The medial frontal cortex, performance monitoring, cognitive control, and decision making

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Key points

- Brief description of the neuroanatomy of the posterior medial frontal cortex (pMFC)
- Outline interindividual variability of pMFC anatomy
- Overview of performance monitoring signals represented in the pMFC
- Integration of findings into theories of performance monitoring
- Discuss involvement of pMFC in strategic and global behavioral changes based on feedback (i.e., decision making)
- Discuss how the pMFC facilitates complex reward and environment structure learning

Abstract

This article outlines the involvement of the posterior medial frontal cortex (pMFC) in performance monitoring, cognitive control, and decision making. We first describe the neuroanatomy of the pMFC. We then review the functional contributions of the pMFC to performance monitoring, resulting adaptations, and decision making. Based on the evidence reviewed in this article, we conclude that a broad array of performance monitoring and decision-making signals are represented in the pMFC. Specific properties of these signals allow the pMFC to monitor performance, implement necessary adjustments, and to perform complex reward and environment structure learning. Future research should consider the substantial interindividual variability of pMFC anatomy to parse out the representations of these signals within the pMFC into finer level of detail.

Introduction

The medial walls of the frontal lobes cover a large cortical area and comprise multiple regions that differ with respect to their cytoarchitecture, receptor architecture, and connectivity. A broad range of cognitive and affective functions have been associated
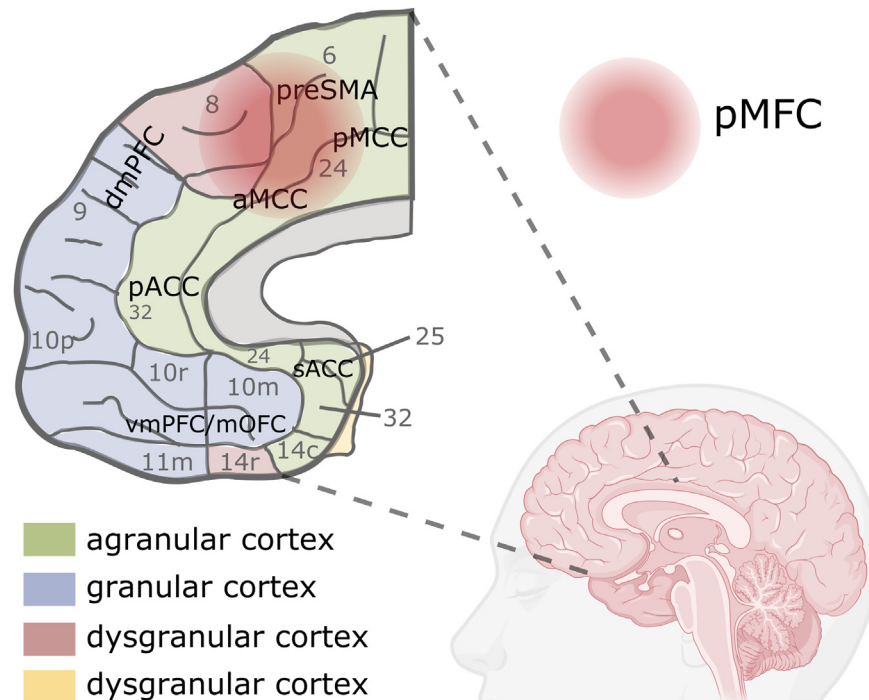
Fig. 1   Subregions of the medial frontal cortex. Functional regions in the medial and orbital frontal cortex in relation to cytoarchitecture maps. Cingulate areas include: the subcallosal and pregenual anterior cingulate cortices (sACC and pACC, respectively), the anterior and posterior midcingulate cortices (aMCC and pMCC, respectively), and the posterior cingulate cortex (not shown here). The isocortical regions can be divided into ventromedial prefrontal cortex/medial orbitofrontal cortex (vmPFC/mOFC), and dorsomedial prefrontal cortex (dmPFC). Hemodynamic signals in neuroimaging studies often coactivate several neighboring regions. As a consequence the descriptive term posterior medial frontal cortex (pMFC) has been used to commonly refer to pre-SMA and aMCC, in addition to adjacent SMA, posterior dmPFC, and pMCC (Ridderinkhof et al., 2004). Based on Ongür et al. (2003), Wise (2008), Klein-Flügge et al. (2022), Ullsperger et al. (2014b). Note: Parts of this figure were created using BioRender.com and published with permission.

with the medial frontal cortices. The gross anatomy and subregions of the medial frontal wall is shown in Fig. 1. Valuation and decision-making functions of other parts of the medial frontal wall, such as the ventromedial prefrontal and orbitofrontal cortices, are covered elsewhere. In this article, we will focus on cognitive control and the involvement of the (posterior) medial wall of the frontal lobe.

Nearly continuously humans are faced with the demand for flexible adaptation. Adaptations are needed to achieve one's goals efficiently or avoid harmful outcomes. The ability to flexibly adapt to unfavorable outcomes, changing demands, and novel or uncertain situations is classically summarized as cognitive control. Cognitive control represents a major executive function; often the term is used even synonymously with executive functions. Neurological and mental disorders impairing cognitive control massively deteriorate activities of daily living and quality of life: The dysexecutive syndrome is characterized by erratic, perseverative and erroneous behavior, often despite knowing that a chosen action is incorrect. In contrast, hyperactive cognitive control in obsessive-compulsive disorder can lead to disabling compulsions like excessive checking behavior (Endrass and Ullsperger, 2014). Research has identified the posterior medial frontal cortex (pMFC; Fig. 1) as a crucial node for performance monitoring and cognitive control. In addition, pMFC has been implicated in pain and negative affect (Shackman et al., 2011; Kragel et al., 2018). In this article, we will first describe the neuroanatomy of the pMFC and then discuss the functional contributions of the pMFC to performance monitoring as well as the behavioral and neural adaptations that result from performance-monitoring processes. A further consequence of performance monitoring is to update stimulus and action values to guide future decisions. Therefore, we will also address the role of the pMFC in decision making.

