differences across the sets of ROIs, we explored whether individuals who showed a greater difference in decoding accuracy between conditions in one set of ROIs showed a similar pattern in the other sets of ROIs. To this end, we averaged the differences between switch and repeat decoding accuracy across all ROIs in each set. Next, we tested for age group differences in the correlations among the three sets of ROIs by comparing the correlations of each pair of ROI sets between the two age groups using *cocor* (version 1.1-4; Diedenhofen and Musch, 2015) in R.

2.8 Associations between decoding accuracy and performance

To anticipate the outcome of our analyses, we did not observe any differences in decoding accuracy between individual ROIs within each set. As a result, we deviated from the preregistration and tested whether decoding accuracy across ROIs in a set predicted task performance. We used a linear mixed model with performance accuracy as the dependent variable, average decoding accuracy across the ROIs in one set, condition (repeat vs. switch), and age group (adults vs. children) as fixed effects, and a random intercept modeling the individual participants. We used leave-one-out cross-validation (*loo* package; Vehtari et al., 2022) to compare the model including all interactions between the fixed effects to models including fewer interaction terms. We only tested models that included an interaction of age group and condition to account for differences in behavioral performance between children and adults. For both behavioral accuracy and RT, and the models in all ROI sets, model comparisons indicated better fit for the model including only the main effect of decoding accuracy and the interaction between age group and condition, but no interaction of decoding accuracy with either age group or condition. Thus, the effect of interest was the main effect of decoding accuracy. The same model setup and comparison approach was used for linear mixed models of RT.

3. Results

3.1 Greater switch costs in children than adults

Adults exhibited higher overall performance accuracy than children (estimate (est.) = -0.16 ; 95%-CI: $-0.20, -0.11$) as well as shorter RTs on correct trials (est. = 0.28 ; 95%-CI: $0.22, 0.33$). Both groups exhibited switch costs, with higher accuracy on repeat than on switch trials (est. = -0.03 ; 95%-CI: $-0.04, -0.02$); as well as shorter correct RTs on repeat than on switch trials (est. = 0.24 ; 95%-CI: $0.21, 0.27$).

Critically, children exhibited greater switch costs than adults in terms of accuracy (condition x group interaction: est. = -0.05 ; 95%-CI: $-0.07, -0.03$; Figure 1C), albeit not in terms of RTs (condition x group interaction: est. = 0.01 ; 95%-CI: $-0.03, 0.05$; Figure 1C). In sum, both children and adults showed switch costs in accuracy and RT, with greater accuracy switch costs in children than in adults.

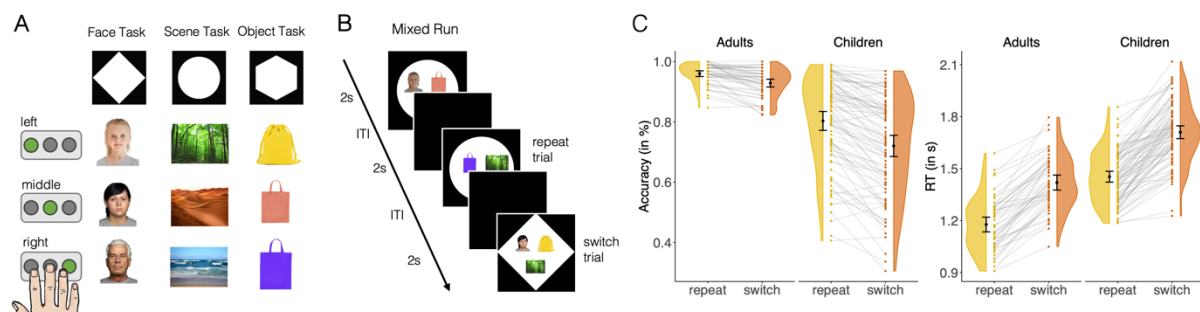


Figure 1: Task-switching paradigm and age differences in performance. (A) The task-switching paradigm consisted of three tasks: the face task, the scene task, and the object task. Participants had to perform the task indicated by the simultaneously presented shape in the background. Depending on the stimulus presented, one of three buttons had to be pressed in response (indicated here by the green button). Faces had to be categorized according to the age of the person shown, scenes according to the location (i.e., forest, desert, or sea), and objects according to the color. (B) The mixed runs included trials on which the task of the previous trial was repeated (50%) or switched to a different task (50%) in an unpredictable manner. (C) Performance accuracy (in %) and response times (in seconds) for repeat (yellow) and switch (orange) trials split by age group. Gray lines connect performance measures for each individual. Image credits: Young and old adult faces were taken from the FACES collection (Ebner et al., 2010).

3.2 Higher decoding accuracy for repeat than for switch trials across age groups

Decoding accuracy for each ROI is shown in Figure 2. We predicted lower decoding accuracy on switch than on repeat trials across groups in all sets of ROIs, with greater reductions in decoding accuracy for children. To test these hypotheses, we used Bayesian linear mixed models for each set of ROIs to predict decoding accuracy by age group, condition, and ROI.

In each set of ROIs, we found evidence of a main effect of condition (switch vs. repeat; FP ROIs: est. = -0.10 ; 95%-CI: $-0.14, -0.06$; CO ROIs: est. = -0.09 ; 95%-CI: $-0.13, -0.05$; TO ROIs: est. = -0.15 ; 95%-CI: $-0.19, -0.11$), with higher decoding accuracy on repeat than on switch trials. There was no evidence for effects of age group in any of the ROI sets, showing that, contrary to our hypothesis, decoding accuracy was comparable between children and adults. Finally, there were no effects of specific ROI within a set, suggesting that all tested ROIs showed higher decoding accuracy on repeat trials relative to switch trials in both age groups.

ROI-specific analyses indicated that all ROIs showed above-chance (> 0.33) decoding accuracy on repeat trials (all t s > 6.85 ; all lower bounds of 95%-CI > 0 ; see Figure 2). By contrast, decoding accuracy on switch trials did not differ from chance in the majority of ROIs (i.e., the bilateral SPL and IFJ for the FP ROIs, the bilateral al and dACC of the CO ROIs, and the face- and scene-selective ROI; $-1.04 < t < 1.36$; all lower bounds of 95%-CI < 0), with only two exceptions. The dlPFC showed above-chance decoding accuracy for switch trials in adults ($t = 1.96$; lower bound of 95%-CI = 0.005) but not in children ($t = 0.64$; lower bound of 95%-CI = -0.015), and the object-selective ROI showed above-chance decoding accuracy for switch trials in children ($t = 2.55$; lower bound of 95%-CI = 0.012), but not in adults ($t = 1.2$; lower bound of 95%-CI = -0.0077).

Taken together, in line with our hypothesis and in accordance to the observed behavioral switch costs, decoding accuracy was greater for repeat than for switch trials across all sets of ROIs. Above-chance decoding of the currently relevant task was only evident for repeat trials, while the newly-updated relevant task on a switch trial could not be distinguished from the two irrelevant tasks based on the neural activation pattern. Of note, contrary to our hypothesis, children showed comparably distinct task-set representations as adults.

To explore whether the TO ROIs showed preference for stimuli in the currently relevant task, given their putative functional specialization for processing different kinds of stimuli (Cantlon et al., 2011; Natu et al., 2016; Golarai et al., 2017; Tian et al., 2021), we tested decoding accuracy for the preferred compared to the non-preferred tasks on repeat trials in each ROI. The face-selective ROI showed greater decoding accuracy on repeat trials for the face task compared to the object and scene tasks (est. = -0.06 ; 95%-CI: -0.8 , -0.03) even though each trial presented a face, object, and scene stimulus simultaneously on the screen and at unpredictable locations. By contrast, neither the object- nor scene-selective ROI showed a preference for object or scene tasks, respectively. Thus, only the face-selective ROI showed a preference for the stimuli it was expected to prefer.

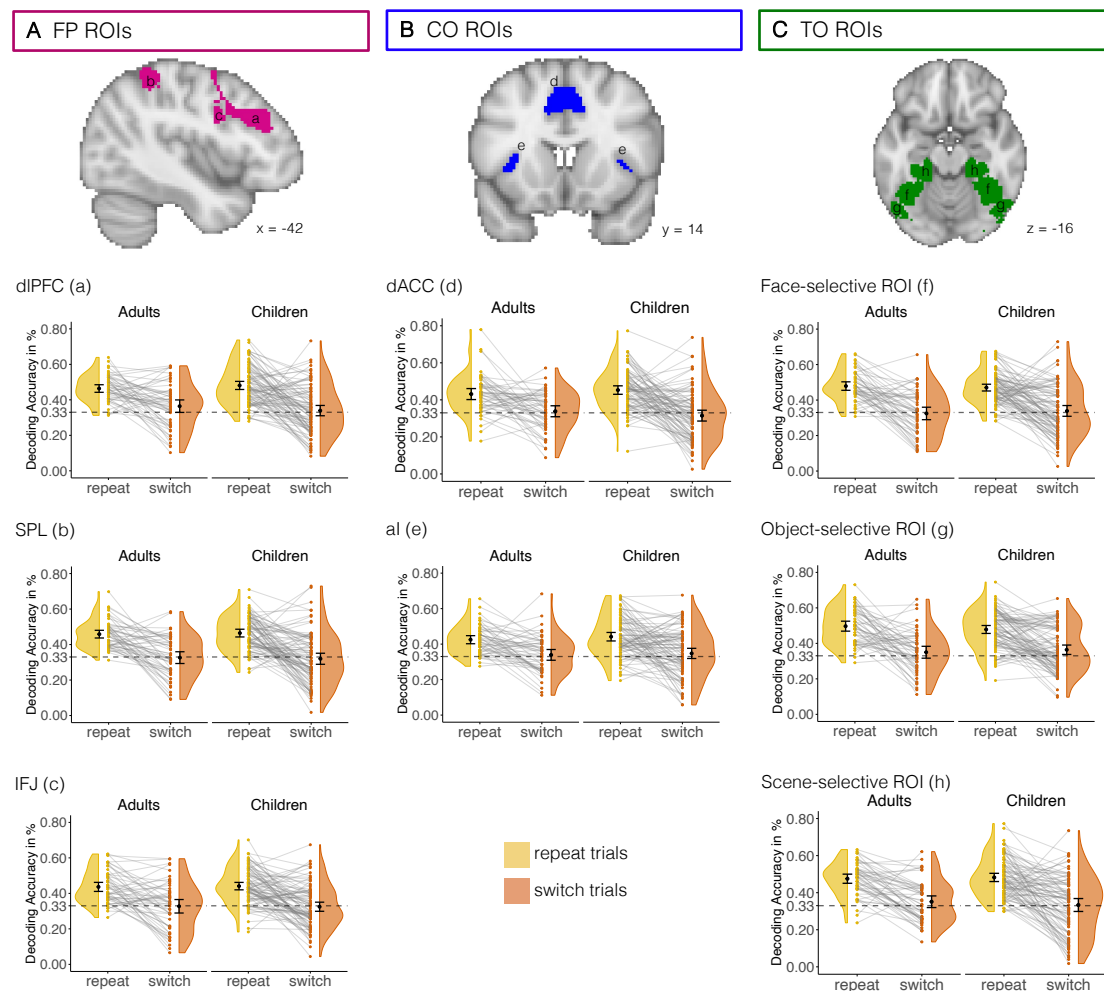


Figure 2: Regions of interest (ROIs) and decoding accuracy results. The dashed line in each plot indicates chance (0.33). (A) Decoding accuracy for repeat trials (yellow) and switch trials (orange) in adults and children of frontoparietal (FP) regions: (a) dorsolateral prefrontal

cortex (dlPFC), (b) superior parietal lobe (SPL), and (c) inferior frontal junction (IFJ). (B) Decoding accuracy of cingulo-opercular (CO) regions: (d) dorsal anterior cingulate cortex (dACC) and (e) anterior insula (al). (C) Decoding accuracy of temporo-occipital (TO) regions: (f) face-selective ROI in the fusiform gyrus, (g) object-selective ROI in the lateral occipital cortex, (h) scene-selective ROI in the parahippocampal gyrus.

3.3 Higher decoding accuracy for temporo-occipital ROIs

As the effect of condition was present in all three sets of ROIs, we next sought to directly compare whether it differed between the sets of ROIs. A model comparing the effects of age group, condition, and ROI set on decoding accuracy revealed that relative to the TO ROIs, decoding accuracy was lower in the FP ROIs (est. = -0.03 ; 95%-CI: $-0.06, -0.01$) and CO ROIs (est. = -0.06 ; 95%-CI: $-0.06, -0.04$). The difference between the CO and the TO ROIs was further qualified by an interaction with condition (est. = 0.06 ; 95%-CI: $0.02, 0.1$), indicating a greater difference in decoding accuracy between switch and repeat trials in the TO compared to the CO ROIs. There was neither evidence for differences between the FP and the CO ROIs nor for any differences between the age groups. Thus, while all investigated regions showed greater decoding accuracy on task repetitions compared to task switches, this condition difference, as well as overall decoding accuracy, was greater in the TO ROIs than in regions classically associated with cognitive control processes in children and adults.

3.4 No evidence for task-set inertia effects on representations

Next, we investigated whether task-set inertia contributed to less distinct task-set representations on switch trials. To this end, we compared the percentage of trials on which the classifier falsely predicted the previously relevant task to the percentage of trials on which it predicted the third task that was neither relevant on the current nor on the previous trial. Separate models for each set of ROIs included the fixed effects of incorrectly predicted task (previous vs. third task), age group, and region. None of the investigated sets of ROIs showed a higher probability of predicting the previous task over the third task in both children and adults (all 95%-CI included zero; Figure 3). Thus, we did not find any evidence that lower decoding accuracy on switch trials was related to task-set inertia, whereby the representation

of the task relevant on the immediately preceding trial would linger after ceasing to be relevant.

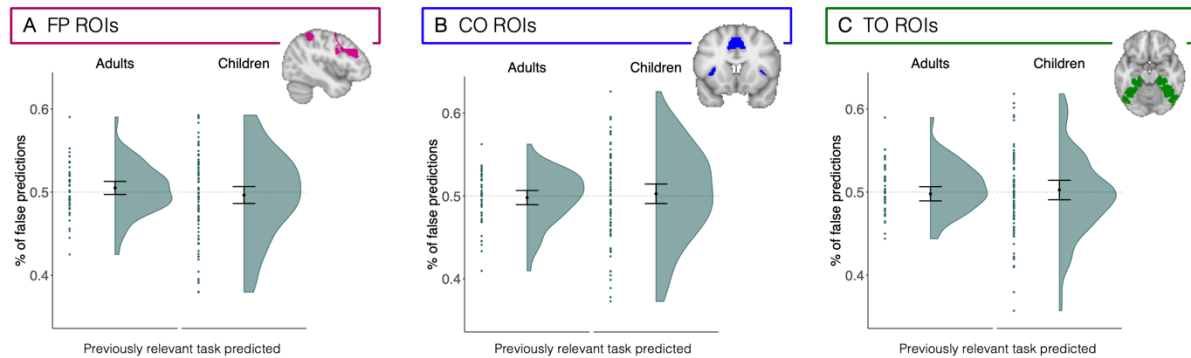


Figure 3: Percentage of predictions of the previously relevant task of all false predictions of the currently relevant task (i.e., task-set inertia) for (A) the frontoparietal (FP) ROIs, (B) the cingulo-opercular (CO) ROIs, and (C) the temporo-occipital (TO) ROIs. As none of the analyses within each set of ROIs indicated differences between regions, data were averaged across ROIs in each set for visualization.

3.5 Children showed similar condition differences in decoding accuracy in CO and FP ROIs

Next, to assess whether switch demand affected different brain regions similarly within an individual, we conducted a set of exploratory analyses testing whether children and adults showed similar patterns of switch-related reductions in decoding accuracy across ROI sets. To this end, we calculated the average difference in decoding accuracy between switch and repeat trials (i.e., difference scores) across all ROIs of the same set. The association between difference scores in the FP and in the CO ROIs differed between the age groups ($p = .018$; Figure 4): children showed a moderate to strong correlation between decoding accuracy difference scores in FP and CO ($r = .64$; $p_{\text{FDR}} < .001$, FDR-corrected for multiple comparisons), whereas adults showed a weak to moderate correlation ($r = .33$; $p_{\text{FDR}} = .027$). Difference scores showed a moderate correlation between FP and TO ROIs in children ($r = .54$; $p_{\text{FDR}} < .001$) and in adults ($r = .38$; $p_{\text{FDR}} = .015$), and did not differ between age groups ($p = .27$). Difference scores between CO and TO ROIs showed weak to moderate correlations in both children ($r = .31$; $p_{\text{FDR}} = .004$) and adults ($r = .30$; $p_{\text{FDR}} = .03$), and did not differ between age groups ($p = .98$). In sum, children showed

greater similarity than adults in the impact of switching demands on FP and CO ROIs, while group differences were neither evident for the correlations between FP and TO nor for those between CO and TO.

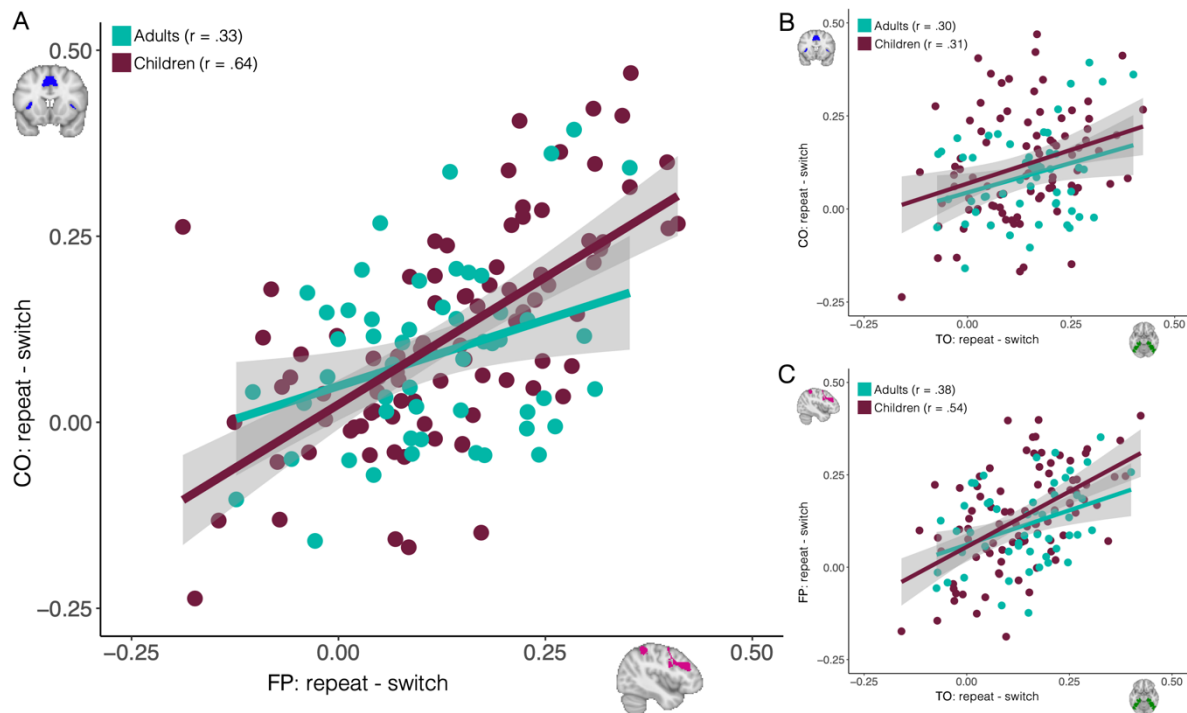


Figure 4: Correlations of condition differences in decoding accuracy between sets of ROIs split by age group. (A) In children (shown in magenta), greater differences in decoding accuracy between repeat and switch trials in frontoparietal (FP) ROIs were associated with greater differences on the same measure in the cingulo-opercular (CO) ROIs. This was not the case in adults (shown in turquoise). (B) Correlations in CO and temporo-occipital (TO) ROIs did not differ between children and adults. (C) Correlations in FP and TO ROIs did not differ between children and adults.

3.5 Decoding accuracy was not related to task-switching performance

Finally, to investigate whether having more distinct neural representations of the currently relevant task set was related to better task-switching performance, we tested whether decoding accuracy averaged across all ROIs within each set was associated with higher performance accuracy and/or lower RTs. Model comparisons indicated that the best fitting model included the main effect of decoding accuracy and the interaction between age group and condition, but no interaction of decoding

accuracy with either age group or condition. This suggests that there were no differences between children and adults in the potential association between decoding accuracy and performance. In these models across all participants, none of the ROI sets showed an effect of decoding accuracy on either performance accuracy or correct RTs (all 95%-CI included zero). Thus, we found no evidence that higher decoding accuracy was associated with better performance during task switching in the present paradigm.

