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Review

Performance monitoring across the lifespan: Still maturing post-conflict regulation in children and declining task-set monitoring in older adults

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A R T I C L E   I N F O

A B S T R A C T

Conditions that render the selection of correct actions difficult require the monitoring of the execution and outcomes of one's own actions. Such performance monitoring abilities undergo maturational and aging-related changes across the lifespan. This review highlights evidence for qualitative differences in behavior and physiological correlates of performance monitoring across the lifespan. Few developmental studies examine both stimulus-locked as well as response-locked components. Here, we examine a lifespan pattern of stimulus- as well as response-locked ERPs during performance monitoring to inform age differences in subprocesses of performance monitoring. Findings from functional magnetic resonance imaging (fMRI) studies that lend further support for the observed age differences in performance monitoring are also reviewed. Together, the evidence suggest that suboptimal performance monitoring during maturation is characterized by a reduced ability to flexibly translate experienced conflicts into top-down control, whereas declined performance monitoring in aging is characterized by difficulties in maintaining task set representations. Such age specific deficits are apparent in performance monitoring related to response conflicts as well as in performance monitoring during reinforcement learning and value-based decision making.

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Contents

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1. Introduction

The observation of electrophysiological markers that are specific to response or action errors was first made in the early 1990s (Falkenstein et al., 1990, 1991; Gehring et al., 1993a,b). Two decades later, considerable progress has been made in understanding how we monitor erroneous responses or error-prone situations and how we adapt to those critical events in order to increase the likelihood of accurate performance or obtaining desired action outcomes. Such processes have been summarized under the cognitive concept of performance monitoring (Ridderinkhof et al., 2004, see also Botvinick et al., 2001; Falkenstein et al., 2000; Holroyd and Coles, 2002; Ullsperger et al., 2014). Specifically, performance monitoring denotes a set of neurocognitive processes that signal the occurrence of events that threaten overall task goals (e.g., errors or losses that conflict with the goals of performing as correctly as possible or the goal of maximizing gains). Furthermore, performance monitoring is thought to support flexible adaptation of behavior in order to reach and maintain an optimal level of performance. Performance monitoring is thus of vital importance for goal-directed and flexible behavior.

Clearly, especially cognitive systems that operate with either not yet fully developed or already declining neurocognitive functions would be particularly in need of an efficient performance monitoring system. However, the brain substrates and cognitive processes of performance monitoring undergo changes across the lifespan. Children, adolescents and older adults have been consistently observed to perform worse on tasks that require performance monitoring (see Li et al., 2009; Segalowitz and Dywan, 2009; Segalowitz et al., 2010 for reviews). This review focuses on age-specific differences in performance monitoring functions across the lifespan. To this end, we review electrophysiological studies that reveal age differences in ERPs associated with different aspects of performance monitoring (e.g., the monitoring of conflicting stimulus inputs, the monitoring of response execution or undesired action outcomes). Electrophysiological measures are a particularly useful tool in characterizing age differences during performance monitoring, as they allow the separation of neurocognitive processes that are closely spaced in time, such as the monitoring of stimulus inputs and the monitoring of response outputs.

1.1. Organization and key themes

This review is organized as follows. We start with a discussion of brain substrates involved in performance monitoring and their development across the lifespan. Next, evidence for age-specific difficulties across the lifespan in the behavioral performance during response conflict tasks is reviewed. In particular, during response conflicts, children and adolescents are more prone to committing errors whereas older adults are more prone to slowed responding, as compared to younger adults. We then relate these behavioral age differences to age differences in electrophysiological correlates (ERPs) of performance monitoring during stimulus inputs and during response execution. The amplitude of ERPs associated with stimulus- or response-related processing differ across the lifespan and suggest a changing emphasis of subprocesses of performance monitoring across the lifespan. Drawing on this behavioral and electrophysiological evidence, we postulate age-specific difficulties in different aspects of performance monitoring during childhood and old age. Specifically, we argue that performance monitoring during maturation is characterized by a reduced ability to flexibly translate experienced conflicts into top-down control, whereas performance monitoring in aging is characterized by difficulties in maintaining task set representations. This postulate is then evaluated in light of developmental findings in functional magnetic resonance imaging (fMRI) studies of performance monitoring. Finally, as a yet outstanding question, we compare performance monitoring during response conflicts and during decision making across the lifespan.

2. Assessing performance monitoring during response conflict tasks

This section outlines common aspects of response conflict tasks that are used to measure performance monitoring. In doing so, we hope to illustrate more precisely the role of performance monitoring and cognitive control in the context of response conflicts. Cognitive control is a comparatively broad concept that has been discussed with respect to a variety of cognitive functions, such as working memory, episodic memory, selective attention or performance monitoring. Here we focus on processes of cognitive control as understood in the context of performance monitoring (e.g. Ridderinkhof et al., 2004; Yeung et al., 2004) and illustrate the key aspects of performance monitoring in a commonly used set of response conflict tasks (i.e., Flanker, Go/Nogo, AX-CPT, and Stroop tasks) that are relatively well delineated with respect to the presumed cognitive processes involved. Of specific interest, in these tasks, specific stimulus inputs have to be met with specific responses (or the withholding of a response) according to predefined stimulus-response mappings that are part of the task set. Although the sources for response conflict in these tasks are different (cf. Mansouri et al., 2009; Egner et al., 2007), the monitoring and control processes required during these tasks have been accounted for within the same computational model (cf. conflict monitoring model; Botvinick et al., 2001) and are reflected in similar neural markers (cf. Nieuwenhuis et al., 2003; Rubia et al., 2006; see

below for more details). Thus, the monitoring and control aspects observed with these tasks may share overlapping processes.

During such typical response conflict tasks, the demands of performance monitoring increase particularly when stimulus inputs map onto – and thereby trigger – unwanted or contextually inappropriate responses (cf. Botvinick et al., 2001). For instance, in the Stroop or Go/NoGo tasks stimulus inputs automatically trigger a preferential or habitual response that has to be inhibited. In the case of the Flanker task, distractors prime the incorrect conflicting response. Apart from situations involving conflicting stimulus inputs, response errors also signal higher demands on performance monitoring as they indicate the need for corrective actions. Taken together, there are hence two particular instances of critical events during response conflict tasks that require stronger performance monitoring: (a) conflicting stimulus inputs that require selective sensory processing in order to follow the correct stimulus-response mapping and (b) conflicting response tendencies that require a stronger focus on the correct response tendency in order to avoid an error. The specific electrophysiological potentials that arise during those two types of critical events as well as the underlying cognitive processes they presumably reflect are reviewed in a later section.

Finally, apart from the monitoring of events that impede the goal of performing as accurately as possible, theories of cognitive control (Botvinick et al., 2001; Miller, 2000; Miller and Cohen, 2001; Yeung et al., 2004) assume that in response conflict tasks, cognitive control biases the processing of task- relevant stimulus inputs as well as the execution of correct responses. Performance monitoring is hence not only thought to detect critical events but also to provide the basis for the initiation of an increase in cognitive control to decrease the likelihood of errors in the future. For instance, after error commissions, a stronger attentional focus on stimulus inputs and a more cautious response strategy have been observed that were related to stronger performance monitoring signals (King et al., 2010).

In the following, brain regions and neurotransmitters relevant for performance monitoring and cognitive control processes are briefly reviewed in order to further substantiate the different subprocesses at work during performance monitoring. Age differences in these brain regions and neuromodulation are also reviewed to provide a basis for considering age differences in behavioral and electrophysiological data during performance monitoring.

3. Brain substrates of performance monitoring

The most important cortical brain regions involved in performance monitoring and cognitive control are lateral (BA 9/46/6) and medial frontal cortex (anterior cingulate cortex, ACC (BA 24/32/33)) as well as the pre-supplementary motor area, preSMA (BA 6/8), and the parietal cortex (BA 7/39). Subcortical structures, such as the basal ganglia, dorsal striatum and the thalamus (e.g., Chudasama and Robbins, 2006; Miller, 2000; Munakata et al., 2011; Velanova et al., 2008) are also involved through the fronto-striatal pathway. Source localization studies as well as concurrent EEG-fMRI studies have localized generators of electrophysiological correlates of performance monitoring (see below for more details) in the medial frontal cortex (e.g., Yeung et al., 2004; Santesso and Segalowitz, 2008; Debener et al., 2005). EEG source localization measures, however, do not provide sufficient spatial precision to answer the question whether different ERPs related to performance monitoring reflect the same or different underlying cortical dipoles. Apart from the detection of the need for cognitive control (such as during response conflicts or errors), medial frontal areas are also thought to signal to lateral prefrontal areas that then exert top-down cognitive control (Botvinick et al., 2001; King et al., 2010; Danielmeier and Ullsperger, 2011; Kerns et al., 2004; Miller and

Cohen, 2001; Ridderinkhof et al., 2004). Lateral prefrontal areas target higher order sensory and motor cortices to bias stimulus and response processing (Miller, 2000; Nigbur et al., 2012). In terms of controlling brain areas, a distinction has been made between prefrontal and parietal areas (superior frontal lobe and superior parietal lobe) that exert top-down control and regions that are more driven by sensory inputs and are thus providing bottom-up control of actions (temporo-parietal junction and inferior frontal gyrus; Corbetta and Shulman, 2002). Finally, subcortical structures are thought to relay cognitive control via dorsal striatum and thalamus as well as the subthalamic nucleus to motor areas, thereby inhibiting or disinhibiting the thalamic control over motor outputs (Aron, 2007; Chudasama and Robbins, 2006).

With respect to neuromodulatory processes, the neuromodulator dopamine plays an important role in performance monitoring and cognitive control (see Arnsten and Li, 2005; Cools and D'Esposito, 2009; Montague et al., 2004 reviews). Dopamine levels are thought to affect the ability for maintaining and flexibly updating task sets that guide response and stimulus selection (Braver et al., 1999; Chudasama and Robbins, 2006). For instance, phasic midbrain dopaminergic signals are thought to be particularly relevant for updating task sets in accordance with contextual demands (Braver and Cohen, 1999; D'Ardenne et al., 2012; Holroyd and Coles, 2002). In the following, the development of these anatomical and neurochemical substrates across the lifespan is reviewed with a view on identifying first hints on age-specific deficits in performance monitoring.

3.1. Delayed maturation of prefrontal cortex and long-range prefrontal connections in children and adolescents

Developmental differences in volumetric and connectivity measures as well as in neuromodulation suggest particular difficulties in prefrontally-based top-down control during maturation. Volumetric studies show a protracted development of frontal brain areas in children and adolescents (Gogtay et al., 2004; Sowell et al., 2003). Long-range white matter connections that link the frontal cortex to sensory and motor control areas also develop gradually and continue to mature until early adulthood (Edin et al., 2009; Giorgio et al., 2010b). Functional connectivity evidence from resting-state connectivity analyses also indicate that interactions between medial and lateral prefrontal cortices and cerebellum, occipital, thalamic as well as parietal areas are weaker in children than in younger adults (Fair et al., 2007, 2009). Of direct relevance, Liston and colleagues observed greater Go/Nogo accuracy in children with stronger frontostriatal white matter connections (Liston, 2003). Also, larger gray matter volume in prefrontal cortex as well as basal ganglia has been related to better Go/Nogo performance (Casey et al., 1997a,b). With regard to neuromodulators, a protracted development in the cortical dopamine system is observed, which reaches adult levels only in late adolescence (Diamond et al., 2004; Wahlstrom et al., 2010; see Li, 2013 for review). This might also impair the monitoring of performance as well as the initiation of cognitive control.

3.2. Decreased prefrontal integrity and dopaminergic modulation in aging

Similar to the age differences observed during maturation, the frontal areas are particularly affected during aging. Prefrontal gray matter volume declines markedly during aging (Raz et al., 2005; Resnick et al., 2003). Furthermore, white matter – including long-range connections – declines during aging as well (Giorgio et al., 2010a). With regard to neuromodulators, ample evidence exists for attenuated cortical and subcortical dopaminergic modulation that underlie various aspects of cognitive aging (see Bäckman et al., 2006

for review; see Li et al., 2001, for a theoretical account). Studies examining the link between age-related biological changes and the decline in performance monitoring functions point to impaired prefrontal processes. For instance, a reduced integrity of the right inferior frontal cortex and its connections to the subthalamic nucleus are predictive of prolonged stop signal reaction times in older adults (Coxon et al., 2012). Moreover, in older adults, decreases in prefrontal white matter volume have been associated with hyperactivity during conflicting stimulus inputs on a flanker task (Colcombe et al., 2005) and on an attentional shift task (Hedden et al., 2012). These results hint at higher control demands or less efficient control-related activations in older adults due to compromised integrity in frontal white matter.

Taken together, brain networks implicating cognitive control undergo substantial neuroanatomical and neurochemical changes across the lifespan. Volumetric and neuromodulatory studies point to particular deficits of performance monitoring and cognitive control processes attributed to the prefrontal cortex in children as well as older adults. In addition, there is ample evidence on a reduced dopaminergic modulation in subcortical structures in older adults. A decline of prefrontally based functions might indicate difficulties in maintaining task sets, or difficulties in exerting top-down control in situations of conflicting stimulus inputs or response tendencies. The few existing studies that link structural brain development and performance monitoring functions appear to support this view. For instance, as reviewed above, worse performance on response conflict tasks has been observed in individuals with reduced frontal gray matter volume and reduced frontal white matter connections. However, at the current stage, studies that address the relationship between structural changes and cognitive changes related to performance monitoring across the lifespan are still too scarce to provide a clear picture as to which cognitive processes of performance monitoring are particularly affected across the lifespan. In the following, we thus review behavioral as well as electrophysiological evidence in different age groups to shed light on age-specific difficulties in subprocesses of performance monitoring.

4. Behavioral evidence of lower accuracy and prolonged reaction times during maturation but only prolonged reactions in older adults during performance monitoring

A review of behavioral findings from child developmental and aging studies of response conflict monitoring (see Table 1) reveals qualitative differences in behavioral performance that hint at age-specific deficits. Children show prolonged reaction times and have a greater tendency to commit errors in conditions involving response conflicts (Davies et al., 2004; Hämmerer et al., 2010; Johnstone et al., 2005; Jonkman et al., 2003; Jonkman, 2006; Santesso et al., 2006; Van Meel et al., 2012; Wiersema et al., 2007); whereas older adults often do not commit more errors than younger adults, but only respond much slower (Nieuwenhuis et al., 2002; Hämmerer et al., 2010; Falkenstein et al., 2001; Endrass et al., 2012; Themanson et al., 2006; Wascher et al., 2011). In a recent study using the Go-NoGo paradigm, we controlled for potential age differences in speed-accuracy tradeoffs and confirmed that this pattern of behavioral results is not attributable to age differences in speed-accuracy tradeoff (Hämmerer et al., 2010). Similarly, another recent study, which manipulated speed-accuracy tradeoffs experimentally in a Flanker task, also did not observe adult age differences in accuracy, but only in reaction times (Endrass et al., 2012). These qualitative differences in behavioral performance thus provide a first hint that different subprocesses of performance monitoring may be affected during development and aging.

The fact that children are more prone to respond erroneously suggests that processes separating relevant and misleading stimulus inputs or correct and incorrect response tendencies are affected during maturation. Indeed, a child developmental study that varied the difficulty of stimulus-response compatibility both with respect to perceptual discrimination and with respect to response preparation in a flanker task shows deficits in children in the resistance to interference in stimulus-response translation but not in perceptual filtering of correct and incorrect responses or general aspects of motor preparation (Ridderinkhof et al., 1997). It hence seems that monitoring and selectively focusing on relevant stimulus inputs or correct response tendencies are the most challenging aspects of cognitive control for children and adolescents. This notion is also in line with the observed protracted development of prefrontal control structures during maturation reviewed above. Prefrontal control structures have been implicated in the top-down regulation of correct and erroneous response options during response conflicts (Miller, 2000; Miller and Cohen, 2001) and in post-error adjustments of cognitive control (King et al., 2010).