Neuroanatomical parcellation of the posterior medial frontal cortex

The cingulate sulcus is a very prominent feature on the medial wall, dividing the cingulate gyrus from the remaining cortical areas. Based on cytoarchitectural data, Brent Vogt has proposed a four-regions parcellation of the cingulate cortex (Vogt, 2009), which is further supported by receptor architecture (Palomero-Gallagher et al., 2009). The cingulate gyrus can thus be divided into the anterior cingulate (ACC, further divided into pregenual and subcallosal ACC), midcingulate (MCC, further divided into anterior and posterior parts, aMCC and pMCC, respectively), posterior cingulate (PCC), and retrosplenial cortices (RSc). The region most

consistently involved in performance monitoring and cognitive control, the pMFC (Ridderinkhof et al., 2004; Ullsperger et al., 2014b), is rather vaguely defined based on neuroimaging results and comprises the aMCC, pre-supplementary motor area (pre-SMA) and adjacent medial Brodmann area 8 in the dorsomedial prefrontal cortex (dmPFC). In the literature, the terms dorsal anterior cingulate cortex (dACC, a term deviating from Vogt's nomenclature) and (anterior) rostral cingulate zone (RCZa; Picard and Strick, 1996) are often used nearly synonymously to aMCC.

Representations of latent variables reflecting the need, magnitude and type of cognitive control are conceivably bound to the anatomy and physiological/computational capabilities of the underlying structure. The connections of a brain region constrain the information it can access and the influence it can exert on the rest of the brain. They are a unique identifier of each cortical area —a "connectivity fingerprint" (Passingham et al., 2002). Cortical cytoarchitecture is determined by cell types and densities, identifiable layers, receptor expressions, and intracortical connectivity. It presumably affects the type of representations and computations that can be processed by a given region (Palomero-Gallagher et al., 2009, 2013; van Heukelum et al., 2020). In-vivo connectivity- and post-mortem cytoarchitecture-based parcellations of the cingulate cortex and adjacent regions appear to yield similar results (Vogt, 2005, 2009; Beckmann et al., 2009; Neubert et al., 2015). It is thus conceivable that different subregions along the rostrocaudal axis of the cingulate gyrus and along the radial (ventrodorsal) axis of the pMFC differ with respect to their functional specialization, i.e., the information they are able to represent and process. However, replicable mapping of functional representations in the pMFC onto its anatomical subregions has been difficult. In human fMRI research, a major reason for the inability to differentiate clear functional boundaries may be substantial interindividual variability of pMFC anatomy. The most consistent sulcus on the medial wall is the cingulate sulcus (CS) which delineates the cingulate gyrus (CG) forming a belt around the corpus callosum. A single uninterrupted CS is the most common anatomical variant in the pMFC (Ono et al., 1990; Paus et al., 1996; Vogt et al., 2004; Wei et al., 2017; Selahi et al., 2023). Many people, however, show a double parallel pattern where a more-or-less prominent paracingulate sulcus (PCS) forms a dorsal sulcus delineating the paracingulate gyrus (PCG) dorsal to the CG. The PCS is more frequent in the left hemisphere than in the right hemisphere; its presence, prominence and asymmetry is moreover modulated by sex and handedness (Wei et al., 2017; Amiez et al., 2018; Selahi et al., 2023). Axonal tension forces during brain development are important for the formation of gyri and sulci (Van Essen, 1997), which suggests that regional gyrification is closely related to connectivity and cytoarchitecture. In line with this, PCS presence seems associated with a relative expansion of cyto-architectural area 32′: in single-CS configurations it is confined to the dorsal bank of the CS and in gyral doubling configurations it stretches over the crown of the PCG (Vogt et al., 1995). Moreover, gray matter volumes and cortical thickness are affected by the presence of the PCS (Fornito et al., 2004, 2006a, 2008; Huster et al., 2007; Paus et al., 1996). This may explain why variations in pMFC gyrification are associated with individual differences in cognition (Fornito et al., 2004, 2006a,b, 2008; Tissier et al., 2018; Del Maschio et al., 2018; Amiez et al., 2018) and risk for mental disorders (Garrison et al., 2015, 2018; Lorenzetti et al., 2015; Park et al., 2013; Shim et al., 2009; Yucel et al., 2003). fMRI studies showed that the spatial distribution of feedback-related activity depends on pMFC gyrification (Amiez et al., 2013; Amiez and Petrides, 2014): feedback-related activity during exploration was systematically located in the CS when the PCS was absent, but in the PCS when it was present. In a go/nogo task, pMFC gyrification predicted performance and response-conflict-related EEG dynamics (Huster et al., 2009). This suggests that pMFC gyrification —and the presumably underlying cytoarchitecture and connectivity— have a major influence on the spatiotemporal representation of cognitive-control signals. However, hitherto only few studies considered single-subject anatomical features (e.g., Amiez et al., 2013, 2016; Derrfuss et al., 2012).

Functional contributions of the medial frontal wall to performance monitoring and decision making

Performance monitoring

Based on evidence from neuroimaging, electrophysiological recordings and lesion studies in humans and non-human primates it is well established that the pMFC is essential for performance monitoring (see **Fig. 3**Aii; Ridderinkhof et al., 2004; Fu et al., 2019, 2023; Sajad et al., 2019; Shenhav et al., 2016; Ullsperger et al., 2014b; Alexander and Brown, 2011). This conviction is based on more than half a century of investigations into how the brain knows whether and when to implement adaptation, for example by recruiting control processes, to facilitate goal-directed behavior. Adaptations triggered by performance monitoring signals are manifold and occur at multiple time scales and levels of processing (for a detailed discussion see Danielmeier and Ullsperger, 2011; Ullsperger et al., 2014b).

