

Review

Cognitive flexibility across the lifespan: developmental differences in the neural basis of sustained and transient control processes during task switching

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The ability to flexibly switch between task sets increases early and decreases late in life. This lifespan pattern differs between mixing costs, denoting performance decrements during task switching compared with single tasking, and switch costs, denoting performance decrements on trials after the task has switched relative to trials where the task repeats. Generally, mixing costs reach their lifespan minimum later and increase again earlier than switch costs. We propose that lifespan changes in cognitive flexibility are associated with neural processes implementing sustained and transient control processes that underlie mixing and switch costs, respectively. To better understand the lifespan development of sustained and transient control processes, future research needs to delineate longitudinal changes in functional connectivity patterns and task-set representations.

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Introduction

Flexibly adapting to changing environmental demands is a challenge individuals face on a daily basis, already at a

young age. As a key component of executive functions [1,2], cognitive flexibility enables goal-directed behavior and is positively associated with multiple real-life outcomes, including academic achievement [3] and the maintenance of higher cognitive functioning and independence in later adulthood [4,5].

Task switching represents one typical situation requiring cognitive flexibility. When a new task becomes relevant, individuals need to engage transient, trial-based control processes to update the newly relevant task set (i.e. the set of rules that link specific stimuli with their corresponding actions) and to inhibit the previous, no-longer-relevant task set. Transient control processes are immediately relevant when switching occurs and are reflected in slower and less accurate responses (i.e. switch costs) when switching from one task to another (i.e. switch trial) compared with repeating the same task (i.e. repeat trial) within mixed-task blocks of a task-switching paradigm [6–8].

Furthermore, task switching entails sustained (i.e. continuous) control processes reflected in performance differences between two different contexts — in the task-switching paradigm, these contextual differences refer to performance differences between single-task blocks, in which the same task is executed repeatedly across trials, and mixed-task blocks, in which different tasks are intermixed (i.e. global switch costs). Thus, each trial in mixed-task blocks could potentially require a switch to a different task. Global switch costs [9] can be conceptualized as behavioral expressions of the underlying sustained processes of maintenance, selection and monitoring of multiple task sets, and the readiness to switch [10–12]. These costs are inherently associated with switch costs as both repeat and switch trials within mixed-task blocks are considered. In contrast, mixing costs, or the comparison of trials in single-task blocks to repeat trials in mixed-task blocks [13], are assumed to be largely independent of switch costs. However, mixing costs may not capture the demands on sustained control to the extent that global switch costs do, as they only regard selected trials (i.e. repeat trials) within mixed-task blocks (for a detailed discussion, see Ref. [14]).

Task-switching ability increases across childhood and early adolescence and decreases in later adulthood [15–17]. Cross-sectional evidence comparing different age groups suggests that patterns of age differences differ between mixing and switch costs [17–20]: for instance, Reimers and Maylor [17] investigated task switching between 10 and 66 years using an alternating-runs task-switching paradigm in which the task changed every second trial during mixed blocks. The authors showed that compared with switch costs, global costs decreased later in childhood and increased earlier with aging. However, given the lack of longitudinal studies and limitations of the tasks used with very young children, it is unclear whether switch costs might show a similar magnitude of age differences when investigating very young children or older old adults. The patterns of cross-sectional age differences in mixing and switch costs are consistent with different developmental trajectories for these costs and offer a starting point for considering the role of sustained and transient processes for cognitive flexibility development. Elucidating the particular shape of these developmental trajectories requires longitudinal studies to test within-person change in transient and sustained processes across the lifespan.

On the neural level, task switching engages frontoparietal regions, including the inferior frontal junction (IFJ), the superior parietal lobe, the dorsolateral prefrontal cortex (PFC), and the dorsal anterior cingulate cortex [21,22]. These regions support task switching as parts of larger networks [23]. Particularly, the frontoparietal and the cingulo-opercular networks play a key role for cognitive flexibility [24,25]. While frontoparietal activation has been associated with task switching relatively consistently, evidence for the involvement of cingulo-opercular regions is less consistent [26]. These differences may reflect a more prominent role of the frontoparietal network for cognitive flexibility or the limited number of studies that have examined sustained control processes [26].