In contrast, during tasks involving monitoring stimulus-response conflicts older adults tend to perform slower but at accuracy levels comparable to younger adults. Their overall slowing in the absence of a greater tendency for commission errors suggests rather a general deficit in stimulus or response processing that affects correct and incorrect processes alike. Conceivable candidates for specific performance monitoring deficits during aging are hence a reduced attentional processing of stimulus inputs, a compromised retrieval of the current response demands based on the task set, or a general tendency for cautiously slow responding in older adults (cf. Band and Kok, 2000a,b). Again, the decline in prefrontal structures in the elderly might contribute to the deficit in maintaining task sets. Studies that control for age-related differences in speed-accuracy trade-off show that the typical pattern of slower responses in the elderly and more errors in children is not entirely attributable to age differences in response strategies (Hämmerer et al., 2010; Endrass et al., 2012) and thus suggest a general tendency for children for premature responses and for slowed responding in older adults. Moreover, adult age differences in the ability to adapt response strategies have been observed (cf.; Smith and Brewer, 1995; Forstmann et al., 2011). Existing studies suggest, for instance, a reduced ability of children to monitor the accuracy of responses (Brewer and Smith, 1989) and a reduced ability of older adults to control the speed of responses (Smith and Brewer, 1995).

In the following, we discuss evidence from electrophysiological studies, which provide more detailed evidence of affected physiological processes than the anatomical evidence reviewed in the previous section. This will provide the basis for identifying which of the above suggested cognitive processes are the most likely candidates for deficits in performance monitoring during maturation and aging.

5. Event-related potentials related to performance monitoring: evidence for distinct cognitive processes associated with stimulus-locked and response-locked ERPs

Given that stimulus- and response-locked ERPs have been linked to different processes during performance monitoring, we compare stimulus-related and response-related electrophysiological indicators of performance monitoring (cf. also Fig. 1). A comparison of these ERPs will then help to delineate age differences in different subprocesses of performance monitoring.

Various ERPs are observed during performance monitoring. Among the most important are the error-related negativity (Ne/ERN) that appears about 100 ms after errors and the correct response negativity (Nc/CRN), which can be observed shortly after correct responses (Falkenstein et al., 1990, 1991). As a stimulus-locked component, the N2 is a frequently investigated

component. The N2 emerges about 250 ms following stimulus inputs that are mapped onto specific responses. It is larger in conditions evoking conflicting response tendencies (Falkenstein et al., 2000).

Several theoretical accounts of the cognitive processes reflected in the response-locked and stimulus-locked ERPs exist. Among these are: (a) the detection of errors (Falkenstein et al., 1990, 1991, 2000; Steinhauser et al., 2008); (b) the inhibition of incorrect response tendencies (Falkenstein et al., 1999, 2000); (c) response conflict monitoring (Botvinick et al., 1999; Yeung et al., 2004); (d) response selection (Roelofs et al., 2006; Gajewski et al., 2008); (e) error prediction or action outcome prediction (reinforcement learning theory; Holroyd and Coles, 2002, predicted response-outcome model; Alexander and Brown, 2010). It is beyond the scope of our review to suggest which of the theories on the processes reflected in ERPs related to performance monitoring is most appropriate. In the following we will therefore review empirical evidence regarding the cognitive processes reflected in Ne/ERN and N2 in the age range of younger adults. This allows us to base our review of lifespan age differences in these processes on an empirically supported common ground of existing theories. Given that we observe a differential development of in particular Ne/ERN and N2 amplitudes across the lifespan, we focus on empirical and theoretical accounts that lend themselves more readily to differentiating processes reflected in these two ERPs.

Regarding the Ne/ERN, one of the most consistently observed findings is an increase in Ne/ERN amplitude when errors are more significant (see also van Noordt and Segalowitz, 2012 for a review). For instance, the Ne/ERN is increased after errors if participants are asked to focus more on correct than on fast responding (Falkenstein et al., 1990; Gehring et al., 1993a,b). Likewise, the Ne/ERN is higher if errors weight heavier because they result in monetary losses (Potts, 2011) and is associated with interindividual differences in error relevance (see Segalowitz and Dywan, 2009 for a review). Also, evidence from studies with patients suffering from obsessive-compulsive disorder (Endrass et al., 2008) or generalized anxiety disorder (Weinberg et al., 2010) shows that individuals who attribute more relevance to errors exhibit higher Ne/ERN amplitudes. In healthy samples of younger adults, a positive correlation across participants between Ne/ERN size and response accuracy has also been observed (Herrmann et al., 2004), suggesting that participants who focus more on correct responses show larger Ne/ERN amplitudes.

The Ne/ERN is specifically sensitive to errors resulting from response conflicts. It is larger for errors due to premature responding as compared to errors related to ambiguous stimulus inputs (Scheffers and Coles, 2000). However, the evidence as to whether the Ne/ERN varies with different degrees of overlap in motor effectors (i.e., a conflict between more or less different response tendencies) is mixed. When the overlap in motor effectors was varied (four possible responses distributed about two fingers and two hands or two hands and two feet), one study observed a higher Ne/ERN with higher overlap between correct and error responses (Gehring and Fencsik, 2001). However, another study observed a lower Ne/ERN with more overlap in motor effectors (Bernstein et al., 1995). An explanation for these contradictory results – apart from differences in overlap between specific motor effectors – might be that a subjective perception of error severity influences the evaluation of errors. This subjective perception might very well vary across studies independent of the assumed degree of overlap in motoric effectors during errors. Indeed, there are now several studies which report a dissociation of the overlap between conflicting motoric responses and the amplitude of the Ne/ERN (Burlé et al., 2004; Carbonnell and Falkenstein, 2006). Finally, unlike later positive ERPs after errors (Pe), which will be discussed further below, the Ne/ERN does not require conscious error detection and does not vary with the detectability of an error (Nieuwenhuis et al., 2003; Steinhauser and Yeung, 2010).

Taken together, in response conflict tasks, the Ne/ERN amplitude is more sensitive to errors following conflicting response tendencies than following ambiguous stimulus inputs. However, the Ne/ERN appears to reflect the monitoring of critical response events at a higher level rather than the more effortful specific response selection or the overlap in motor activations. Intra- and interindividual differences in error relevance modulate the Ne/ERN amplitude. The more a correct performance is emphasized or the more likely a correct performance is, the higher is the Ne/ERN amplitude in case of an error. Finally, a variation of the detectability of errors does not reflect in Ne/ERN amplitude, suggesting that the amplitude of the Ne/ERN is rather modulated by an a priori, task-set related emphasis of correct performance than by a retrospective conscious appraisal of an error.

Following a similar line of reasoning as in the case of the Ne/ERN, the Nc/CRN – a negativity observed after correct responses – has been regarded as an index of response conflict in the form of increased processing of erroneous response tendencies during a correct response. A larger Nc/CRN would thus indicate a correct response that is less certain (Yeung et al., 2004). Lending support to views that suggest similar processes in Ne/ERN and Nc/CRN, recent studies found that one independent EEG component is sufficient to account for both Ne/ERN and Nc/CRN (Hoffmann and Falkenstein, 2010; Roger et al., 2010).

The N2 in response conflict tasks is usually examined after conflicting stimulus inputs that nonetheless still result in correct responses. The N2 reflecting performance monitoring can be differentiated from an N2 as evident in mismatch, oddball or novelty tasks (cf. Folstein and Van Petten, 2008). Unlike the mismatch N2, which is associated with perceptually deviant stimuli, a higher N2 in conflict tasks is observed on Nogo stimuli that are perceptually more similar to Go stimuli (Azizian et al., 2006). Similarly, in the flanker task a higher N2 is observed on incongruent stimulus inputs that are as frequent as congruent stimulus inputs. During performance monitoring, it is hence not the perceptual saliency (related to stimulus frequency) or perceptual deviance of stimuli that modulate the N2 amplitude but instead the propensity of stimulus inputs to result in conflicting response tendencies. Similar to the Ne/ERN, the N2 in response conflict tasks thus varies with a conflict in response tendencies rather than being sensitive to a conflict in stimulus processing. If multiple stimuli are mapped onto specific responses that are presented at the same time, a larger N2 is observed only if the stimuli are mapped onto conflicting responses (Van Veen and Carter, 2002). Moreover, the N2 is sensitive to conflicting response tendencies irrespective of whether the weaker response tendency is one of inhibiting or executing a response (Nieuwenhuis et al., 2003). Indeed, the N2 appears to be independent of response execution per se as the mere imagination of inhibiting or executing responses in a Go/Nogo task results in a higher N2 to Nogo stimuli (Burlé et al., 2004). As is true for the Ne/ERN, the N2 amplitude is larger when more is at stake, i.e., when errors result in punishments (Potts, 2011). Finally, higher N2 amplitudes are observed in contexts of low error likelihood and slower responses (Yeung and Nieuwenhuis, 2009).

Taken together, the N2 in response conflict tasks is higher following stimulus inputs that engender conflicting response tendencies. Similar to the Ne/ERN, the N2 is more sensitive to response-related as compared to stimulus-related conflicts. Moreover, again similar to the Ne/ERN, the N2 appears to be unrelated to actual response execution or inhibition but rather reflects a conflict of response tendencies on a level of monitoring motor responses. Finally, prolonged uncertainty about the correct response is related to higher N2 amplitudes as evident in higher N2 amplitudes to slower responses.

In summary, both Ne/ERN and N2 reflect difficulties in response monitoring rather than stimulus perception. Both ERPs are modulated when manipulating the relevance of performance outcomes. Of particular relevance for this review, however, there are also distinct differences between the two components. The most obvious difference is that the Ne/ERN – observed after errors – varies with the strength of correct response tendencies while the N2 – examined before correct responses – varies with the strength of stimulus inputs that prime incorrect response tendencies. This difference between these two ERPs is nicely exemplified in an elegant recent study that varied the strength of conflicting stimulus inputs by varying their spatial distance to the target stimuli. As should be expected, participants made more errors on trials with incongruent stimulus inputs when distracting inputs were closer to the target. In line with the assumption that the N2 increases with more conflicting input, the increase of the N2 on incongruent trials was larger when the distractors were close to the targets. In contrast, the Ne/ERN was smaller when distractors where closer to the target, hence when the correct response tendency was stronger during incorrect responses (Danielmeier et al., 2009).

In light of current theories that address response control (response selection theory, response inhibition theory, conflict monitoring theory), effects of the strength of correct response tendencies on the amplitude of Ne/ERN can be understood as a greater conflict between erroneous and correct response tendencies during errors (Botvinick et al., 2001; Yeung et al., 2004). This might then reflect in more effortful response selection or response inhibition as well as more prominent errors (Falkenstein et al., 1999, 2000; Gajewski et al., 2008; Roelofs et al., 2006).

A larger N2 following more conflicting inputs is thought to reflect more conflict between correct and incorrect response tendencies primed by the conflicting stimulus inputs (Yeung et al., 2004; Yeung and Nieuwenhuis, 2009; Falkenstein et al., 1999, 2000; Gajewski et al., 2008; Roelofs et al., 2006). Again, the notion of conflicting responses triggered by stimulus inputs is in line with suggestions of the N2 reflecting a greater need for response selection or inhibition (Falkenstein et al., 1999, 2000; Gajewski et al., 2008; Roelofs et al., 2006).

In turn, theories that emphasize the evaluation of response or outcome expectations during performance monitoring (reinforcement learning theory or predicted response-outcome model) suggest that a higher Ne/ERN during errors reflects the fact that an error is a less expected event in contexts with a strong focus on correct responses (Holroyd and Coles, 2002; Alexander and Brown, 2011). Likewise, regarding the N2, correct responses after more prevalent conflicting inputs are the less expected event (Alexander and Brown, 2011) and thereby result in increased N2 amplitudes.

In summary, a common ground of empirical evidence is a variation of the Ne/ERN amplitude with the strength of the focus on correct responses and a variation of the N2 amplitude with the strength of conflicting stimulus inputs. Although existing theories differ in their view on the precise processes reflected in performance monitoring signals, we feel that this common ground of empirical evidence can be accounted for within the diverse existing theories. In the following, we will examine age differences across the lifespan in Ne/ERN and N2 amplitudes in light of the reviewed evidence and theoretical accounts. In doing so, we will in particular focus on accounts that inform the observed differences across the lifespan in the amplitudes of Ne/ERN and N2.

5.1. Lifespan age differences in stimulus- and response-locked ERPs during performance monitoring

When comparing ERP amplitudes across the lifespan, comparable measurement properties have to be assumed. We have recently shown that test-retest stability and reliability of ERPs related to performance monitoring are comparable across the lifespan (Hämmerer et al., 2013). Nonetheless, age differences in latency jitter between trials might affect the overall amplitude of ERPs. As of yet, few studies directly addressed whether age differences in ERP amplitudes are related to age differences in latency jitter of ERPs across trials. One that did – for the P3 – did not observe age differences in latency jitter between younger and older adults (Walhovd et al., 2008). On the other hand, Papenberg et al. (2013) recently observed lower inter-trial phase coherence in the theta range during NoGo trials in developing and aging individuals, indicating higher temporal variability in children, adolescents and older adults in comparison to younger adults. Moreover, age and individual differences in inter-trial theta coherence are related to performance indicators, for instance reaction time variability (Papenberg et al., 2013). However, direct empirical evidence is too scarce to be conclusive about the extent to which age differences in latency jitter may systematically contribute to amplitudes in ERPs in different age groups. As will be outlined in more detail below, relative to young adults, the N2 amplitudes are in general larger in children and smaller in older adults. Given higher variability in children as well as older adults, it is thus unlikely that age differences in temporal jitter alone contribute to lifespan age differences in ERP amplitudes.

Most of the evidence on lifespan age differences in ERPs during performance monitoring comes from studies that employed the Flanker or the Go/Nogo tasks (see Table 1 for an overview). Few developmental studies report both stimulus-locked as well as response-locked components. Here, we examine a lifespan pattern of stimulus- as well as response-locked ERPs during performance monitoring to inform age differences in subprocesses of performance monitoring. An empirical example from a lifespan study that included children, adolescents, younger and older adults is provided in Fig. 1 (cf. also Hämmerer et al., 2010). As shown in Table 1 and Fig. 1, when comparing response- and stimulus-locked components across the lifespan, a distinct pattern of ERP amplitudes during stimulus and response processing is apparent (indicated in italic font in Table 1). Compared to younger adults, children show larger N2 and smaller Ne/ERN amplitudes. In contrast, older adults show smaller N2 as well as smaller Ne/ERN amplitudes relative to younger adults. In the following, we will review age differences in response-locked ERPs and stimulus-locked ERPs during performance monitoring in more detail and outline their significance with respect to age differences in performance monitoring processes.

5.1.1. Lifespan age differences in response-locked ERPs: ERPs that reflect a focus on correct responses are reduced in children and older adults

An example of stimulus- and response-locked ERPs during performance monitoring in a lifespan study is given in Fig. 1 and Box 1. An overview of the current literature on this topic can be found in Table 1. As can be seen in Fig. 1 and Table 1, relative to younger adults, the majority of studies observed smaller Ne/ERN amplitudes in children or adolescents (Davies et al., 2004; Hogan et al., 2005; Kim et al., 2007; Ladouceur et al., 2004; Santesso et al., 2006; Van Meel et al., 2012; Wiersema et al., 2007) as well as older adults (Beste et al., 2010; Endrass et al., 2012; Falkenstein et al., 2001; Themanson et al., 2006). As reviewed above, a large Ne/ERN can be taken as an index of a stronger focus on correct response tendencies (Miller, 2000; Botvinick et al., 2001; Yeung et al., 2004; Yeung and Cohen, 2006). The consistent findings of reduced Ne/ERN amplitudes in children and older adults might thus indicate reduced top-down control to assure correct performance, or, relatedly, a reduced relevance of correct performance (cf. Segalowitz and Dywan, 2009; Falkenstein et al., 2000). A recent study that assessed the electrophysiological correlates of a speed versus accuracy instruction in older adults showed overall reduced

Table 1
Overview of studies using electrophysiological recordings to assess age differences in response conflict tasks.