This research was boosted by the discovery of the error-related negativity (ERN; also called error negativity, Ne) in the scalp-recorded EEG in the 1990s (Falkenstein et al., 1991; Gehring et al., 1993) making the performance monitoring process observable by non-invasive techniques (see **Fig. 2**). The ERN is a fronto-central negative voltage deflection that peaks 50−100 ms after erroneous responses in speeded choice reaction time tasks. It is elicited independently of stimulus modality (i.e., independent of whether visual, tactile, or auditory stimuli are presented (Falkenstein et al., 2000; Gruendler et al., 2011)) and effector modality (i.e., independent of whether responses are given via hand, foot, or eye-movement (Ganushchak and Schiller, 2006, 2009; Holroyd et al., 1998; Masaki et al., 2001; Nieuwenhuis et al., 2001; Van 't Ent and Apkarian, 1999; Wessel et al., 2011)). Interestingly, an ERN-like ERP (often revered to as observational ERN) has also been reported during the observation of action errors committed by other persons (Bates et al., 2005; Miltner et al., 2004; van Schie et al., 2004). Yet, this component appears to only be elicited when the observed error has direct consequences for personal adjustments (de Bruijn et al., 2007). Moreover, the ERN shows
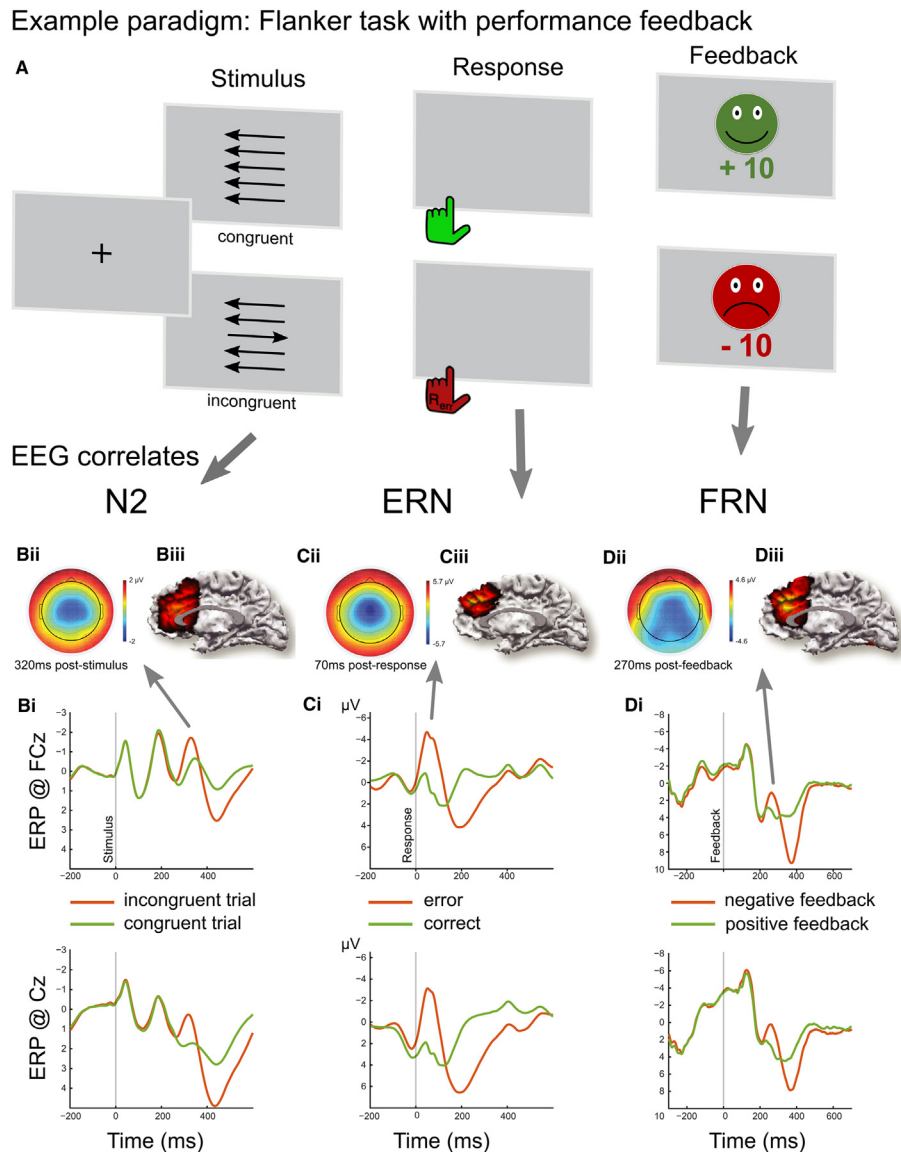
Fig. 2 Performance monitoring signals in the human EEG. This figure shows the representation of performance monitoring (PM) signals during stimulus processing, response generation, and feedback evaluation. (A) Example of different performance monitoring stages in a Flanker task with performance feedback. After the fixation cross, either congruent or incongruent flankers (four surrounding arrows) and a central target are presented on each trial. Participants must respond as quickly and correctly as possible to the direction of the target. Finally, feedback on the performance is presented (B) Following stimulus presentation, response conflict instigates a negative scalp potential (the N2) followed by a short-latency positivity (P3a). The N2/P3a complex is modulated by response conflict, task engagement, and surprise (Wessel et al., 2012; Folstein and Van Petten, 2008; Eichele et al., 2010). (C) The frontocentral error-related negativity (ERN) occurs within the first 100 ms after the erroneous response in reaction time tasks. (Cii) shows scalp topography of the difference error-correct. (Ciii) Source localization reveals a source in the aMCC. The ERN is followed by an early frontocentral and later centroparietal error positivity (Pe). The ERN has been associated with incoming objective evidence indicating a performance error, whereas the Pe seems to reflect the accumulated subjective evidence and correlates with conscious perception of the error (Kirschner et al., 2021; Overbeek et al., 2005; Steinhauser and Yeung, 2010; Wessel et al., 2011). (D) Errors signaled via explicit feedback elicits the frontocentral feedback-related negativity (FRN), followed by a frontocentral P3a and a parietal P3b. The FRN has been suggested to code prediction errors and surprise (Kirsch et al., 2022; Ullsperger et al., 2014a; Walsh and Anderson, 2012). The P3b has been associated with adjustments of future behavior (Kirschner et al., 2022; Fischer and Ullsperger, 2013; Nassar et al., 2019a). Comparison of topography and generator structures of the ERN (Aii-Aiii), FRN (Bii-Biii) and N2 (Cii-Ciii) suggest an overlapping topography and pMFC source for the three ERP components. Adapted from Gruendler et al. (2011).

high consistency within participants at lower trial numbers, but when event-related potentials are calculated at least 12 error trials are needed for sufficient statistical reliability (Fischer et al., 2017). Single-trial ERN amplitudes are often associated with behavioral adjustments like post-error slowing (Fischer et al., 2015, 2016; Fu et al., 2019; Sajad et al., 2019; Debener et al., 2005). Yet it should be noted that there is an ongoing debate whether PES is adaptive or maladaptive. Evidence for both views has been shown

(Danielmeier and Ullsperger, 2011, Fischer et al., 2018; Notebaert et al., 2009; Purcell and Kiani, 2016; Ridderinkhof et al., 2004; Wessel, 2018; Choo et al., 2023). Taken together, these results render the ERN a robust and reliable neural substrate of error monitoring and subsequent recruitment of cognitive control. In group studies with patients suffering from focal lesions, e.g., the basal ganglia, thalamus, or lateral prefrontal cortex, the ERN has proven to be a sensitive and functionally specific marker of the integrity of the performance monitoring network (Ullsperger and von Cramon, 2006; de Bruijn and Ullsperger, 2011; Seifert et al., 2011; Wessel et al., 2014; Gehring and Knight, 2000; Peterburs et al., 2011). Yet, although the ERN has proven to be a useful workhorse for research into performance monitoring and cognitive control, until recently rather little was known about the underlying mechanisms that give rise to it.