4. Discussion

Using MVPA, we examined the extent to which the distinctiveness of neural task-set representations contributed to age differences in task switching. Both children and adults showed lower decoding accuracy on switch compared to repeat trials across FP, CO, and TO regions, suggesting less distinct task-set representations on switch trials. We observed above-chance classification of the currently relevant task for repeat trials in all ROIs, while classification performance was largely at chance level for switch trials (except for the left dIPFC in adults and the object-selective ROI in children). Contrary to our expectations, we found no evidence that decoding accuracy differed between children and adults. In addition, task-set representations of the previously relevant task were not more likely to be (erroneously) decoded than the representations of the third task that was irrelevant on the previous and current trials. Thus, our analyses do not provide any evidence that task-set inertia contributed to lower distinctiveness for switch trials. The distinctiveness of the representation of the currently relevant task set decreased during switching in regions beyond the FP network, including CO regions associated with task control (Braver et al., 2003; Sestieri et al., 2014; Han et al., 2019; Palenciano et al., 2019; Cocuzza et al., 2020; Wood and Nee, 2023) as well as TO regions associated with the task-relevant stimuli (cf. Tsumura et al., 2021). Notably, children showed higher correlations in these decoding accuracy costs between FP and CO regions than adults, suggesting that switch demand affected task-set representations in FP and CO regions in a manner that was more similar among children than among adults.

4.1 More distinct representations on repeat than switch trials

The finding that the currently relevant task set could be decoded with an accuracy that was above chance for repeat but not for switch trials supports the notion that task-set representations in the present task were less stable when they had recently been updated (i.e., on switch trials; Meiran, 1996; Mayr and Kliegl, 2000). The lower distinctiveness on switch trials has partly been attributed to the lingering representation of the (no-longer relevant) task set from the previous trial (Rogers and Monsell, 1995; Wylie and Allport, 2000; Qiao et al., 2017; Rangel et al., 2023).

Directly testing this task-set inertia hypothesis in the present study, we did not find any evidence for this pattern, contrary to the previous findings reported by Qiao

et al. (2017) based on representational similarity between consecutive trials. Note that compared to Qiao et al. (2017), our participants had to switch among three different tasks. This allowed us compare whether a multivariate pattern of brain activation contained more information of the previously relevant task than a third task (relevant on neither the previous nor the current trial), and thus directly test predictions made by the task-set inertia hypothesis.

Taken together with previous studies investigating neural representations during task switching (Loose et al., 2017; Qiao et al., 2017), the present results indicate that differences in neural task-set representations may depend on the specific kind of switching demand. Specifically, our paradigm and the one used by Qiao et al. (2017) required switches between different arbitrary rules and their corresponding response mappings that may be more likely to modulate the distinctiveness of task-set representations (cf. Woolgar et al., 2011), as indicated by a condition difference in decoding accuracy. In contrast, the paradigm by Loose et al. (2017) required switches between responses while the task remained the same conceptually, which resulted in comparable (above-chance) decoding for both switch and repeat trials (cf. Brass and De Baene, 2022).

4.2 Similar distinctiveness of task-set representations in children and adults

By demonstrating that the currently relevant task can be reliably predicted from neural activation patterns during task switching not only in adults but also in children, our results provide novel insights into children's ability to flexibly switch between rules. These findings add to an emerging research direction investigating the role of neural representations for cognitive development across childhood and adolescence (e.g., Fandakova et al., 2019; Jung et al., 2023).

Contrary to our expectations based on comparisons of univariate task-based activation during task switching (e.g., Crone et al., 2006b; Wendelken et al., 2012), we did not find evidence for less distinct neural task-set representations in children compared to adults. However, a similar level of decoding accuracy between children and adults should not be taken as evidence that representations were identical or used in the same way in both age groups. Even with similar distinctiveness of task-set representations, there may still be differences in the application of the task set. Specifically, decoding techniques only indicate differences between task-set

representations but do not reveal the processes through which these representations come to be or how they influence behavior (cf. Kriegeskorte and Douglas, 2018).

For example, tasks eliciting different levels of task performance in adults were shown to have comparable levels of decoding accuracy, suggesting that differences in complexity were not captured by the decoder (Ruge et al., 2019). This may be especially relevant when comparing groups of individuals of different ages, given that the neural systems that are being decoded differ in organization due to maturation and experience. In line with this consideration, Crone and colleagues (2006c) found that age differences in univariate activation were more pronounced when representations in working memory needed to be manipulated not just maintained. Finally, univariate analyses of the present sample revealed that children upregulated frontoparietal activation on switch compared to repeat trials to a smaller extent than adults did (Schwarze et al., 2023), further supporting the idea that children and adults may differ with respect to implementing the newly relevant task-set representation on switch trials.

4.3 Differences between networks

Corroborating and extending previous studies of neural task-set representations during rule-based tasks (Woolgar et al., 2011; Zhang et al., 2013; Loose et al., 2017; Qiao et al., 2017) with respect to regional heterogeneity, we showed greater decoding accuracy in TO regions compared to FP and CO regions, not only in children but also in adults. TO regions may be more strongly driven by the visual input of the task, support sensory representations within working memory (cf. Olivers and Roelfsema, 2020), or carry representations of lower dimensionality rendering them more distinct in their neural pattern (cf. Buschman, 2021). Note that the present task did not include multiple cues (i.e., a single cue was used for each task) and the cue was presented simultaneously with the stimuli. We can thus not rule out that the cue contributed to the distinctiveness of task-set representations (cf. Loose et al., 2017). Given the relatively earlier position of the TO regions in the ventral visual processing stream (e.g., Kravitz et al., 2013), the extent to which the cue might have impacted task-set representations may differ between ROIs and thus contribute to differences in decoding accuracy between ROIs.

Our exploration of regional heterogeneity led to the finding that the difference between switch versus repeat decoding accuracy was correlated more strongly between the CO and FP ROIs (but not the TO ROIs) in children than in adults. It has been noted before that differences in the functional roles of CO and FP networks increase in the course of child and adolescent development (e.g., Fair et al., 2009; Keller et al., 2022; Tooley et al., 2022). In light of the individual differences observed here, we could speculate that the closer functional association between FP and CO regions in children is associated with the representation of more similar features in these regions in children as compared to adults. This idea is consistent with suggestions that representational structure is crucial for efficient cognitive control (Badre et al., 2021; Garner and Dux, 2023) and differs between regions in adults (Vaidya and Badre, 2022). A recent study examined how representational structures change during the acquisition of new tasks in adults (Mill and Cole, 2023) and demonstrated regional differences in compositional representations, that is, task-general activation patterns, and conjunct representations, that is task-specific activation patterns. Specifically, with learning, compositional representations in cortical regions were replaced by conjunct representations previously only found in subcortical regions.

4.3 Conclusion

Taken together, our results demonstrate that task-set representations were affected by switch demands – not only in adults but also in children. Individual differences in the degree to which effects of switch demands were correlated between sets of brain regions raise the possibility that the closer functional association between frontoparietal and cinguloopercular regions in children is related to the representation of more similar task features across regions in childhood. These findings raise further questions about the role of representations in the development of cognitive control during childhood that merit further study: What is the role of regional heterogeneity and overlapping feature representation for the learning and generalization of task rules in childhood? Future work focusing on developmental changes in neural representations could provide fruitful in elucidating the mechanisms underlying cognitive control development.

5. References

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C: Paper 3

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Intensive task-switching training and single-task training differentially affect behavioral and neural manifestations of cognitive control in children

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Running title: Task-switching training in children

Abstract

The ability to flexibly switch between tasks develops during childhood. Children's task-switching performance improves with practice, but the underlying processes remain unclear. We examined how nine weeks of task-switching training affect performance and task-related activation and connectivity as assessed by functional magnetic resonance imaging. Children (8–11 years) were pseudo-randomly assigned to three groups: high-intensity task switching (SW; n = 70), high-intensity single tasking (SI; n = 72), and passive control (n = 41). After three weeks, drift-diffusion modeling revealed faster evidence accumulation and more cautious responding in both training groups relative to the control group. At the end of training, these changes were maintained in the SW group only, that also showed activation decreases in dorsolateral prefrontal cortex. Functional connectivity increases associated with task-switching demands became less pronounced with practice in both training groups, with more persistent decreases in the SI group. We conclude that task-switching training altered performance by accelerating evidence accumulation and promoting more cautious responding. Faster evidence accumulation along with decreased task-related activations suggest increased processing efficiency in frontoparietal regions with training. More intense task-switching training helped maintain these changes, possibly by facilitating plastic change through the protracted mismatch between processing supplies and environmental demands.

Keywords: child development, drift-diffusion modeling, prefrontal cortex, task switching

1. Introduction

Executive functions describe a set of control processes supporting goal-directed behavior (Diamond 2013). Task switching, the ability to flexibly switch between different tasks, constitutes a key component of executive functions (Miyake et al. 2000; Miyake and Friedman 2012) and continues to improve across childhood (Cepeda et al. 2001; Crone et al. 2004; Reimers and Maylor 2005; Crone, Bunge, et al. 2006; Huizinga and van der Molen 2007; Weeda et al. 2014). Accordingly, a number of studies have aimed to improve children's task-switching abilities with training (Karbach and Kray 2009; Kray, Karbach, Haenig, et al. 2012; Zinke et al. 2012; Kray et al. 2013; Dörrenbächer et al. 2014; Karbach et al. 2017; Zuber et al. 2023). However, the mechanisms underlying training-related task-switching improvements in childhood are not yet well understood. The present study seeks to close this gap by examining changes in the cognitive and neural processes underlying task switching in children aged 8 to 11 years, an age period during which children continue to show major improvements in executive functions (Tervo-Clemmens et al. 2023).

1.1 Age differences in task-switching

To examine task switching in the laboratory, task-switching paradigms require individuals to perform two or more tasks in an intermixed fashion, such that each trial constitutes either a repeat of the previous task or a switch to a different one (cf. Koch and Kiesel 2022). The demand to switch to a different task elicits performance costs (i.e., switch costs), evident in lower accuracy and longer response times (RTs). Switch costs are assumed to reflect the updating of the relevant task set and inhibition of the no-longer relevant task set (e.g., Allport et al. 1994; Rogers and Monsell 1995; Meiran 1996; Mayr and Kliegl 2000; Wylie and Allport 2000). Blocks of trials involving task switches are referred to as *mixed blocks* and can be compared to *single blocks* in which participants perform the different tasks separately. The comparison of mixed and single blocks allows one to capture processes that are common to repeat and switch trials within mixed blocks (i.e., mixing costs), in particular the increased

demands to maintain and monitor multiple task sets (e.g., Rubin and Meiran 2005; Pettigrew and Martin 2016). Compared to young adults, children show greater mixing and switch costs, with switch costs approaching adult levels around age 10, while age differences in mixing costs continue to be evident up to adolescence (Cepeda et al. 2001; Crone et al. 2004; Reimers and Maylor 2005; Crone, Bunge, et al. 2006; Huizinga and van der Molen 2007; Manzi et al. 2011).

Cognitive processes involved in task switching can be assessed in a more granular manner using drift-diffusion models (Ratcliff 1978; for a review see Schmitz and Voss 2012). Specifically, drift rates – the speed of evidence accumulation for the correct response – are generally greater on repeat compared to switch trials, thus allowing a participant to reach a decision for the correct response more quickly on repeat trials (Schmitz and Voss 2012). The boundary-separation parameter, also referred to as the decision threshold, has been associated with response caution. It has been suggested to capture interindividual differences in strategy during task switching as well as intraindividual differences between conditions, such that boundary separation is greater on switch than on repeat trials, especially when switches are unpredictable (Karayanidis et al. 2009; Schmitz and Voss 2012). Finally, the non-decision time parameter reflects the encoding of cues and stimuli and preparatory processes, including the reconfiguration of the task set, which are thought to be more demanding on switch than repeat trials (Schmitz & Voss, 2012). Studies have further suggested that the non-decision time parameters additionally capture processes after the decision has been made, reflecting the continuous processing of the stimuli (Resulaj et al. 2009; Schroeder and Verrel 2014). Note however that these post-decision aspects of the non-decision time parameter have not been systematically examined in task-switching studies.

To date, drift-diffusion parameters during task switching have rarely been examined in developmental studies. Weeda and colleagues (2014) investigated drift-diffusion parameters on showed that children become more efficient at accumulating evidence for the correct response between ages 7 and 15 years, reflected in increased drift rates with age.

Compared to 7–11-year-olds, 15-year-olds showed smaller boundary separation, suggestive of less cautious responses, and more efficient stimulus encoding and response selection, indexed by lower non-decision time. All parameters approached adult levels between ages 11 and 15 years, indicating that most developmental changes in evidence accumulation, response caution, and preparatory processes during task switching mature during late childhood to mid-adolescence (Weeda et al. 2014; see also Schuch and Konrad 2017). Notably, studies to date only investigated drift-diffusion parameters for switch and repeat trials within mixed-task blocks and did not include a single-task condition. The contributions of these processes to developmental improvements in mixing costs are thus unknown. This constitutes a significant gap in our understanding of task-switching development, since mixing costs show greater improvements in late childhood than do switch costs (Cepeda et al. 2001; Reimers and Maylor 2005), and thus greater potential for training-related improvements.

1.2 Task-switching training

Task-switching abilities can be improved with training across the lifespan (Kray and Lindenberger 2000; Cepeda et al. 2001; Minear and Shah 2008; Berryhill and Hughes 2009; Strobach et al. 2012; von Bastian and Oberauer 2013; Dörrenbächer et al. 2014). During task-switching training, participants typically train switching between tasks over the course of several sessions, with studies consistently showing improved performance on the trained tasks (Kray and Dörrenbächer 2020). By comparing performance improvements with task-switching training to an active control group that practices the same tasks in a single-task condition, studies have demonstrated that it is specifically switching between tasks as opposed to repeated practice of the task rules that leads to improved performance (Minear and Shah 2008).

In studies with adults, mixing costs were substantially reduced or even eliminated upon training (Berryhill and Hughes 2009; Strobach et al. 2012), while switch costs were mostly reduced but remained present after training (Kray and Lindenberger 2000; Cepeda et

al. 2001; Strobach et al. 2012). This pattern of results suggests that the demands on task-set maintenance and monitoring processes associated with mixing costs (Rubin and Meiran 2005; Pettigrew and Martin 2016) can be met more effectively with training, resulting in comparable performance in mixed- and single-task blocks. From a developmental perspective, these results stress the potential of training to mitigate age differences in task switching, which are particularly pronounced with respect to the ability to maintain and monitor multiple task sets (Cepeda et al. 2001; Reimers and Maylor 2005).

Indeed, task-switching training in children leads to improvements in both mixing and switch costs (Cepeda et al. 2001; Karbach and Kray 2009; Kray, Karbach, Haenig, et al. 2012; Zinke et al. 2012; Kray et al. 2013; Dörrenbächer et al. 2014; Karbach et al. 2017; Zuber et al. 2023). Some studies showed even greater training gains in children than adults (Cepeda et al. 2001; Karbach and Kray 2009; Karbach et al. 2017) suggesting that task switching abilities may be especially malleable while they are still developing (cf. Wass et al. 2012; Kühn and Lindenberger 2016).

While these studies demonstrate that children approach adult levels of task-switching performance upon training, it is unclear whether neural activation patterns associated with task switching also become more adult-like or whether children improve their performance by strengthening different, potentially child-specific activation patterns. Moreover, varying switching demands during training, in combination with the opportunity to train the task rules during single tasks, may be particularly beneficial in children, as they may have additional difficulties in representing the different task-relevant rules (Karbach and Kray 2009).

1.3 Changes in neural processes with training

Task switching has been associated with increased fMRI activation in frontoparietal brain regions (for recent meta-analyses, see Worringer et al. 2019; Zhang et al. 2021), in particular in the inferior frontal junction (IFJ; cf. Derrfuss et al. 2005), the superior parietal lobe (SPL), and the dorsolateral prefrontal cortex (dlPFC), along with functional connections among them (Yin et al. 2015; Dajani et al. 2020). Training studies of task switching or dual

tasking in adults suggest that activation in these regions decreases with training (Dux et al. 2009; Jimura et al. 2014; Garner and Dux 2015). These results obtained for task-switching training are consistent with training studies of executive functions in general, which also showed decrements in brain activation with training (Landau et al. 2004; Landau et al. 2007; Dux et al. 2009; Schneiders et al. 2011; Jimura et al. 2014). At the same time, a substantial number of executive-function training studies has also reported training-related increases in activation (Olesen et al. 2004; Erickson et al. 2007; Westerberg and Klingberg 2007; Jolles et al. 2010; Schweizer et al. 2013; Buschkuhl et al. 2014). As a result, the overall picture of training-induced quantitative changes in fMRI activation is mixed (Landau et al. 2004; Kelly and Garavan 2005; Buschkuhl et al. 2012; Hsu et al. 2014; Constantinidis and Klingberg 2016). Decreased activation has been interpreted as improved efficiency of rule processing in frontoparietal regions, while increased activation has been interpreted as stronger involvement of the corresponding brain regions in task execution (Poldrack 2000; Kelly and Garavan 2005; Kelly et al. 2006). Additionally, connectivity among frontoparietal regions has been found to increase with cognitive training, both at rest (Jolles et al. 2013; Mackey et al. 2013; Guerra-Carrillo et al. 2014) and during task performance (Kundu et al. 2013; Thompson et al. 2016).

Neuroimaging studies of age differences in task switching have shown that children recruit similar brain regions as adults, albeit less adaptively modulating task-related activation with increasing switching demands (Bunge and Wright 2007; Velanova et al. 2008; Wendelken et al. 2012; Mogadam et al. 2018; Engelhardt et al. 2019; Kupis et al. 2021; Zhang et al. 2021; Schwarze et al. 2023; but see Crone, Donohue, et al. 2006; Morton et al. 2009). To date, no studies have investigated the changes in neural processes associated with task-switching training in childhood. Based on the existent cognitive training literature, we hypothesized two alternative patterns of neural change. First, with training, children may show reduced activation in frontoparietal brain regions, similar to one of the training-related patterns observed in adults (Landau et al. 2004; Landau et al. 2007; Dux et al. 2009; Schneiders et al. 2011; Jimura et al. 2014). Such a pattern has been previously

demonstrated with attention training in children: investigating the time course of activation using electroencephalography, Rueda et al. (2012) showed faster recruitment of the attention network after training.

Second, cognitive training in children may have similar effects on neural processes as age-dependent maturation (Jolles and Crone 2012), such that with training, children's brain activation becomes increasingly similar to the activation seen in adults (Rueda et al. 2005; Jolles et al. 2012). For task switching, such a pattern would be reflected in more pronounced increases of brain activation with greater task-switching demands (e.g., Wendelken et al. 2012; Schwarze et al. 2023). Consistent with this hypothesis, studies have reported more adult-like connectivity patterns with working-memory training in children (Astle et al. 2015; but see Jolles et al. 2013) and a combined executive function training in adolescents (Lee et al. 2022). Note that training-induced increases in activation reported in previous studies in adults (Olesen et al. 2004; Erickson et al. 2007; Westerberg and Klingberg 2007; Jolles et al. 2010; Schweizer et al. 2013; Buschkuhl et al. 2014) may be indistinguishable from activation increases due to more adult-like activation with training.

Alternatively or additionally, children may also show qualitative changes by recruiting additional or different brain regions to meet increased demands on task-switching upon training (Buschkuhl et al. 2012; Jolles and Crone 2012). This would speak to fundamentally different training effects in children compared to adults, potentially due to the continuing development of the underlying neural circuitry (Galván 2010).

1.3 Present study

The goal of the present study was to shed light on the cognitive and neural processes supporting training-induced improvements in task switching in children aged between 8 and 11 years. To this end, we leveraged computational approaches to model cognitive processes during task switching (cf. Reinhartz et al. 2023) in combination with the examination of neural processes in two groups that trained with different dosages of task-switching over nine weeks. To elucidate trajectories of change beyond pre- and post-training measures (cf.

Lindenberger and Lövdén 2019; Lövdén et al. 2020), participants performed task switching in the MRI scanner or MRI simulator on two occasions during the training period in addition to the pre- and post-training sessions. We expected task-switching performance to improve with training in both groups, resulting in increasing drift rates, decreasing boundary separation, and decreasing non-decision times during mixed blocks, with changes potentially happening on different trajectories in the different training groups. Specifically, we expected less extensive or slower changes in children who trained smaller doses of task switching. We further sought to test the hypotheses regarding neural changes outlined above. All hypotheses were preregistered (<https://osf.io/by4zq/>).