Study	Age groups examined	Task used	Accuracy	Reaction time	Ne/ERN (error-related negativity)	Nc/CRN (correct-related negativity)	N2	PE (error positivity), post-error slowing	Other examined ERPs
Child developmental studies									
Davies et al. (2004)	Children, adolescents, younger adults (7–25 years)	Flanker task	Increases with increasing age[a]	Decreases with increasing age[a]	Increases with increasing age	Decreases with increasing age	–	No post-error slowing age effect, np Pe effect with age	–
Hogan et al. (2005)	Adolescents, younger adults (12–18; 18–22 years)	2 Forced-Choice task	Adolescents = younger adults[a]	Adolescents = younger adults[a]	Adolescents < younger adults	Adolescents = younger adults	–	No Pe age effect	–
Johnstone et al. (2005)	Children, adolescents, younger adults (7–47 years)	Go/Nogo task	Increases with increasing age	Decreases with increasing age	–	–	Decreases with increasing age	–	N1, P2, P3
Jonkman et al. (2003)	Children, younger adults (9–10 years; 19–23 years)	CPT-AX task	Children < adults	Children = younger adults	–	–	Children > younger adults	–	CNV, P3
Jonkman (2006)	Children, younger adults (6–7; 9–10; 19–23 years old)	CPT-AX task	Children < younger adults	Children > younger adults	–	–	Children > younger adults	–	P2, CNV, Cue-P3
Kim et al. (2007)	Children, younger adults (7–11; 21–25 years)	Go/Nogo task	Children = younger adults	Decreases with increasing age	Children = younger adults	(children > younger adults)	–	–	–
Lamm et al. (2006)	Children, adolescents (7–16 years)	Go/Nogo task	–	Decreases with increasing age	–	–	Children > adolescents	–	–
Santesso and Segalowitz (2008)	Adolescents, younger adults (15–16 years; 18–20 years)	Flanker task (Go/Nogo task)	Adolescents = younger adults (Adolescents < younger adults)	Adolescents = younger adults (Adolescents = younger adults)	Adolescents < younger adults (Adolescents < younger adults)	Adolescents = younger adults (Adolescents = younger adults)	–	Adolescents < younger adults in post-error slowing, no Pe age effects	–
Santesso et al. (2006)	Children, younger adults (10; 18–30 years)	Flanker task	Children < younger adults	Children > younger adults	Children < younger adults	(Children > younger adults)	–	No age effect	–
Van Meel et al. (2012)	Children, younger adults (6–9; 10–12 years)	Flanker task	Children < younger adults	Children > younger adults	Children < younger adults	Children > younger adults	Children > younger adults	–	–
Wiersema et al. (2007)	Children, adolescents, younger adults (7–8; 13–14; 23–24 years)	Go/Nogo task	Increases with increasing age	Decreases with increasing age	Children < adolescents = younger adults	–	–	No Pe age effect, no post-error slowing age effect	–
Lifespan studies									
Hämmerer et al. (2010)	Children, Adolescents, Younger Adults, Older Adults (9–10; 13–14; 20–30; 65–75 years)	AX-CPT task	Children < Adolescents < younger adults = older adults[b]	Children > Adolescents = younger adults < older adults; older adults > children[b]	–	–	Children = adolescents = younger adults > older adults; children > younger adults.	–	CNV, P3, Cue-P3,
Aging studies									
Beste et al. (2010)	Younger and older adults (21–51; 41–75 years)	Go/Nogo Task	Older adults > Younger adults	Older adults > young adults	–	–	Older adults < younger adults	–	P3

Table 1 (Continued)

Study	Age groups examined	Task used	Accuracy	Reaction time	Ne/ERN (error-related negativity)	Nc/CRN (correct-related negativity)	N2	PE (error positivity), post-error slowing	Other examined ERPs
Endrass et al. (2012)	Younger adults, older adults (19–28; 62–80 years)	Flanker task (speed or accuracy instruction)	Older adults = younger adults	Older adults > younger adults	Older adults < younger adults	Older adults = younger adults	–	–	–
Falkenstein et al. (2001)	Younger adults, older adults (19–25; 54–65 years)	Flanker task	Older adults = younger adults	Older adults > younger adults	Older adults < younger adults	Older adults = younger adults	–	–	–
Nieuwenhuis et al. (2002)	Younger adults, older adults (18–23; 60–80 years)	Flanker task	Older adults > younger adults	Older adults > younger adults	Older adults < younger adults	–	–	–	–
Themanson et al. (2006)	Younger adults, older adults (18–21; 60–71 years)	Switch task	Older adults = younger adults	Older adults > younger adults	Older adults < younger adults	–	–	No post-error slowing age effect	–
Wascher et al. (2011)	Younger adults, older adults (19–26; 50–70 years)	AX-CPT task	–	Older adults > younger adults	–	–	Older adults < younger adults	–	Cue-P3

CNV: Contingent negative variation.
a Controlled for inter-individual speed-accuracy trade off.
b Controlled for inter- and intraindividual speed-accuracy trade-off.

Box 1: Lifespan age differences in stimulus- and response-locked ERPs during a Go/Nogo task.

A distinct pattern of ERP amplitudes across the lifespan can be observed in stimulus-locked and response-locked components. Stimulus-locked ERPs (N2 to Go and Nogo stimuli) are largest in children and smallest in older adults (linear lifespan contrast: $t = 3.78$, $p < .01$, $d = 0.68$ for Go stimuli; $t = 8.76$, $p < .01$, $d = 1.65$ for Nogo stimuli). With respect to the response locked ERPs (lower panels), Ne/ERN amplitudes after errors are smaller in children and older adults (curvilinear lifespan contrast: $t = -2.31$, $p < .01$, $d = .36$) while Nc/CRN amplitudes after correct responses are larger (curvilinear lifespan contrast: $t = 3.56$, $p < .01$, $d = .55$), suggesting a reduced focus on the correct response tendency and higher uncertainty during correct responses in children and older adults. For data preprocessing methods and task details, see Hämmerer et al. (2010).

Although there is a higher level of experienced conflict in children, the conflict signal may not trigger top-down control effectively to focus on the correct response tendency, due to an immature prefrontal network. In contrast, in older adults, a strong reduction in stimulus-locked ERPs is observed, suggesting weaker stimulus inputs or a reduced processing of stimulus inputs based on task set representations. Reduced stimulus inputs might then engender less discernable response tendencies and explain the observed reduced focus on correct response tendencies in older adults (see text for details). (Data adapted and reanalyzed from Hämmerer et al., 2010 with permission. Copyright 2010 Elsevier)

Ne/ERN amplitudes but an increase of the Ne/ERN under the accuracy instruction (Endrass et al., 2012). If a larger Ne/ERN is taken as an indicator of stronger top-down control, this would suggest that an adaptation of the strength of the focus on correct responses is still possible in old age, although overall levels of top-down control are reduced. It is an interesting topic for future studies whether emphasizing performance accuracy may modulate Ne/ERN amplitude in children.

Fewer and less reliable findings exist with respect to developmental effects in the Nc/CRN (cf. Table 1). In children, a higher Nc/CRN has been repeatedly observed (Kim et al., 2007; Santesso et al., 2006; Van Meel et al., 2012; but see Davies et al., 2004 for a smaller Nc/CRN in children as compared to younger adults). If the Nc/CRN is to be taken as an index of uncertainty during execution of the correct response, this would suggest that children are less certain about their correct responses. In the elderly, increased Nc/CRN amplitudes have been observed in the context of reinforcement learning tasks (see also below). While the Nc/CRN decreased with learning in younger adults, it remained high in older adults (Pietschmann et al., 2008). In response conflict tasks, two studies have shown similar Nc/CRN amplitudes in younger and older adults (Endrass et al., 2012; Falkenstein et al., 2001). To date, there is hence too little evidence to conclusively suggest that response-locked components in older adults are indicative of higher uncertainty during correct responses.

Taken together, reduced Ne/ERN amplitudes and a trend for increased Nc/CRN amplitudes in children suggest a reduced focus on correct response tendencies during child development. Such a reduced focus on correct responses might relate to a reduced emphasis on correct performance as well as to more uncertainty during correct responses. With regard to existing theories of performance monitoring this might be indicative of a reduced ability or willingness to ensure correct responses by exerting response control in the form of enhanced response selection or response inhibition. Somewhat analogously, according to theories that emphasize the evaluation of response or outcome expectations, this might indicate a reduced certainty or expectation of a
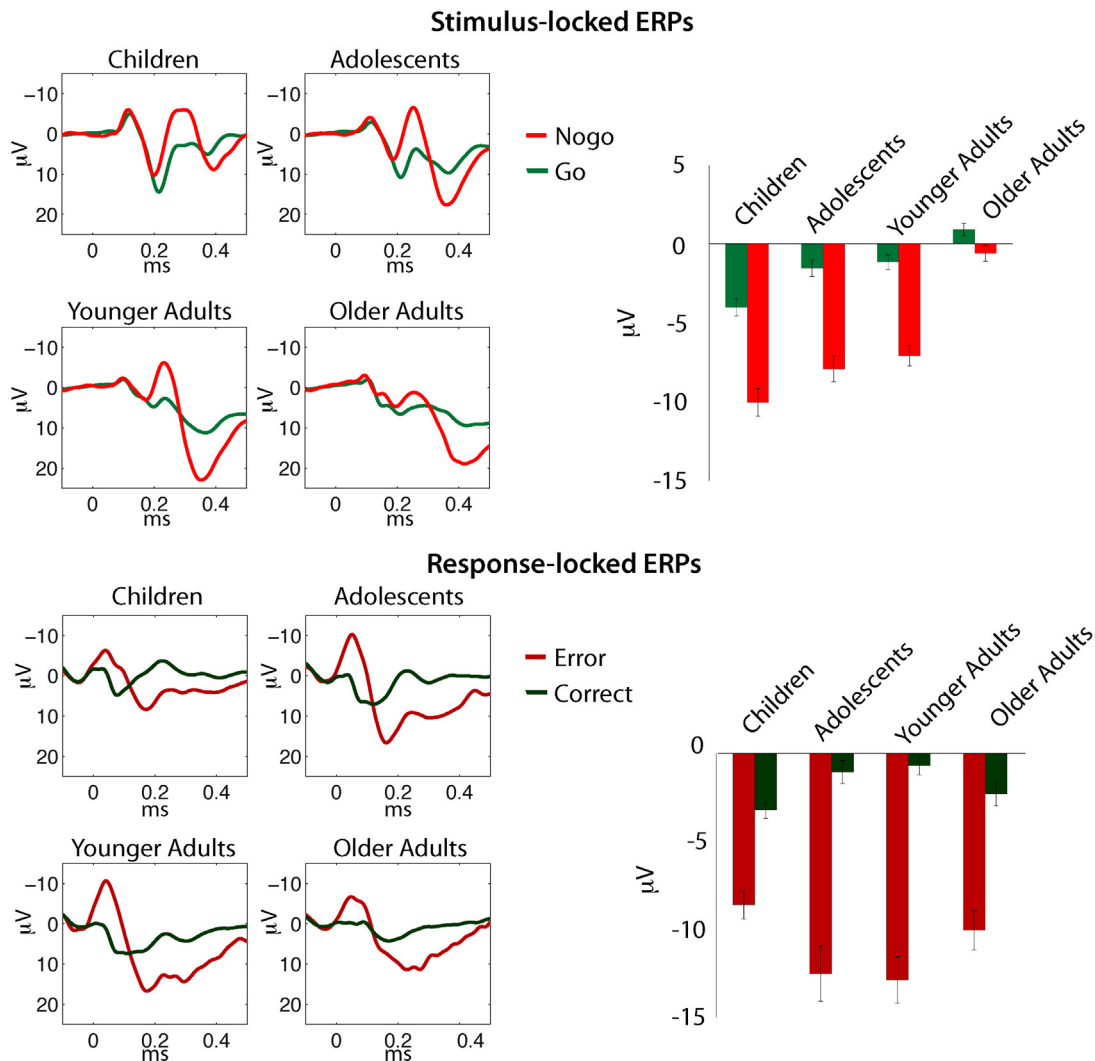
Fig. 1. Lifespan age differences in stimulus- and response-locked ERPs during a Go/Nogo task at electrode FCz (Bar graphs indicate mean amplitude for each age group. Error bars denote 1 SE of the mean). This exemplary result (as well as findings from the majority of studies, see Table 1) suggests different neural correlates for the maturation and senescence of cognitive control processes during performance monitoring.

correct response. The fact that children and adolescents commit more errors during response conflicts is coherent with the assumption of a reduced ability or willingness to assure correct responses. However, older adults do not commit more errors than younger adults, a reduced focus on correct responses alone can thus not explain the observed reduced ERN amplitudes during aging.

5.1.2. Lifespan age differences in stimulus-locked ERPs: ERPs that reflect processing of conflicting stimulus inputs are increased during maturation and reduced during aging

Differences between age groups seem to be more pronounced in stimulus-locked ERPs. The N2 component is larger in children (Hämmerer et al., 2010; Johnstone et al., 2005; Jonkman, 2006; Jonkman et al., 2003; Lamm et al., 2006), suggesting that they react more sensitively to conflicting stimulus inputs and/or that stimulus-induced response conflict is experienced to a greater extent (cf. also upper part of Fig. 1). Compared to evidence from children and adolescents, a rather different pattern of ERP components is observed in older adults (cf. upper part of Fig. 1). Here, the N2 following incongruent or distracting stimuli during response conflict tasks is clearly reduced in comparison with younger adults (Beste et al., 2010; Wascher et al., 2011; Hämmerer et al., 2010; Nieuwenhuis et al., 2002). This suggests reduced

levels of stimulus-induced conflicts or a reduced sensitivity to stimulus-induced conflicts in older adults as compared to the other age groups. The frequently observed slowing of older adults during response conflicts might thus be related to a weaker or prolonged accumulation of response-related stimulus evidence.

Taken together, response-related ERPs suggest a reduced ability or willingness to focus on correct responses during maturation as well as during aging. This matches well with the increased error rates observed in children and adolescents. Higher N2 amplitudes – which increase with a stronger impact of distracting stimulus inputs – also suggest that the filtering of relevant inputs during stimulus processing is still subject to further development in these two maturing age groups. This inability to filter inputs might further contribute to the observed greater tendency to fall prey to misleading stimulus inputs. In contrast, older adults show smaller Ne/ERN amplitudes but are rather prone to slowed responding than to committing more errors. In addition, their N2 amplitudes are clearly reduced as compared to the other age groups. Unlike children and adolescents, in whom a reduced ability to isolate relevant stimulus inputs and response tendencies might be assumed, in the case of older adults, the reduced N2 suggests that their ability to focus on correct responses during performance monitoring may be compromised by a reduction in the strength of stimulus inputs. In the

following, we examine these hypotheses in more detail in light of current empirical and modeling evidence. In doing so, we put specific emphasis on theories that differentiate the processes reflected in response- and stimulus-locked ERPs.