The evidence on age differences in the neural correlates of sustained and transient control and their contributions to variability in cognitive flexibility has not been integrated across child development and aging research. To fill this gap, we summarize the current state of research on cognitive flexibility development with a selective focus on neuroimaging studies of task switching in children and older adults. We then outline future research directions that can enhance our understanding of the ways in which changes in sustained and transient control processes relate to changes in cognitive flexibility across the lifespan.

Child and adolescent development of cognitive flexibility: refined frontoparietal and cingulo-opercular recruitment

Cognitive flexibility continues to improve throughout childhood and adolescence [17,18,27–29], presumably

reflecting the increasingly refined recruitment of frontoparietal and cingulo-opercular brain regions. Specifically, during task switching, children recruit similar brain regions as adults (see Ref. [22] for a recent meta-analysis) but show less pronounced upregulation of activation from single-task blocks to mixed-task blocks and from repeat to switch trials within mixed-task blocks [29–34]. This pattern of results suggests that children have difficulties adapting activation as efficiently as adults when control demands increase during task switching. One contributing factor may be related to the protracted structural development of these regions [35] and the white matter tracts connecting them [36]. Behavioral and neuroimaging findings converge to suggest that transient control processes approach adult levels earlier than sustained control processes. For instance, we recently investigated the role of sustained and transient control processes for cognitive flexibility in 8- to 11-year-old children and young adults using a cued task-switching paradigm with three tasks [29]. We observed greater differences between age groups for mixing costs and sustained control activation than for switch costs and transient control activation in frontoparietal and cingulo-opercular regions (Figure 1a; [29], see also Ref. [32]).

In addition to shifting, task-switching paradigms like the one implemented in Ref. [29] involve further transient control processes, such as inhibition, working memory updating, and stimulus-driven attention. They also rely on sustained control processes, including working memory maintenance and selection, monitoring, and readiness to switch. Beyond studies investigating task switching, stimulus-driven performance relying on transient processes has been suggested to reach adult levels earlier than proactively prepared performance relying on sustained processes [37]. Proactive control of task sets relies heavily on the ability to represent multiple relevant task sets over an extended period (e.g. throughout blocks of task-switching blocks) [38] and has been linked to the development of active task-set maintenance in working memory [39,40]. Proactive control can be observed by 8 years of age [41] and continues to improve throughout adolescence [15,17]. For instance, in a recent eye-tracking study of cued task switching, children fixated the rule information more extensively than adults during a preparatory period, with more pronounced differences for younger (8–11 years) than for older children (11–13 years) [42]. Children also showed less preparation-related activation in frontoparietal and cingulo-opercular regions than adults during a cued task-switching paradigm [31], suggesting that the greater reliance on reactive control might reflect limited recruitment of sustained neural processes to enable proactive control.

Taken together, these results suggest that younger children show difficulties with the sustained preparation of task execution and instead rely more strongly on transient rule updating, whereas older children and

adolescents approach adult levels of sustained control supporting a more proactive state that allows for faster processing of the cue information and less reliance on reactive control.

Normal aging of cognitive flexibility: less-specific frontoparietal and cingulo-opercular recruitment

Cognitive flexibility, and task switching in particular, declines in later adulthood [20]. Compared with younger adults, older adults consistently show larger mixing costs [9,20], whereas age-related deficits in switch costs are less pronounced or even absent [20,43]. Neuroimaging evidence supports the notion that sustained control shows more pronounced age-related declines. In a cued task-switching paradigm differentiating between sustained and transient neural processes [44], older adults (65–87 years) showed reduced sustained activation in the anterior PFC (aPFC) relative to younger adults, potentially reflecting less efficient maintenance and readiness to switch between rules. In parallel, older, but not younger, adults showed increased transient aPFC activation for switch trials. While increased sustained aPFC activation was associated with lower mixing costs in younger adults, increased transient aPFC activation was associated with higher switch costs in older adults. These findings suggest that with age, brain regions involved in sustained control may be engaged during transient control with detrimental effects on performance [45,46]. However, multiple studies [46–48] did not find age differences in transient activation on switch and repeat trials between younger and older adults.