Where does the ERN arise and what is the underlying mechanism?

To understand the underlying mechanism of the ERN, it is important to understand where it arises. Source modeling consistently suggest that the spatial distribution of the ERN and its magnetoencephalography (MEG) equivalent can be accounted for by a dipole or a more distributed source in the pMFC, specifically in the aMCC (Dehaene et al., 1994; Gruendler et al., 2011; Holroyd et al., 1998; Keil et al., 2010; Miltner et al., 2003; Ullsperger and von Cramon, 2001). Consistent with these findings, error signals in the aMCC have been found in fMRI (Ullsperger et al., 2014a) and combined fMRI and EEG studies (Beldzik et al., 2022; Debener et al., 2005; Iannaccone et al., 2015). Importantly, the inverse problem in EEG source modeling and individual morphological differences in cortical folding patterns preclude firm conclusions about the origins of the ERN (Fu et al., 2023). Likely there are multiple sources even within the MCC. The ERN therefore is a manifestation of multiple neural signals arising in different cortical areas (Cohen, 2017). Recently our understanding of origins and mechanism of the ERN were advanced by single neuron recordings in pMFC (Fu and Rutishauser, 2024).

Evidence from human single neuron recordings

A robust finding from single neuron recordings in human and non-human primates in the in the medial wall is error related single-neuron spiking responses (Emeric et al., 2008, 2010; Fu et al., 2019, 2023; Godlove et al., 2011; Ito et al., 2003; Schall et al., 2002; Niki and Watanabe, 1979). Specifically in humans, neurons that signal errors have been found in the pre-SMA (or more broadly SFG) and aMCC (Fu et al., 2019). Here, two types of error-related neurons have been identified: "type I" neurons in aMCC produce more spikes on average on error trials compared to correct trials, "type II" neurons do the opposite (Fu et al., 2019). The proportion of type II error neurons is larger in the pre-SMA (40%) than in the aMCC (26%). Moreover, there is evidence for a hierarchical relationship between the aMCC the pre-SMA, whereby action errors are first detected by error neurons in the pre-SMA and then broadcast to the aMCC (Bonini et al., 2014; Fu et al., 2019, 2023). Interestingly, the latency of error neuron activity falls in time window of the ERN and this spiking activity is exclusively related to macrolevel error signals (Fu et al., 2019; Sajad et al., 2019). Based on this line of evidence, Fu et al. (2023) suggest that ERN reflects highly synchronous and aligned electric dipoles within error neurons in the pre-SMA and aMCC that respond specifically to error computation. In a recent study, the same research group investigated the question whether spiking by these error neurons is task specific or domain general. In a subset of neurons, their results demonstrated remarkable similarity in the timing, magnitude, and overall dynamics in two different tasks (Fu et al., 2022). This evidence indicates that these neurons generate a domain-general performance monitoring signal abstracted away from task-specific requirements. In line with these results, laminar recordings in human aMCC suggest that several aMCC microdomains in superficial layers can respond fairly similar to quite different cognitive tasks and performance contrasts within tasks (Wang et al., 2005). Interestingly, there is also evidence for domain-specific performance monitoring signals in aMCC (Fu et al., 2022). Here, a subset of neurons signaled errors and conflict related signals exclusively for either a Stroop task or multisource interference task. These signals are useful for performance monitoring, as they provide task-specific information about performance disturbances.

Spectral decomposition of error signals

Time-frequency decomposition of midfrontal EEG signals has revealed additional insights into the neural processes that are linked to performance monitoring. For example, conflict and error processing coincide with increased midfrontal theta-band (4−8 Hz) activity, at least partly generated in the pMFC (Cavanagh and Frank, 2014; Cohen and Cavanagh, 2011; Cohen and Donner, 2013; Cohen and van Gaal, 2014; Nigbur et al., 2012; Wang et al., 2005). Likely, both power increase and phase-locking of ongoing theta oscillations contribute to the ERN (Luu et al., 2004; Trujillo and Allen, 2007; Yeung et al., 2007). On a theoretical level, rise-to-threshold models suggest that the increase in theta activity adjusts response thresholds or "hold your horses" recruitment of cognitive control (Cavanagh and Frank, 2014; Frank et al., 2005; Cavanagh et al., 2011). Using a Flanker and Simon task, Muralidharan et al. (2023) found that theta events (i.e., transient theta events in single trials) could be dissociated into two modes when a partial error occurred. Here, one mode of theta was linked to the stimulus-response conflict possibly reflecting a caution signal that "holds" responses. The second mode was strongly linked to partial errors and thereby reflecting processes specifically related to erroneous responses. Together, these results suggest that midfrontal theta is not only involved in the detection or monitoring of errors but also in their correction.

Other performance monitoring signals in the medial wall

Besides the ERN, several other signals in the medial wall have been linked to different performance monitoring stages (i.e., monitoring events before, during, or after the action; see Fig. 2). For example, if actions are performed under uncertainty, external feedback is needed to disambiguate whether the intended outcome was obtained or not. Here, negative and unexpected feedback elicits

the feedback-related negativity (FRN; Miltner et al., 1997), more recently also called reward positivity (Holroyd et al., 2008). The ERN and FRN have overlapping frontocentral scalp voltage distributions, with likely overlapping generator structures in the pMFC (Gentsch et al., 2009; Gruendler et al., 2011; see Fig. 2). These results have led to the assumption that both signals are functionally equivalent and may index the computation of prediction errors (Holroyd and Coles, 2002; Miltner et al., 1997). Consistent with this, there is evidence that the FRN not only codes outcomes but also the expectation of the outcomes in opposite fashion (Fischer and Ullsperger, 2013; Schuller et al., 2020). Thus the FRN is obeying to necessary and sufficient criteria of a reward prediction error (RPE) signal (Sambrook and Goslin, 2015). Interestingly, the FRN appears to only track RPE signals if rewards were actually obtained rather than counterfactual (Fischer and Ullsperger, 2013; Kirschner et al., 2022; Schuller et al., 2020) and not in observational learning (Burnside et al., 2019).