According to the conflict monitoring theory (Botvinick et al., 2001; Yeung et al., 2004), a larger conflict signal (e.g., as reflected in a larger N2 amplitude) should lead to more deployment of top-down control, which, in turn, reduces performance errors that are usually associated with a smaller amplitude of the Ne/ERN. Specifically, the initiation of top-down control via lateral prefrontal areas is thought to be associated with stronger conflict-related activation in medial frontal cortex (Kerns, 2006; King et al., 2010). This does not seem to be the case in children and adolescents. Instead, the fact that children and adolescents are more prone to committing errors (Davies et al., 2004; Hämmerer et al., 2010; Hogan et al., 2005; Lorsbach and Reimer, 2008; Santesso et al., 2006; Van Meel et al., 2012; Johnstone et al., 2005) while showing larger N2 amplitudes suggests that they experience more conflict or react stronger to conflicting inputs. The experienced conflict does not trigger sufficient top-down control to focus on the correct response tendency in the future. Interestingly, the same pattern—high N2 components and low Ne/ERN components—has also been observed in a patient with left hemispheric ACC lesions, a structure that is implicated in the detection of conflicts and the targeting of controlling areas (Swick and Turken, 2002). This parallel is especially interesting given evidence of a reduced volume of the ACC during child development (Gogtay et al., 2004; Sowell et al., 2003). Computational models that alter specific subprocesses of performance monitoring and predict ERP amplitudes might provide further indicators of the subprocesses affected during child development. In particular, a model with reduced translation of conflict into attentional control replicated the pattern of higher N2 and lower Ne/ERN amplitude observed in children and adolescents (Yeung and Cohen, 2006). One possible interpretation of the pattern of increased N2 amplitudes and reduced Ne/ERN amplitudes during maturation is hence that response conflicts trigger top-down control to a lesser extent in children and adolescents compared to younger adults. This might be related to the fact that their medial and lateral prefrontal cortex is not yet fully developed (Gogtay et al., 2004; Sowell et al., 2003) as well as less well-connected than in younger adults (Hwang et al., 2010).

As outlined above, older adults often show slower responses in conditions involving response conflicts (Nieuwenhuis et al., 2002; Hämmerer et al., 2010; Falkenstein et al., 2001; Endrass et al., 2012; Themanson et al., 2006; Wascher et al., 2011) while they do not commit more errors than younger adults (Falkenstein et al., 2001; Nieuwenhuis et al., 2002; Hämmerer et al., 2010; Themanson et al., 2006; Endrass et al., 2012). Together with the reduced Ne/ERN as well as reduced N2 amplitudes in older adults, this suggests that both the focus on a correct response as well as the impact of distracting stimulus inputs is reduced in the elderly. This reduction in ERP amplitudes cannot be attributed to overall reduced ERP amplitudes in older adults as, e.g., the Nc/CRN amplitude has been shown to be the same or even larger in the elderly as compared to younger adults (see above).

Since both the fostering of correct response tendencies as well as the monitoring of distracting stimulus inputs are reduced in elderly, a likely candidate for an aging-related change in performance monitoring is a reduction in the strength of relevant as well as distracting inputs. Such a reduction might be explained by weaker stimulus inputs or a weaker attentional modulation of stimulus inputs according to the current task set. The smaller N2 observed in older adults might hence be related to less distinct representations of conflicting stimulus inputs and consequently weaker emerging response tendencies. Indeed, reduced N2 amplitudes have been observed in those elderly who show larger ERPs

indicating attentional distractability (P3a) during a Go/Nogo task (Hämmerer et al., 2010). Besides, modeling work also shows that reduced stimulus inputs as well as a reduced attentional focus on stimulus inputs in general can result in lower N2 amplitudes as well as prolonged reaction times (Yeung and Cohen, 2006). Also, computational studies have suggested that aging-related declines in dopaminergic modulation of neuronal gain control result in less distinctive stimulus or task representations (Li et al., 2001, 2005; Eppinger et al., 2011).

A less distinctive task-set guided attentional bias compromises the build-up of correct and incorrect response tendencies alike and should result in less discernable response tendencies during correct responses as well as during incorrect ones. Such a deficit might explain the less distinct Nc/CRN and Ne/ERN amplitudes that have been observed in older adults[1] (Falkenstein et al., 2001; Endrass et al., 2012; Pietschmann et al., 2008) as well as the prolonged reaction times during aging.

Indeed, there is evidence of increased global switch costs in elderly that occur in conditions of increased need for maintaining different task sets (Kray, 2006; Kray and Lindenberger, 2000), as well as evidence of an outsourcing of task set representations in the form of a stronger reliance on guiding cue stimuli (Mayr, 2001; Lindenberger and Mayr, 2013; Spieler, 2006; see also below). This also points to a particular deficit of older adults in maintaining task set information.

Taken together, during maturation, we observe a strong response to critical stimulus inputs and weak ERPs associated with the monitoring of errors. In contrast, during aging, we observe a reduced response to conflicting stimulus inputs and weak ERPs associated with the monitoring of errors. These age-specific patterns of stimulus- and response-related ERPs during performance monitoring can be interpreted in light of existing performance monitoring theories and concurrent evidence and provide a basis for developing hypotheses on age-specific deficits in performance monitoring across the lifespan. Specifically, a strong monitoring response to conflicting inputs during maturation and a weak response to errors suggest a particular deficit to translate experienced conflicts into stronger top-down control on correct inputs and responses. This assumption is guided by modeling work that details the processing of conflicts and fostering of control and is in line with empirical evidence on an underdeveloped control system in medial and lateral frontal cortices during maturation. During aging, a different ERP pattern suggests different age-specific deficits. Specifically, a weak monitoring response to conflicting inputs as well as to correct response tendencies suggests a general reduction in the monitoring of correct and incorrect response tendencies. As outlined above, such a general reduction might be explained by weaker stimulus inputs or a weaker attentional modulation of stimulus inputs according to the current task set. As a first hint for the correctness of these assumptions, older adults that show reduced N2 amplitudes to conflicting stimulus show also increased attentional distractability during a performance monitoring task.

In the following, we review these hypotheses further in light of evidence from fMRI studies that assess lifespan age differences in performance monitoring. Here, we put a particular emphasis on age differences in prefrontal structures that support the initiation of top-down control as well as the maintenance of task set

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[1] Note that a response strategy that emphasizes accuracy over speed should contribute to higher Ne/ERN amplitudes in older adults than in younger adults (cf. Gehring et al., 1993a,b), which have, in fact, not been observed, suggesting that reduced N2 amplitudes in elderly are not indicative of a stronger focus on relevant stimulus inputs.

representations as these subprocesses have been identified as being in particular affected.

6. Lifespan age differences during performance monitoring in fMRI studies

6.1. Under-recruitment of prefrontal areas during higher task demands in children and adolescents

The majority of fMRI studies on the maturation of performance monitoring report an under-recruitment of lateral prefrontal areas especially during challenging task conditions both in children and adolescents (Bunge et al., 2002; Crone et al., 2006; Rubia et al., 2006). Furthermore, connectivity analyses with resting state data have shown a general trend of more short-range, but less long-range connections in children as compared to younger adults (Fair et al., 2007, 2009). Specifically, during the transition from adolescence to adulthood, an increase in the strength of effective connectivity between lateral and medial frontal cortex, lateral prefrontal cortex and parietal cortex as well as lateral prefrontal cortex and thalamus has been observed (Hwang et al., 2010). This finding is of particular relevance as a link between medial and lateral prefrontal areas is implicated in the initiation of top-down control following conflicting stimulus inputs. Overall, findings from developmental connectivity studies thus lend support for the conjecture of a failure to exert top-down control when stronger cognitive control is required.

So far, only few studies have attempted to disentangle age-related and performance-related differences in prefrontal activations during development. Crone et al. (2006) observed positive correlations of frontal activations and better performance during a 2-choice rule switch task that were independent of age differences within the sample. Rubia and colleagues (2006) observed a positive correlation between performance on the Simon task and inferior frontal activations in addition to performance-independent age-related increases in frontal brain areas. In line with the assumption of a particular deficit to initiate top-down control, fMRI studies thus suggest an increase in prefrontal control-related activations during maturation that is associated with developmental improvements in performance.

Interestingly, some studies show greater parietal activations in children as compared to adults during response conflict tasks (Casey et al., 2005). For instance, a study by Rubia and colleagues observed an increase in prefrontal and a decrease in parietal activations during maturation (Rubia et al., 2006). This might suggest that immature prefrontal control in children and adolescents might be countered by a greater orientation toward bottom-up processing of task inputs that implicate the parietal regions. In line with this, a recent review by Posner and colleagues (2012) suggests that a maturational shift from externally toward internally driven control, is accompanied by a shift from cholinergically toward dopaminergically modulated control networks. Cholinergic projections from the basal forebrain are thought to regulate orienting behavior that is necessary for noticing the need for adaptive actions (Posner et al., 2012). Further support for this interpretation comes from a study that shows higher parietal and insula activations in children that is correlated with better performance, whereas more active frontal areas were predictive of better performance in younger adults (Bunge et al., 2002). Finally, children show stronger connections within parietal cortex as compared to adolescents and younger adults, while adults show stronger connections between lateral and medial frontal cortex, lateral prefrontal cortex and parietal cortex as well as lateral prefrontal cortex and thalamus (Hwang et al., 2010). Taken together, these findings suggest that during childhood, the top-down control network that exerts response control

via top-down regulation of lateral prefrontal areas is not yet in place; instead, parietal areas appear to contribute more to cognitive control than in adult samples. Future studies should address whether this stronger involvement of parietal areas is related to a greater reliance on stimulus-oriented processing and bottom-up control during maturation.

6.2. Over-recruitment of prefrontal areas during lower task demands in older adults

In older adults, the contribution of prefrontal control areas to performance monitoring and cognitive control is less consistent across studies. In some studies, relative to younger adults, older adults over-recruit the prefrontal areas already at easier task levels (DiGirolamo et al., 2001; Hedden et al., 2012; Nagel et al., 2009, 2011) suggesting that non-challenging tasks have to be met with greater top-down control in older adults than in younger adults. However, whether stronger prefrontal activations in older adults are indicative of compensatory or impedimentary recruitment of prefrontal areas differs between studies. Additional prefrontal activations in older adults have been found to be associated with better performance (Hedden et al., 2012) or worse performance (Colcombe et al., 2005; Nielson et al., 2002). This may, in part, reflect the increased between-person heterogeneity during aging. To better understand the inconsistencies across studies, a better anatomical delineation of the involved prefrontal areas is also in order. For instance, a recent meta-analysis by Spreng and colleagues (2010) showed that worse performing older adults tended to show higher activations in the right inferior and middle frontal gyri, while older adults with relatively better performance showed higher activations in left middle frontal gyrus in a range of perceptual, executive and memory tasks.

Taken together, in comparison to younger adults, older adults tend to over-recruit prefrontal areas already at lower task demands. Interestingly, a study that contrasted task periods that require the maintenance of one or two task sets showed similar lateral prefrontal recruitment in older adults in both conditions, while younger adults only showed increased activation in the condition with more demanding task-set maintenance (DiGirolamo et al., 2001). This suggests that increased prefrontal activations already at lower task demands in the elderly might in part be related to more effortful task set maintenance. Finally, studies that focus on age-specific deficits in cognitive control suggest that older adults find it particularly difficult to exert proactive, task-set based control during stimulus processing (Braver et al., 2001; Paxton et al., 2008) and to suppress irrelevant information in working memory paradigms (Clapp et al., 2011; Gazzaley et al., 2005). Interestingly, the suppression deficit in working memory contexts is related to a less differentiated early processing of target and distractor stimuli (Gazzaley, 2011; Störmer et al., 2013), pointing again to particular difficulties of older adults in anticipatory stimulus selection, possibly due to weaker task representations that limit anticipatory filtering of task-relevant inputs.

In summary, evidence from developmental fMRI studies during response conflict tasks corroborates our conjecture of age-specific deficits postulated based on the pattern of stimulus-related and response-related ERP components across the lifespan. In particular, the conjecture of a reduced ability to initiate top-down control in children is supported by evidence of reduced lateral prefrontal activations during task conditions of stronger control demands. Furthermore, resting-state and functional connectivity studies suggest underdeveloped medial-lateral frontal connections in children, which might affect the translation of monitored conflicts into stronger top-down control. Additionally, stronger parietal activations during tasks demanding cognitive control raise the question whether a stronger tendency to employ stimulus-driven
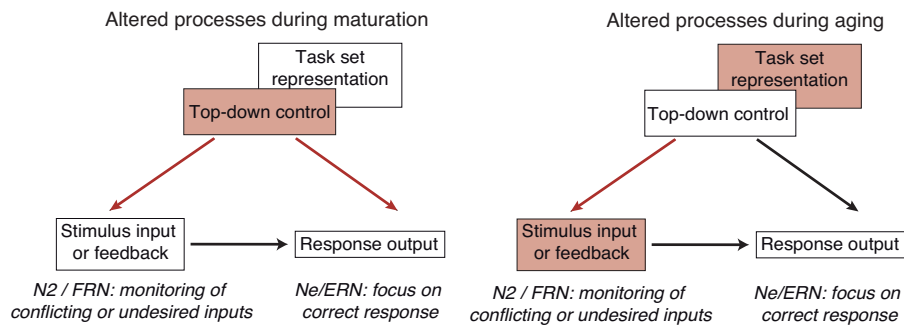
Fig. 2. Schematic overview of lifespan age differences in performance monitoring during response conflicts and decision making tasks. Subprocesses which appear to be particularly difficult during maturation or aging are marked in red. During maturation (left graph), a strong response to undesired or conflicting inputs (N2 or FRN) is observed, while the Ne/ERN that reflects the focus on correct responses is reduced. A particular deficit during maturation appears to be hence the translation of experienced conflicts during stimulus processing into stronger top-down control during response processing. In contrast, during aging (right graph), reduced N2/FRN as well as reduced Ne/ERN amplitudes are observed. A deficit in processing stimuli based on task set representations could explain this particular ERP pattern. Weaker stimulus representations might then in turn lead to a reduced ability to focus on the correct response. More effortful task set maintenance as well as less distinct stimulus inputs thus affect both, stimulus and response-related potentials (see text for details).

control mechanisms exists in childhood. With respect to aging, an increase in prefrontal activations is frequently observed. However, the evidence as to whether these increased activations support or hinder performance monitoring is mixed. Tasks that varied the relevance or difficulty of maintaining task set representations however showed more effortful and less anticipatory task set maintenance in older adults. These findings are in line with the suggested greater difficulties of older adults to monitor critical events based on task-set representations (for an overview of these age-specific differences in performance monitoring see Fig. 2).

7. New insights about lifespan development of performance monitoring

The present review has put a particular emphasis on electrophysiological indicators to understand the development of performance monitoring across the lifespan. A range of well-established ERPs related to performance monitoring has been heavily researched in the last decades in adults as well as in developmental and aging samples. Existing theories on the cognitive processes reflected in these ERPs provide – also with the help of computational models – a rich literature for interpreting age differences in these ERPs and for formulating conjectures about age differences in cognitive processes during performance monitoring. The higher temporal resolution of electrophysiological data allows for a separation of performance monitoring processes related to stimulus or response processing (Ullsperger et al., 2014). The ability to separate such processes has proven especially helpful in understanding age-related differences. We have provided a summary of the pattern of stimulus- and response-related ERPs across the lifespan during performance monitoring and evaluated the related cognitive age differences in light of existing theories of performance monitoring. Age-specific deficits in performance monitoring ERPs explain age-specific deficits observed in behavioral data and are supported by evidence observed in fMRI studies. Our review hence offers new insights into age differences in the dynamics of performance monitoring that are helpful in interpreting the observed qualitative differences across the lifespan.

7.1. Experienced conflicts trigger less top-down control in children

In children and adolescents, the greater propensity to commit errors during response conflicts can be understood as a reduced ability to react to response conflicts with an increase in top-down control. Increased susceptibility to distracting stimulus inputs – as evident in larger N2 amplitudes – but reduced error-related ERPs

(Ne/ERN), that indicate a reduced focus on correct responses, are observed during maturation. Experienced conflicts should result in increased top-down control to bias processing of relevant stimulus inputs and correct response tendencies. Increased responses to conflicts and a reduced focus on correct response during maturation indicate thus a reduced ability to initiate top-down control. Neuroanatomical and neurochemical changes of prefrontal structures and in particular a prolonged development of long-range connections as well as medial-to-lateral connections in prefrontal cortex might underlie the reduced ability to initiate top-down control following response conflicts. Finally, parietal areas are more active during cognitive control in children and adolescents as compared to younger adults. This suggests a qualitative change in cognitive control functions during child development, progressing from parietally-related bottom-up, stimulus driven task control to prefrontally-based top-down control (Luna and Sweeney, 2004; Munakata et al., 2012; Posner et al., 2012).