In sum, age-related declines in sustained control might elicit a shift from proactive to reactive control during tasks requiring cognitive flexibility [38,49]. This shift may be partly associated with the loss of frontal gray matter volume in late adulthood [50] and changes in structural connections linking frontal and parietal regions [51].

Interim summary

Taken together, we propose that the development of task switching across the lifespan reflects the interaction between developmental changes in (1) transient control processes allowing for moment-to-moment adjustments in task-set updating and inhibition, which develop relatively early on and show less pronounced declines in aging; and (2) sustained control processes related to the readiness to switch, and the maintenance, selection, and monitoring of relevant task sets, which continue to develop well into adolescence and show relatively earlier age-related declines. During child development, frontoparietal and cingulo-opercular regions become more adaptively recruited in service of transient and sustained control during switching. In contrast, normal cognitive

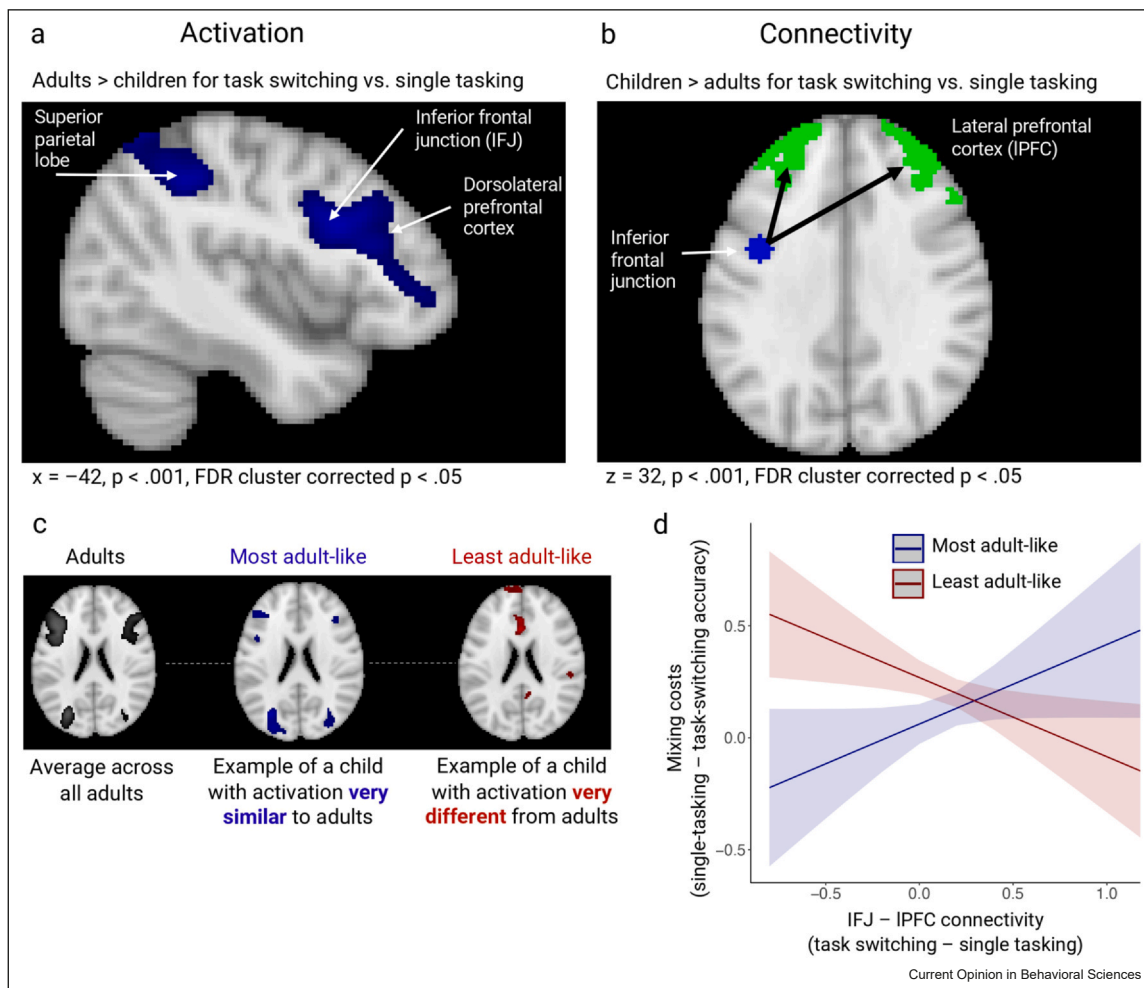
aging is marked by less adaptive recruitment of frontal regions for sustained control. The divergence of lifespan development in transient and sustained processes is intriguing, given that the underlying neural correlates of both processes encompass frontal, parietal, and cingulo-opercular areas, which show pronounced structural changes across the lifespan [35,50]. We propose that two relatively underexplored factors might contribute to this divergence: (1) changes in the fine-tuning of connections among frontoparietal and cingulo-opercular brain regions; and (2) changes in the distinctiveness of abstract representation of task rules. Our considerations build on frameworks considering the role of representations and control in lifespan cognitive development [52] and extend those to the neural basis of task-switching development.