To briefly preview the results, drift rates and boundary separation increased for both groups after the first three weeks of intensive training, indicating both faster evidence accumulation and more cautions responses, respectively. The observed increases in drift rate and boundary separation were greater for the intensive task-switching group, particularly in the mixed blocks. The high-intensity task-switching group maintained these increases for the rest of training, while the initial increases in the high-intensity single-tasking group returned to pre-training levels by the end of training.

On the neural level, children in the high-intensity task-switching training group showed decreased activation in the dlPFC across conditions. Functional connectivity among frontoparietal regions was higher on repeat than on single trials and decreased in both training groups. These changes were more pronounced in the intensive single-tasking group towards the end of training. Taken together, these results provide first insights into the dynamics of training-related change in the cognitive and neural processes supporting task switching in childhood and suggest that with training, children became more efficient in dealing with the demands of task switching.

2. Materials and Methods

Hypotheses and plans for analysis were preregistered before the start of data analysis at <https://osf.io/by4zq/>.

2.1 Research participants and study overview

A total of 183 children aged between 8 and 11 years ($M = 9.95$ years, $SD = 0.70$) were pseudo-randomly assigned to one of three groups: two training groups and a passive control group. An overview of the study design is depicted in Figure 1A.

The two training groups practiced for nine weeks on a tablet at home for a total of 27 training sessions (30–40 min per session). In each session, participants completed a task-switching training game. A high-intensity task-switching (SW) training group ($N = 70$, 35 girls; age: $M = 9.85$ years, $SD = 0.65$) completed 17% single-task blocks and 83% mixed-task blocks per training game. A high-intensity single-tasking (SI) training group ($N = 72$, 34 girls; age: $M = 9.83$ years, $SD = 0.68$) trained on 83% single-task blocks and 17% mixed-task blocks per training game. The stimuli and rules in each game were identical between the two training groups such that the groups differed only in their relative demands on task switching (see section 2.2). The passive control (PC) group ($N = 41$, 20 girls; age: $M = 10.34$ years, $SD = 0.72$) did not perform any training games.

In addition to at-home training, both training groups performed four sessions of a task-switching paradigm (described in section 2.3) in the MRI scanner or MRI simulator: before training (pre-test, session A), after approximately 3 weeks of training (session B), after approximately 6 weeks of training (session C), and again after approximately 9 weeks, after the training was completed (post-test, session D). No MRI data were collected for the MRI simulator participants, who performed the task-switching paradigm in a mock scanner that looked just like the MRI scanner. The PC group performed the same task-switching paradigm in the MRI scanner at sessions A and D, while sessions B and C only included structural scans.

All participants were screened for MRI suitability, had no history of psychological or neurological diseases, and spoke German as their primary language. All participants who provided MRI data were right-handed. Parents and children provided informed written consent. All participants were reimbursed with 10€ per hour spent at the laboratory. The training groups received an additional bonus of 40€ for the completion of all training games and MRI/MRI-simulator sessions. Additionally, children in the training groups received a toy as a reward for their performance on the training games (see details below). The study was approved by the ethics committee of the Freie Universität Berlin and conducted in line with the Declaration of Helsinki.

Behavioral analyses were based on the four (for the SW and SI group) or two (for the PC group) sessions of the experimental task-switching paradigm performed in the MRI scanner or simulator. To ensure that participants included in the analyses performed this paradigm meaningfully, we excluded data in a session-specific manner based on preregistered performance criteria. Specifically, if a child performed below 50% accuracy in the run of single blocks (run 1, see below for more details on the paradigm) in a given session of the task-switching paradigm or below 35% accuracy in either of the two runs of mixed blocks (run 2 and 3) their data of that session were excluded from analyses. Additionally, we excluded 4 participants (2 from each training group) from all analyses because they did not complete at least half of the 27 training games. Based on these criteria, behavioral analyses included 160 children at session A (SW = 60 [9 excluded based on session-specific performance], SI = 64 [6], PC = 36 [4]), 115 at session B (SW = 57 [6 excluded], SI = 58 [6]), 115 at session C (SW = 54 [7 excluded], SI = 61 [4]), and 133 at session D (SW = 47 [11 excluded], SI = 57 [7]), PC = 29 [5]).

Of the children included in behavioral analyses, we additionally excluded children from neuroimaging analyses based on in-scanner head motion. fMRI volumes with framewise displacement (Power et al. 2012) above 0.4 mm were labeled as low-quality (cf. Dosenbach et al. 2017). If any of the fMRI runs of a specific session exceeded 50% of low-quality volumes, the session was excluded for that participant. Thus, fMRI analyses included

87 children at session A (SW = 32 [3 excluded], SI = 30 [7], PC = 25 [2]), 55 at session B (SW = 33 [2 excluded], SI = 22 [6]), 55 at session C (SW = 31 [4 excluded], SI = 24 [4]), and 72 at session D (SW = 24 [4 excluded], SI = 24 [4]), PC = 24 [1]).

Note that 2 of the 4 participants who were excluded from all analyses due to having completed too few training games were included in the neuroimaging analysis for session A, on which we defined the regions of interest (ROIs). Very few participants left the study after session A, i.e., dropout was minimal: SW = 3, SI = 4, PC = 7.

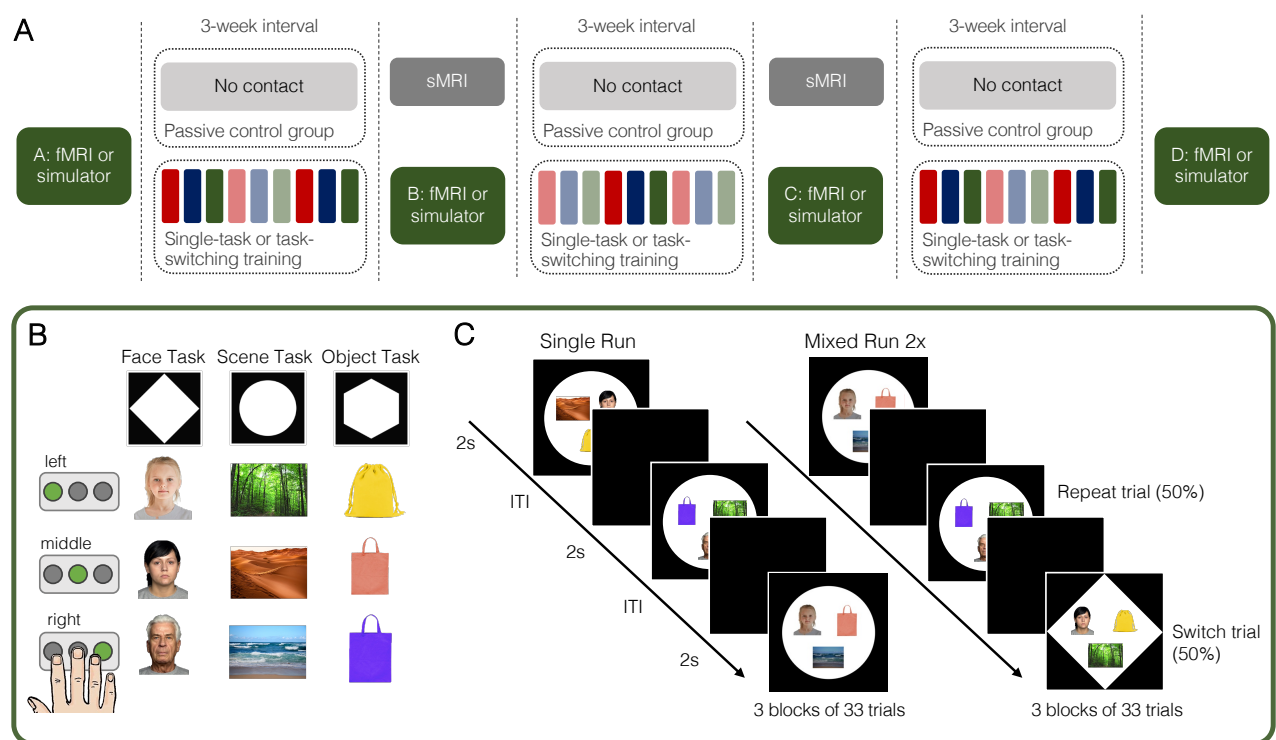


Figure 1. Outline of study design and experimental task-switching paradigm. (A) The timeline of training and assessment across the nine weeks for the three groups. fMRI or simulator indicates that the main task-switching paradigm (see B and C) was performed in the MRI scanner or MRI simulator, sMRI indicates structural scan. The colored bars indicate the training games: opaque colored bars indicate one of the three repeating games and translucent bars indicate one of the unique games, with the color indicating which of the repeating tasks matched the structure of the unique task. (B) The task-switching paradigm that all groups completed in the fMRI scanner or simulator. The shape cue indicated one of the three tasks. As indicated by three exemplar stimuli of each task, participants selected one of three buttons based on the face's age in the Face Task, the type of environment in the Scene Task and the color of the object in the Object Task. (C) Showing 3 sequential trials of the

single and mixed blocks; in the single run depicted here, participants performed the scene task on every trial. In the mixed task, the shape cues (and therefore tasks) repeated on some trials and switched on others. ITI: inter-trial interval. Image credits: Young and old adult faces were taken from the FACES collection (Ebner et al. 2010). B & C: Adapted from Schwarze et al. (2023), Figure 1.

2.2 At-home training

Children in the SW and SI groups received a tablet after their first MRI or MRI simulator session and were instructed to complete three training games per week for nine weeks (i.e., 27 games in total; Figure 1A). The training games on the tablet were programmed using Unity (Version 5.6.1; Unity Technologies). Completion of the games was self-paced; however, a new game only became available 24 hours after the completion of the previous game. Three games were repeated every other week in the same order (i.e., 5 repetitions of each of the 3 games across training). One of the repeating games was identical to the paradigm performed in the MRI-scanner/-simulator sessions. Each repetition of the three games was interspersed with three unique games that were performed only once (for a total of 12 unique games). The unique games were designed to have the same rule structure as one of the repeating games, while using different stimuli. Each game started with task instructions followed by 3 practice blocks of 15 trials each, during which feedback was provided. No feedback was given during the rest of the game.

Two thirds (i.e., 18) of the training games consisted of 486 trials, one third (i.e., 9) consisted of 485 trials, resulting in a minimally different number of single trials performed at each game (see Supplementary Table 1 for details). In each game, the SW group completed 17% single-block trials and 83% mixed-block trials, while the SI group completed 83% single-block trials and 17% mixed-block trials. For both groups, mixed blocks included 50% repeat and switch trials with unpredictable cues that appeared simultaneously with the target. For all games, each trial lasted up to 3 s and responses had to be given within this period, with stimuli presentation ending when a response was given. There was a 50 ms interval between response and presentation of the next trial. After each block, children could

decide independently when to start the next block by pressing a button. Each game lasted between 30 and 40 minutes.

To encourage the completion of the games, children received stars at the end of each game block that were converted into coins at the end of each game. Children could trade the coins for toys at any of the MRI/MRI-simulator sessions, with a greater number of coins allowing children to receive larger toys. The number of stars received after each block depended on accuracy, with bonus points being awarded for faster responses compared to the previous blocks as long as performance did not drop below 80% accuracy for the SW group and 90% accuracy for the SI group. On average, children in the SW and SI group completed 25.2 (SD = 3.52) and 25.4 (SD = 3.02) training games, respectively (no difference between groups: $t = 0.00$, $p = 1$).

2.3 Experimental task-switching paradigm

For the training groups, all four laboratory sessions included a task-switching paradigm (see Schwarze et al. 2023, for detailed paradigm description) that participants performed in the MRI scanner or simulator. Participants were familiar with the paradigm from an assessment session completed prior to the first MRI-scanner/-simulator session, and two practice blocks completed in the MRI simulator right before the actual task. The task-switching paradigm consisted of three tasks: the Face Task, the Scene Task, and the Object Task. Participants had to perform the task cued by the shape of the background, based on previously learned rules linking each shape with one of the three tasks (Figure 1B). Specifically, the Face Task required the presented face to be categorized by age (child, young adult, older adult), the Scene Task required the presented scene to be categorized by its location (forest, desert, ocean), and the Object Task required the presented object to be categorized by color (yellow, red, purple). Responses were given via button press with three fingers of the right hand. The stimuli and the task cue appeared at the same time. The arrangement of the target images varied randomly on each trial independent of the categorization rule. In each session, participants performed 3 runs of 99 trials each (Figure 1C). Every trial lasted 2 s,

followed by a fixation cross (1–6s, jittered) along with an extended fixation period (20 s) after every 33 trials. In the first run (i.e., single run), tasks were presented sequentially in a single-task manner. In runs two and three (i.e., mixed runs), the three tasks were intermixed with a switch rate of 50% and switches were unpredictable. The first trial of each run was excluded from all analyses. At each session, the experimental paradigm was performed in the MRI scanner after an initial T1-weighted scan during which participants watched a muted cartoon. The PC group followed the same protocol for their sessions A and D, while sessions B and C only included structural scans. For comparability, children who performed the task in the MRI simulator also watched a muted cartoon accompanied by scanner noise before they completed the task. Performance in this task-switching paradigm did not differ between children in the MRI-scanner and MRI-simulator group at any of the sessions.

2.4 Behavioral analyses

Trials with response times (RTs) below 200 ms and above 3000 ms, and trials with no responses, were excluded from analyses. Accuracy was calculated as the percentage of correct responses across all given responses for each condition. Median RTs were based on correct trials only. Outliers were defined as accuracy or RT values differing by more than 3.5 SD from the condition- and session-specific mean across all groups, and were removed from analyses of accuracy and RTs separately. To further examine training-related changes in the cognitive processes underlying task switching while accounting for potential speed–accuracy tradeoffs, we applied drift-diffusion modeling for the two training groups across the four laboratory sessions (Ratcliff 1978). Drift-diffusion models have previously been applied to task-switching paradigms in young adults (Schmitz and Voss 2012), children (Weeda et al. 2014; Schuch and Konrad 2017) and older adults (Ging-Jehli and Ratcliff 2020). Drift-diffusion parameters (i.e., drift rate, boundary separation, and non-decision time) were estimated for each group and session using a hierarchical drift-diffusion models (HDDM) in the HDDM toolbox (Version 0.9.8; Wiecki et al. 2013).

Specifically, the HDDM was fitted to correct and incorrect trials, with outlier probability set to 5%. Since all three parameters (boundary separation, drift rate, and non-decision time) have been associated with different cognitive processes during task switching (cf. Schmitz & Voss, 2012), the model of interest allowed all three parameters to vary between conditions and groups across sessions. Compared to models fixing one or multiple parameters, the model of interest proved a better fit to the data. Individual-specific estimates were averaged across all iterations (N = 5000) of the model and used for subsequent analyses of training-related change described below (cf. Katahira 2016).

All analyses were performed using Bayesian linear mixed models with the *brms* package in R (Bürkner 2017). Reported effects are based on 95% credible intervals (CI), meaning that we can make a statement with 95% probability (cf. Bürkner 2017; see also Morey et al. 2016).

2.4.1 Changes from pre- to post-training: Accuracy and RTs

For accuracy and RTs, we examined change in the SW and SI groups relative to the PC group from the pre-test (session A) to post-training (sessions D). Deviating from the preregistration, we included the SW and SI groups separately in these models, as opposed to combining them, to capture differences for each training group. More specifically, group (SW, SI, and PC, with PC as reference level), session (A vs. D), and condition (single vs. repeat vs. switch) were modeled as fixed effects, allowing for interactions among them. Models included random intercepts and slopes for individual participants. We started with a full model that included all interactions between fixed effects and compared this to models with fewer interaction terms, using leave-one-out cross-validation in the *loo* package (Vehtari et al. 2022). Across all analyses, the model including all interaction terms either outperformed or did not differ from the models with fewer interaction terms (see Supplementary Table 2).

2.4.2 Changes across all four sessions: HDDM parameters

To test for differences in change between the two training groups in the course of training, we compared HDDM parameters between the SW and SI groups across all four sessions. Change across more than two sessions is not necessarily linear; to describe these trajectories as precisely as possible, we thus opted to model the four sessions of the present study as a factor with four levels (sessions A, B, C, and D). In the results reported below, we compare each of the sessions B, C, and D against the pre-test session A to test whether the training completed up to that point was associated with improved performance relative to before the start of training. Group (SW vs. SI), session (B vs. A, C vs. A, D vs. A), and condition (single vs. repeat vs. switch) were modeled as fixed effects allowing for interactions among them with random intercepts and slopes for individual participants. Across all analyses, the models including all interaction terms outperformed or did not differ from the models with fewer interaction terms (see Supplementary Table 2).

We opted to analyze HDDM parameters using linear mixed models for consistency with all remaining analyses. An alternative approach for testing differences in HDDM parameters is the pairwise comparison of the posterior distributions of a parameter, for instance, testing whether the posterior distributions of a parameter differ between the SW and SI group at a specific session. These analogous, preregistered analyses revealed the same pattern of results as the mixed models reported below (see Supplementary Table 3).

2.4 fMRI data acquisition and preprocessing

As reported by Schwarze et al. (2023), structural and functional MR images were collected on a 3-Tesla Siemens Tim Trio MRI scanner. Functional runs consisted of 230 whole-brain echo-planar images of 36 interleaved slices (TR = 2000 ms; TE = 30 ms; 3 mm isotropic voxels). The imaging protocol included functional imaging during the performance of the task-switching paradigm on all four sessions for the SW and SI group and on the first and last MRI session for the PC group. Structural MRI scans were acquired for all groups at all

four sessions (220 slices; 1 mm isotropic voxels; TR = 4500 ms; TE = 2.35 ms; FoV = 160 × 198 × 220).

Preprocessing was performed using fMRIPrep (Version 20.2.0; Esteban et al. 2019). For a detailed description see the fMRIPrep documentation (<https://fmriprep.org/en/stable/>). Briefly, functional images were co-registered to individual anatomical templates using FreeSurfer (Greve and Fischl 2009). The anatomical template was created from anatomical scans across all sessions, removing scans that were of poor quality based on the MRIQC classifier (Version 0.15.2; Esteban et al. 2017) and additional visual inspection. Images were slice-time corrected (using AFNI; Cox and Hyde 1997), realigned (using FSL 5.0.9; Jenkinson et al. 2002), resampled into MNI152NLin6Asym standard space with an isotropic voxel size of 2 mm, and spatially smoothed with an 8mm FWHM isotropic Gaussian kernel using SPM12 (Functional Imaging Laboratory, University College London [UCL], UK).

2.5 fMRI data analysis

2.5.1 General linear models (GLM)

GLM analyses were performed using SPM12 software (Functional Imaging Laboratory, UCL, UK). For each participant, we estimated an event-related GLM for each session. Each stimulus presentation was coded as an event with zero duration, and convolved with a canonical hemodynamic response function (HRF). Separate regressors were included for correct single, correct repeat, and correct switch trials. Incorrect trials, trials with no responses, and the first trial of each run were modeled in a nuisance regressor. Data were high-pass filtered at 128 s. To minimize head motion artifacts, we included the amount of framewise displacement per volume in mm (Power et al., 2012), realignment parameters (three translation and three rotation parameters), and the first six anatomical CompCor components (as provided by fMRIPrep; Behzadi et al. 2007) as regressors of no interest. The first five volumes of each run were discarded to allow for stabilization of the magnetic field. Temporal autocorrelations were estimated using first-order autoregression. To identify

regions that showed activation associated with mixing demand, we compared activation on repeat trials in mixed blocks to single-block trials (repeat > single) across all three groups at session A (N = 89; voxel-level $p < .001$, FDR-corrected at cluster level). To identify regions modulated by switch demand, we compared activation on switch to repeat trials in the mixed blocks (switch > repeat) across all three groups at session A (N = 89; voxel-level $p < .001$, FDR-corrected at cluster level).

2.5.2 ROI definition and analyses

ROIs were defined on the repeat > single contrast and switch > repeat contrast across all children at session A described above. To ensure anatomical specificity, we anatomically restricted activation-based ROIs in the dlPFC, SPL, and precuneus using the middle frontal gyrus, SPL, and precuneus regions of the Harvard-Oxford atlas, respectively (thresholded at 30%; Makris et al. 2006). The IFJ was restricted based on coordinates from a meta-analysis of task switching (Derrfuss et al. 2005), as no anatomical mask is available for this functionally defined region associated with task-switching (cf. Richter and Yeung 2014). We extracted activation parameters for these ROIs using Marsbar (Brett et al. 2002).