7.2. Weaker stimulus processing and task set maintenance in older adults

Older adults are not more likely to commit errors during response conflicts, but show prolonged reaction times. Given that error rates are similar to younger adults but electrophysiological indices of experienced conflict during stimulus processing (N2 amplitudes) are lower, their performance monitoring deficit is suggested to arise from difficulties in stimulus processing that affect correct and incorrect response tendencies alike, namely weaker task-set representations. Electrophysiological evidence shows a reduced response to conflicting stimulus inputs as well as reduced error-related ERPs. It is thus possible that the focus on correct responses during errors is compromised by weaker stimulus inputs that prime these responses. Neuroanatomical and neurochemical changes support the assumption of a deficit in task set representations, given the decline in prefrontal cortex and dopaminergic modulation of frontal areas, which is thought to be relevant for task set maintenance (D'Ardenne et al., 2012). Electrophysiological (Hämmerer et al., 2010) as well as fMRI (Paxton et al., 2008) evidence further confirms a reduced ability to use task-set related information in guiding stimulus processing.

7.3. Similarities between lifespan age differences in monitoring response conflicts and value-based decisions

It is conceivable that insights in age differences of performance monitoring during response conflict tasks generalize to age differences in monitoring during decision making tasks. Performance

monitoring encompasses both, response conflict monitoring as well as action outcome monitoring, e.g., during decision making or reinforcement learning (Ridderinkhof et al., 2004). Response conflict and outcome monitoring rely on partially overlapping brain areas, with motivational control processes involving mostly ventral prefrontal and striatal areas, and cognitive control processes supported mostly by medial dorsal and lateral prefrontal as well as dorsal striatal areas (see Haber and Knutson, 2010 for a review). Moreover, ERP potentials observed during reinforcement learning tasks (Ne/ERN, Nc/CRN, and FRN – Feedback-related negativity, an N2-like component; Miltner et al., 1997; Holroyd and Coles, 2002) resemble those observed during response conflict tasks.

Before assessing similarities in age effects in these two domains of performance monitoring, we first assess similarities and differences in ERPs during response conflicts and decisions. ERPs related to performance monitoring during decision making or reinforcement learning have been reviewed extensively elsewhere (Santesso et al., 2011; Walsh and Anderson, 2012; San Martin, 2012). The FRN is typically observed to be largest following loss or error feedback in reinforcement learning or gambling tasks (Miltner et al., 1997; Gehring and Willoughby, 2002). However, an increased FRN can be observed after positive and negative events alike, as long as they are unexpected or undesired in a given context (Talmi et al., 2013). Moreover, the FRN does not reflect an absolute or graded appraisal of potential outcomes, but rather a dichotomous evaluation of desired and undesired outcomes given a certain context (Holroyd et al., 2004). In line with this, studies that explored the relationship of positive and negative prediction errors and N2 on the single trial level showed that the distinction of positive and negative outcomes is reflected in the FRN, while the size of the prediction error varies with the ensuing P3 amplitude (Philiastides et al., 2010; Fischer and Ullsperger, 2013). Finally, the FRN is larger if errors are consequences of own volitional actions as compared to instructed actions (Yeung et al., 2005).

Evidence on processes reflected in response-locked components is comparatively sparse. A larger Ne/ERN is observed if the correct response is more certain (Holroyd and Coles, 2002; Nieuwenhuis et al., 2002; Eppinger et al., 2008, 2009). In turn, a larger Nc/CRN is thought to reflect more uncertainty during correct responses (Scheffers and Coles, 2000; Pailing and Segalowitz, 2004; Santesso et al., 2011).

Taken together, parallel processes in performance monitoring signals during decision making and during response conflicts emerge. In both contexts, the Ne/ERN varies with the certainty of correct responses or the focus on correct responses. Likewise, increased Nc/CRN amplitudes are thought to reflect uncertain responses in both domains. In response conflict tasks, the N2 is larger for conflicting stimulus inputs, whereas in decision making or reinforcement learning tasks, the FRN is larger for undesired or unexpected action outcomes. A common theme for stimulus-locked components is hence that they are larger for events that indicate a threat to correct performance. Moreover, FRN as well as N2 reflect a monitoring of events at a higher level, independent of the actual nature of the event (response inhibition or response execution; gain or loss outcome). Also, both N2 components are larger if correct performance is emphasized (Potts, 2011; Santesso et al., 2011), and thus appear to be in part driven by the strength of the monitoring focus. Given the many parallels, it is thus conceivable that the processes reflected in stimulus-locked N2 amplitudes during response conflicts and during decision making are comparable.

An important conceptual difference, however, is that the experimental variation of expected action outcomes – and thereby the importance of unexpected or undesired events – is easier in decision making or reinforcement learning tasks as compared to response conflict tasks. It is for instance possible to compare the relative importance of positive, neutral or negative outcomes or to assess the change of outcome values in different reward contexts. Such a relative evaluation of outcome expectations in monitoring responses has been a particular focus in studies of performance monitoring during decision making, also in age comparative studies.

Studies investigating lifespan age differences in ERPs of performance monitoring during decision making or reinforcement learning are summarized in Table 2. As in the case of the N2 during monitoring conflicting stimulus inputs, reduced FRN amplitudes are consistently observed in older adults during reinforcement learning and decision making tasks (Nieuwenhuis et al., 2002; Eppinger et al., 2008; Mathewson et al., 2008; Bellebaum et al., 2011; Eppinger and Kray, 2011; Hämmerer et al., 2011; Pietschmann et al., 2008, 2011). Apart from absolute amplitude differences during aging, a reduction in the separation of gains and losses in the monitoring of outcomes as evident in less distinct FRN amplitudes to the two outcomes has also frequently been observed (Nieuwenhuis et al., 2002; Hämmerer et al., 2011). More distinct FRN amplitudes to different outcomes are thereby understood as reflecting a stronger focus on desired action outcomes (Holroyd et al., 2004). Importantly, less differentiated responses to gain and loss feedback in older adults are observed specifically in conditions where feedback is less reliable (probabilistic) (Nieuwenhuis et al., 2002; Eppinger et al., 2008; Hämmerer et al., 2011). If a formation of outcome expectations is more challenging, older adults apparently fail to form expectations that allow for a distinct evaluation of action outcomes (cf. also Eppinger et al., 2011; Hämmerer and Eppinger, 2012 for a more thorough discussion of this view). Analogously, older adults are less able than younger adults to develop relational outcome representations during learning (i.e. distinct FRN amplitudes in ambiguous reward contexts: neutral versus gain or neutral versus loss feedback; Eppinger and Kray, 2011). Older adults are hence less able to rely on value representations or outcome expectations during feedback evaluation. This finding is compatible with the notion of a reduced attentional focus based on reduced task set representations as observed during response conflict monitoring in elderly outlined above.

Also during maturation, initial evidence suggests parallels between the development of response conflict monitoring and outcome monitoring. Regarding stimulus-locked components, a decrease in FRN amplitudes during maturation as in the case of response conflict monitoring is observed in the majority of studies (Eppinger et al., 2009; Hämmerer et al., 2011; Zottoli and Grose-Fifer, 2012; Crowley et al., 2013). However, as in the case of the older adults, despite an overall larger ERP amplitude, a less distinct response to gain and loss outcomes is observed in particular in children (Hämmerer et al., 2011; Zottoli and Grose-Fifer, 2012). Behavioral and heart rate responses show that children differentiate less than younger adults between informative and uninformative feedback (Crone et al., 2004, 2006). This suggests that their ability to use feedback to orient future actions is not yet fully developed. A reduced ability to translate the observed strong monitoring response to critical events into a behavioral adaptation appears thus to be a common theme of the monitoring of response conflicts and action outcomes during maturation.

Evidence in response-locked components is less consistent, some studies observed comparable Ne/ERN amplitudes (Pietschmann et al., 2008, 2011; Eppinger et al., 2009), some reduced NE/ERN amplitudes in older adults as compared to younger adults (Nieuwenhuis et al., 2002; Eppinger and Kray, 2011). Two studies examined the Nc/CRN in older adults and found similar amplitudes as compared to younger adults. These have been attributed to increased uncertainty during responses in older adults (Pietschmann et al., 2008, 2011). Interestingly, children as well as older adults showed particular decreases in Ne/ERN amplitudes if the feedback was less reliable, and a focus on the correct

Table 2
Overview of studies using electrophysiological recordings to assess age differences in reinforcement learning and decision making tasks.

Study	Age groups examined	Task used	Accuracy	Reaction time	Ne/ERN (error-related negativity)	Nc/CRN (correct-related negativity)	FRN (feedback-related negativity)	Other examined ERPs
Child developmental studies								
Crowley et al. (2013)	Children, adolescents (10–17 years)	Gambling task	–	–	–	–	*Children > late adolescents*	–
Eppinger et al. (2009)	Children, younger adults (10–12, 19–24 years)	Probabilistic reinforcement learning task	Children < younger adults	–	Children > younger adults	–	*Children > younger adults*	P3
Santesso et al. (2011)	Adolescents, younger adults (16–17, 18–29 years)	Gambling task	–	–	–	–	Adolescents = younger adults	–
Shephard et al. (2013)	Children, younger adults (10.2, 25.5 years)	Reversal learning task	Children < younger adults	Children > younger adults	–	–	*Children > younger adults*	Stimulus-related P3
Zottoli and Grose-Fifer (2012)	Adolescents, younger adults (14–27, 22–26 years)	Gambling task	Adolescents = younger adults	–	–	–	*Adolescents > younger adults*	–
Lifespan studies								
Hämmerer et al. (2011)	Children, adolescents, younger adults, older adults (9–10; 13–14; 20–30; 65–75 years)	Probabilistic reinforcement learning task	Children < adolescents < younger adults > older adults	–	–	–	*Children > adolescents > younger adults > older adults; children > younger adults*	–
Aging studies								
Bellebaum et al. (2011)	Younger adults, older adults (20–31, 52–67 years)	Probabilistic reinforcement learning task	Younger adults > older adults	–	–	–	*Younger adults > older adults*	P3
Eppinger and Kray (2011)	Younger adults, older adults (22.1, 69.7 years)	Probabilistic reinforcement learning task with neutral versus positive or neutral versus negative feedback	Younger adults > older adults	–	Younger adults > older adults	–	*Younger adults > older adults*	P3
Eppinger et al. (2008)	Younger adults, older adults (20.8, 68.5 years)	Probabilistic reinforcement learning task	Younger adults > older adults	–	Younger adults = older adults	–	*Younger adults > older adults*	P3
Ferdinand and Kray (2013)	Younger adults, older adults (20–27, 70–77 years)	Time estimation task	Younger adults > older adults	–	–	–	*Younger adults > older adults*	P3
Mathewson et al. (2008)	Younger adults, older adults (18–26, 65–87 years)	Maze learning task	Younger adults > older adults	Younger adults < older adults	–	–	*Younger adults > older adults*	P3
Nieuwenhuis et al. (2002)	Younger adults, older adults (18–23, 60–80 years)	Probabilistic reinforcement learning task	Younger adults > older adults	Younger adults = older adults	Younger adults > older adults	–	*Younger adults > older adults*	–
Pietschmann et al. (2008)	Younger adults, older adults (18–28, 60–71 years)	Reinforcement learning task	Younger adults > older adults	Younger adults < older adults	Younger adults = older adults	Younger adults = older adults	–	–
Pietschmann et al. (2011)	Younger adults, older adults (23.7, 66.1 years)	Probabilistic reinforcement learning task	Younger adults = older adults	Younger adults = older adults	Younger adults = older adults	Younger adults = older adults	*Younger adults > older adults*	P3

Note. Italics indicate study results that are in line with general picture across the lifespan as outlined in the text, i.e. children having larger N2 and smaller Ne/ERN components than younger adults and older adults showing smaller FRN and smaller Ne/ERN components.

responses therefore harder to establish (Eppinger et al., 2008, 2009; Pietschmann et al., 2011). Taken together, evidence in response-locked ERPs during decision making in different age groups thus confirms the increase in Ne/ERN with a stronger focus on correct responses. During decision making, a decrease in Ne/ERN during maturation and aging is less prominent as compared to response conflict tasks. This might be related to the fact that the certainty of the correctness of a response is more variable in decision making and probabilistic reinforcement learning tasks – in all age groups.

7.4. Summary

We have reviewed evidence of lifespan age differences in performance monitoring during response conflicts and decision making. A coherent picture of age-specific challenges emerges across behavioral, imaging, and in particular electrophysiological evidence of age differences during performance monitoring. In children and adolescents, a particular deficit to ensure correct response execution has been identified. ERPs that reflect the monitoring of response conflicts suggest an increased sensitivity to distracting stimulus inputs and a reduced focus on correct responses. Together with imaging evidence of a reduced connectivity of prefrontal top-down control areas, this suggests a weaker ability to initiate cognitive control following experienced response conflicts or undesired action outcomes. Likewise, during reinforcement learning or decision making, monitoring responses to undesired action outcomes are larger during maturation than in adulthood. However, children appear to make less use of the information provided by the feedback to adapt future choices. In general, performance monitoring during maturation is thus characterized by a strong sensitivity to external feedback that indicates the necessity for a behavioral adaptation, but a reduced ability or willingness to implement the relevant changes via internal control structures.

In older adults, prolonged reaction times during response conflicts have been observed. More importantly, a striking reduction in ERP amplitudes that reflect the monitoring of conflicting stimulus inputs or undesired actions outcomes is characteristic for older adults. In the domain of decision making or reinforcement learning, this is evident as a reduced separation of desired and undesired action outcomes. This is particularly evident in reward contexts that require the formation of outcome expectations. In light of imaging evidence that suggests particular difficulties of older adults to maintain or develop task set representations, we suggest that the aging performance monitoring system is in general characterized by weaker task set representations and task-set-related attentional modulation that impairs selective stimulus and response processing during performance monitoring.

8. Outlook and future research questions

The present review summarized behavioral, electrophysiological and fMRI results that reflect changes in performance monitoring across the lifespan. We hope to have provided an important first step toward identifying age-specific deficits in performance monitoring across the lifespan. Future studies should follow up on this attempt to understand mechanisms of these age-specific differences in performance monitoring. In the following, we outline three aspects of research on age differences in performance monitoring that in our view might be most relevant in this regard.

8.1. Formalizing lifespan age differences in performance monitoring using computational models

Model-based approaches provide an excellent tool to further test the hypotheses outlined in this review. They allow for the quantification of qualitative age differences within the same conceptual framework via an age-specific pattern of weights of nonlinearly interacting dynamic cognitive processes (see also Munakata et al., 2012 for a review of another successful example of using computational models to pinpoint qualitative age differences). In addition, experimental manipulations as well as training of specific cognitive subprocesses that are affected in different age groups (e.g. the difficulty in maintaining task sets or the difficulty of applying cognitive control) should be employed more often. This is for instance relevant to identify whether deficits observed during maturation or aging are due to capacity or strategy-related limitations. A combination of experimentally manipulated and computationally modeled target processes provides a powerful tool for the investigation of age-related limitations in functional subprocesses of performance monitoring, such as focusing on accurate responding or reacting to conflicting stimulus inputs.

8.2. Lifespan age differences in electrophysiological correlates of error awareness (Error positivity Pe)

Following the Ne/ERN, positive-going ERPs – often termed error positivity or Pe – are observed (Falkenstein et al., 1990). Unlike the Ne/ERN, which does not differentiate between conscious and unconscious error, the Pe is related to the conscious detection of errors and is larger with more error awareness (Falkenstein et al., 1990, 2000; Leuthold and Sommer, 1999; Steinhauser and Yeung, 2010; Hughes and Yeung, 2011). Up to now, few studies investigated developmental differences in conscious post-error adaptational processes as evident in the error positivity (Pe). Of those that did, many studies observe no age effect (cf. Table 1) while some did observe smaller Pe amplitudes during aging (Falkenstein et al., 1998; Band and Kok, 2000a,b). Future studies should investigate whether Pe amplitudes vary with error awareness to a similar extent across the lifespan. This would provide first insights into age differences in conscious post-error adaption.