Lifespan changes in the specialization of brain networks

During child development, brain networks show a complex pattern of strengthening and weakening of functional connections that have been suggested to support flexible behavior [53]. Network organization (e.g. measured via the segregation and integration between functional networks) and the strength of connections within and between networks during rest continues to mature until early adulthood (see Ref. [54] for a review of brain network development across multiple measures), with the degree of network segregation and integration depending on a network's respective position along the sensorimotor-association axis [55,56]. For instance, Pines et al. [55] demonstrated that association networks, including the frontoparietal and cingulo-opercular networks, showed increasing segregation with age (8–23 years), while sensorimotor networks showed increasing integration. Likewise, normal aging is associated with changes in the functional network architecture of the brain: compared with younger adults, connections within frontoparietal and cingulo-opercular networks in older adults are weaker, whereas connections between these networks are stronger [57] (see Ref. [87] for a review of brain network aging).

One study investigated dynamic resting-state connectivity among frontoparietal and cingulo-opercular networks in the context of cognitive flexibility across the lifespan (6–85 years). Multiple patterns of connectivity were defined by their specific within- and between-network connectivity and differed in the amount of time they were present during a scan [58]. A greater number of switches between these connectivity patterns over time was associated with better cognitive flexibility across age groups. However, the number of pattern switches was reduced in children and older adults, suggesting that differences in functional network architecture due to maturation and senescence may limit

Figure 1



Summary of developmental findings of Schwarze et al. [29]. **(a)** Adults showed greater upregulation of activation in frontal and parietal brain regions with increased task-switching demand (task switching compared with single tasking) than children. **(b)** Compared with adults, children showed greater increases of connectivity between the IFJ and the IPFC with higher task-switching demands. **(c)** Left panel: Task-based activation (task switching > single tasking) across adults ($P < .05$, FWE corrected) used as reference for estimating how similar an individual child's activation pattern was to the average adult pattern. Middle panel: Example of a child showing more adult-like activation for the contrast shown in blue ($P < .001$, uncorrected). Right panel: Example of a child showing less adult-like activation for the contrast shown in red ($P < .001$, uncorrected). **(d)** The relationship between the increase in connectivity and performance depended on how adult-like a child's brain activation was. Children who showed less adult-like activation (red line) showed better performance with increased connectivity, whereas children who showed more adult-like activation (blue line) showed worse performance with increased connectivity.