We performed Bayesian linear mixed models to investigate whether activation in the ROIs changed with training and differed between training groups. First, we explored trajectories of training-related change in activation across all four sessions in the two training groups. As for the analyses of HDDM parameters described above, models included fixed effects of group (SW vs. SI), session – modeled as a factor with four levels (A, B, C, D) –, and condition. Condition included repeat vs. single for models of activation in ROIs defined by the repeat > single contrast, and switch vs. repeat for activation in ROIs defined by the switch > repeat contrast. Random intercepts of participant and random slopes of session were also included in all models.

In a second step, to test whether changes in task-related activation were training-related, we compared the SW and SI groups to the PC group on sessions A and D, for which data from all groups was available. Models included fixed effects of group (SW vs. PC, SI vs.

PC), session (A vs. D), and condition (repeat vs. single; switch vs. repeat) and their interactions, as well as random intercepts of individuals and random slopes of session. Results of these analyses are included in the main results for ROIs that showed changes in the two training groups across all four sessions; detailed model outputs for all ROIs are reported in Supplementary Tables 9 and 11.

To test for training-related changes in the adult task-switching network, we additionally defined ROIs from 53 adults (20–30 years) who performed the same task-switching paradigm at a single timepoint (see Schwarze et al. 2023 for details). Results for these preregistered ROI analyses are reported in Supplementary Tables 4–6, and were generally consistent with the results reported below.

2.5.3 Whole-brain longitudinal analyses

Since the ROI-based analysis is biased towards the activation patterns observed in session A, we additionally performed longitudinal whole-brain analyses to test for training-related changes outside the ROIs, as well as how these differed between groups. We constructed mixed ANOVAS in SPM with group as a between-participant factor and session as a within-participant factor. Specifically, we tested for differences between the SW and SI groups and the PC group comparing sessions A and D, and for differences between the SW and SI groups across all four sessions. The input contrast images included the repeat > single contrast to investigate changes in modulation of activation with mixing demand, and the switch > repeat contrast for changes in modulation of activation with switch demand. There were no significant clusters showing changes in activation with training at the predefined threshold ($p < .001$, uncorrected), neither when comparing sessions A and D nor when testing for any effects across all sessions.

2.5.4 Psychophysiological interactions

To examine training effects in task-related functional connectivity, we conducted gPPI (generalized psychophysiological interaction) analyses (McLaren et al. 2012) using the

CONN toolbox (Version 20b; Whitfield-Gabrieli and Nieto-Castanon 2012). gPPI can be used to model how connectivity strength differs between conditions, thus making it possible to investigate how brain networks are flexibly adapting to task demands. gPPI parameters were estimated separately for each condition, that is, correct single, correct repeat, and correct switch trials (McLaren et al. 2012). The main effect of the three conditions and the nuisance regressors from the activation GLM were regressed out of the fMRI timeseries before analysis. We calculated ROI-to-ROI gPPI for connections among ROIs associated with mixing demand, identified by the repeat > single contrast (i.e., bilateral IFJ, bilateral SPL, and left dlPFC). In a separate but identical model, we calculated ROI-to-ROI gPPI for connections among the ROIs associated with switch demands, identified by the switch > repeat contrast (i.e., left IFJ, bilateral SPL, bilateral precuneus).

The gPPI models provided two connectivity parameters for each connection between any two ROIs representing connectivity estimates in both directions. Therefore, we first tested whether the direction had an effect on the connectivity parameter. We modeled estimated connectivity for each connection with a linear mixed model including the direction, condition, session, and training group as fixed effects, allowing for all interactions and including random intercepts of individuals and random slopes of session. We compared this model to one without any interactions involving seed region. As model comparisons indicated better fit for models without interaction effects of seed region, we averaged parameters across directions for each connection to be used in the subsequent analysis.

Individuals' condition-specific gPPI parameters (averaged across directions) for each connection and session were analyzed using Bayesian linear mixed models to examine differences in the changes of these parameters between the SW and SI groups. Specifically, mirroring the models of activation above, we tested whether connectivity values among the ROIs associated with mixing demands (defined on the basis of the repeat > single contrast) changed across sessions (i.e., session B, C, and D compared to A as the reference level). In addition to the fixed effect of session, models included fixed effects for group (SW vs. SI) and condition (repeat vs. single) and random intercepts of participant and connection, as

well as random slopes for session. For the connectivity parameters among the ROIs associated with switch demand, we tested the same model, except that the condition levels consisted of switch vs. repeat.

Additionally, to characterize whether key task-switching regions changed connectivity to brain regions outside of the ROIs defined by brain activation, we analyzed seed-to-voxel PPIs. Here, we used a seed in the left IFJ and in the left SPL, based on their prominent roles in task switching (e.g., Kim et al. 2012; Richter and Yeung 2014) and our analyses of age differences in task switching between children and adults (Schwarze et al. 2023). Results of these seed-to-voxel analyses and further preregistered connectivity analyses are reported in Supplementary Results 1–3.

3. Results

3.1 Training-related improvements in accuracy and RTs in the SW group

To examine changes in task-switching performance with training, we first examined changes in accuracy and RT between sessions A to D (for analyses of accuracy and RTs across all sessions, see Supplementary Table 7). Here, we were primarily interested in differences between the training groups and the control group. To this end, we predicted accuracy and RT by fixed effects of group (SW, SI, and PC), condition (single, repeat, switch), and session (A vs. D). Across all models, the models including all interactions fit best or did not differ from the best fitting model (see Supplementary Table 2), suggesting that training-related changes in performance differed between groups and conditions. To further characterize how the groups changed with training, we used the PC group as the reference to evaluate change in each training group relative to the control group. There were no differences in accuracy or RTs among the three groups at session A prior to training.

For both accuracy (Figure 2A) and RTs (Figure 2B), we observed mixing costs (i.e., lower accuracy and longer RTs on repeat than single trials) and switch costs (i.e., lower accuracy and longer RTs on switch than repeat trials) across both sessions and all groups (see Table 1 for model estimates).

RT switch costs decreased from session A to D across all groups due to faster RTs on switch trials. Compared to the PC group, the SW group showed increasing accuracy and decreasing RTs from session A to D across conditions. Compared to the PC group, the SI group maintained higher single-task accuracy across sessions A and D, but did not differ in the repeat or switch conditions (see Supplementary Figure 1 for condition-specific changes). Taken together, the SW group – but not the SI group – showed a greater training-related increase in accuracy and decrease in RTs relative to the PC group. The lack of interactions between session and condition on accuracy change suggests that improvements were similar across all conditions.

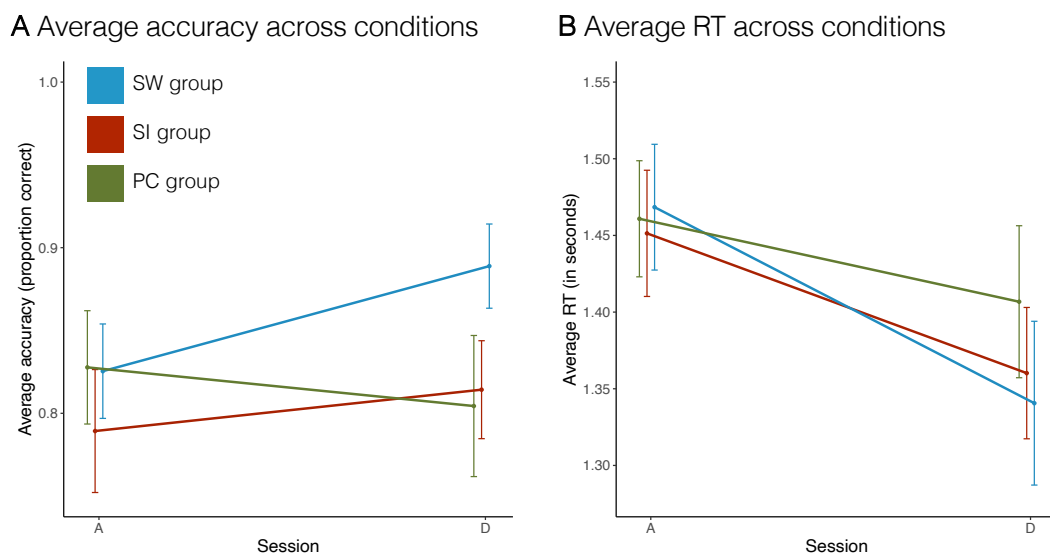


Figure 2: Training-related changes in overall performance. Accuracy (A) and RTs (B) averaged across conditions. Overall performance improved from session A to D in accuracy and RTs in the task-switching (SW) training group (blue) relative to the passive control (PC) group (green). The single-task (SI) training group is shown in red. Error bars denote 95%-confidence intervals.

Table 1: Model outputs for accuracy and RT. Models included condition (single, repeat, switch; with repeat as the reference level), session (A, D; with A as the reference level), and group (SW, SI, PC; with PC as the reference level) as fixed effects, and random intercepts for individuals and random slopes for sessions. Note that because the PC group was defined as a reference level, the model output only includes the comparisons of the SW group to the PC group and of the SI group to the PC group. Bold values indicate estimates whose 95%-CI did not include zero. Est.: Estimate.

Effect	Accuracy			RT		
	Est.	CI		Est.	CI	
Intercept	0.81	0.77	0.86	1.47	1.41	1.52
condition: single vs. repeat	0.13	0.1	0.16	-0.28	-0.32	-0.23
condition: switch vs. repeat	-0.07	-0.11	-0.04	0.26	0.22	0.3
session: D vs. A	-0.02	-0.07	0.03	-0.02	-0.09	0.04
group: SW vs. PC	0.01	-0.04	0.07	0	-0.07	0.07
group: SI vs. PC	-0.02	-0.08	0.03	-0.01	-0.08	0.06
condition (single vs. repeat) x session (D vs. A)	-0.05	-0.1	0.01	0.01	-0.05	0.07
condition (switch vs. repeat) x session (D vs. A)	0.03	-0.02	0.08	-0.08	-0.14	-0.02
condition (single vs. repeat) x group (SW vs. PC)	-0.04	-0.08	0	0.02	-0.03	0.07
condition (switch vs. repeat) x group (SW vs. PC)	-0.02	-0.06	0.02	0.01	-0.04	0.06
condition (single vs. repeat) x group (SI vs. PC)	-0.03	-0.07	0.01	0.03	-0.03	0.08
condition (switch vs. repeat) x group (SI vs. PC)	-0.01	-0.05	0.03	-0.01	-0.06	0.05
session (D vs. A) x group (SW vs. PC)	0.08	0.02	0.14	-0.09	-0.18	-0.01
session (D vs. A) x group (SI vs. PC)	0.03	-0.03	0.09	-0.07	-0.15	0.01
condition (single vs. repeat) x group (SW vs. PC) x session (D vs. A)	0.01	-0.05	0.08	0.06	-0.02	0.14
condition (switch vs. repeat) x group (SW vs. PC) x session (D vs. A)	0.02	-0.04	0.08	-0.01	-0.08	0.07
condition (single vs. repeat) x group (SI vs. PC) x session (D vs. A)	0.07	0.01	0.13	0.05	-0.02	0.13
condition (switch vs. repeat) x group (SI vs. PC) x session (D vs. A)	-0.01	-0.07	0.05	-0.01	-0.09	0.07

3.2 Hierarchical drift-diffusion models across all four sessions

For a more detailed understanding of the training-related changes in the cognitive processes contributing to task switching, we analyzed HDDM parameters (Wiecki et al. 2013) across all four sessions in the SW and SI groups. There were no differences between the SW and SI groups in any of the HDDM parameters at session A. We predicted different HDDM parameters (drift rate, boundary separation, and non-decision time) by training group (SW vs. SI), condition (single, repeat, and switch), and session (A, B, C, and D). In all analyses, the models including all interactions fit best or did not differ from the best fitting model (see Supplementary Table 2), suggesting that the SW and SI groups differed in changes in HDDM parameters across conditions. To characterize group differences in change, session A was set as the reference level, and the other three sessions (i.e., sessions B, C, D) were compared to this reference. For clarity, we focus on effects showing a probability of 95% below (see Supplementary Table 8 for complete model outputs).

3.2.1 Condition effects across sessions.

Across sessions and groups, drift rates were lower on switch than on repeat trials (switch vs. repeat: est. = -0.28 ; 95%-CI $-0.39, -0.18$) and lower on repeat trials than on single trials (single vs. repeat: est. = 0.69 ; 95%-CI $0.58, 0.81$), indicating faster evidence accumulation for the correct response on trials with lower mixing and switch demands (Figure 3A).

Boundary separation parameters were greater for single compared to repeat trials (single vs. repeat: est. = 0.10 ; 95%-CI $0.01, 0.18$), and for repeat compared to switch trials (switch vs. repeat: est. = -0.17 ; 95%-CI $-0.25, -0.09$), suggesting that participants were more cautious on single-task blocks than on repeat trials within mixed blocks, and more cautious on repeat trials than on switch trials (Figure 3B). Non-decision time was shorter for single compared to repeat trials (single vs. repeat: est. = -0.1 ; 95%-CI $-0.13, -0.06$), and for repeat than for switch trials (switch vs. repeat: est. = 0.22 ; 95%-CI $0.17, 0.27$), showing that preparation time was shorter on trials with lower mixing and switch demands (Figure 3C). Thus, with increasing mixing (repeat vs. single) and switch (switch vs. repeat) demands, children were

slower at accumulating evidence for the correct response, followed a less cautious response strategy, and took longer to prepare the response.

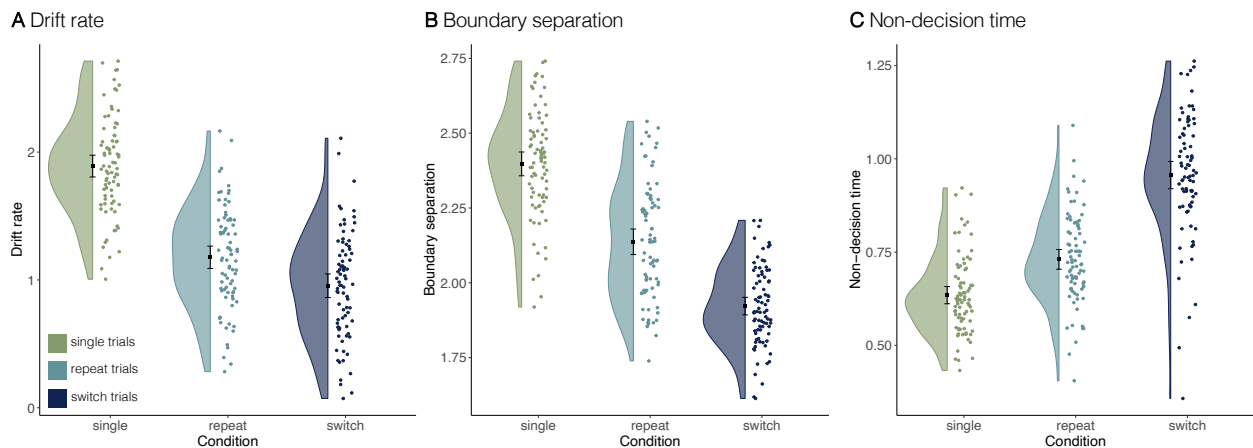


Figure 3: Condition differences in hierarchical drift-diffusion model parameters. Showing (A) drift rate, (B) boundary separation, and (C) non-decision time for single trials (light green), repeat trials (light blue), and switch trials (purple) across sessions and groups. Scatters show individuals' parameter values averaged across sessions. Error bars denote 95%-confidence intervals. Note that parameter values were averaged across sessions within individuals for visualization purposes only; no analyses were calculated on these averaged data.

3.2.2 Training-related increases in drift rates in the SW group

Across training groups and task conditions, drift rates increased from session A to B (est. = 0.27; 95%-CI 0.13, 0.41) and remained higher on session C compared to A (est. = 0.28; 95%-CI 0.13, 0.43; Figure 4A). Of note, these overall effects of training were further qualified by interactions with group and condition.

First, across groups, increases early in training were larger for single than for repeat trials (Session [B vs. A] x condition [single vs. repeat]: est. = 0.29; 95%-CI 0.13, 0.44) whereas the maintenance of increased drift rates later in training was more pronounced for switch than repeat trials (session [D vs. A] x condition [switch vs. repeat]: est. = 0.15; 95%-CI 0.01, 0.29). Second, the SW group benefited more from training in the first three weeks of training: drift rate increases from A to B were greater in the SW group compared to the SI group (session [B vs. A] x group [SW vs. SI]: est. = 0.24; 95%-CI 0.04, 0.45). These initial

differences in drift rate between the SW and SI groups were especially pronounced for repeat and switch trials relative to single trials (session [B vs. A] x condition [single vs. repeat] x group [SW vs. SI]: est. = -0.30 ; 95%-CI $-0.52, -0.08$; no interaction for difference between repeat and switch trials). Third, a further benefit of SW compared to SI training became evident at session D: compared to the SI group, the SW group maintained increased drift rates at session D compared to A across conditions (session [D vs. A] x group [SW vs. SI]: est. = 0.34 ; 95%-CI $0.1, 0.58$).

Taken together, both training groups showed an increase in evidence accumulation after the first three weeks of training, with the SW group showing greater increases than the SI group. Of note, the SW group – but not the SI group – maintained these improvements at the end of training.

3.2.3 Greater boundary separation in the SW group

Changes in boundary separation were qualified by interactions with condition and group, suggesting differences in training-related changes between groups and conditions (Figure 4B). First, the SW group showed greater increases in boundary separation than the SI group from session A to B across all conditions (session [B vs. A] x group [SW vs. SI]: est. = 0.20 ; 95%-CI $0.06, 0.32$). The SW group maintained these condition-independent increases at session D to a greater extent than the SI group (session [D vs. A] x group [SW vs. SI] = est. = 0.22 ; 95%-CI $0.07, 0.36$). Second, relative to session A, boundary separation parameters on single trials were higher in session B (session [B vs. A] x condition [single vs. repeat]: est. = 0.53 ; 95%-CI $0.42, 0.65$) and session C (session [C vs. A] x condition [single vs. repeat]: est. = 0.26 ; 95%-CI $0.14, 0.37$). This change was further qualified by an interaction with group (session [B vs. A] x condition [single vs. repeat] x group [SW vs. SI]: est. = -0.23 ; 95%-CI $-0.40, -0.06$), indicating that the difference in boundary-separation increase between single and repeat trials was particularly pronounced in the SI group.

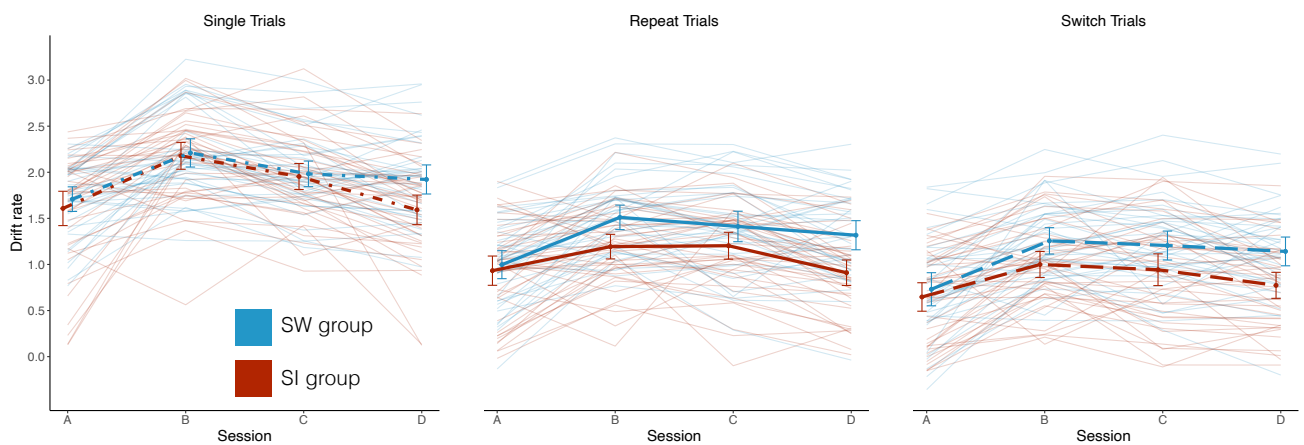
Thus, response caution increased within the first three weeks of training, with similar increases across conditions for the SW group and specific increases for single trials in the SI

group. At the end of training, the SW group showed greater maintenance of the increased boundary separation than the SI group.