Recently, evidence from single neuron recordings in pMFC in macaques challenge the assumption that both, the ERN and FRN are functionally equivalent, and suggest a distinction between the representation of action errors and reward prediction errors (Fu et al., 2023). For example, Sajad et al. (2019) demonstrated that action error neurons in the macaques' SFG predict the ERN while neurons who signal gain or loss of reward do not. Yet, this might be specific to SFG and not aMCC. Error neurons in aMCC might be more abstract and code both action and prediction errors (Ito et al., 2003; Krigolson and Holroyd, 2007). Hence, action error signals from the SFG may be one of many inputs to the aMCC (Fu et al., 2023). However, this hypothesis has yet to be established in humans.

Another important performance monitoring signal that is observable in the EEG is related to response conflict. For example, when during an action it turns out that more effort is needed and invested - for example by resolving simultaneous activation of competing response tendencies—an increased frontocentral negativity in the EEG is observable (N2; Folstein and Van Petten, 2008; Kopp et al., 1996; Van Veen and Carter, 2002). A comparison of the generator structures of the ERN, FRN and N2 suggest an overlapping pMFC source for the three ERP components (Gruendler et al., 2011; see Fig. 2). Consistent with this, neurophysiological evidence in humans suggest, that response conflict neurons can be found in both the aMCC and pre-SMA (Fu et al., 2022; Sheth et al., 2012; Smith et al., 2019). Recently, Fu et al. (2022) demonstrated, that response conflict signals in a Stroop task are not only observables in MFC during action selection but also after a response has been given. Here, specific neurons in the pre-SMA and aMCC code if correct actions were executed under high or low conflict. Interestingly, using multivariate analyses of single neurons the authors found that these two types of conflict signals are represented by different neurons. Based on these findings Fu et al. (2023) suggest a distinction between two types of response conflict signals in pMFC: (1) one that occurs during action selection, aimed to resolve conflict proactively (2) one that occurs after action selection that serves as an ex post/after the fact evaluation signal.

Interestingly, besides monitoring conflict during action selection and execution, humans can estimate conflict probability from the history of experienced conflict (Fu et al., 2022; Jiang et al., 2014, 2015). Specifically, the probability of different conflict types is distinctly represented in aMCC neurons and associated with reaction time and accuracy (Fu et al., 2022; Jiang et al., 2015). Interestingly, the conflict probability signal in pMFC appears to explain more variance than experienced conflict in the previous trial alone, suggesting that this signal reflects the integration of experienced conflict over a longer time scale.

Theories of performance monitoring

Since the discovery of the ERN in 1990, various theories of performance monitoring have been put forward. They share the notion that the pMFC indicates the need for adaptation, but researchers have debated what signals are represented there and how they inform about the need for adaptation. In this article we will focus on the currently most widely accepted theories that are more or less directly based on principles of reinforcement learning and response conflict monitoring.

The mismatch theory (Brooks, 1986; Falkenstein et al., 1991; Miltner et al., 1997; Coles et al., 2001; Gehring et al., 1993; Ullsperger and von Cramon, 2001) proposes that error signals in aMCC are instigated by a comparator which is signaling a mismatch between the representation of the correct response and the executed erroneous response. According to the mismatch theory, the representation of the executed response is a corollary discharge of the motor response. The representation of the correct response is assumed to be the result of on-going perceptual stimulus processing and task relevant stimulus-response mapping. Borrowing key elements of this theory, Fu et al. (2023) formulated an updated conceptual framework of performance monitoring processes. A key difference between the models is that the representation of correct actions is not a result of ongoing stimulus processing but rather a result of predictions made by forward models. Moreover, this model included different types of performance-monitoring signals. A mismatch (control prediction error) is signaled in situations where action error or ex post conflict occur unexpectedly. These performance monitoring signals indicated that the current control settings (i.e., mechanisms used to influence action selection) derived from forward modeling are ill posed to the situation at hand and consequently used to train the control inverse model in the aMCC. Based on the evidence reviewed above, the authors hypothesize that the SFG first computes ex post performance monitoring signals and then passes them on to the aMCC. In situations where the SFG ex post performance monitoring signals occur unexpectedly, the aMCC uses this information to revise forward and inverse models (Fu et al., 2023).

In the *response conflict monitoring theory* (Botvinick et al., 2001) it is assumed that error signals arise from conflicts between incompatible response tendencies. Within this theory, neurons in the pMFC are positioned as conflict detectors that are assumed to recruit cognitive control processes and fast erroneous responses are a special case of high response conflict (Carter et al., 1998). While on correct trials involving response conflict the conflict is maximal before the response, on errors resulting from (prematurely) executing the incorrect response tendency the response conflict is largest after the response (Yeung et al., 2004). Neuroimaging studies have shown that the pMFC represents experienced response conflict (Ullsperger et al., 2014a) and conflict prediction

(see discussion above and Fu et al., 2022; Jiang et al., 2015), yet the response conflict monitory theory has repeatedly been a matter of debate (Burle et al., 2005, 2008; Carbonnell and Falkenstein, 2006; Grinband et al., 2011; Steinhauser et al., 2008; Yeung et al., 2011; Fu et al., 2023). For example, recordings in the human MFC suggest a clear distinction between error and conflict neurons (see above). Moreover, there is evidence that error and conflict related theta activity has distinct frequency signatures and sources (Beldzik et al., 2022). These results challenge the assumption that action errors are merely computed as a conflict signal (Fu et al., 2019, 2023).

The reinforcement learning theory of performance monitoring (Holroyd and Coles, 2002) proposes that the ERN arises from the transmission of prediction errors through dopaminergic inputs to the pMFC. This error signal is assumed to trigger a temporary pause in dopamine release, putatively leading to the disinhibition of pyramidal neurons in the pMFC, which, in turn, is assumed to generate the ERN. While this theory offers plausible explanation how the midbrain dopaminergic systems is facilitating task learning in the prefrontal cortex (Wang et al., 2018), the mesoprefrontal dopaminergic system lacks the temporal precision needed to generate the fast paced error signals described above (Fu et al., 2023; Ullsperger et al., 2014a). Moreover, recent evidence suggests independent error computations in the human MFC (Fu et al., 2019, 2022, 2023) which might precede prediction error signals in the midbrain (Noritake et al., 2018).