flexible network recruitment during task switching [58]. These findings suggest that resting-state networks associated with transient and sustained control become increasingly specialized during child development and allow more flexible transitions between brain states, while network specialization and flexibility decline in aging. This pattern suggests that young adults' network architecture allows for more adaptive recruitment of functional connections depending on task demands. However, determining whether children and older adults recruit connections within and between networks

differently than young adults to achieve flexible behavior requires investigations of connectivity during task performance.

Using task-based functional connectivity, we examined whether children recruit connections differently than young adults with increased sustained control demands during task switching. Children (8–11 years) showed increased connectivity between the IFJ and the anterior lateral PFC (IPFC) during mixed-task blocks compared with single-task blocks [29] (Figure 1b; see also Ref. [59])

for similar results). Children with less adult-like sustained control activation along with increased IFJ–IPFC connectivity showed lower mixing costs, while increased IFJ–IPFC connectivity in children with more adult-like sustained control activation was associated with greater mixing costs (Figure 1c,d). These findings suggest that increased connectivity with additional prefrontal regions might represent an alternative, potentially developmentally earlier mechanism to support sustained control that might be afforded by less segregated association networks in late childhood. Less adult-like activation suggests limited sustained control such that these children might benefit from increased IFJ–IPFC connectivity to provide additional support of task-set management and selection [60,61] or increased involvement of metacontrol [62,63]. However, longitudinal studies of task-based connectivity are needed to clarify the role of such a mechanism during the development of cognitive flexibility. Our findings that for children with more adult-like activation patterns, increased IFJ–IPFC connectivity was detrimental for performance (red line in Figure 1d) suggest that ongoing network segregation during development might offer room for selecting inefficient or inappropriate strategies. These findings underline the complexity and nonlinearity of the relationship between task-related activation, connectivity, and behavior [64–66].

At the other end of the lifespan, using task-based connectivity during cued task switching, one study found stronger frontoparietal connectivity in younger adults compared with older adults (60–85 years) during the cue period, with no age differences in frontoparietal and cingulo-opercular connectivity during presentation of the target [48]. Thus, older adults may have difficulty engaging proactive control due to reduced communication among frontoparietal and cingulo-opercular regions [49].

In summary, the extent to which functional connections can be dynamically adapted to changing task demands appears to change across the lifespan, thereby affecting cognitive flexibility. The cingulo-opercular network [11] might be particularly critical for co-ordinating dynamic adaptations of network configuration in the context of sustained control [67–69]. While the cingulo-opercular network has not received as much attention as the frontoparietal network in cognitive flexibility development, the proposed protracted development of sustained control warrants the re-evaluation of this focus, especially in a lifespan context. Studies directly contrasting task-related connectivity associated with transient and sustained processes across ages can help advance our understanding of the ways in which network segregation followed by desegregation across the lifespan, including frontoparietal and cingulo-opercular networks, enables flexible adjustments of network configuration and connection strength with varying task demands.

Changing distinctiveness of abstract representations across the lifespan

When switching to a different task, the demand to update the relevant task sets has been suggested to result in less stable task-set representations on switch than on repeat trials, thereby contributing to increased switch costs [6]. Additionally, the previously relevant task set is thought to linger and thus dilute the currently relevant task set [8,70].