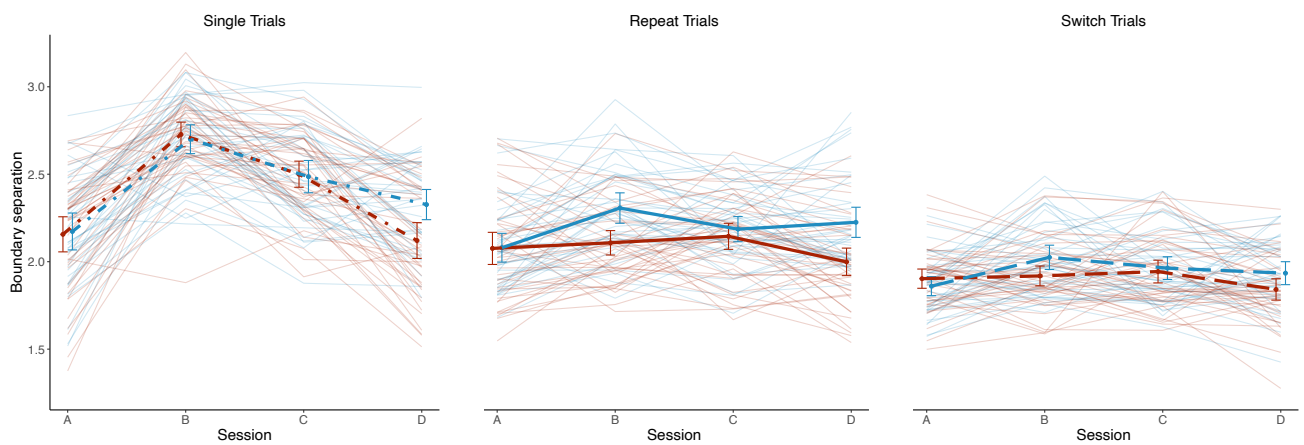
3.2.4 Decrease of non-decision time across the SW and SI groups

Across both training groups, non-decision time decreased with training, such that non-decision times at sessions B, C, and D were lower than at session A (B vs. A: est. = -0.05 ; 95%-CI $-0.08, -0.02$; C vs. A: est. = -0.07 ; 95%-CI $-0.11, -0.04$; D vs A: est. = -0.08 ; 95%-CI $-0.11, -0.05$; Figure 4C). Decreases were particularly pronounced for single trials relative to repeat trials at session B (session [B vs. A] x condition [single vs. repeat]: est. = -0.06 ; 95%-CI $-0.1, -0.01$). Thus, across training groups, non-decision time decreased, suggesting reduced preparation time with training.

A Drift rate



B Boundary separation



C Non-decision time

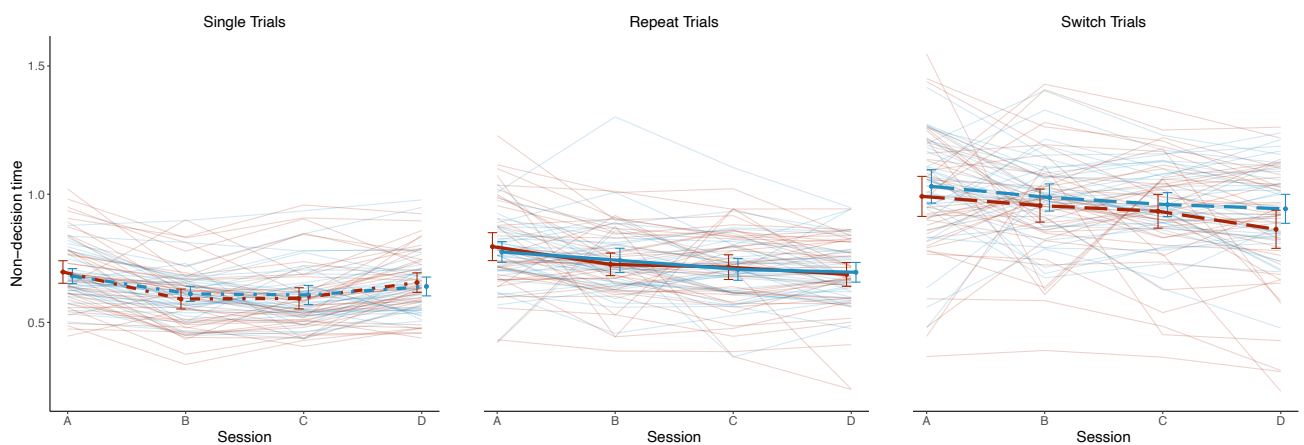


Figure 4: Training-related changes in hierarchical drift-diffusion model parameters. Showing (A) drift rate, (B) boundary separation, and (C) non-decision time for single trials (left panels, dot-dashed line), repeat trials (central panels, solid line), and switch trials (right panels, dashed line). The SW group is depicted in blue, and the SI group in red. Thin lines show individual trajectories colored according to training group. Error bars denote 95%-confidence intervals.

3.3 Changes in activation and connectivity associated with mixing demands

Whole-brain activation across all children at session A revealed stronger activation for repeat > single trials in multiple frontal and parietal regions, including the bilateral IFJ, bilateral SPL, and left dlPFC (Figure 5A). Accordingly, we investigated training-related change in activation and ROI-to-ROI connectivity in the following ROIs: left and right IFJ, left and right SPL, and left dlPFC. First, in line with the behavioral analyses above, we tested whether activation and connectivity changed at any of the sessions during or at the end of training (i.e., sessions B, C, D) relative to the pre-test session A. Second, to test whether these changes were indeed related to training, we compared changes in the training groups to the PC group, focusing on sessions A and D where data from all groups were available.

3.3.1 Reduced frontoparietal activation with training in the SW group

Within each ROI, we analyzed activation parameters for the effects of session (B, C, and D compared to A as the reference level) and interactions with group (i.e., differences between SW and SI groups). Below, we report effects involving session and interactions of session with group (see Supplementary Tables 9 and 10 for an overview of all effects).

In the right SPL (Figure 5B), activation on repeat trials decreased such that the difference between single and repeat trials decreased with training across both groups. The decrease in activation for repeat trials became evident at session C (est. = -1.06 ; 96%-CI: $-2.03, -0.1$) and remained evident at session D (est. = -1.15 ; 95%-CI: $-2.09, -0.19$). While a descriptively similar pattern was evident in the left SPL, the data did not support the effect with 95% probability. Comparison to the PC group for sessions A and D caution the interpretation of these changes as related to the training program: the decreases in repeat activation from session A to D became evident across all three groups (est. = -1.19 ; 95%-CI: $-2.15, -0.22$) and neither the SW nor the SI group differed reliably from the PC group at session D (all 95%-CI include zero).

Compared to session A, activation in the left dIPFC (Figure 5B) decreased across both single and repeat conditions for the SW group but not the SI group (group [SW vs. SI] x session [D vs. A]: est. = -0.87 ; 95%-CI: $-1.79, -0.01$). Descriptively, the left IFJ showed a similar effect as the dIPFC, but we did not find evidence for the effect with the predefined criterion of 95% probability. Comparison to the PC group for sessions A and D provided support that this change was specific to the SW group: compared to the PC group, the SW group showed lower activation in the left dIPFC and left IFJ across conditions at session D compared to A (left dIPFC: est. = -1.48 ; 95%-CI: $-2.47, -0.5$; left IFJ: est. = -0.84 ; 95%-CI: $-1.6, -0.07$).

To summarize, the dIPFC and SPL showed decreases in activation across sessions. The effects in the dIPFC were observed across the single and repeat conditions and were only present in the SW group. In the SPL, the differences between single and repeat trials decreased in both training groups as well as in the PC group and were therefore unlikely to be related to the intensive training manipulation in the study.

3.3.2 Decreased task-based connectivity in the SI training group

To test whether task-based connectivity among the ROIs (i.e., left IFJ, left SPL, left dIPFC, right IFJ, right SPL) showed training-related changes, we analyzed connection-specific PPI parameters for the effects of session (B, C, and D compared to A) and interactions with group (i.e., differences between SW and SI groups).

Across sessions, connectivity was greater for repeat than for single trials (repeat vs. single: est. = 1.91 ; 95%-CI: $1.46, 2.38$), indicating that regions interacted more closely in response to mixing demands. As shown in Figure 5C, this condition difference was influenced by training. Specifically, connectivity for the repeat condition decreased with training (condition [repeat vs. single] x session [B vs. A]: est. = -0.75 ; 95%-CI: $-1.46, -0.05$; C vs. A: est. = -2.17 ; 95%-CI: $-2.85, -1.49$; D vs. A: est. = -1.57 ; 95%-CI: $-2.25, -0.88$), with especially pronounced decreases in the SI group towards the end of training (condition [repeat vs. single] x group [SW vs. SI] x session [C vs. A]: est. = 2.14 ; 95%-CI: $1.23, 3.05$;

[D vs. A]: est. = 1.41; 95%-CI: 0.47, 2.36). Comparison to the PC group for sessions A and D indicated that this late change was specific to the SI group: compared to the PC group, the SI group showed lower connectivity on repeat trials at session D compared to A (condition [repeat vs. single] x group [SI vs. PC] x session [D vs. A]: est. = -1.58; 95%-CI: -2.60, -0.58).

In summary, connectivity among frontoparietal ROIs during task repeats decreased with training across both groups, suggesting less upregulation of connectivity in the mixed- vs. single-task context over time. Towards the end of training (i.e., sessions C and D) this decrease was particularly pronounced for the SI group relative to the SW group.

Training-related changes in activation and connectivity associated with mixing costs

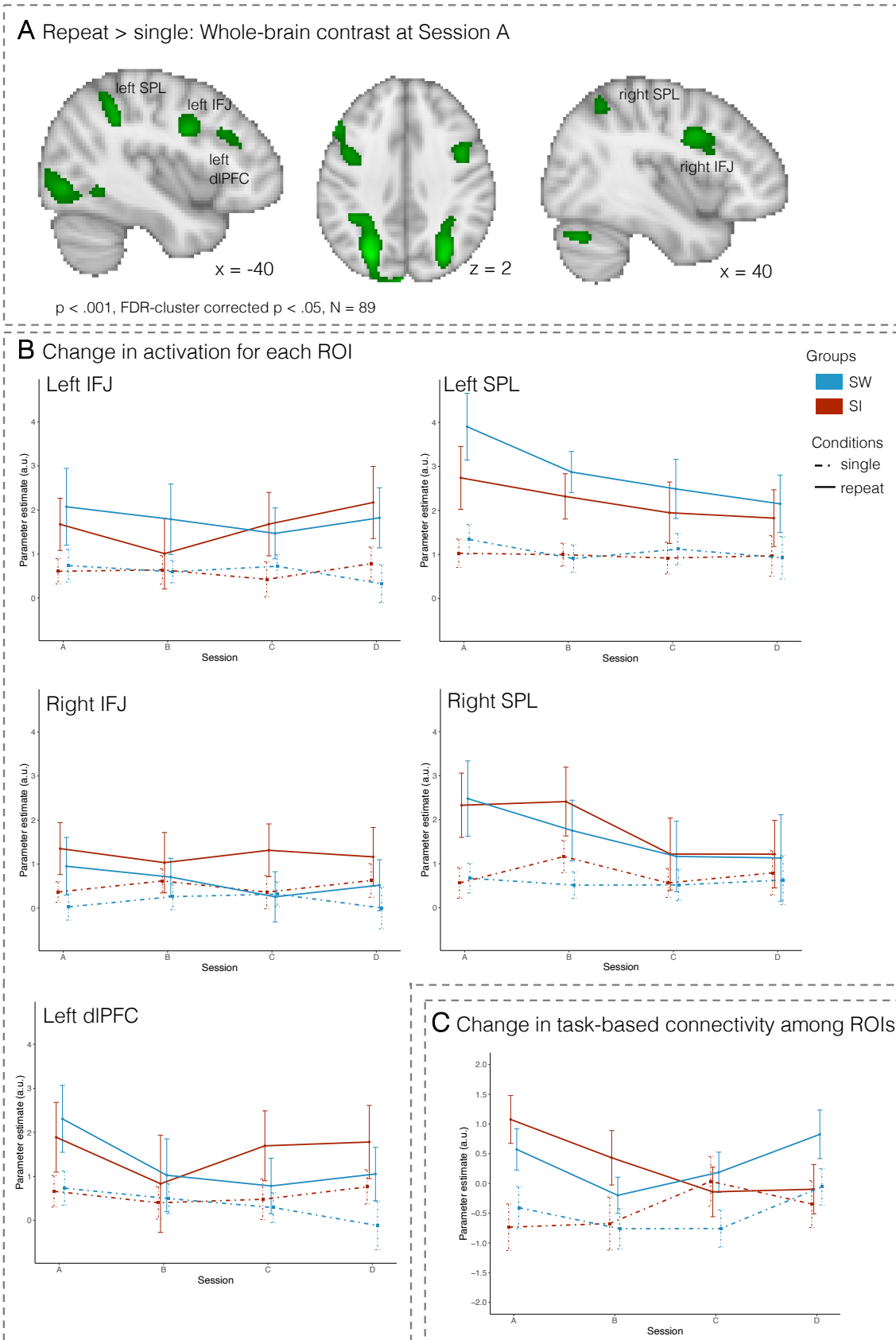


Figure 5: Training-related changes in activation and connectivity associated with mixing costs. (A)

Brain regions showing greater activation on repeat than on single trials at session A across all

children ($N = 89$; $p < .001$, FDR-cluster corrected $p < .05$). (B) Change in activation for each ROI. (C) Change in connectivity (i.e., PPI parameters across all connections) among these ROIs. The SW group is shown in blue and the SI group is shown in red. Error bars denote 95%-confidence intervals.

3.4 Training-related changes in activation and connectivity associated with switch demand

Whole-brain activation across all children at session A indicated increased activation for switch than for repeat trials in the left IFJ, bilateral SPL, and bilateral precuneus.

Accordingly, we investigated training-related changes in activation and ROI-to-ROI connectivity in the following ROIs: left IFJ, left and right SPL, and left and right precuneus (Figure 6A). First, we tested whether activation and connectivity had changed at any of the sessions during or at the end of training (i.e., sessions B, C, D) relative to the pre-test session A. Second, to test whether these changes were indeed related to training, we compared changes in the training groups to the PC group, focusing on sessions A and D, where data from all groups were available.

3.4.1 Transient changes in switch-related brain activation with training

We analyzed activation parameters for repeat and switch trials for the effects of session (B, C, D compared to A) and interactions with group (SW vs. SI group) in each ROI. Below, we report effects that involved session and interactions of session with group (see Supplementary Tables 11 and 12 for an overview of all effects).

Across both groups and conditions (Figure 6B), activation in the left IFJ decreased from session A to B (effect of session B vs. A: est. = -1.03 ; 95%-CI: $-1.89, -0.20$). In the right precuneus, activation increased from session A to B (effect of session B vs. A: est. = 0.95 ; 95%-CI: $0.21, 1.69$). These changes returned to baseline towards the end of training as indicated by no differences of sessions C and D compared to A (all 95%-CI include zero). Accordingly, the training groups did not show any differences in activation compared to the PC group at session D in the IFJ and in the precuneus (all 95%-CI include zero). The right SPL showed an overall decrease in activation across switch and repeat trials from session A

to D in both groups (est. = -0.61 ; 95%-CI: $-1.18, -0.06$). The comparisons to the PC group did not show clear evidence that this change in the training groups differed from the PC group: the interactions of group and session did not become evident (95%-CI included zero).

To summarize, across groups, the IFJ and the precuneus showed early changes in activation between sessions A and B after three weeks of training, with increases in the right precuneus and decreases in the left IFJ across conditions. The right SPL showed slower decreases in overall activation that only became evident at the end of training at session D; however, a lack of difference to the PC group at session D caution against the interpretation of this decrease as related to the intensive training manipulation in the study.

3.4.2 Inconclusive results regarding changes in task-based connectivity with training

We next analyzed connection-specific PPI parameters among left IFJ, left SPL, left precuneus, right SPL, and right precuneus for the effects of session (B, C, D compared to A) and interactions with group (SW vs. SI group).

As shown in Figure 6C, connectivity for switch trials decreased from session A to B in the SI group, while the SW group showed an increase of connectivity for switch trials and a decrease for repeat trials (session [B vs. A] x group [SW vs. SI] x condition [switch vs. repeat]: est. = 1.77 ; 95%-CI: $0.76, 2.77$). However, we did not observe clear differences in connectivity between switch and repeat trials across the two groups independent of training. Thus, the observed differences between groups in training-related changes cannot be meaningfully interpreted as changes in adaptively adjusted connectivity among regions based on switch demands. Compared to the PC group, the SW group also showed a different pattern of change from session A to D between conditions (session [D vs. A] x group [SW vs. PC] x condition [switch vs. repeat]: est. = 1.41 ; 95%-CI: $0.33, 2.49$), but again the lack of condition effects across groups and sessions limits the interpretability of these findings. The SI group showed no compared to the PC group when comparing sessions A and D.

Training-related changes in activation and connectivity associated with switch costs

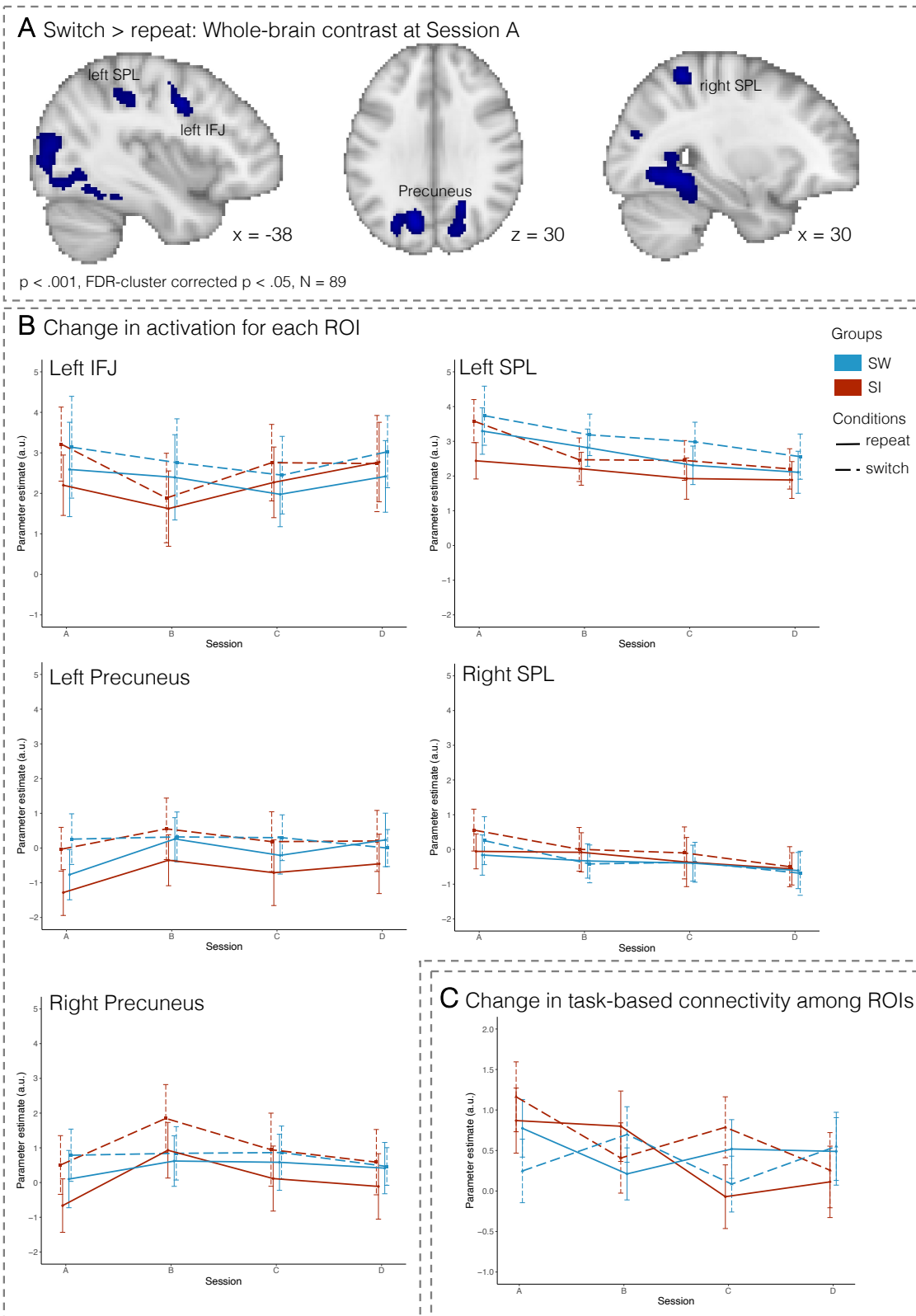


Figure 6: Training-related changes in activation and connectivity associated with switch costs. (A)

Brain regions showing greater activation on switch than on repeat trials at session A across all

children ($N = 89$; $p < .001$, FDR-cluster corrected $p < .05$). (B) Change in activation for each ROI. (C)

Change in connectivity (i.e., PPI parameters across all connections) among these ROIs. The SW group is shown in blue and the SI group in red. Error bars denote 95%-confidence intervals.