8.3. Lifespan age differences in the temporal coherence of performance monitoring signals

Finally, in lifespan developmental research, the investigation of oscillatory electrophysiological processes during performance monitoring is still in its early stages (Beste et al., 2011; Müller and Anokhin, 2012; Papenberg et al., 2013; Schmiedt-Fehr and Basar-Eroglu, 2011). These studies, however, yield important insights into age-specific differences in performance monitoring. For instance, improved performance during response conflict tasks has been shown to relate to the temporal coherence of electrophysiological oscillations (faster target detection with faster synchronization of oscillations in stimulus-processing areas; Müller and Anokhin, 2012). In lifespan developmental studies, temporal coherence – also in monitoring-related oscillations – changes markedly across the lifespan (Müller et al., 2009; Papenberg et al., 2013; Sander et al., 2012; Werkle-Bergner et al., 2012). These age-related differences in temporal coherence also relate to behavioral age differences. For instance, increased response variability during response conflict tasks in children and older adults was related to a decreased inter-trial theta phase coherence of monitoring signals (Papenberg et al., 2013). Future studies should extent this research to investigate age differences in the temporal coherence between frontal areas that implicate top-down control and motor or sensory areas during performance monitoring.

in this paper. At the time of preparing this review, the first and third authors were affiliated with TU Dresden. The first author is currently at the University College in London. We thank other project members, Ulman Lindenberger and Hauke Heekeren, for valuable contributions to prior work associated with the FOR 778 research group.

References

Alexander, W.H., Brown, J.W., 2010. Computational models of performance monitoring and cognitive control. Top. Cogn. Sci. 2, 658–677, http://dx.doi.org/10.1111/j.1756-8765.2010.01085.

Alexander, W.H., Brown, J.W., 2011. Medial prefrontal cortex as an action-outcome predictor. Nat. Neurosci. 14 (10), 1338–1344, http://dx.doi.org/10.1038/nn.2921.

Arnsten, A.F.T., Li, B.M., 2005. Neurobiology of executive functions: catecholamine influences on prefrontal cortical functions. Biol. Psychiatry 57, 1377–1384, http://dx.doi.org/10.1016/j.biopsych.2004.08.019.

Aron, A.R., 2007. The neural basis of inhibition in cognitive control. Neuroscientist 13 (3), 214–228, http://dx.doi.org/10.1177/1073858407299288.

Azizian, A., Freitas, A.L., Parvaz, M.A., Squires, N.K., 2006. Beware misleading cues: perceptual similarity modulates the N2/P3 complex. Psychophysiology 43 (3), 253–260, http://dx.doi.org/10.1111/j.1469-8986.2006.00409.

Bäckman, L., Nyberg, L., Lindenberger, U., Li, S.C., Farde, L., 2006. The correlative triad among aging, dopamine, and cognition: current status and future prospects. Neurosci. Biobehav. Rev. 30 (6), 791–807, http://dx.doi.org/10.1016/j.neubiorev.2006.06.005.

Band, G.P.H., Kok, A., 2000a. Age effects on response monitoring in a mental-rotation task. Biol. Psychol. 51, 201–221, http://dx.doi.org/10.1016/S0301-0511(99)00038-1.

Band, G.P.H., Kok, A., 2000b. Age effects on response monitoring in a mental-rotation task. Biol. Psychol. 51 (2), 201–221, http://dx.doi.org/10.1016/S0301-0511(99)00038-1.

Bellebaum, C., Kobza, S., Thiele, S., Daum, I., 2011. Processing of expected and unexpected monetary performance outcomes in healthy older subjects. Behav. Neurosci. 125 (2), 241–251, http://dx.doi.org/10.1037/a0022536.

Bernstein, P.S., Scheffers, M.K., Coles, M.G., 1995. Where did I go wrong? A psychophysiological analysis of error detection. J. Exp. Psychol. Hum. Percept. Perform. 21 (6), 1312–1322.

Beste, C., Ness, V., Falkenstein, M., Saft, C., 2011. On the role of fronto-striatal neural synchronization processes for response inhibition – evidence from ERP phase-synchronization analyses in pre-manifest Huntington's disease gene mutation carriers. Neuropsychologia 49, 3484–3493.

Beste, C., Willemssen, R., Saft, C., Falkenstein, M., 2010. Response inhibition subprocesses and dopaminergic pathways: basal ganglia disease effects. Neuropsychologia 48, 366–373.

Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. Psychol. Rev. 108 (3), 624–652.

Botvinick, M., Nystrom, L.E., Fissell, K., Carter, C.S., Cohen, J.D., 1999. Conflict monitoring versus selection-for-action in anterior cingulate cortex. Nature 402 (6758), 179–181, http://dx.doi.org/10.1038/46035.

Braver, T.S., Cohen, J.D., 1999. Dopamine, cognitive control, and schizophrenia: the gating model. Prog. Brain Res. 121, 327–349, http://dx.doi.org/10.1016/S0079-6123(08)63082-4.

Braver, T.S., Barch, D.M., Cohen, J.D., 1999. Cognition and control in schizophrenia: a computational model of dopamine and prefrontal function. Biol. Psychiatry 46 (3), 312–328, http://dx.doi.org/10.1016/S0006-3223(99)00116-X.

Braver, T.S., Barch, D.M., Keys, B.A., Carter, C.S., Cohen, J.D., Kaye, J.A., Janowski, J.S., Taylor, S.F., Yesavage, J.A., Mumenthaler, M.S., Jagust, W.J., Reed, B.R., 2001. Context processing in older adults: evidence for a theory relating cognitive control to neurobiology in healthy aging. J. Exp. Psychol. Gen. 130 (4), 746–763, http://dx.doi.org/10.1037/0096-3445.130.4.746.

Brewer, N., Smith, G.A., 1989. Developmental changes in processing speed: influence of speed-accuracy regulation. J. Exp. Psychol. Gen. 118, 298–310, http://dx.doi.org/10.1037/0096-3445.118.3.298.

Bunge, S.A., Dudukovic, N.M., Thomason, M.E., Vaidya, C.J., Gabrieli, J.D., 2002. Immature frontal lobe contributions to cognitive control in children: evidence from fMRI. Neuron 33 (2), 301–311, pii:S0896627301005839.

Burlé, B., Vidal, F., Bonnet, M., 2004. Electroencephalographic nogo potentials in a no-movement context: the case of motor imagery in humans. Neurosci. Lett. 360 (1–2), 77–80, http://dx.doi.org/10.1016/j.neulet.2004.02.034, pii:S030439400400223X.

Carbonnell, L., Falkenstein, M., 2006. Does the error negativity reflect the degree of response conflict? Brain Res. 1095 (1), 124–130, http://dx.doi.org/10.1016/j.brainres.2006.04.004.

Casey, B.J., Tottenham, N., Liston, C., Durston, S., 2005. Imaging the developing brain: what have we learned about cognitive development? Trends Cogn. Sci. 9 (3), 104–110, http://dx.doi.org/10.1016/j.tics.2005.01.011, pii:S1364-6613(05)00030-6.

Casey, B.J., Trainor, R.J., Orendi, J.L., Schubert, A.B., Nystrom, L.E., Giedd, J.N., Castellanos, F.X., Haxby, J.V., Noll, D.C., Cohen, J.D., Forman, S.D., Dahl, R.E., Rapoport, J.L., 1997a. A developmental functional MRI study of prefrontal activation during performance of a Go-No-Go task. J. Cogn. Neurosci. 9 (6), 835–847, http://dx.doi.org/10.1162/jocn.1997.9.6.835.

Casey, B.J., Trainor, R., Giedd, J., Vauss, Y., Vaituzis, C.K., Hamburger, S., Kozuch, P., Rapoport, J.L., 1997b. The role of the anterior cingulate in automatic and controlled processes: a developmental neuroanatomical study. Dev. Psychobiol. 30 (1), 61–69, http://dx.doi.org/10.1002/(SICI)1098-2302(199701)30:1<61::AID-DEV6>3.0.CO;2-T.

Chudasama, Y., Robbins, T.W., 2006. Functions of frontostriatal systems in cognition: comparative neuropsychopharmacological studies in rats, monkeys and humans. Biol. Psychol. 73 (1), 19–38, http://dx.doi.org/10.1016/j.biopsycho.2006.01.005, pii:S0301-0511(06)00023-8.

Clapp, W.C., Rubens, M.T., Sabharwal, J., Gazzaley, A., 2011. Deficit in switching between functional brain networks underlies the impact of multitasking on working memory in older adults. Proc. Natl. Acad. Sci. U. S. A. 108 (17), 7212–7217, http://dx.doi.org/10.1073/pnas.1015297108.

Colcombe, S.J., Kramer, A.F., Erickson, K.I., Scalf, P., 2005. The implications of cortical recruitment and brain morphology for individual differences in inhibitory function in aging humans. Psychol. Aging 20 (3), 363–375, http://dx.doi.org/10.1037/0882-7974.20.3.363, pii:2005-13210-001.

Cools, R., D'Esposito, M., 2009. Dopaminergic modulation of flexible cognitive control in humans. In: Dopamine Handbook. Oxford University Press, Oxford, http://dx.doi.org/10.1093/acprof:oso/9780195373035.003.0017.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3 (3), 201–215, http://dx.doi.org/10.1038/nrn755.

Coxon, J.P., Van Impe, A., Wenderoth, N., Swinnen, S.P., 2012. Aging and inhibitory control of action: cortico-subthalamic connection strength predicts stopping performance. J. Neurosci. 32 (24), 8401–8412, http://dx.doi.org/10.1523/JNEUROSCI.6360-11.2012.

Crone, E.A., Donohue, S.E., Honomichl, R., Wendelken, C., Bunge, S.A., 2006. Brain regions mediating flexible rule use during development. J. Neurosci. 26 (43), 11239–11247, http://dx.doi.org/10.1523/JNEUROSCI.2165-06.2006.

Crone, E.A., Somsen, R.J., Van Beek, B., Van Der Molen, M.W., 2004. Heart rate and skin conductance analysis of antecendents and consequences of decision making. Psychophysiology 41 (4), 531–540.

Crowley, M.J., Wu, J., Hommer, R.E., South, M., Molfese, P.J., Fearon, R.M., Mayes, L.C., 2013. A developmental study of the feedback-related negativity from 10–17 years: age and sex effects for reward versus non-reward. Dev. Neuropsychol. 38 (8), 595–612, http://dx.doi.org/10.1080/87565641.2012.694512.

D'Ardenne, K., Eshel, N., Luka, J., Lenartowicz, A., Nystrom, L.E., Cohen, J.D., 2012. Role of prefrontal cortex and the midbrain dopamine system in working memory updating. Proc. Natl. Acad. Sci. U. S. A. 109 (49), 19900–19909, http://dx.doi.org/10.1073/pnas.1116727109.

Danielmeier, C., Ullsperger, M., 2011. Post-error adjustments. Front. Psychol. 2, 233, http://dx.doi.org/10.3389/fpsyg.2011.00233.

Danielmeier, C., Wessel, J.R., Steinhauser, M., Ullsperger, M., 2009. Modulation of the error-related negativity by response conflict. Psychophysiology 46 (6), 1288–1298, http://dx.doi.org/10.1111/j.1469-8986.2009.00860.

Davies, P.L., Segalowitz, S.J., Gavin, W.J., 2004. Development of response-monitoring ERPs in 7- to 25-year-olds. Dev. Neuropsychol. 25 (3), 355–376, http://dx.doi.org/10.1207/s15326942dn2503_6.

Debener, S., Ullsperger, M., Siegel, M., Fiehler, K., von Cramon, D.Y., Engel, A.K., 2005. Trial-by-trial coupling of concurrent electroencephalogram and functional magnetic resonance imaging identifies the dynamics of performance monitoring. J. Neurosci. 25 (50), 11730–11737, http://dx.doi.org/10.1523/JNEUROSCI.3286-05.2005, pii:25/50/11730.

Diamond, A., Briand, L., Fossella, J., Gehlbach, L., 2004. Genetic and neurochemical modulation of prefrontal cognitive functions in children. Am. J. Psychiatry 161 (1), 125–132, http://dx.doi.org/10.1176/appi.ajp.161.1.125.

DiGirolamo, G.J., Kramer, A.F., Barad, V., Cepeda, N.J., Weissman, D.H., Milham, M.P., Wszalek, T.M., Cohen, J.N., Banich, M.T., Webb, A., Belopolsky, A., McAuley, E., 2001. General and task-specific frontal lobe recruitment in older adults during executive processes: a fMRI investigation of task-switching. Neuroreport 12 (9), 2065–2071, http://dx.doi.org/10.1007/s002210100712.

Edin, F., Klingberg, T., Johansson, P., McNab, F., Tegner, J., Compte, A., 2009. Mechanism for top-down control of working memory capacity. Proc. Natl. Acad. Sci. U. S. A. 106 (16), 6802–6807, http://dx.doi.org/10.1073/pnas.0901894106.

Egner, T., Delano, M., Hirsch, J., 2007. Separate conflict-specific cognitive control mechanisms in the human brain. Neuroimage 35 (2), 940–948, http://dx.doi.org/10.1016/j.neuroimage.2006.11.061, pii:S1053-8119(06)01179-7.

Endrass, T., Klawohn, J., Schuster, F., Kathmann, N., 2008. Overactive performance monitoring in obsessive-compulsive disorder: ERP evidence from correct and erroneous reactions [Comparative Study]. Neuropsychologia 46 (7), 1877–1887, http://dx.doi.org/10.1016/j.neuropsychologia.2007.12.001.

Endrass, T., Schreiber, M., Kathmann, N., 2012. Speeding up older adults: age-effects on error processing in speed and accuracy conditions. Biol. Psychol. 89 (2), 426–432, http://dx.doi.org/10.1016/j.biopsycho.2011.12.005.

Eppinger, B., Kray, J., 2011. To choose or to avoid: age differences in learning from positive and negative feedback. J. Cogn. Neurosci. 23, 41–52, http://dx.doi.org/10.1162/jocn.2009.21364.

Eppinger, B., Hämmerer, D., Li, S.-C., 2011. Neuromodulation of reward-based learning and decision making in human aging. Ann. N. Y. Acad. Sci. 1235, 1–17, http://dx.doi.org/10.1111/j.1749-6632.2011.06230.

Eppinger, B., Kray, J., Mock, B., Mecklinger, A., 2008. Better or worse than expected? Aging, learning, and the ERN. Neuropsychologia 46

(2), 521–539, http://dx.doi.org/10.1016/j.neuropsychologia.2007.09.001, pii:S0028-3932(07)00321-1.

Eppinger, B., Mock, B., Kray, J., 2009. Developmental differences in learning and error processing: evidence from ERPs. Psychophysiology 46 (5), 1043–1053, http://dx.doi.org/10.1111/j.1469-8986.2009.00838, pii:PSYP838.

Fair, D.A., Cohen, A.L., Power, J.D., Dosenbach, N.U., Church, J.A., Miezin, F.M., Schlaggar, B.L., Petersen, S.E., 2009. Functional brain networks develop from a local to distributed organization. PLoS Comput. Biol. 5 (5), e1000381, http://dx.doi.org/10.1371/journal.pcbi.1000381.

Fair, D.A., Dosenbach, N.U., Church, J.A., Cohen, A.L., Brahmbhatt, S., Miezin, F.M., Barch, D.M., Raichle, M.E., Petersen, S.E., Schlaggar, B.L., 2007. Development of distinct control networks through segregation and integration. Proc. Natl. Acad. Sci. U. S. A. 104 (33), 13507–13512, http://dx.doi.org/10.1073/pnas.0705843104.