Recent task-switching studies used multivariate classification methods for neuroimaging data, including applying classifiers to predict the currently relevant task from neural activation patterns (i.e. multivariate pattern analysis) or quantifying the similarity among neural activation patterns between different tasks (i.e. representational similarity analysis). They showed that in young adults, task-set representations were less distinct on switch compared to repeat trials [71,72] (but see Refs. [73,74]). These results are particularly intriguing with respect to task-switching development. One recurring explanation for less flexible behavior in children and older adults is that their task-set representations are less distinct compared with young adults [27,32,40]. We tested this hypothesis in childhood by comparing 8- to 11-year-olds and young adults during cued task switching [72]. In both groups, neural task-set representations of the currently relevant task were less distinct on switch than on repeat trials in frontoparietal, cingulo-opercular, and temporo-occipital brain regions. Switch-related reductions in neural distinctiveness were comparable between children and young adults, indicating relatively mature task-set representations (see also Ref. [75]), but were more highly correlated across frontoparietal and cingulo-opercular regions in children than in adults. In a related study comparing 7- to 9-year-olds and young adults during a one-back working memory task requiring participants to attend to one of two dimensions, both task-relevant and task-irrelevant information could be decoded in children in visual cortex regions, while only task-relevant information could be reliably decoded in adults [76]. While these studies offer initial hints at possible differences in task-set representations between children and adults, they also suggest that age differences might depend on the required manipulations of task-set representations and might differ between cognitive control domains (i.e. task switching [72] vs working memory and attention in [76]). Thus, while we propose a key role of increasingly distinct representations to support cognitive flexibility development, further research is needed to disentangle their precise trajectory depending on the task demands.

At the other end of the lifespan, aging has been associated with general neural dedifferentiation [77–80] resulting in less specific representations of incoming information during passive viewing, episodic [81] and

working memory tasks [82]. Of particular relevance to the present discussion, Weeks et al. [83] applied a whole-brain pattern classifier to neuroimaging data of a delayed match-to-sample task, including face and scene categories, of which only one category was subsequently cued and tested. Older adults (60–77 years) showed more evidence for sustained representation of the irrelevant information during the working memory delay period compared with young adults.

The investigation of the role of task-set representations' distinctiveness for the development of cognitive flexibility has only recently begun, and a direct lifespan comparison may be particularly informative. First, we expect that older adults (but not children) will already demonstrate overall less distinct representations of the relevant task set in the execution of single tasks that will propagate further and affect sustained control. Second, when only parts of the task set change, both children and older adults experience difficulties with the transient updating of task sets [84]. Based on recent findings of performance being most efficient if tasks are represented in a conjunct manner in the brain, including corresponding cues, stimuli, responses, and the mappings among them [70,85], we expect that age differences in representations might be especially relevant for transient control processes.

Outlook

To move toward a mechanistic understanding of lifespan changes in cognitive flexibility, and task switching in particular, we need to chart the development of sustained and transient control processes at behavioral and neural levels of analysis. Cross-sectional age group comparisons suggest that sustained processes show more protracted development in childhood and earlier decline in later adulthood than transient processes, indicating differential lifespan trajectories of general/mixing and switch costs. A closer look at age differences in functional connectivity and neural task-set representations is likely to refine our understanding of the development of sustained and transient control processes. We expect developmental differences in network characteristics and task-based connectivity to be particularly important for the development of sustained control, whereas changes in task-set representations might be especially relevant for transient control development. Initial evidence suggests neural distinctiveness and network segregation are positively related in sensorimotor networks across younger and older adults [86], underlining the need to investigate the codevelopment of representations and connectivity for cognitive flexibility. Longitudinal evidence delineating concurrent (e.g. linking current levels of sustained and transient control) and lead-lag relations (i.e. how transient and/or sustained control at an earlier time point impacts change in

sustained/transient control at a later time point) will advance our understanding of the underlying developmental dynamics. Longitudinal studies can further provide hints for prevention and intervention, such as specific age ranges that might benefit from training or forms of environmental support targeted at either sustained or transient control processes. Finally, future studies should explore the domain generality of sustained and transient control by testing how their development trajectories differentially impact other executive functions such as working memory or inhibition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that have influenced or might appear to have influenced the work reported in this article.

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