4. Discussion

In the present study we investigated behavioral and neuroimaging data of 8–11-year-olds to elucidate behavioral and neural changes as a function of different doses of task-switching training. We analyzed task performance in terms of drift-diffusion parameters, fMRI activation, and task-based functional connectivity before and after training, as well as twice during the nine-week training phase, to shed new light on the behavioral and neural changes that take place during task-switching training.

Comparing the pre- and post-training sessions, accuracy increased and RTs decreased with training across conditions in the group with the higher dose of task-switching training. These findings corroborate and extend previous findings demonstrating that task-switching performance in children can be improved with intensive training (Karbach and Kray 2009; Kray, Karbach, Haenig, et al. 2012; Zinke et al. 2012; Dörrenbächer et al. 2014; Karbach et al. 2017). We leveraged drift-diffusion modeling to provide a more detailed picture of how the different training schedules influenced cognitive processes during task switching. We observed rapid changes after three weeks (i.e., from session A to B) across all parameters in both training groups: the boundary-separation and drift-rate parameters increased, while non-decision time decreased. Children in the high-intensity task-switching group showed more pronounced increases in drift rate and boundary separation that were maintained for the duration of the training. The sustained increase in boundary separation in the high-intensity task-switching group is somewhat surprising, given that previous training studies have shown reductions in boundary separation (Reinhartz et al. 2023; Schmiedek et al. 2023). In our view, the combination of increasing drift rates with widening decision boundaries reveals that children were approaching the task in a more cautious manner with increasing practice. Additionally, both groups showed decreases in the non-decision time parameter with training. Thus, even small doses of task switching during training, in combination with extensively practicing the task rules separately, improved preparatory processes such as reconfiguration of the task set (Schmitz and Voss 2012) and more

efficient response execution in light of potentially conflicting or distracting information (cf. Resulaj et al. 2009; Schroeder and Verrel 2014).

On the neural level, we observed different patterns of changes in activation associated with mixing demands (i.e., repeat vs. single trials) and switch demands (i.e., switch vs. repeat trials). Activations associated with both single and repeat trials decreased in lateral prefrontal ROIs (i.e., left dlPFC and to a smaller extent, left IFJ) in the high-intensity task-switching group, but not in the high-intensity single-tasking group. Additionally, task-related activations on repeat trials decreased in the right SPL in both training groups, but also the PC group, resulting in a smaller difference between repeat and single conditions. In parallel, connectivity among frontal and parietal regions decreased with training for repeat trials, with more pronounced changes in the high-intensity single-tasking group than in the high-intensity task-switching group. Brain regions specifically associated with greater switch demands prior to training showed a rapid training-related change in activation in session B, but returned to baseline by the end of training.

Taken together, more intensive task-switching training led to faster accumulation of information for the correct response while simultaneously promoting a more cautious response strategy. The accompanying neural analyses indicate that intensive task-switching training was associated with decreases in task-related activation in the prefrontal cortex (PFC) as well as in connectivity among PFC and parietal regions, presumably indicating more efficient task processing with training.

4.1 Training improves efficiency of processing in frontoparietal regions

Both training groups showed increases in drift rates with training, suggesting faster, more efficient evidence accumulation for the correct response (Radcliff, 1978). Higher drift-rate parameters have been associated with faster response selection during task switching (Schmitz and Voss 2012), potentially due to less interference from the previous stimulus-response (S-R) mapping (Weeda et al. 2014). Previous studies on the flexibility of task-set updating in children have suggested that such an interference from the previous S-R

mapping contributes to the costs of switching, especially in children (Hommel et al. 2011). Thus, with training, children might become better at resolving interference or selecting the correct S-R mapping more quickly. Furthermore, increased drift rates have been associated with more efficient extraction of high-quality information from the task (Ratcliff et al. 2012) along with increased efficiency of rule processing (cf. Schmitz and Voss 2012). Gains in evidence accumulation during perceptual decision making have been found to be positively associated with working memory gains on a completely different set of tasks (Schmiedek et al. 2023), pointing to a connection between drift rate and mechanisms supporting working memory. Increased efficiency with multitasking training has also been proposed by Dux and colleagues (2009), based on decreased activation in lateral PFC, which is consistent with the activation decreases that we observed specifically in the high-intensity task-switching group.

Specifically, activation in lateral prefrontal regions associated with mixing demands (i.e., repeat > single contrast), especially in the left dlPFC, showed a decrease across both conditions from the first to the second session. Notably, only the high-intensity task-switching group maintained these changes by the end of training. Previous studies in adults have associated such activation decreases with increased efficiency of rule processing (Kelly and Garavan 2005; von Bastian et al. 2022). Poldrack (2000) has suggested that a key contributor to training-related activation decreases are more precise neural representations of task sets that enable more efficient processes. Accordingly, Garner and Dux (2015) showed training-related performance improvements with dual-task training alongside reduced task-related activations and more distinct task-set representations in the PFC in adults.

The present results extend the observation that increased efficiency underlies training-related improvements in executive functions from adulthood (cf. von Bastian et al. 2022) to late childhood, by demonstrating decreases in frontal activation that were accompanied by increased drift rates with intensive task switching training. This observation is relevant in light of suggestions that training in children may speed up maturation with children becoming more adult-like in activation and connectivity patterns (Jolles et al. 2012;

Jolles and Crone 2012). Our previous work (Schwarze et al. 2023) showed the present task-switching paradigm elicited smaller upregulation of frontoparietal activation in (untrained) children compared to adults. This pattern indicates a potential for children's activation patterns to become more adult-like by condition-specific increases in activation. However, we did not observe such changes in any of the ROIs (see also Supplementary Results 3). Rather than showing more adult-like activation, children revealed a similar training-related change of decreasing PFC activation as previously reported in adults. Future studies are needed to elucidate how these training-related changes in neural processes depend on the targeted executive function (e.g., task-switching as opposed to working-memory training; Jolles et al. 2012; Astle et al. 2015) or the investigated age range (Rueda et al. 2005; Lee et al. 2022).

4.2 Rapid temporary changes in switch-related activation

Most changes of activation associated with switch costs were similar across training groups and relatively short lived, such that they became evident at the second session but were no longer present at the end of training. While this pattern matches the initial changes of the drift rate and boundary separation parameters, it does not match the maintenance of the later changes, especially in the high-intensity task-switching group.

In line with the well-established evidence that switch costs approach adult levels earlier than mixing costs do (Cepeda et al. 2001; Crone et al. 2004; Reimers and Maylor 2005; Crone, Bunge, et al. 2006; Huizinga and van der Molen 2007; Manzi et al. 2011), children in the present study showed smaller switch costs than mixing costs prior to training (see Schwarze et al. 2023). Thus, the different patterns of change observed for neural processes associated with mixing and switch costs may reflect differences in the mismatch between current ability and demands imposed on the cognitive control system during training (cf. Lövdén et al. 2010; Lövdén et al. 2020). According to this interpretation, the supply–demand mismatch was greater for mixing costs than for switch costs, leading to the

observed sustained changes in neural activation, whereas the relatively smaller mismatch for switch costs could be met by temporary changes of control processes.

4.3 Return to baseline performance and activation in the SI group

While we had predicted slower or less extensive behavioral improvements and neural changes with lower dosages of task switching, the high-intensity single-tasking group showed behavioral and neural changes as quickly and almost as extensively as the high-intensity task-switching group. However, the high-intensity single-tasking group returned to baseline levels of performance and dIPFC activation by the end of training. There are different potential explanations for the return to baseline with intensive single-task training. First, the lower doses of task switching in each training game (i.e., 17%) may not have posed enough demands to evoke sustained challenge to the task-switching networks to maintain the initial changes (Lövdén et al. 2010). Hence, the changes observed at the beginning of training may rather reflect the reconfiguration of existing resources, also referred to as flexibility (Lindenberger and Lövdén 2019; Lövdén et al. 2020; cf. Baltes 1987), than structural alterations of brain and behavior that would qualify as plasticity.

Second, the lower dosage of task-switching demands during training in the high-intensity single-tasking group may have favored adopting a strategy that is tailored to the demands of the single-task context, which, however, might be less well suited for task switching. Group differences in boundary separation are especially interesting to consider in light of such potential strategy differences. Specifically, boundary separation captures response caution, both on an individual level as well as on a trial level that is likely to correspond to the perceived risk of making an error (Schmitz and Voss, 2012). While both groups showed greater boundary separation for single trials at the second session, only the high-intensity task-switching group showed these increases for repeat and switch trials as well. The increased boundary-separation parameter may reflect greater control allocation to switch and repeat trials or the increased sensitivity to the cue and its changes within mixed blocks. With children in the high-intensity single-tasking group mainly practicing on the

relatively easier condition of single-task blocks, they may have adopted a different strategy for the allocation of control than the high-intensity task-switching group (Shenhav et al. 2013; see Steinbeis 2023 for a developmental perspective). This may have hindered them in correctly judging the required control on mixed blocks, in line with our observation that group differences in the increase in boundary separation were especially pronounced for repeat and switch trials as opposed to single trials. Such differences in control allocation might have been especially prominent in the second half of training, when children had become more familiar with the type of task-switching paradigm and the amount of cognitive control required for successful performance.

Another key difference between the two training groups may be related to the need to track changes in task demands indicated by changes in context. The ability to track changes in contexts continues to develop in late childhood (Waskom et al. 2014; Frick and Chevalier 2023) and contributes to the development of self-directed control (Frick et al. 2022). In the present training paradigm, the demands for context tracking were greater for the high-intensity task-switching group, in which participants performed more mixed blocks during training and thus faced more frequent switches of the cue. During the training games, the cue was always presented along with the target stimulus, effectively rendering it the context of the stimulus. Thus, the high-intensity task-switching group not only learned the mappings between each stimulus and the corresponding response, but also more intensively practiced tracking the context in which these were presented, which was crucial for successful task performance. In turn, the improved ability to track the context might have enabled more efficient rule implementation in the dlPFC (Hyafil et al. 2009; Ruge et al. 2013) and thus reduced activation in this region to a greater extent in this group than in the high-intensity single-tasking group.

Finally, children in the two training groups may have learned the rule structure differently, based on their experience with the tasks during training. Mixed blocks require the application of the rules in a hierarchical manner: mappings between a stimulus and a response are nested within a cue indicating which stimulus is relevant. While the ability to

identify and apply such hierarchical rule structures has been demonstrated in infants and toddlers (Werchan et al. 2015; Werchan et al. 2016), it is continually refined throughout childhood and adolescence (Kray, Karbach, and Blaye 2012; Unger et al. 2016). During the instruction phase of each training game, the hierarchical structure of each task was made explicit to both groups. Nonetheless, children in the high-intensity single-tasking group may have represented the mappings between stimulus and response separately from the cue, as the cue was only relevant at the beginning of a block. Such a flat rule structure could be more efficient when single-tasking, but ineffective in mixed blocks where the cue is crucial for successful performance on each trial (cf. Verbeke and Verguts 2023).

4.4 Limitations

We would like to acknowledge some important limitations of the present study. First, the sample size for the analyses of activation and connectivity is relatively small, limiting our ability to find smaller effects, especially for whole-brain analyses over time as they require complete datasets with currently available data-analysis pipelines. Thus, the reported training-related changes in activation and connectivity patterns should be interpreted with caution and seen as a starting point for further research. Additionally, changes in performance and brain function may happen at different time scales (Baykara et al. 2021). For example, the limited changes in activation associated with switch costs may be due to session B being too far into training to capture the potentially early onset of such changes. Also, in keeping with earlier work on task switching (Schmitz and Voss 2012; Schmitz and Voss 2014; Weeda et al. 2014; Schuch and Konrad 2017; Ging-Jehli and Ratcliff 2020), we did not estimate all possible parameters of the drift-diffusion model (Henrich et al. 2023), given the limited number of trials per condition and group. Finally, while we were able to demonstrate that different doses of task-switching during training (i.e., high-intensity task switching vs. high-intensity single tasking) were associated with differential changes in performance and activation patterns, it seems worthwhile to investigate the effects of other training regimes in future work. In particular, we recommend examining the effects of a

sequential training regime in which single-task training precedes task-switching training. Possibly, task-switching training is more effective if preceded by a training phase during which the decision rules governing each task have been firmly established.

4.5 Conclusion

In this study, we show that high-intensity task-switching training speeds up evidence accumulation, induces more cautious response strategies, and reduces activation and connectivity in frontal regions in children aged between 8 and 11 years. By comparing different doses of practicing switching between rules, we were able to demonstrate that greater experience with task switching is associated with more efficient rule processing in the PFC. In summary, we conclude that high-intensity task-switching may facilitate the efficient allocation of cognitive control, such as the continuous tracking of contextual information and the flexible, hierarchical representation of currently relevant tasks. Our findings provide initial evidence on the ways in which task-switching processes change with training at both behavioral and neural levels of analysis in late childhood. Future research can build on these findings by investigating which training regimes are most effective in promoting efficient task switching at different ages, with the aim to better understand the interplay between maturational and experiential factors and timescales in the ontogeny of cognitive control.

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Supplementary Material

Intensive task-switching training and single-task training differentially affect behavioral and neural manifestations of cognitive control in children

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Supplementary Materials

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Supplementary Table 1. Details of the distribution of trials in single and mixed blocks for the three types of training games for the high-intensity single-tasking (SI) and high-intensity task-switching (SW) groups.

Training task	SI group		SW group	
	single	mixed	single	mixed
Face-scene task and unique tasks of the same structure	405	81	81	405
Monster task and unique tasks of the same structure	405	81	81	405
Robot tasks and unique tasks of the same structure	404	81	80	405

Supplementary Table 2. Model comparisons showing that for behavioral measures (accuracy, RT, HDDM parameters) the model including all interactions fit best or did not differ from best-fitting model. Models were compared using the LOO function within the loo package in R (Vehtari et al. 2022). ELPD difference indicates the difference between each model's Bayesian leave-one-out estimate of the expected log pointwise predictive density (ELPD) and the best fitting model, whole ELPD difference is zero. SE indicates the standard error of this difference. Note that there is not a fixed ratio of SE to ELPD difference to indicate significant differences between models. Until these exist, developers' suggestions are that an ELPD difference around five times the SE can be interpreted as indicating differences between models. Note that models for accuracy and response time (RT) included all three groups and sessions A and D, while models for HDDM parameters (drift rate, boundary separation, and non-decision time) included the SI and SW group and all four sessions (A,B,C,D). Bold values indicate the best fitting model.

Model	Accuracy		RT		Drift rate		Boundary separation		Non-decision time	
	ELPD difference	SE	ELPD difference	SE	ELPD difference	SE	ELPD difference	SE	ELPD difference	SE
condition x session x group	0	0	0	0	0	0	0	0	-1.7	5.5
condition + session x group	-14.4	7.5	-54	11.1	-13.1	8.9	-92.7	15.1	-16.1	6.5
condition x session + group	-8.7	6.6	-0.5	4.7	-4.9	6.6	-6.8	6.3	0	0
session + condition x group	-14.4	7.2	-50	10.9	-5.4	7.9	-95.1	15.4	-12.8	7
condition + session + group	-15.8	7.9	-53.8	11.1	-11.9	9.2	-96.8	15.5	-13.6	6.4

Supplementary Table 3. Paired comparisons of posterior distributions of HDDM parameters. Bold values indicate comparisons for which the probability was above 95%.

Condition	Group	session	Drift rate (v)	Boundary separation (a)	Non-decision time (t)	
Single	SW > SI	A	0.8	0.589	0.508	
		B	0.608	0.402	0.772	
		C	0.581	0.445	0.692	
		D	0.994	0.994	0.383	
	SW	A > B	0.0	0.0	0.996	
		A > C	0.018	0.0	0.996	
		A > D	0.0	0.001	0.831	
	SI	A > B	0.0	0.0	0.961	
		A > C	0.001	0.0	0.975	
		A > D	0.0	0.001	0.9	
	Repeat	SW > SI	A	0.709	0.57	0.452
			B	0.996	0.99	0.699
C			0.948	0.688	0.564	
D			1.0	0.999	0.8	
SW		A > B	0.0	0.272	0.931	
		A > C	0.0	0.272	0.975	
		A > D	0.0	0.14	0.999	
SI		A > B	0.0	0.005	0.807	
		A > C	0.007	0.005	0.948	
		A > D	0.009	0.1	0.968	
Switch		SW > SI	A	0.761	0.283	0.961
			B	0.981	0.91	0.909
	C		0.994	0.605	0.936	
	D		0.999	0.861	0.999	
	SW	A > B	0.0	0.414	0.586	
		A > C	0.0	0.414	0.846	
		A > D	0.0	0.317	0.999	
	SI	A > B	0.0	0.005	0.72	
		A > C	0.007	0.005	0.881	
		A > D	0.003	0.1	0.966	

Supplementary Table 4. Changes in activation across all sessions (A–D) in the two training groups (SI vs. SW) for repeat and single trials in the regions of interest (ROIs) defined on the repeat > single contrast in the adult comparison sample. CI indicates 95% credible intervals; bold values indicate estimates whose 95%-CI did not include zero. Dorsal anterior cingulate cortex (dACC), dorsolateral prefrontal cortex (dlPFC), inferior frontal junction (IFJ), superior parietal lobe (SPL)

Effect	Left dACC			Left dlPFC			Left IFJ			Left SPL			Right dACC			Right dlPFC			Right IFJ			Right SPL		
	Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI	
Intercept	3.01	2.44	3.58	2.09	1.49	2.69	1.61	1.12	2.11	2.41	1.95	2.88	2.32	1.84	2.82	1.18	0.59	1.76	1.53	1.05	2.02	2.09	1.50	2.68
group: SW vs. SI	0.98	0.22	1.78	0.13	-0.69	0.95	0.15	-0.59	0.89	1.01	0.32	1.70	0.59	-0.08	1.27	0.11	-0.70	0.92	-0.79	-1.48	-0.09	0.07	-0.73	0.86
session: B vs. A	0.05	-0.72	0.82	-1	-1.89	-0.10	-0.45	-1.19	0.26	-0.31	-0.93	0.31	0.11	-0.60	0.80	-0.11	-0.94	0.75	-0.4	-1.04	0.27	0.09	-0.72	0.89
session C vs. A	0.72	0.03	1.43	-0.21	-0.99	0.57	0.06	-0.60	0.72	-0.73	-1.39	-0.09	0.26	-0.38	0.93	0.02	-0.83	0.88	-0.21	-0.83	0.44	-1.26	-2.08	-0.42
session D vs. A	-0.04	-0.76	0.69	-0.38	-1.16	0.41	0.54	-0.10	1.19	-0.71	-1.33	-0.10	-0.38	-1.04	0.28	-0.4	-1.17	0.39	-0.23	-0.84	0.40	-1.22	-1.99	-0.44
condition: single vs. repeat	-1.23	-1.85	-0.63	-1.3	-1.95	-0.63	-0.99	-1.50	-0.46	-1.4	-1.94	-0.86	-1.11	-1.68	-0.55	-0.64	-1.32	0.03	-1.07	-1.60	-0.55	-1.53	-2.18	-0.87
group SW x session B	-0.64	-1.65	0.36	-0.09	-1.25	1.06	0.09	-0.86	1.04	-0.69	-1.56	0.20	-0.61	-1.55	0.32	-0.64	-1.74	0.43	0.52	-0.34	1.38	-0.69	-1.73	0.35
group SW x session C	-1.57	-2.53	-0.65	-0.95	-2.00	0.11	-0.37	-1.26	0.51	-0.47	-1.35	0.47	-0.99	-1.90	-0.10	-1.17	-2.31	-0.05	-0.02	-0.89	0.83	0.12	-0.91	1.18
group SW x session D	-1.21	-2.19	-0.23	-0.63	-1.72	0.47	-0.39	-1.33	0.55	-0.71	-1.61	0.18	-0.82	-1.78	0.12	-0.96	-2.07	0.12	0.09	-0.80	0.94	-0.04	-1.13	1.04
group SW x single	-1.04	-1.89	-0.20	-0.14	-1.06	0.77	0.01	-0.76	0.76	-0.79	-1.57	0.01	-0.63	-1.43	0.14	-0.31	-1.26	0.64	0.37	-0.36	1.12	0.03	-0.86	0.92
session B x single	-0.49	-1.44	0.47	0.76	-0.32	1.83	0.47	-0.39	1.35	0.34	-0.44	1.12	-0.39	-1.26	0.47	0.02	-1.01	1.05	0.6	-0.21	1.41	0.42	-0.60	1.40
session C x single	-0.79	-1.71	0.11	0	-0.98	1.00	-0.24	-1.04	0.55	0.62	-0.17	1.42	-0.21	-1.05	0.64	-0.19	-1.23	0.85	0.08	-0.70	0.86	1.15	0.16	2.16
session D x single	0.06	-0.85	0.99	0.37	-0.61	1.33	-0.47	-1.27	0.29	0.78	-0.00	1.57	0.21	-0.64	1.05	0.66	-0.34	1.63	0.4	-0.39	1.17	1.37	0.40	2.34
group SW x session B x single	0.83	-0.41	2.09	0.09	-1.27	1.49	-0.29	-1.42	0.84	0.26	-0.85	1.34	0.74	-0.39	1.92	0.53	-0.86	1.90	-0.49	-1.58	0.59	0.05	-1.23	1.39
group SW x session C x single	1.26	0.05	2.50	0.69	-0.66	2.01	0.42	-0.67	1.51	0.4	-0.74	1.51	0.91	-0.23	2.07	1.29	-0.12	2.67	0.54	-0.53	1.58	-0.15	-1.47	1.16
group SW x session D x single	0.54	-0.72	1.78	-0.22	-1.56	1.15	-0.32	-1.45	0.85	0.2	-0.95	1.32	0.51	-0.66	1.69	0.33	-1.08	1.74	-0.4	-1.50	0.72	-0.32	-1.66	1.03