Furthermore, the pMFC has been suggested to be involved in **action outcome prediction.** The error-likelihood theory states that the pMFC learns to predict error likelihood based on context features (Brown and Braver, 2005). The magnitude of the pMFC signal reflects the learned error likelihood and serves as an early warning signal recruiting cognitive control. More recently, a **predicted response-outcome model** of pMFC function has been suggested (Alexander and Brown, 2011). In this model, pMFC neurons are assumed to code the learned prediction of the probability and timing of the various possible outcomes of the action at hand. The predicted response-outcome model is thus based on a generalized temporal difference error algorithm, with the important feature that it can predict multiple possible action-outcome relationships simultaneously. Outcomes are evaluated with respect to their deviation from prediction, irrespective of their positive or negative valence. As a result, surprising outcomes are associated with greater pMFC signals and then recruit adaptive control. Surprise-related pMFC signals have been described at neuronal, EEG, and fMRI levels (Ferdinand et al., 2012; Hayden et al., 2011; Jessup et al., 2010; Matsumoto et al., 2007; Sallet et al., 2007; Wessel et al., 2012).

The expected value of control theory

So far, we discussed how the pMFC detects errors and conflict and uses these signals to implement behavioral adjustments. But how do we decide how much cognitive control we want to engage at a given time? Recruiting control is costly: there are constraints due to metabolic resources depleted by controlled processing, limited capacity of control systems, and constraints due to interference in task processing pathways (Shenhav et al., 2017). Within the expected value of control theory, it has been suggested that the aMCC represents the expected value of control (EVC) and utilizes a cost-benefit analysis for control allocation (Shenhav et al., 2013, 2016). Specifically, aMCC monitors for information relevant to evaluating EVC and specifies the optimal control allocation to downstream regions (Shenhav et al., 2016; Yee et al., 2021). The basic idea is that this region is not doing all the evaluation but instead is collecting afferent signals that are relevant for the evaluation process (errors, conflict, reward etc.) and then through its efferent to downstream regions is implementing downstream control signal specifications. This allocation of control is further guided by reward expectation and efficacy (Fromer et al., 2021).

Lower-level action control vs. higher-level strategy control within pMFC

Several studies suggest that control abstraction may be hierarchically organized along pMFC's rostrocaudal axis. Here, lower-level action control is represented more caudal in pMFC and higher-level strategy control more rostral in pMFC (Shenhav et al., 2018; Taren et al., 2011; Venkatraman et al., 2009; Zarr and Brown, 2016; Ritz and Shenhav, 2022). This organization may reflect a more general hierarchy of abstraction within PFC (Badre and D'Esposito, 2009; Badre and Nee, 2018; Koechlin and Summerfield, 2007; Taren et al., 2011). Yet, there is also evidence for a dissociation of the neural representation of conflict and errors at task (higher-level strategy control) and response (lower-level action control) level in pMFC, whereby errors and conflict at task level are represented more posterior (Desmet et al., 2011).

Decision making

This part of the article focuses on more strategic and global behavioral changes based on feedback (vs. short-term adjustments). For example, we can learn from our mistakes and adjust choice preferences strategically to achieve global goals. The reinforcement learning theory and related theories placed performance monitoring signals into the learning context (Alexander and Brown, 2011, 2015; Holroyd and Coles, 2002; Shahnazian and Holroyd, 2018; Silvetti et al., 2011; Vassena et al., 2017). In line with this assumption, pMFC activity has consistently been related to reward prediction errors. Thus, this activity could reflect a teaching signal for subsequent learning and decision making (Ullsperger et al., 2014a). Several lines of research validate this claim. First, evidence from EEG and fMRI data suggests that in classical learning paradigms outcome related pMFC activity changes as a function of learning (Holroyd and Coles, 2002; Holroyd et al., 2009; Krigolson and Holroyd, 2007; Mars et al., 2005). Here, early in learning—when feedback is most informative—feedback-related activity is largest and decreases as learning is progressing. Second, feedback-related activity in the aMCC has been related to learning success. For example, aMCC activity predicted error correction in subsequent trials in an associative learning task and a Go/No Go task (Hester et al., 2008, 2009). Moreover, feedback-related

aMCC activity during a probabilistic learning task was associated with performance in a delayed memory task (Klein et al., 2007). In addition, ultrasound stimulation of the aMCC-homolog during a learning task in non-human primates reduced learning efficiency and prolonged information sampling (Banaie Boroujeni et al., 2022). Third, results from functional connectivity analyses revealed stronger aMCC connectivity with hippocampus and ventral striatum during early learning when feedback is highly informative, compared to later stages in learning (Klein et al., 2007). Together, these data provide compelling evidence that outcome monitoring related aMCC activity resembles key characteristics of a learning signal. Building on reinforcement learning theory, where the aMCC activity is thought to reflect merely RPE coding (Holroyd and Coles, 2002), the action value model suggests that adaptive learning is facilitated by weighting the prediction error according to the statistical properties of the environment and reinforcement history (Behrens et al., 2007; Jocham et al., 2009; Kennerley et al., 2006). Hence, aMCC may have a key role in representing and adaptively updating choice values and internal beliefs more generally. In line with this, after lesions in the MCC sulcus, macaques choices no longer reflected integration of reward over time but were exclusively guided by the most recent outcomes (Kennerley et al., 2006).
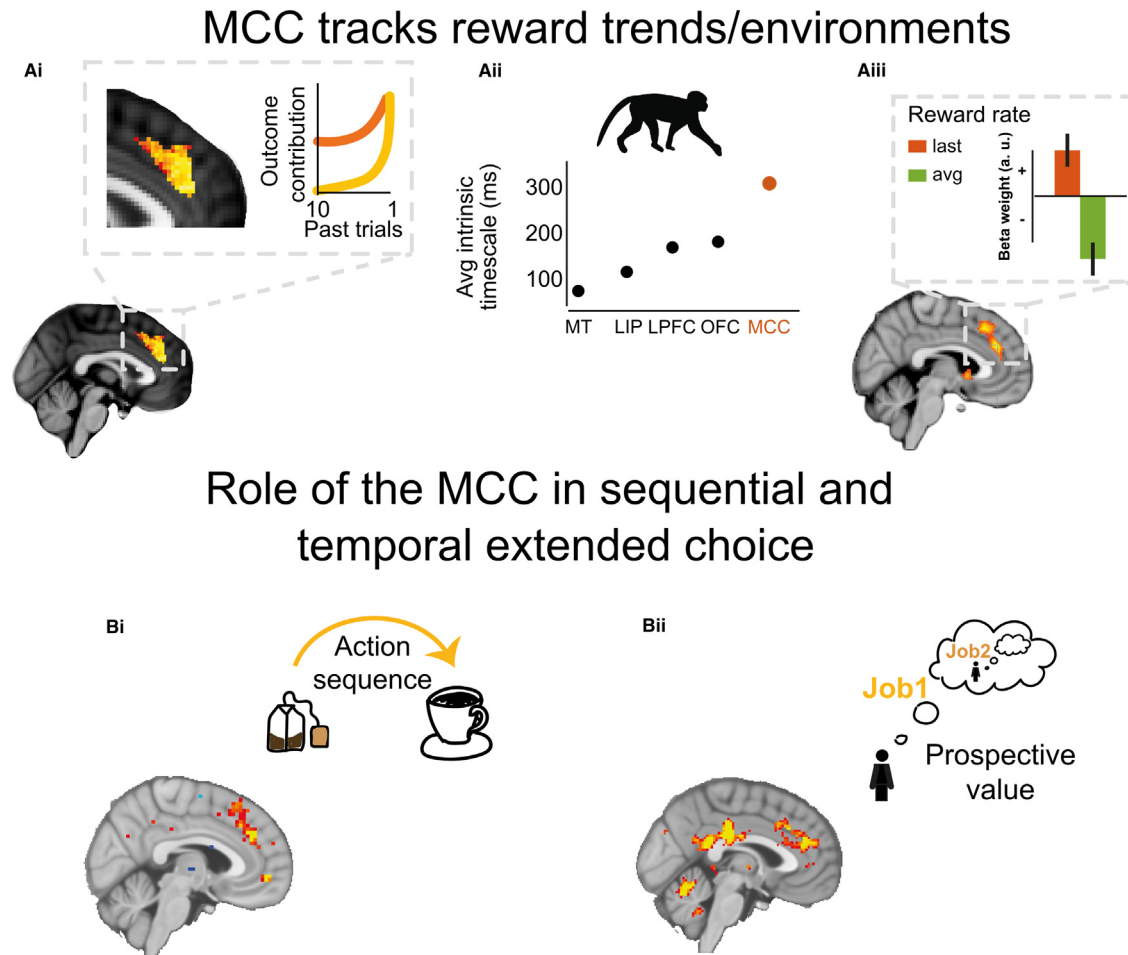
The role of aMCC in monitoring changing reward environments