Falkenstein, M., Hohnsbein, J., Hoormann, J., Blanke, L., 1990. Effects of errors in choice reaction tasks on the ERP under focused and divided attention. In: Brunia, C.H.M., Gaillard, A.W.K., Kok, A. (Eds.), Psychophysiological Brain Research, vol. 1. Tilburg University Press, Tilburg, pp. 192–195.

Falkenstein, M., Hohnsbein, J., Hoormann, J., Blanke, L., 1991. Effects of cross-modal divided attention on late ERP components. II. Error processing in choice reaction tasks. Electroencephalogr. Clin. Neurophysiol. 78, 447–455.

Falkenstein, M., Hoormann, J., Hohnsbein, J., 1999. ERP components in Go/Nogo tasks and their relation to inhibition. Acta Psychol. (Amst.) 101, 267–291.

Falkenstein, M., Hoormann, J., Hohnsbein, J., 1998. EKP-Korrelate der Fehlerverarbeitung in Abhängigkeit von Alter und Ermüdung. In: Falkenstein, M., Hohnsbein, J., Ullsperger, P. (Eds.), Cognitive Changes due to Aging and Fatigue as Revealed in the Electrical Brain Activity. Bundesanstalt für Arbeitsschutz und Arbeitsmedizin, Berlin, pp. 57–66.

Falkenstein, M., Hoormann, J., Hohnsbein, J., 2001. Changes of error-related ERPs with age. Exp. Brain Res. 138 (2), 258–262.

Falkenstein, M., Hoormann, J., Christ, S., Hohnsbein, J., 2000. ERP components on reaction errors and their functional significance: a tutorial. Biol. Psychol. 51 (2-3), 87–107, pii:S0301051199000319.

Ferdinand, N.K., Kray, J., 2013. Age-related changes in processing positive and negative feedback: is there a positivity effect for older adults? Biol. Psychol. 94 (2), 235–241, http://dx.doi.org/10.1016/j.biopsycho.2013.07.006.

Fischer, A.G., Ullsperger, M., 2013. Real and fictive outcomes are processed differently but converge on a common adaptive mechanism. Neuron 79 (6), 1243–1255, http://dx.doi.org/10.1016/j.neuron.2013.07.006.

Folstein, J.R., Van Petten, C., 2008. Influence of cognitive control and mismatch on the N2 component of the ERP: a review. Psychophysiology 45 (1), 152–170, http://dx.doi.org/10.1111/j.1469-8986.2007.00602.

Forstmann, B., Tittgemeyer, M., Wagenmakers, E.-J., Derrfuss, J., Imperati, D., Brown, S., 2011. The speed-accuracy tradeoff in the elderly brain: a structural model-based approach. J. Neurosci. 31 (47), 17242–17249, http://dx.doi.org/10.1523/JNEUROSCI.0309-11.2011.

Gajewski, P.D., Stoerig, P., Falkenstein, M., 2008. ERP-correlates of response selection in a response conflict paradigm. Brain Res. 1189, 127–134, http://dx.doi.org/10.1016/j.brainres.2007.10.076, pii:S0006-8993(07)02603-0.

Gazzaley, A., 2011. Influence of early attentional modulation on working memory. Neuropsychologia 49 (6), 1410–1424, http://dx.doi.org/10.1016/j.neuropsychologia.2010.12.022.

Gazzaley, A., Cooney, J.W., Rissman, J., D'Esposito, M., 2005. Top-down suppression deficit underlies working memory impairment in normal aging. Nat. Neurosci. 8 (10), 1298–1300, http://dx.doi.org/10.1038/nn1543, pii:nn1543.

Gehring, W.J., Fencsik, D.E., 2001. Functions of the medial frontal cortex in the processing of conflict and errors. J. Neurosci. 21 (23), 9430–9437.

Gehring, W.J., Willoughby, A.R., 2002. The medial frontal cortex and the rapid processing of monetary gains and losses. Science 295 (5563), 2279–2282.

Gehring, W.J., Goss, B., Coles, M.G.H., Meyer, D.E., Donchin, E., 1993a. A neural system for error detection and compensation. Psychol. Sci. 4 (6), 385–390, http://dx.doi.org/10.1111/j.1467-9280.1993.tb00586.

Gehring, W.J., Goss, B., Coles, M.G.H., Meyer, D.E., Donchin, E., 1993b. A neural system for error detection and compensation. Psychol. Sci. 4 (6), 385–390.

Giorgio, A., Santelli, L., Tomassini, V., Bosnell, R., Smith, S., De Stefano, N., Johansen-Berg, H., 2010a. Age-related changes in grey and white matter structure throughout adulthood. Neuroimage 51 (3), 943–951, http://dx.doi.org/10.1016/j.neuroimage.2010.03.004.

Giorgio, A., Watkins, K.E., Chadwick, M., James, S., Winmill, L., Douaud, G., De Stefano, N., Matthews, P.M., Smith, S.M., Johansen-Berg, H., James, A.C., 2010b. Longitudinal changes in grey and white matter during adolescence. Neuroimage 49 (1), 94–103, http://dx.doi.org/10.1016/j.neuroimage.2009.08.003.

Gogtay, N., Giedd, J.N., Lusk, L., Hayashi, K.M., Greenstein, D., Vaituzis, A.C., Thompson, P.M., 2004. Dynamic mapping of human cortical development during childhood through early adulthood. Proc. Natl. Acad. Sci. U. S. A. 101 (21), 8174–8179, http://dx.doi.org/10.1073/pnas.0402680101.

Haber, S.N., Knutson, B., 2010. The reward circuit: linking primate anatomy and human imaging. Neuropsychopharmacology 35 (1), 4–26, http://dx.doi.org/10.1038/Npp.2009.129.

Hämmerer, D., Biele, G., Muller, V., Thiele, H., Nurnberg, P., Heekeren, H.R., Li, S.C., 2013. Effects of PPP1R1B (DARPP-32) polymorphism on feedback-related brain potentials across the life span. Front. Psychol. 4, 89, http://dx.doi.org/10.3389/fpsyg.2013.00089.

Hammerer, D., Eppinger, B., 2012. Dopaminergic and prefrontal contributions to reward-based learning and outcome monitoring during child development

and aging. Dev. Psychol. 48 (3), 862–874, http://dx.doi.org/10.1037/a0027342 [Review].

Hämmerer, D., Li, S.C., Müller, V., Lindenberger, U., 2010. An electrophysiological study of response conflict processing across the lifespan: assessing the roles of conflict monitoring, cue utilization, response anticipation, and response suppression. Neuropsychologia 48 (11), 3305–3316, http://dx.doi.org/10.1016/j.neuropsychologia.2010.07.014, pii:S0028-3932(10)0009-X.

Hämmerer, D., Li, S.C., Muller, V., Lindenberger, U., 2011. Life span differences in electrophysiological correlates of monitoring gains and losses during probabilistic reinforcement learning. J. Cogn. Neurosci. 23 (3), 579–592, http://dx.doi.org/10.1162/jocn.2010.21475.

Hedden, T., Van Dijk, K.R., Shire, E.H., Sperling, R.A., Johnson, K.A., Buckner, R.L., 2012. Failure to modulate attentional control in advanced aging linked to white matter pathology. Cereb. Cortex 22 (5), 1038–1051, http://dx.doi.org/10.1093/cercor/bhr172.

Herrmann, M.J., Rommler, J., Ehlis, A.C., Heidrich, A., Fallgatter, A.J., 2004. Source localization (LORETA) of the error-related-negativity (ERN/Ne) and positivity (Pe). Cogn. Brain Res. 20 (2), 294–299, http://dx.doi.org/10.1016/j.cogbrainres.2004.02.013, pii:S0926641004000898.

Hoffmann, S., Falkenstein, M., 2010. Independent component analysis of erroneous and correct responses suggests online response control. Hum. Brain Mapp. 31 (9), 1305–1315, http://dx.doi.org/10.1002/hbm.20937.

Hogan, A.M., Vargha-Khadem, F., Kirkham, F.J., Baldeweg, T., 2005. Child development of action monitoring from adolescence to adulthood: an ERP study. Dev. Sci. 8 (6), 525–534.

Holroyd, C.B., Coles, M.G., 2002. The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. Psychol. Rev. 109 (4), 679–709.

Holroyd, C.B., Larsen, J.T., Cohen, J.D., 2004. Context dependence of the event-related brain potential associated with reward and punishment. Psychophysiology 41, 245–253.

Hughes, G., Yeung, N., 2011. Dissociable correlates of response conflict and error awareness in error-related brain activity. Neuropsychologia 49 (3), 405–415, http://dx.doi.org/10.1016/j.neuropsychologia.2010.11.036 [Research Support, N.I.H., Extramural Research Support, Non-U.S. Gov't].

Hwang, K., Velanova, K., Luna, B., 2010. Strengthening of top-down frontal cognitive control networks underlying the development of inhibitory control: a functional magnetic resonance imaging effective connectivity study. J. Neurosci. 30 (46), 15535–15545, http://dx.doi.org/10.1523/JNEUROSCI.2825-10.2010.

Johnstone, S.J., Pleffer, C.B., Barry, R.J., Clarke, A.R., Smith, J.L., 2005. Development of inhibitory processing during the Go/Nogo task. J. Psychophysiol. 19 (1), 11–23, http://dx.doi.org/10.1027/0269-8803.19.1.11.

Jonkman, L.M., 2006. The development of preparation, conflict monitoring and inhibition from early childhood to young adulthood: a Go/Nogo ERP study. Brain Res. 1097 (1), 181–193, http://dx.doi.org/10.1016/j.brainres.2006.04.064, pii:s0006-8993(06)01151-6.

Jonkman, L.M., Lansbergen, M., Stauder, J.E., 2003. Developmental differences in behavioral and event-related brain responses associated with response preparation and inhibition in a Go/Nogo task. Psychophysiology 40 (5), 752–761, http://dx.doi.org/10.1111/1469-8986.00075.

Kerns, J.G., 2006. Anterior cingulate and prefrontal cortex activity in an FMRI study of trial-to-trial adjustments on the Simon task. Neuroimage 33 (1), 399–405, http://dx.doi.org/10.1016/j.neuroimage.2006.06.012, pii:S1053-8119(06)00666-5.

Kerns, J.G., Cohen, J.D., MacDonald 3rd, A.W., Cho, R.Y., Stenger, V.A., Carter, C.S., 2004. Anterior cingulate conflict monitoring and adjustments in control. Science 303 (5660), 1023–1026, http://dx.doi.org/10.1126/science.1089910.

Kim, E.Y., Iwaki, N., Imashioya, H., Uno, H., Fujita, T., 2007. Error-related negativity in a visual go/no-go task: children vs. adults. Dev. Neuropsychol. 31 (2), 181–191, http://dx.doi.org/10.1080/87565640701190775.

King, J.A., Korb, F.M., von Cramon, D.Y., Ullsperger, M., 2010. Post-error behavioral adjustments are facilitated by activation and suppression of task-relevant and task-irrelevant information processing. J. Neurosci. 30 (38), 12759–12769, http://dx.doi.org/10.1523/JNEUROSCI.3274-10.2010.

Kray, J., 2006. Task-set switching under cue-based versus memory-based switching conditions in younger and older adults. Brain Res. 1105 (1), 83–92, http://dx.doi.org/10.1016/j.brainres.2005.11.016, pii:S0006-8993(05)01603-3.

Kray, J., Lindenberger, U., 2000. Adult age differences in task switching. Psychol. Aging 15 (1), 126–147.

Ladouceur, C.D., Dahl, R.E., Carter, C.S., 2004. ERP correlates of action monitoring in adolescence. Ann. N. Y. Acad. Sci. 1021, 329–336, http://dx.doi.org/10.1196/annals.1308.040.

Lamm, C., Zelazo, P.D., Lewis, M.D., 2006. Neural correlates of cognitive control in childhood and adolescence: disentangling the contributions of age and executive function. Neuropsychologia 44 (11), 2139–2148, http://dx.doi.org/10.1016/j.neuropsychologia.2005.10.013, pii:S0028-3932(05)00336-2.

Leuthold, H., Sommer, W., 1999. ERP correlates of error processing in spatial S-R compatibility tasks. Clin. Neurophysiol. 110 (34), 2–357, http://dx.doi.org/10.1016/S1388-2457(98)00058-3.

Li, S.-C., 2013. Neuromodulation and developmental contextual influences on neural and cognitive plasticity across the life span. Neurosci. Biobehav. Rev. 37, 2201–2208.

Li, S.-C., Hämmerer, D., Müller, V., Hommel, B., Lindenberger, U., 2009. Lifespan development of stimulus-response conflict cost: similarities and differences between child development and senescence. Psychol. Res. 73, 777–785, http://dx.doi.org/10.1007/s00426-008-0190-2.

Li, S.-C., Lindenberger, U., Sikström, S., 2001. Aging cognition: from neuromodulation to representation. Trends Cogn. Sci. 5, 479–486, http://dx.doi.org/10.1016/S1364-6613(00)01769-1.

Li, S.-C., Naveh-Benjamin, M., Lindenberger, U., 2005. Aging neuromodulation impairs associative binding: a neurocomputational account. Psychol. Sci. 16, 445–450.

Lindenberger, U., Mayr, U., 2013. Cognitive aging: is there a dark side to environmental support? Trends Cogn. Sci., http://dx.doi.org/10.1016/j.tics.2013.10.006 [Epub ahead of print].

Liston, C., 2003. Developmental differences in diffusion measures of cortical fiber tracts. J. Cogn. Neurosci. 15, S57–S58.

Lorsbach, T.C., Reimer, J.F., 2008. Context processing and cognitive control in children and young adults. J. Genet. Psychol. 169 (1), 34–50, http://dx.doi.org/10.3200/GNTP.169.1.34-50.

Luna, B., Sweeney, J.A., 2004. The emergence of collaborative brain function: FMRI studies of the development of response inhibition. Ann. N. Y. Acad. Sci. 1021, 296–309, http://dx.doi.org/10.1196/annals.1308.035.

Mansouri, F.A., Tanaka, K., Buckley, M.J., 2009. Conflict-induced behavioural adjustment: a clue to the executive functions of the prefrontal cortex. Nat. Rev. Neurosci. 10 (2), 141–152, http://dx.doi.org/10.1038/nrn2538.

Mathewson, K.J., Dywan, J., Snyder, P.J., Tays, W.J., Segalowitz, S.J., 2008. Aging and electrocortical response to error feedback during a spatial learning task. Psychophysiology 45 (6), 936–948, http://dx.doi.org/10.1111/j.1469-8986.2008.00699.

Mayr, U., 2001. Age differences in the selection of mental sets: the role of inhibition, stimulus ambiguity, and response-set overlap. Psychol. Aging 16 (1), 96–109, http://dx.doi.org/10.1037/0882-7974.16.1.96.

Miller, E.K., 2000. The prefrontal cortex and cognitive control. Nat. Rev. Neurosci. 1 (1), 59–65, http://dx.doi.org/10.1038/35036228.

Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci. 24, 167–202, http://dx.doi.org/10.1146/annurev.neuro.24.1.167.

Miltner, W.H.R., Braun, C.H., Coles, M.G.H., 1997. Event-related brain potentials following incorrect feedback in a time-estimation task: evidence for a generic neural system for error detection. J. Cogn. Neurosci. 9 (6), 788–798.

Montague, P.R., Hyman, S.E., Cohen, J.D., 2004. Computational roles for dopamine in behavioural control. Nature 431, 760–767, http://dx.doi.org/10.1038/nature03015.

Müller, V., Anokhin, A.P., 2012. Neural synchrony during response production and inhibition. PLoS ONE 7, e38931.

Müller, V., Gruber, W., Klimesch, W., Lindenberger, U., 2009. Lifespan differences in cortical dynamics of auditory perception. Dev. Sci. 12, 839–853.

Munakata, Y., Herd, S.A., Chatham, C.H., Depue, B.E., Banich, M.T., O'Reilly, R.C., 2011. A unified framework for inhibitory control. Trends Cogn. Sci. 15 (10), 453–459, http://dx.doi.org/10.1016/j.tics.2011.07.011.