Supplementary Table 5: Changes in activation across all sessions (A – D) in the two training groups (SI vs. SW) for switch and repeat trials in the ROIs defined on the switch > repeat contrast in the adult comparison sample. CI denotes 95%-Credible Intervals; bold values indicate estimates whose 95%-CI did not include zero. Supplementary motor area (SMA)

Effect	Left dACC			Left IFJ			Left Precuneus			Left SMA			Left SPL			Right dACC			Right Precuneus			Right SMA		
	Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI	
Intercept	2.01	1.34	2.66	2.16	1.36	2.98	-0.81	-1.43	-0.19	2.62	1.94	3.28	2	1.46	2.53	1.74	1.17	2.29	-0.18	-0.89	0.53	1.96	1.29	2.63
group: SW vs. SI	0.48	-0.40	1.39	0.45	-0.67	1.58	0.36	-0.49	1.22	0.96	0.06	1.87	0.45	-0.29	1.18	0.26	-0.51	1.03	0.66	-0.30	1.67	0.86	-0.05	1.77
session: B vs. A	-0.03	-0.75	0.66	-0.99	-1.83	-0.15	0.51	-0.19	1.25	0.11	-0.69	0.90	-0.38	-0.98	0.20	0.03	-0.70	0.77	0.93	0.16	1.71	0.3	-0.47	1.07
session C vs. A	0.84	0.08	1.60	-0.25	-1.02	0.54	0.15	-0.67	0.98	0.67	-0.10	1.45	-0.48	-1.18	0.22	0.44	-0.36	1.25	0.36	-0.63	1.36	0.4	-0.52	1.35
session D vs. A	-0.1	-0.87	0.65	0.41	-0.43	1.20	0.38	-0.43	1.16	-0.33	-1.15	0.46	-0.81	-1.45	-0.21	-0.18	-0.93	0.58	0.38	-0.47	1.23	-0.02	-0.91	0.90
condition: switch vs. repeat	0.59	0.10	1.07	0.71	0.34	1.11	1.03	0.46	1.63	0.61	0.13	1.11	0.63	0.24	1.03	0.49	-0.02	1.01	0.83	0.25	1.42	0.62	0.09	1.16
group SW x session B	-0.22	-1.17	0.73	0.69	-0.39	1.77	0.26	-0.74	1.20	-0.67	-1.69	0.37	-0.12	-0.90	0.67	-0.24	-1.20	0.73	-0.39	-1.42	0.63	-1.01	-2.00	-0.02
group SW x session C	-1.3	-2.31	-0.31	-0.39	-1.42	0.61	0.07	-1.02	1.18	-0.86	-1.90	0.19	-0.18	-1.10	0.75	-0.76	-1.86	0.32	-0.14	-1.49	1.19	-0.55	-1.78	0.70
group SW x session D	-0.51	-1.56	0.51	-1.2	-2.28	-0.08	0.1	-0.99	1.21	-0.21	-1.33	0.93	-0.24	-1.09	0.64	-0.43	-1.48	0.60	-0.19	-1.39	0.99	-0.51	-1.78	0.74
group SW x single	0.01	-0.64	0.66	-0.19	-0.73	0.33	-0.34	-1.18	0.48	-0.09	-0.76	0.55	-0.25	-0.86	0.32	-0.06	-0.78	0.64	-0.29	-1.10	0.52	-0.18	-0.89	0.54
session B x switch	-0.51	-1.21	0.20	-0.42	-1.04	0.15	-0.24	-1.15	0.64	-0.75	-1.46	-0.05	-0.4	-1.01	0.17	-0.41	-1.21	0.36	0.08	-0.83	0.96	-0.79	-1.59	0.02
session C x switch	-0.56	-1.25	0.14	-0.29	-0.88	0.31	-0.46	-1.31	0.40	-0.48	-1.19	0.22	-0.38	-0.98	0.20	-0.5	-1.25	0.25	-0.21	-1.07	0.63	-0.43	-1.19	0.34
session D x switch	0.09	-0.61	0.79	-0.41	-1.01	0.19	-0.52	-1.40	0.37	-0.38	-1.08	0.32	-0.37	-0.96	0.19	0.07	-0.68	0.81	-0.22	-1.09	0.65	-0.64	-1.42	0.13
group SW x session B x switch	0.22	-0.73	1.18	0.12	-0.64	0.94	-0.23	-1.42	1.00	0.77	-0.17	1.74	0.36	-0.43	1.19	0.56	-0.45	1.61	-0.4	-1.56	0.84	0.85	-0.21	1.89
group SW x session C x switch	0.41	-0.53	1.33	0.09	-0.67	0.87	0.2	-0.94	1.38	0.22	-0.71	1.16	0.49	-0.31	1.31	0.43	-0.55	1.46	0.07	-1.09	1.26	-0.03	-1.09	1.01
group SW x session D x switch	-0.08	-1.05	0.89	0.59	-0.21	1.40	-0.33	-1.57	0.94	0.53	-0.45	1.56	0.33	-0.50	1.16	-0.06	-1.13	1.01	-0.26	-1.46	1.00	0.7	-0.42	1.80

Supplementary Table 6. Details on ROIs defined on the adult comparison sample

Contrast	Hemisphere	ROI	Size	Peak		
Repeat > single	left	dIPFC	243	-44	24	28
		IFJ	381	-42	4	32
		dACC	122	-4	12	52
		SPL	332	-28	-58	48
	right	dIPFC	239	48	30	26
		IFJ	410	38	0	40
		SPL	249	32	-52	50
		dACC	107	8	12	52
Switch > repeat	left	dACC	218	-6	10	50
		SMA	407	-6	8	52
		IFJ	102	-48	2	32
		SPL	509	-32	-52	58
	right	Precuneus	569	-10	-72	40
		dACC	123	12	20	36
		SMA	216	2	2	56
		Precuneus	451	20	-58	6

Supplementary Table 7. Model outputs of performance (accuracy and response times) across all sessions (A–D) in the two training groups (SW vs. SI) for single, repeat, and switch trials (repeat as reference level). CI denotes 95%-Credible Intervals; bold values indicate estimates whose 95%-CI did not include zero.

Effect	Accuracy			RT		
	Estimate	CI		Estimate	CI	
Intercept	0.81	0.77	0.86	1.47	1.41	1.52
condition: single vs. repeat	0.13	0.1	0.16	-0.28	-0.32	-0.23
condition: switch vs. repeat	-0.07	-0.11	-0.04	0.26	0.22	0.3
session: D vs. A	-0.02	-0.07	0.03	-0.02	-0.09	0.04
group: SI vs. PC	-0.02	-0.08	0.03	-0.01	-0.08	0.06
group: SW vs. PC	0.01	-0.04	0.07	0	-0.07	0.07
condition (single vs. repeat) x session (D vs. A)	-0.05	-0.1	0.01	0.01	-0.05	0.07
condition (switch vs. repeat) x session (D vs. A)	0.03	-0.02	0.08	-0.08	-0.14	-0.02
condition (single vs. repeat) x group (SI vs. PC)	-0.03	-0.07	0.01	0.03	-0.03	0.08
condition (switch vs. repeat) x group (SI vs. PC)	-0.01	-0.05	0.03	-0.01	-0.06	0.05
condition (single vs. repeat) x group (SW vs. PC)	-0.04	-0.08	0	0.02	-0.03	0.07
condition (switch vs. repeat) x group (SW vs. PC)	-0.02	-0.06	0.02	0.01	-0.04	0.06
session (D vs. A) x group (SI vs. PC)	0.03	-0.03	0.09	-0.07	-0.15	0.01
session (D vs. A) x group (SW vs. PC)	0.08	0.02	0.14	-0.09	-0.18	-0.01
condition (single vs. repeat) x group (SI vs. PC) x session (D vs. A)	0.07	0.01	0.13	0.05	-0.02	0.13
condition (switch vs. repeat) x group (SI vs. PC) x session (D vs. A)	-0.01	-0.07	0.05	-0.01	-0.09	0.07
condition (single vs. repeat) x group (SW vs. PC) x session (D vs. A)	0.01	-0.05	0.08	0.06	-0.02	0.14
condition (switch vs. repeat) x group (SW vs. PC) x session (D vs. A)	0.02	-0.04	0.08	-0.01	-0.08	0.07

Supplementary Table 8. Complete model outputs drift diffusion parameters (drift rate, boundary separation, non-decision time) across all sessions (A–D) in the two training groups (SW vs. SI) for single, repeat, and switch trials (repeat as reference level). CI denotes 95%-Credible Intervals; bold values indicate estimates whose 95%-CI did not include zero.

Effect	Drift rate (v)			Boundary separation (a)			Non-decision time (t)		
	Estimate	CI		Estimate	CI		Estimate	CI	
Intercept	0.93	0.78	1.08	2.07	2	2.14	0.79	0.75	0.83
condition: single vs. repeat	0.69	0.58	0.81	0.1	0.01	0.18	-0.1	-0.13	-0.06
condition: switch vs. repeat	-0.28	-0.39	-0.18	-0.17	-0.25	-0.09	0.22	0.17	0.27
session: B vs. A	0.27	0.13	0.41	0.04	-0.05	0.13	-0.05	-0.08	-0.02
session: C vs. A	0.28	0.13	0.43	0.08	-0.01	0.17	-0.07	-0.11	-0.04
session: D vs. A	-0.02	-0.19	0.14	-0.07	-0.17	0.03	-0.08	-0.11	-0.05
group: SW vs. SI	0.07	-0.15	0.29	0	-0.1	0.11	-0.01	-0.07	0.05
session B x single	0.29	0.13	0.44	0.53	0.42	0.65	-0.06	-0.1	-0.01
session B x switch	0.09	-0.05	0.24	-0.02	-0.14	0.1	0.02	-0.03	0.08
session C x single	0.04	-0.11	0.19	0.26	0.14	0.37	-0.03	-0.08	0.02
session C x switch	0.02	-0.13	0.16	-0.04	-0.15	0.08	0.02	-0.05	0.08
session D x single	0.03	-0.12	0.18	0.03	-0.09	0.14	0.04	-0.01	0.08
session D x switch	0.15	0.01	0.29	0.01	-0.1	0.12	-0.02	-0.08	0.04
single x group SW	0.02	-0.14	0.18	0	-0.12	0.12	0	-0.04	0.05
switch x group SW	0.02	-0.13	0.17	-0.05	-0.16	0.07	0.09	0.02	0.16
session B x group SW	0.24	0.04	0.45	0.2	0.06	0.32	0.01	-0.04	0.05
session C x group SW	0.13	-0.09	0.35	0.04	-0.1	0.17	0.01	-0.04	0.06
session D x group SW	0.34	0.1	0.58	0.22	0.07	0.36	-0.01	-0.05	0.04
session B x single x group SW	-0.3	-0.52	-0.08	-0.23	-0.4	-0.06	0.03	-0.03	0.1
session B x switch x group SW	-0.08	-0.28	0.13	-0.05	-0.22	0.12	-0.08	-0.16	0
session C x single x group SW	-0.17	-0.39	0.04	-0.06	-0.23	0.11	0.03	-0.04	0.1
session C x switch x group SW	0.05	-0.16	0.26	0.03	-0.14	0.19	-0.08	-0.16	0.01
session C x single x group SW	-0.14	-0.35	0.08	-0.01	-0.18	0.15	0.01	-0.06	0.07
session D x switch x group SW	-0.06	-0.27	0.15	-0.08	-0.25	0.08	-0.04	-0.12	0.05

Supplementary Table 9. Changes in activation between session A and D in all three groups (SI vs. PC [passive control group], SW vs. PC) for repeat and single trials in the ROIs defined on the repeat > single contrast at session A. CI denotes 95%-Credible Intervals; bold values indicate estimates whose 95%-CI did not include zero.

Effect	Left IFJ			Left SPL			left dIPFC			Right IFJ			Right SPL		
	Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI	
Intercept	0.62	0.11	1.13	0.99	0.5	1.45	0.15	-0.41	0.7	0.5	0.05	0.95	0.56	0.04	1.1
group: SI vs. PC	0	-0.69	0.69	0.03	-0.61	0.69	0.55	-0.19	1.3	-0.1	-0.72	0.53	0.01	-0.73	0.73
group: SW vs. PC	0.14	-0.53	0.83	0.34	-0.28	0.97	0.63	-0.11	1.37	-0.45	-1.06	0.17	0.15	-0.57	0.87
session: D vs. A	0.28	-0.27	0.82	0.42	-0.2	1.04	0.63	-0.05	1.33	0.15	-0.41	0.7	0.37	-0.31	1.04
condition: repeat vs. single	1.99	1.4	2.56	2.69	2.04	3.36	1.94	1.27	2.63	1.6	1	2.19	2.26	1.61	2.93
groupSI x sessionD	-0.22	-0.95	0.51	-0.35	-1.24	0.51	-0.52	-1.48	0.4	-0.01	-0.78	0.76	-0.21	-1.15	0.73
groupSW x sessionD	-0.84	-1.6	-0.07	-0.89	-1.75	-0.02	-1.48	-2.47	-0.5	-0.28	-1.05	0.51	-0.53	-1.44	0.4
group SI x repeat	-0.95	-1.7	-0.18	-1.02	-1.93	-0.13	-0.7	-1.63	0.25	-0.69	-1.48	0.12	-0.47	-1.42	0.47
group SW x repeat	-1.06	-1.86	-0.26	-0.14	-1.04	0.76	-0.53	-1.46	0.38	-0.81	-1.6	-0.01	-0.55	-1.46	0.34
session D x repeat	-0.09	-0.89	0.7	-0.66	-1.59	0.27	-0.99	-2.03	0.02	-0.58	-1.43	0.26	-1.19	-2.15	-0.22
group SI x session D x repeat	0.35	-0.76	1.43	-0.14	-1.41	1.18	0.63	-0.8	2.01	0.37	-0.77	1.52	-0.02	-1.45	1.39
groupSW x session D x repeat	0.71	-0.42	1.82	-0.48	-1.81	0.8	0.85	-0.54	2.25	0.46	-0.71	1.62	0.12	-1.22	1.47

Supplementary Table 10. Changes in activation across all sessions (A, B, C, and D) in the two practice groups (SI vs. SW) for repeat and single trials in the ROIs defined on the repeat > single contrast at session A. CI denotes 95%-Credible Intervals; bold values indicate estimates whose 95%-CI did not include zero.

Effect	Left IFJ			Left SPL			left dIPFC			Right IFJ			Right SPL		
	Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI	
Intercept	0.67	0.26	1.09	1.05	0.64	1.46	0.76	0.32	1.24	0.44	0.03	0.83	0.63	0.16	1.13
group: SW vs. SI	0.11	-0.46	0.67	0.28	-0.28	0.85	0	-0.64	0.66	-0.37	-0.90	0.19	0.09	-0.60	0.77
session: B vs. A	-0.03	-0.49	0.42	-0.03	-0.58	0.54	-0.25	-0.88	0.38	0.2	-0.30	0.72	0.49	-0.09	1.09
session C vs. A	-0.17	-0.62	0.27	-0.09	-0.67	0.48	-0.22	-0.85	0.41	-0.09	-0.61	0.43	-0.04	-0.62	0.54
session D vs. A	0.01	-0.45	0.46	0.04	-0.54	0.61	0.02	-0.61	0.65	0.14	-0.37	0.64	0.06	-0.57	0.68
condition: repeat vs. single	1.06	0.61	1.51	1.68	1.11	2.26	1.28	0.65	1.9	0.95	0.45	1.47	1.78	1.16	2.41
group SW x session B	-0.13	-0.72	0.48	-0.4	-1.18	0.36	0.08	-0.76	0.92	0	-0.69	0.68	-0.67	-1.47	0.11
group SW x session C	0.03	-0.58	0.65	-0.1	-0.90	0.68	-0.22	-1.06	0.63	0.4	-0.29	1.12	-0.11	-0.90	0.69
group SW x session D	-0.57	-1.20	0.08	-0.53	-1.32	0.27	-0.87	-1.79	-0.01	-0.26	-0.98	0.47	-0.22	-1.07	0.64
group SW x repeat	-0.2	-0.87	0.49	0.83	-0.01	1.64	0.15	-0.70	1.05	-0.2	-0.93	0.5	-0.09	-0.93	0.76
session B x repeat	-0.57	-1.32	0.17	-0.33	-1.15	0.49	-0.98	-2.02	0.06	-0.47	-1.27	0.31	-0.37	-1.30	0.53
session C x repeat	0.16	-0.52	0.86	-0.69	-1.54	0.16	-0.03	-0.96	0.92	0.02	-0.75	0.79	-1.06	-2.03	-0.1
session D x repeat	0.21	-0.48	0.89	-0.81	-1.67	0.02	-0.42	-1.38	0.52	-0.27	-1.05	0.47	-1.15	-2.09	-0.19
group SW x session B x repeat	0.25	-0.75	1.24	-0.25	-1.40	0.92	0.03	-1.36	1.39	0.18	-0.87	1.22	-0.07	-1.30	1.14
group SW x session C x repeat	-0.25	-1.26	0.7	-0.59	-1.77	0.58	-0.83	-2.12	0.43	-0.72	-1.75	0.33	0.14	-1.12	1.41
group SW x session D x repeat	0.45	-0.55	1.45	-0.29	-1.51	0.94	0.31	-1.01	1.62	0.13	-0.91	1.2	0.11	-1.19	1.37

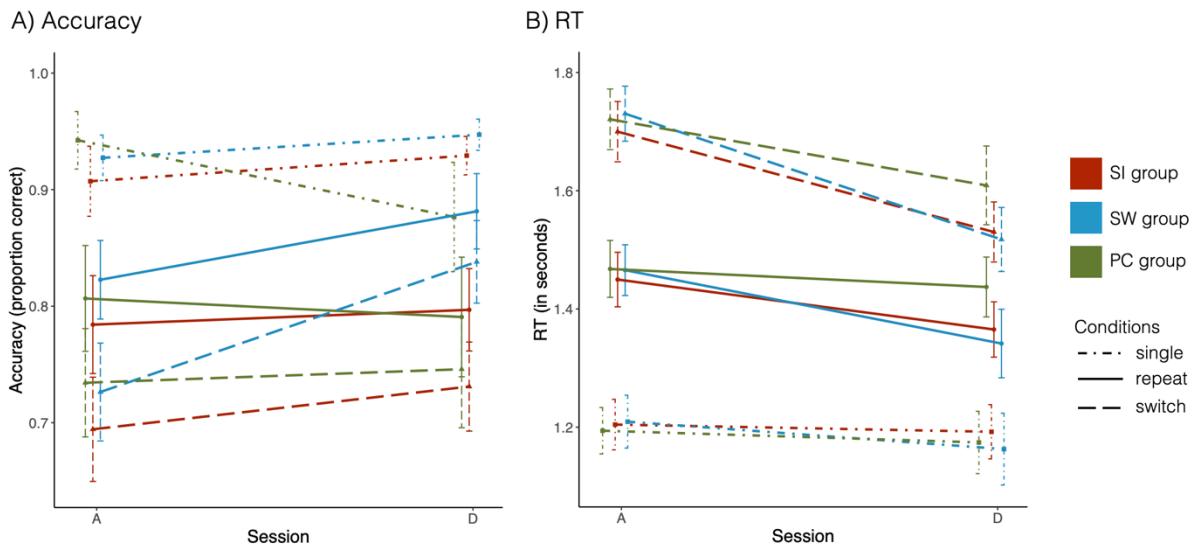
Supplementary Table 11. Changes in activation between session A and D in all three groups (SI vs. PC, SW vs. PC) for switch and repeat trials in the ROIs defined on the switch > repeat contrast at session A. CI denotes 95%-Credible Intervals; bold values indicate estimates whose 95%-CI did not include zero.