A key question in the learning and decision-making domain is how the brain achieves adaptive learning in complex learning situations. That is, in situations in which people are required to adjust their behavior in dynamically evolving environments. Normative learning in changing environments requires increased learning in periods of environmental change and lower learning during periods of stability (Behrens et al., 2007; Nassar et al., 2010, 2012). Converging evidence suggest that humans apply these learning strategies, though to varying degrees (Behrens et al., 2007; Nassar et al., 2010, 2012, 2016, 2021; O'Reilly et al., 2013; Kirschner et al., 2022). On a neural level, evidence from contingency-shift paradigms suggests that aMCC activation is associated with increased learning (i.e., belief updates) during uncertainty, that is predicative of contingency changes in the environment (Behrens et al., 2007; McGuire et al., 2014; Nassar et al., 2019b, 2021; Nour et al., 2018; O'Reilly et al., 2013; Schwartenbeck et al., 2016) (cf. also). In contingency-shifts paradigms surprise and learning are closely related. Here, higher surprise is most often tightly linked to the required learning and belief updating. However, rational integration of surprising information heavily depends on the statistical context of the new information. If surprise is associated with a change in the environment (meaningful surprise), it should be heavily weighted to speed up learning. In contrast, if surprise represents uninformative fluctuations in the environment, this information should be less influential. A recent line of research aimed to tease apart the neural representations of surprise and belief updating. While some studies found dissociable representations of surprise and believe updating, whereby the aMCC was uniquely reflecting updating (Nour et al., 2018; O'Reilly et al., 2013), another study showed aMCC coding of uninformative surprise (d'Acremont and Bossaerts, 2016). Interestingly, the P300 − a feedback-locked EEG response associated with learning adjustments (Fischer and Ullsperger, 2013; Kirschner et al., 2022) − has been suggested to reflect a bidirectional learning signal that takes the statistical properties of the environment into account (Nassar et al., 2019a; Razmi and Nassar, 2022). Specifically, in a context where surprising outcomes reflected changes in the environment, larger P300 amplitudes predicted increased learning. A different pattern was found in a context where surprise was indicative of oddballs (i.e., uninformative surprise). Here, lager P300 amplitudes predicted reduced learning. It remains to be tested, how the aMCC relates to this bidirectional learning signal.

aMCC tracks reward trends in environments

Another key aspect of adaptive decision making in dynamically changing reward environments is the ability to estimate trends in the environment through past experiences. Knowing these trajectories helps to optimize behavior, when rewards are non-stationary, and one must project into the future and plan. Recently, it has been suggested that one way of solving this task in a brain circuit is by wiring up neurons with different time constants, in terms of the time scales over which they integrate reward (Kolling et al., 2016b). Here, by integrating information from neurons weighting very recent reward and neurons weighting rewards over a longer time scale, one can compute a trajectory. Indeed, there is increasing evidence from neuroimaging studies and electrical-physiological recordings in macaques suggesting that aMCC holds representations of experienced reward with multiple time-scales (Bernacchia et al., 2011; Cavanagh et al., 2016; Meder et al., 2017; Murray et al., 2014; Seo and Lee, 2009; Wittmann et al., 2016; Spitmaan et al., 2020; Klein-Flügge et al., 2022). For example, Meder et al. (2017) showed that in humans who played a learning task with changing reward probabilities, neurons in aMCC track the reward history of stimuli with multiple learning rates (see Fig. 3Ai). Here, a subset of voxels in aMCC represent value estimates based on very recent reward experience, while others represent value estimates based on longer term reward experiences. In addition to representing value estimates over different time scales, aMCC neurons in macaques appear to have a larger neural integration time constant (i.e., intrinsic timescale: spiking activity that proceeds direct stimulus processing) compared with other regions (Murray et al., 2014, Fig. 3Aii). Another human fMRI study investigated whether aMCC uses reward representation over different time constants to guide decision about whether to keep foraging in one environment or to explore an alternative environment (Wittmann et al., 2016). They contrasted the different environments reward trends in a way that simple recently weighted reinforcement learning would not help to distinguish between the different environment trajectories. What participants had to due to work out the reward trajectories was to weigh out reward in the past against recent rewards in an opposing manner. Indeed, when participants were offered a leave-stay decision, they were more likely to stay if the recent reward rate was high, while distant high reward rates had a negative effect on the stay decision. Similarly, aMCC showed separate neural responses to recent and distant reward rates at the time of the leave-stay decision (see Fig. 3Aii). Taken together, these results suggest that the aMCC represents reward histories with multiple time constants and one reason why this might be useful is to predict reward trends.