Munakata, Y., Snyder, H.R., Chatham, C.H., 2012. Developing cognitive control: three key transitions. Curr. Direct. Psychol. Sci. 21 (2), 71–77, http://dx.doi.org/10.1177/0963721412436807.

Nagel, I.E., Preuschhof, C., Li, S.C., Nyberg, L., Backman, L., Lindenberger, U., Heekeren, H.R., 2009. Performance level modulates adult age differences in brain activation during spatial working memory. Proc. Natl. Acad. Sci. U. S. A. 106 (52), 22552–22557, http://dx.doi.org/10.1073/pnas.0908238106.

Nagel, I.E., Preuschhof, C., Li, S.C., Nyberg, L., Backman, L., Lindenberger, U., Heekeren, H.R., 2011. Load modulation of BOLD response and connectivity predicts working memory performance in younger and older adults. J. Cogn. Neurosci. 23 (8), 2030–2045, http://dx.doi.org/10.1162/jocn.2010.21560.

Nielson, K.A., Langenecker, S.A., Garavan, H., 2002. Differences in the functional neuroanatomy of inhibitory control across the adult life span. Psychol. Aging 17 (1), 56–71, http://dx.doi.org/10.1037/0882-7974.17.1.56.

Nieuwenhuis, S., Ridderinkhof, K.R., Talsma, D., Coles, M.G., Holroyd, C.B., Kok, A., van der Molen, M.W., 2002. A computational account of altered error processing in older age: dopamine and the error-related negativity. Cogn. Affect. Behav. Neurosci. 2 (1), 19–36, http://dx.doi.org/10.3758/CABN.2.1.19.

Nieuwenhuis, S., Yeung, N., van den Wildenberg, W., Ridderinkhof, K.R., 2003. Electrophysiological correlates of anterior cingulate function in a Go/NoGo task: effects of response conflict and trial type frequency. Cogn. Affect. Behav. Neurosci. 3 (1), 17–26, http://dx.doi.org/10.3758/CABN.3.1.17.

Nigbur, R., Cohen, M.X., Ridderinkhof, K.R., Stürmer, B., 2012. Theta dynamics reveal domain-specific control over stimulus and response conflict. J. Cogn. Neurosci. 24 (5), 1264–1274.

Pailing, P.E., Segalowitz, S.J., 2004. The error-related negativity as a state and trait measure: motivation, personality, and ERPs in response to errors. Psychophysiology 41 (1), 84–95, http://dx.doi.org/10.1111/1469-8986.00124.

Papenberg, G., Hämmerer, D., Müller, V., Lindenberger, U., Li, S.-C., 2013. Lower theta inter-trial phase coherence during performance monitoring is related to higher reaction time variability: a lifespan study. Neuroimage 83, 912–920.

Paxton, J.L., Barch, D.M., Racine, C.A., Braver, T.S., 2008. Cognitive control, goal maintenance, and prefrontal function in healthy aging. Cereb. Cortex 18 (5), 1010–1028, http://dx.doi.org/10.1093/cercor/bhm135.

Philiastides, M.G., Biele, G., Vavatzanidis, N., Kazzer, P., Heekeren, H.R., 2010. Temporal dynamics of prediction error processing during reward-based decision making. Neuroimage 53 (1), 221–232, http://dx.doi.org/10.1016/j.neuroimage.2010.05.052.

Pietschmann, M., Endrass, T., Czerwon, B., Kathmann, N., 2011. Aging, probabilistic learning and performance monitoring. Biol. Psychol. 86 (1), 74–82, http://dx.doi.org/10.1016/j.biopsycho.2010.10.009.

Pietschmann, M., Simon, K., Endrass, T., Kathmann, N., 2008. Changes of performance monitoring with learning in older and younger adults. Psychophysiology 45 (4), 559–568, http://dx.doi.org/10.1111/j.1469-8986.2008.00651, pii:PSYP651.

Posner, M.I., Rothbart, M.K., Sheese, B.E., Voelker, P., 2012. Control networks and neuromodulators of early development. Dev. Psychol. 48 (3), 827–835, http://dx.doi.org/10.1037/a0025530.

Potts, G.F., 2011. Impact of reward and punishment motivation on behavior monitoring as indexed by the error-related negativity. Int. J. Psychophysiol. 81 (3), 324–331, http://dx.doi.org/10.1016/j.ijpsycho.2011.07.020.

Raz, N., Lindenberger, U., Rodrigue, K.M., Kennedy, K.M., Head, D., Williamson, A., Dahle, C., Gerstorf, D., Acker, J.D., 2005. Regional brain changes in aging healthy adults: general trends, individual differences and modifiers. Cereb. Cortex 15 (11), 1676–1689, http://dx.doi.org/10.1093/cercor/bhi044.

Resnick, S.M., Pham, D.L., Kraut, M.A., Zonderman, A.B., Davatzikos, C., 2003. Longitudinal magnetic resonance imaging studies of older adults: a shrinking brain. J. Neurosci. 23 (8), 3295–3301.

Ridderinkhof, K.R., Van der Molen, M.W., Band, G.P.H., Bashore, T.R., 1997. Sources of interference from irrelevant information: a developmental study. J. Exp. Child Psychol. 65 (3), 315–341, http://dx.doi.org/10.1006/jecp.1997.2367.

Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., Nieuwenhuis, S., 2004. The role of the medial frontal cortex in cognitive control. Science 306 (5695), 443–447, http://dx.doi.org/10.1126/science.1100301, pii:306/5695/443.

Roelofs, A., van Turennout, M., Coles, M.G., 2006. Anterior cingulate cortex activity can be independent of response conflict in Stroop-like tasks. Proc. Natl. Acad. Sci. U. S. A. 103 (37), 13884–13889, http://dx.doi.org/10.1073/pnas.0606265103, pii:0606265103.

Roger, C., Bénar, C.G., Vidal, F., Hasbroucq, T., Burle, B., 2010. Rostral Cingulate Zone and correct response monitoring: ICA and source localization evidences for the unicity of correct- and error-negativities. Neuroimage, http://dx.doi.org/10.1016/j.neuroimage.2010.02.005.

Rubia, K., Smith, A.B., Woolley, J., Nosarti, C., Heyman, I., Taylor, E., Brammer, M., 2006. Progressive increase of frontostriatal brain activation from childhood to adulthood during event-related tasks of cognitive control. Hum. Brain Mapp. 27 (12), 973–993, http://dx.doi.org/10.1002/hbm.20237.

San Martin, R., 2012. Event-related potential studies of outcome processing and feedback-guided learning. Front. Hum. Neurosci. 6, 304, http://dx.doi.org/10.3389/fnhum.2012.00304.

Sander, M.C., Werkle-Bergner, M., Lindenberger, U., 2012. Amplitude modulations and inter-trial phase stability of alpha-oscillations differentially reflect working memory constraints across the lifespan. Neuroimage 59, 646–654.

Santesso, D.L., Segalowitz, S.J., 2008. Developmental differences in error-related ERPs in middle- to late-adolescent males. Dev. Psychol. 44 (1), 205–217, http://dx.doi.org/10.1037/0012-1649.44.1.205.

Santesso, D.L., Dzyundzyak, A., Segalowitz, S.J., 2011. Age, sex and individual differences in punishment sensitivity: factors influencing the feedback-related negativity. Psychophysiology 48 (11), 1481–1489, http://dx.doi.org/10.1111/j.1469-8986.2011.01229.

Santesso, D.L., Segalowitz, S.J., Schmidt, L.A., 2006. Error-related electrocortical responses in 10-year-old children and young adults. Dev. Sci. 9 (5), 473–481, http://dx.doi.org/10.1111/j.1467-7687.2006.00514.

Scheffers, M.K., Coles, M.G., 2000. Performance monitoring in a confusing world: error-related brain activity, judgments of response accuracy, and types of errors. J. Exp. Psychol. Hum. Percept. Perform. 26 (1), 141–151.

Schmiedt-Fehr, C., Basar-Eroglu, C., 2011. Event-related delta and theta brain oscillations reflect age-related changes in both a general and a specific neuronal inhibitory mechanism. Clin. Neurophysiol. 122, 1156–1167.

Segalowitz, S.J., Dywan, J., 2009. Individual differences and developmental change in the Ne/ERN response: implications for models of ACC function. Psychol. Res. 73 (6), 857–870, http://dx.doi.org/10.1007/s00426-008-0193-z.

Segalowitz, S.J., Santesso, D.L., Jehta, M.K., 2010. Electrophysiological changes during adolescence: a review. Brain Cogn. 72, 86–100, http://dx.doi.org/10.1016/j.bandc.2009.10.003.

Shephard, E., Jackson, G.M., Groom, M.J., 2013. Learning and altering behaviours by reinforcement: neurocognitive differences between children and adults. Dev. Cogn. Neurosci. 7C, 94–105, http://dx.doi.org/10.1016/j.dcn.2013.12.001.

Smith, G.A., Brewer, N., 1995. Slowness and age: speed-accuracy mechanisms. Psychol. Aging 10 (2), 238–247, http://dx.doi.org/10.1037/0882-7974.10.2.238.

Sowell, E.R., Peterson, B., Thompson, P.M., Welcome, S.E., Henkenius, A.L., Toga, A.W., 2003. Mapping cortical change across the human life span. Nat. Neurosci. 6 (3), 309–315, http://dx.doi.org/10.1038/nn1008.

Spieler, H.D., 2006. Outsourcing cognitive control to the environment: adult age differences in the use of task cues. Psychon. Bull. Rev. 13 (5), 787–793, http://dx.doi.org/10.3758/BF03193998.

Spreng, R.N., Wojtowicz, M., Grady, C.L., 2010. Reliable differences in brain activity between young and old adults: a quantitative meta-analysis across multiple cognitive domains. Neurosci. Biobehav. Rev. 34 (8), 1178–1194, http://dx.doi.org/10.1016/j.neubiorev.2010.01.009.

Steinhauser, M., Maier, M., Hübner, R., 2008. Modeling behavioral measures of error detection in choice tasks: response monitoring versus conflict monitoring. J. Exp. Psychol. Hum. Percept. Perform. 34, 158–176, http://dx.doi.org/10.1037/0096-1523.34.1.158.

Steinhauser, M., Yeung, N., 2010. Decision processes in human performance monitoring. J. Neurosci. 30, 15643–15653, http://dx.doi.org/10.1523/JNEUROSCI.1899-10.2010.

Störmer, V., Li, S.-C., Heekeren, H.R., Lindenberger, U., 2013. Normative shifts of cortical mechanisms of encoding contribute to adult age differences in visual-spatial working memory. Neuroimage 73, 167–175.

Swick, D., Turken, A.U., 2002. Dissociation between conflict detection and error monitoring in the human anterior cingulate cortex. Proc. Natl. Acad. Sci. U. S. A. 99 (25), 16354–16359, http://dx.doi.org/10.1073/pnas.252521499.

Talmi, D., Atkinson, R., El-Deredy, W., 2013. The feedback-related negativity signals salience prediction errors, not reward prediction errors. J. Neurosci. 33 (19), 8264–8269, http://dx.doi.org/10.1523/JNEUROSCI.5695-12.2013.

Themanson, J.R., Hillman, C.H., Curtin, J.J., 2006. Age and physical activity influences on action monitoring during task switching. Neurobiol. Aging 27 (9), 1335–1345, http://dx.doi.org/10.1016/j.neurobiolaging.2005.07.002.

Ullsperger, M., Fischer, A.G., Nigbur, R., Endrass, T., 2014. Neural mechanisms and temporal dynamics of performance monitoring. Trends Cogn. Sci. 18 (5), 259–267, http://dx.doi.org/10.1016/j.tics.2014.02.009 [Research Support, Non-U.S. Gov't].

van Meel, C.S., Heslenfeld, D.J., Rommelse, N.N., Oosterlaan, J., Sergeant, J.A., 2012. Developmental trajectories of neural mechanisms supporting conflict and error processing in middle childhood. Dev. Neuropsychol. 37 (4), 358–378, http://dx.doi.org/10.1080/87565641.2011.653062.

van Noordt, S.J., Segalowitz, S.J., 2012. Performance monitoring and the medial prefrontal cortex: a review of individual differences and context effects as a window on self-regulation. Front. Hum. Neurosci. 6, 197, http://dx.doi.org/10.3389/fnhum.2012.00197.

Van Veen, V., Carter, C.S., 2002. The timing of action-monitoring processes in the anterior cingulate cortex. J. Cogn. Neurosci. 14 (4), 593–602, http://dx.doi.org/10.1162/08989290260045837.

Velanova, K., Wheeler, M.E., Luna, B., 2008. Child developmental changes in anterior cingulate and frontoparietal recruitment support the development of error processing and inhibitory control. Cereb. Cortex 18 (11), 2505–2522, http://dx.doi.org/10.1093/cercor/bhn012.

Wahlstrom, D., Collins, P., White, T., Monica, L., 2010. Developmental changes in dopamine neurotransmission in adolescence: behavioral implications and issues in assessment. Brain Cogn. 72, 146–215, http://dx.doi.org/10.1016/j.bandc.2009.10.013.

Walsh, M.M., Anderson, J.R., 2012. Learning from experience: event-related potential correlates of reward processing, neural adaptation, and behavioral choice. Neurosci. Biobehav. Rev. 36 (8), 1870–1884, http://dx.doi.org/10.1016/j.neubiorev.2012.05.008.

Walhovd, K.B., Rosquist, H., Fjell, A.M., 2008. P300 amplitude age reductions are not caused by latency jitter. Psychophysiology 45 (4), 545–553, http://dx.doi.org/10.1111/j.1469-8986.2008.00661, pii:PSYP661.

Wascher, E., Falkenstein, M., Wild-Wall, N., 2011. Age related strategic differences in processing irrelevant information. Neurosci. Lett. 487 (1), 66–69, http://dx.doi.org/10.1016/j.neulet.2010.09.075.

Weinberg, A., Olvet, D.M., Hajcak, G., 2010. Increased error-related brain activity in generalized anxiety disorder. Biol. Psychol. 85 (3), 472–480, http://dx.doi.org/10.1016/j.biopsycho.2010.09.011.

Werkle-Bergner, M., Freunberger, R., Sander, M.C., Lindenberger, U., Klimesch, W., 2012. Inter-individual performance differences in younger and older adults differentially relate to amplitude modulations and phase stability of oscillations controlling working memory contents. Neuroimage 60, 71–82.

Wiersema, J.R., van der Meere, J.J., Roeyers, H., 2007. Developmental changes in error monitoring: an event-related potential study. Neuropsychologia 45 (8), 1649–1657, http://dx.doi.org/10.1016/j.neuropsychologia.2007.01.004.

Yeung, N., Cohen, J.D., 2006. The impact of cognitive deficits on conflict monitoring. Predictable dissociations between the error-related negativity and N2. Psychol. Sci. 17 (2), 164–171, http://dx.doi.org/10.1111/j.1467-9280.2006.01680, pii:PSCI1680.

Yeung, N., Nieuwenhuis, S., 2009. Dissociating response conflict and error likelihood in anterior cingulate cortex. J. Neurosci. 29 (46), 14506–14510, http://dx.doi.org/10.1523/JNEUROSCI.3615-09.2009.

Yeung, N., Botvinick, M.M., Cohen, J.D., 2004. The neural basis of error detection: conflict monitoring and the error-related negativity. Psychol. Rev. 111 (4), 931–959, http://dx.doi.org/10.1037/0033-295X.111.4.939, pii:2004-19012-005.

Yeung, N., Holroyd, C.B., Cohen, J.D., 2005. ERP correlates of feedback and reward processing in the presence and absence of response choice. Cereb. Cortex 15 (5), 535–544, http://dx.doi.org/10.1093/cercor/bhh153.

Zottoli, T.M., Grose-Fifer, J., 2012. The feedback-related negativity (FRN) in adolescents. Psychophysiology 49 (3), 413–420, http://dx.doi.org/10.1111/j.1469-8986.2011.01312.