Effect	Left IFJ			Left SPL			left Precuneus			Right Precuneus			Right SPL		
	Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI	
Intercept	3.45	2.42	4.45	3.34	2.71	4.00	-0.09	-0.80	0.62	1.03	0.19	1.87	0.09	-0.55	0.74
group: SI vs. PC	-1.07	-2.52	0.4	-0.79	-1.68	0.09	-1.16	-2.13	-0.24	-1.59	-2.75	-0.5	-0.19	-1.05	0.67
group: SW vs. PC	-0.84	-2.21	0.53	-0.08	-0.95	0.79	-0.61	-1.54	0.34	-0.87	-2	0.25	-0.25	-1.1	0.58
session: D vs. A	0.16	-0.74	1.06	-0.35	-1.11	0.39	-0.34	-1.16	0.47	0.61	-1.48	0.29	-0.56	-1.28	0.16
condition: switch vs. repeat	0.24	-0.26	0.73	0.19	-0.25	0.63	0.37	-0.25	0.98	0.57	0.01	1.11	0.3	-0.14	0.74
groupSI x sessionD	-0.06	-1.31	1.17	-0.29	-1.34	0.75	1.26	0.13	2.42	1.13	-0.09	2.36	0.03	-0.97	1.04
groupSW x sessionD	-0.66	-1.83	0.55	-0.82	-1.85	0.2	1.36	0.18	2.53	0.9	-0.33	2.12	0.08	-0.92	1.07
group SI x switch	0.46	-0.18	1.11	0.62	0	1.27	0.72	-0.14	1.59	0.32	-0.46	1.13	0.16	-0.4	0.73
group SW x switch	0.31	-0.32	0.93	0.26	-0.38	0.88	0.58	-0.28	1.42	0.07	-0.69	0.83	0.08	-0.49	0.65
session D x switch	0.59	-0.12	1.28	0.07	-0.57	0.73	0.48	-0.39	1.36	0.29	-0.54	1.12	-0.34	-0.94	0.27
group SI x session D x switch	-0.86	-1.82	0.08	-0.56	-1.52	0.35	-0.97	-2.23	0.26	-0.46	-1.62	0.69	-0.06	-0.88	0.74
groupSW x session D x switch	-0.5	-1.39	0.4	-0.12	-1.03	0.78	-1.74	-2.98	-0.53	-0.81	-1.94	0.3	-0.09	-0.89	0.71

Supplementary Table 12: Changes in activation across all sessions (A, B, C, and D) in the two practice groups (SI vs. SW) for switch and repeat trials in the ROIs defined on the switch > repeat contrast at session A. CI denotes 95%-Credible Intervals.

Effect	Left IFJ			Left SPL			left Precuneus			Right Precuneus			Right SPL		
	Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI		Estimate	CI	
Intercept	2.51	1.52	3.48	2.57	1.97	3.17	-1.18	-1.86	-0.54	-0.41	-1.15	0.34	-0.03	-0.52	0.46
group: SW vs. SI	0.21	-1.15	1.61	0.67	-0.15	1.48	0.49	-0.40	1.38	0.64	-0.45	1.68	-0.22	-0.91	0.44
session: B vs. A	-1.03	-1.89	-0.2	-0.39	-1.10	0.29	0.79	-0.03	1.6	0.95	0.21	1.69	-0.26	-0.84	0.32
session C vs. A	-0.23	-1.11	0.67	-0.59	-1.34	0.14	0.57	-0.30	1.47	0.57	-0.40	1.56	-0.24	-0.9	0.42
session D vs. A	-0.09	-1.03	0.82	-0.67	-1.37	0.02	0.78	-0.12	1.69	0.4	-0.47	1.28	-0.61	-1.18	-0.06
condition: switch vs. repeat	0.66	0.29	1.03	0.76	0.36	1.18	1.12	0.53	1.73	0.98	0.42	1.56	0.44	0.09	0.79
group SW x session B	0.87	-0.22	2.01	0.01	-0.91	0.92	0.22	-0.84	1.28	-0.47	-1.47	0.54	0.13	-0.64	0.89
group SW x session C	-0.47	-1.65	0.68	-0.39	-1.37	0.63	-0.08	-1.25	1.1	-0.29	-1.63	1.06	0.12	-0.78	1.03
group SW x session D	-0.59	-1.79	0.68	-0.5	-1.48	0.47	0.21	-0.99	1.45	-0.22	-1.44	1.04	0.24	-0.55	1.03
group SW x switch	-0.1	-0.61	0.42	-0.29	-0.88	0.31	-0.18	-1.00	0.64	-0.47	-1.27	0.32	-0.07	-0.56	0.43
session B x switch	-0.26	-0.83	0.34	-0.51	-1.11	0.1	-0.22	-1.12	0.66	0	-0.89	0.85	-0.28	-0.81	0.23
session C x switch	0.09	-0.67	0.48	0.39	-0.98	0.2	-0.34	-1.22	0.54	-0.31	-1.16	0.53	-0.42	-0.94	0.11
session D x switch	-0.22	-0.82	0.36	-0.44	-1.04	0.14	-0.51	-1.39	0.39	-0.27	-1.13	0.58	-0.39	-0.91	0.12
group SW x session B x switch	-0.09	-0.86	0.7	0.35	-0.45	1.17	-0.62	-1.82	0.58	-0.27	-1.42	0.91	-0.11	-0.81	0.59
group SW x session C x switch	-0.08	-0.82	0.67	0.62	-0.17	1.42	-0.11	-1.33	1.07	0.19	-0.99	1.36	0.1	-0.63	0.84
group SW x session D x switch	0.28	-0.49	1.09	0.39	-0.44	1.25	-0.71	-1.94	0.52	-0.14	-1.32	1.06	-0.01	-0.73	0.71

Supplementary Figure 1: Training related change in condition-specific performance. Panel A shows accuracy, panel B shows RTs. Mixing costs (i.e., lower accuracy and longer RTs on repeat than single trials) and switch costs (i.e., lower accuracy and longer RTs on switch than repeat trials) were evident across both sessions and all groups. Switch costs in RTs decreased from session A to B across all groups. Overall performance improved from session A to D in accuracy (A) and RTs (B) in the SW group (blue) relative to the PC group (green). The SI group (red) did not differ in change from the PC group for switch and repeat trials, and maintained higher performance on single trials. Error bars denote 95%-confidence intervals.



Supplementary Results 1: Seed-to-voxel connectivity

Connectivity associated with mixing demand

Whole-brain seed-to-voxel analyses with seeds in the left IFJ and SPL for repeat > single did not reveal any clusters that showed changes in connectivity with training ($p < .05$ FDR-corrected, voxel threshold at $p < .001$ uncorrected). As noted in the preregistration, we additionally conducted seed-to-voxel analyses for regions that showed changes in activation with training. More specifically, we analyzed whole-brain connectivity for a seed in the left dlPFC. No clusters showed changes in connectivity with the dlPFC with training ($p < .05$ FDR-corrected, voxel threshold at $p < .001$ uncorrected).

Connectivity associated with switch demand

The whole-brain seed-to-voxel analysis with a seed in the left IFJ revealed a cluster in the left angular gyrus that showed changes in connectivity for switch > repeat with training ($p < .05$ FDR-corrected, voxel threshold at $p < .001$ uncorrected), such that condition differences increased from session A to C in the SI group and then decreased again at session D, while condition differences in the SW group only increased at session D (see Figure SR1.1). There was no significant cluster for the left SPL seed region.

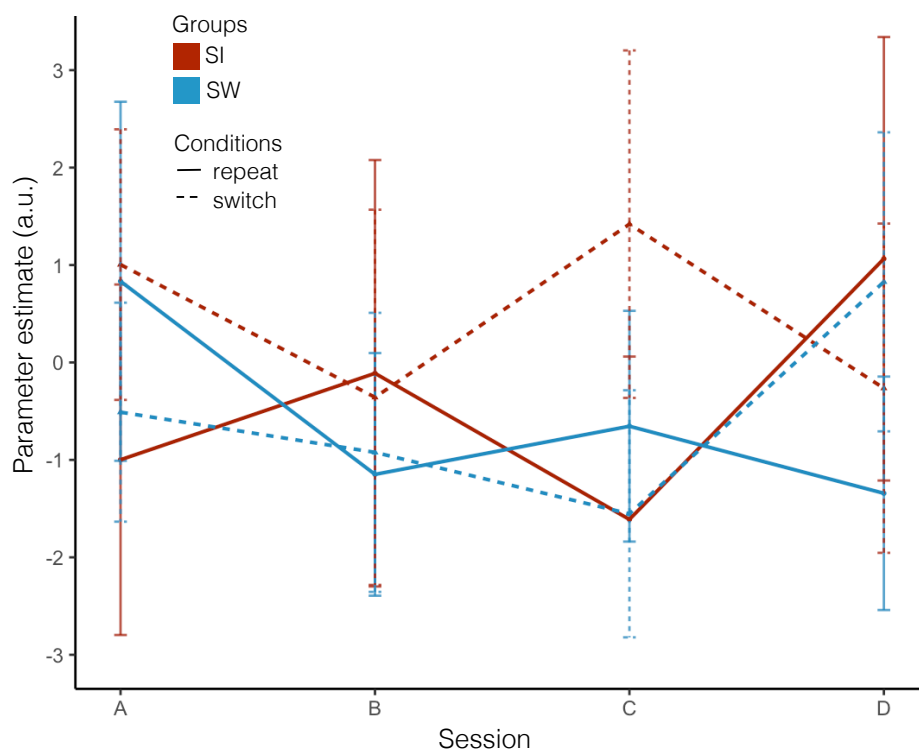


Figure SR1.1: Change in connectivity between the IFJ and a cluster in the left angular gyrus (AG). PPI parameters for the connection between the seed in the IFJ and the cluster in the left AG that showed change in the connectivity difference between repeat and switch trials. Error bars denote 95%-confidence intervals. The single-task (SI) practice group is shown in red and the task-switching practice group in blue. Connectivity for repeat trials is shown in the solid line and for switch trials in the long-dashed line for each session.

Supplementary Results 2: IFJ to IPFC connectivity

Objective. Based on previous findings in age differences between children and adults, where we showed that children showed a greater increase in connectivity between the IFJ and the lateral PFC from single to repeat blocks (Schwarze et al., 2023), we tested whether this connectivity changed with practice.

Methods. For our analyses to be less dependent on the precise location of the IPFC cluster at the first timepoint, we defined two anatomical ROIs (in the frontal polar cortex [FPC] and the middle frontal gyrus [MFG]) based on the Harvard-Oxford Atlas (Makris et al., 2006) thresholded at a probability of 30%. In our previous analyses, we had used these two anatomical regions to restrict the cluster that showed greater connectivity with the IFJ in children compared to adults. Thus, the analyses retained the general location of the cluster without being too dependent on the precise location. We extracted PPI parameters for these ROIs from the session-specific repeat > single PPI model described in the main analyses and subsequently analyzed these for changes between sessions A and D and for differences between the SI, the SW, and the PC groups. Models included random intercepts for participants and random slopes for sessions.

Results. Neither the IFJ to FPC, nor the IFJ to MFG connectivity showed changes with practice. However, connectivity for repeat trials was greater than for single trials across sessions and groups (FPC: est. = 1.48; 95%-CI: 0.19; 2.74; MFG: est. = 2.26; 95%-CI: 1.04; 3.50), suggesting that also after practice children involved these additional regions with increased mixing demand on repeat trials (see Table SR2.1).

Table SR2.1 Model outputs of PPI parameters across sessions A and D, the three groups (SI vs. PC, SW vs. PC), and repeat and single trials. CI denotes 95%-Credible Intervals; bold values indicate estimates whose 95%-CI did not include zero.

Effect	IFJ – FPC			IFJ – MFG		
	Estimate	CI	CI	Estimate	CI	CI
Intercept	-1.73	-2.86	-0.61	-1.84	-2.94	-0.73
group: SI vs. PC	0.33	-1.16	1.84	0.38	-1.11	1.87
group: SW vs. PC	1.17	-0.31	2.63	1.67	0.22	3.14
session: D vs. A	0.91	-0.49	2.32	1.08	-0.24	2.41
condition: repeat vs. single	1.48	0.19	2.74	2.26	1.04	3.5
groupSI x sessionD	-0.07	-1.98	1.82	-1.04	-2.85	0.78
groupSW x sessionD	-0.59	-2.46	1.27	-1.46	-3.3	0.31
group SI x repeat	0.4	-1.35	2.1	-0.56	-2.21	1.13
group SW x repeat	-0.25	-1.94	1.42	-1.02	-2.59	0.57
session D x repeat	-0.33	-2.19	1.48	-1.18	-2.93	0.57
group SI x session D x repeat	-0.31	-2.82	2.24	0.87	-1.57	3.25
group SW x session D x repeat	-0.33	-2.77	2.11	0.47	-1.83	2.79

Supplementary Results 3: Changes in deviation score and association with changes in connectivity

Hypotheses: For detailed hypotheses see pre-registrations at <https://osf.io/by4zq/>. In brief, based on results of the pre-training session (Schwarze et al., 2023), we expected changes in IFJ–IPFC connectivity to depend on how adult-like the pre-training activation of a child was (Hypothesis 5). Additionally, we expected the alignment of changes in activation pattern and connectivity to be associated with practice-related changes in performance (Hypothesis 6).

Methods:

For detailed methods, see pre-registrations at <https://osf.io/by4zq/>.

Deviation Score. Briefly, we computed functional activation deviation scores for repeat > single and switch > repeat activation based on Düzel et al. (2011; see also Fandakova et al. 2015) for each child relative to the adult average of the respective contrast. A more negative score represents more adult-like activation patterns, and a more positive score represents less adult-like patterns.

Deviation score and change in connectivity. To test whether change in IFJ–IPFC connectivity depended on how adult-like a child’s repeat > single activation at session A was, we performed Bayesian linear mixed modeling with IFJ–IPFC connectivity as the dependent variable, and condition (single vs. repeat), session (A vs. D), and deviation score at the first session (high vs. low, based on a median split) as fixed effects, allowing for all interactions. We analyzed only the two training groups (i.e., SW and SI). The model further included a random intercept of individuals and random slope of session.

Given that neither deviation scores nor IFJ–IPFC connectivity changed with practice, we did not further analyze the preregistered Hypothesis 6.

Results: Deviation scores did not change over the course of practice, neither for the repeat > single contrast (Figure SR3.1A), nor the switch repeat contrast (Figure SR3.1B; all 95%-CI included zero). Model outputs are shown in Table SR3.1 for comparisons of session A and D among the three groups (SI vs. PC and SW vs. PC) and in Table SR3.2 for comparisons across all sessions (A, B, C, and D) for the two practice groups (SW vs. SI). The change in connectivity between sessions A and D did not differ between children who showed more and those who showed less adult-like activation patterns at session A (see Table SR3.3).

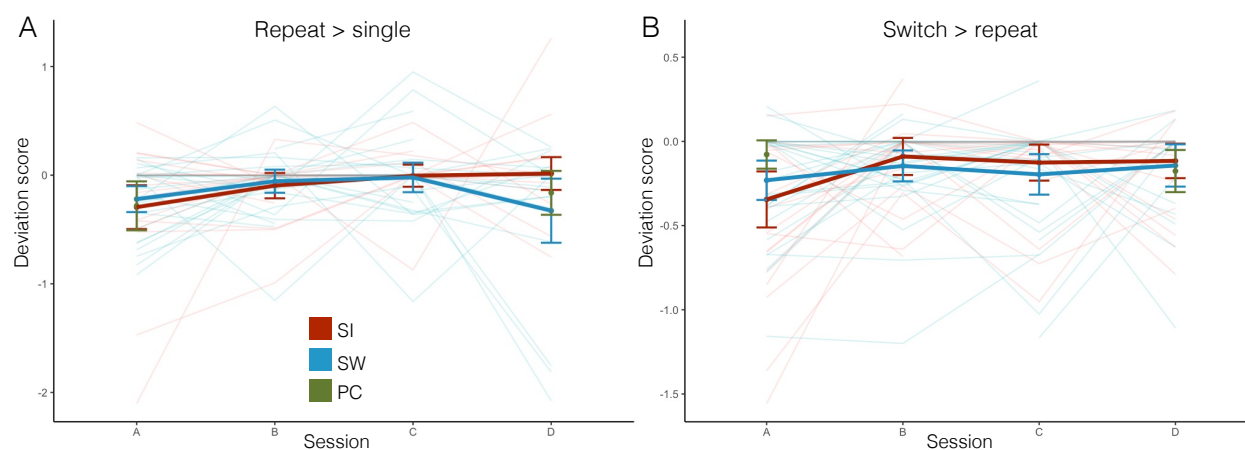


Figure SR3.1 Changes in deviation score. (A) Change in deviation score for the repeat > single contrast. (B) Change in deviation score for the switch > repeat contrast. Higher values denote less adult-like activation pattern. Thin lines show individual trajectories. The passive control (PC) group is shown in green, the single-task practice (SI) group in red, and the task-switching practice (SW) group in blue. Error bars denote 95%-confidence intervals.

Table SR3.1. Model output for comparisons of session A and D among the three groups (SI vs. PC and SW vs. PC). CI denotes 95%-Credible Intervals

Effect	Repeat > Single			Switch > Repeat		
	Estimate	CI		Estimate	CI	
Intercept	-0.01	-0.04	0.02	-0.01	-0.10	0.02
session: D vs. A	-0.01	-0.05	0.04	0	-0.06	0.06
group: SI vs. PC	-0.01	-0.07	0.03	-0.03	-0.22	0.01
group: SW vs. PC	0	-0.05	0.04	-0.01	-0.09	0.03
group SI x session D	0.02	-0.04	0.10	0.03	-0.03	0.23
group SW x session D	0.01	-0.05	0.08	0	-0.06	0.11

Table SR3.2. Model output for comparisons across all sessions (A, B, C, and D) for the two practice groups (SW vs. SI). CI denotes 95%-Credible Intervals

Effect	Repeat > Single			Switch > Repeat		
	Estimate	CI		Estimate	CI	
Intercept	-0.01	-0.05	0.01	-0.03	-0.07	-0.00
session B	0.01	-0.03	0.05	0.02	-0.04	0.08
session C	0.01	-0.02	0.06	0.02	-0.03	0.07
session D	0.01	-0.03	0.06	0.03	-0.02	0.08
group SW vs. SI	0.01	-0.03	0.05	0.02	-0.02	0.07
session B x group SW	0	-0.06	0.04	-0.05	-0.13	0.01
session C x group SW	-0.01	-0.07	0.04	-0.03	-0.09	0.03
session D x group SW	-0.01	-0.07	0.05	-0.03	-0.09	0.03

Table SR3.3. Model output for connectivity at session A and D predicted by deviation score (median split) at session A across both practice groups. CI denotes 95%-Credible Intervals; bold values indicate estimates whose 95%-CI did not include zero.

Effect	IFJ – FPC			IFJ – MFG		
	Estimate	CI		Estimate	CI	
Intercept	-0.52	-1.54	0.5	0.08	-1.01	1.18
session: D vs. A	-0.12	-1.55	1.28	-1.19	-2.61	0.21
condition: repeat vs. single	1.13	-0.02	2.29	0.52	-0.63	1.67
deviation score group: more vs. less adult-like	-0.78	-2.18	0.6	-1.46	-2.94	-0.02
session D x repeat	0.13	-1.7	2	0.83	-0.98	2.69
session D x group more adult-like	1.47	-0.44	3.39	1.86	-0.05	3.78
group more adult-like x repeat	0.77	-0.78	2.34	1.7	0.16	3.25
session D x repeat x group more adult-like	-1.45	-3.96	1.03	-2.39	-4.95	0.12

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