Fig. 3 **The role of aMCC in sequential decision making and monitoring in changing reward environments.** (Ai) aMCC holds multiple representations of experienced success in a simple task based on different timescales. Most recent experience is represented in the lighter, yellow regions. Experience integrated over a longer timescale is reflected in activity in the orange regions (Meder et al., 2017). (Aii) Based on evidence from single neuron recordings in macaques, neurons in MCC additionally appear to have a larger neural integration time constant (i.e., intrinsic timescale: spiking activity that proceeds direct stimulus processing) compared with other regions (Murray et al., 2014). Abbreviations: MT = middle temporal; LIP = lateral intraparietal; LPFC = lateral prefrontal cortex; OFC = orbitofrontal cortex. (Aiii) Knowing whether choice values in a dynamic environment are on an upward or downward trajectory helps to make predictions into the future and facilitates global decision making. One way to work these trends in the environment out, is by comparing recent and past reward rates (i.e., computing the derivative of the reward function). This comparison is reflected by opposing aMCC signals whereby recent reward experience is encoded with a positive sign (shown in red) and reward experienced over a longer timescale is encoded with a negative sign (shown in green) (Wittmann et al., 2016). *Note:* Error bars represent SEM across participants. (B) Oftentimes, we are confronted with the necessity of planning ahead and prospect. (Bi) Evidence from temporally extended decision paradigms revealed that activity in aMCC reflects the sequence of actions needed to acquire a specific goal (Holroyd et al., 2018). (Bii) Activity in aMCC also reflects prospective value of choice options. For example, when deciding whether to accept a job offer or to continue job hunting one should make these decisions prospectively. That is to say, one should consider the set of alternatives, search costs and the available time horizon for the job search (Kolling et al., 2018). Adapted from Klein-Flügge et al. (2022).

Role of the aMCC in sequential and temporally extended choice

Decisions that must be made sequentially or in temporally extended decision paradigms come with a host of novel problems and computational challenges compared to "one shot" preference decisions (Kolling and O'Reilly, 2018). For example, when deciding whether to accept a job offer or to continue job hunting one should make these decisions prospectively. That is to say, one should consider the set of alternatives, search costs and the available time horizon for the job search. Several studies in both macaques and humans suggest that the aMCC integrates the value of the available response options to guide adaptive switching between choices and that this representation is unrelated to the difficulty of choosing between different options (Fouragnan et al., 2019; Klein-Flügge et al., 2022; Kolling et al., 2016a, 2016b, 2018; Vassena et al., 2020; Wittmann et al., 2016). For example, in a seminal study that investigated sequential and temporally extended choice, humans had to decide whether they settle for the most recent offer or to keep searching for alternative offers (see **Fig. 3**Bii; Kolling et al., 2018). The authors show that subjects were capable of planning ahead by incorporating dynamic factors of the task in their choices and that aMCC activity reflected this prospective decision

process. The task of the subjects resembles the job-market problem referred to above and for ecologically valid prospective planning in this situation one need to incorporate at least three key aspects. First, to decide whether to accept an offer or keep searching for alternatives, one need to compare the current job value against the value to search for alternatives. Second, the decision should reflect the anticipation of how the job marketed will change over time (i.e., anticipated change of prospective value). Third, one should consider how much time and resources one can invest in searching for alternatives. The pMFC appears to reflect all these aspects (Kolling et al., 2018). In addition to the representation of prospective values, the pMFC in both rats and humans also encodes distributed, dynamically evolving representations of goal-directed action sequences (see **Fig. 3**Bi; Holroyd et al., 2018; Holroyd and Yeung, 2012; Klein-Flügge et al., 2022; Ma et al., 2014; Shidara and Richmond, 2002; Shima and Tanji, 1998). For example, Holroyd et al. (2018) used a "coffee-tea making" paradigm—in which human subjects are asked to prepare coffee or tea according to specific rules in a sequence of steps—and multivariate pattern analyses of fMRI data to investigate the neural underpinnings of goal-directed sequential decision making. They found that the coffee-tee making task sequences are encoded by distributed representations in aMCC activity that dynamically evolve as the task progresses. Such a distributed and fine-grained representation of action sequences might be useful to guide sequential decisions and perhaps permit action slips across sequences via the separation of task trajectories (Botvinick and Plaut, 2004; Holroyd et al., 2018).

In summary, the pMFC seems to be capable of performing complex reward and environment structure learning. Making decisions in dynamic environments poses unique computational challenges and the evidence reviewed above suggests that the aMCC is well equipped to perform such computations. However, it should be noted that the pMFC/aMCC is obviously not the only brain region concerned with dynamic reward-guided decision making. There are a host of brain regions and systems that control dynamic decision making, for example, the OFC, striatum, dopaminergic (DA) midbrain, and serotonergic (5HT) brainstem (Klein-Flügge et al., 2022; Ullsperger et al., 2014a; Grohn et al., 2020). Identifying the unique contribution made by areas such aMCC and understanding how brain regions and systems interact is not always straightforward and an active area of research (Klein-Flügge et al., 2022).

Conclusions

In this article we outlined the anatomy of the (posterior) medial wall of the frontal lobe and its involvement in cognitive control and decision making. Together, the reviewed evidence suggest that a broad array of performance monitoring and decision-making signals are represented in the pMFC. These signals are assumed to be conveyed to other brain regions, which then implement the necessary adjustments to facilitate goal directed behavior (Ullsperger et al., 2014b; Danielmeier et al., 2011). While some signals (e.g., error signals, RPEs, conflict signals) are assumed to reflect domain-general signals abstracted away from specific task requirements. There is also evidence for domain-specific performance monitoring signals providing task-specific information about performance disturbances. Moreover, specific aspects of performance monitoring and decision-making signals (e.g., control abstraction or representation of reward history) have dissociable representations within the pMFC. Interestingly, some of the pMFC representations reviewed above (particularly RPEs) appear to necessitate a sense of agency and personal engagement. Given the substantial interindividual variability of pMFC anatomy, future research should consider single-subject anatomical features for a more fine-grained mapping of the neural representation of the discussed signals within the pMFC.

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