Beyond Peaks and Troughs: Multiplexed Performance Monitoring Signals in the EEG

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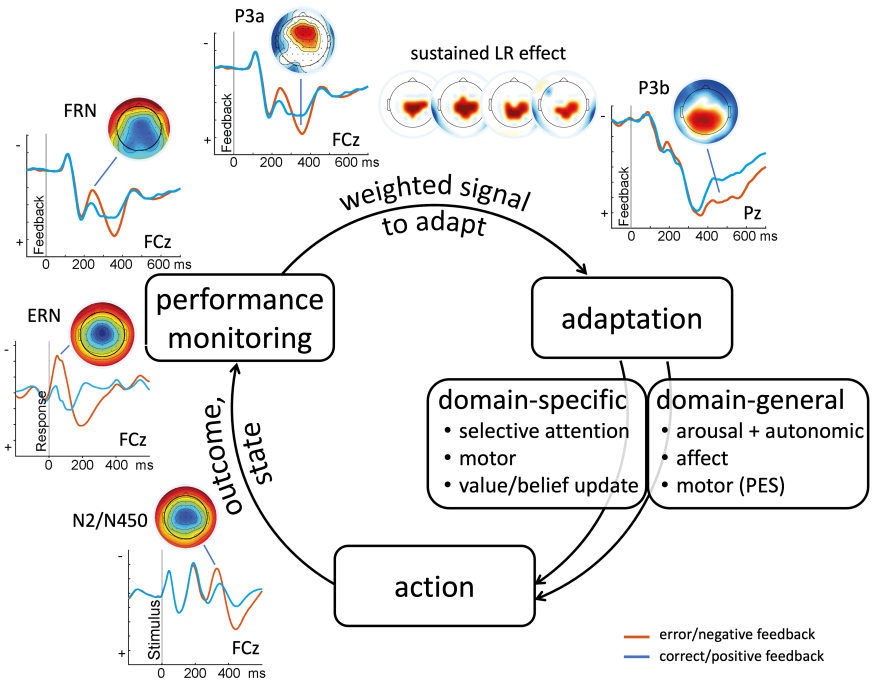

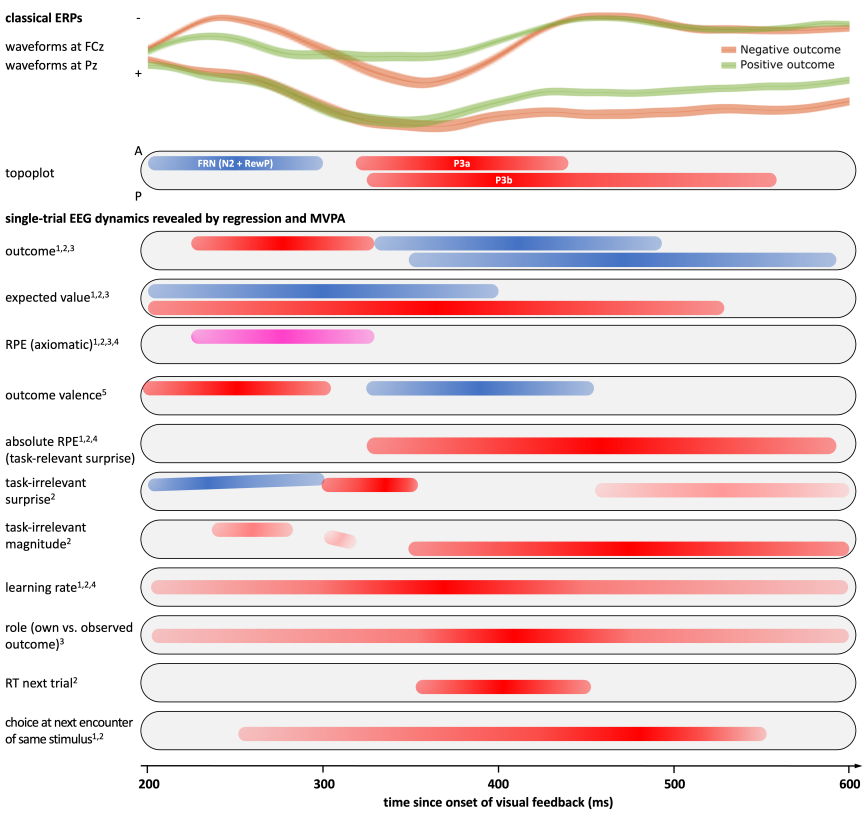

Beyond Peaks and Troughs:
Multiplexed Performance Monitoring Signals in the EEG

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Abstract
With the discovery of event-related potentials elicited by errors more than thirty years ago, a new avenue of research on performance monitoring, cognitive control, and decision making was opened. Since then, the field has developed and expanded fulminantly. After a brief overview on the EEG correlates of performance monitoring, this article reviews recent advancements in the field of performance monitoring based on single-trial analyses using independent component analysis, multiple regression, and multivariate pattern classification. Given the close interconnection between performance monitoring and reinforcement learning, computational modeling and model-based EEG analyses have made a particularly strong impact. The reviewed findings demonstrate that error- and feedback-related EEG dynamics represent variables reflecting how performance monitoring signals are weighted and transformed into an adaptation signal that guides future decisions and actions. The model-based single-trial analysis approach goes far beyond conventional peak-and-trough analyses of event-related potentials and enables testing mechanistic theories of performance monitoring, cognitive control and decision making.

Keywords:
Error processing, performance monitoring, cognitive control, decision making, ERN, FRN, P300, posterior medial frontal cortex, independent component analysis, multiple robust regression, multivariate pattern analysis

Impact Statement:
Performance monitoring and subsequent adaptations are highly dynamic processes. Here, I review recent advances in single-trial EEG dynamics analyses that enabled to rigorously test predictions based on current theories and mathematically formalized computational models of performance monitoring, cognitive control, and decision making. I show that performance monitoring signals reflecting the transformation of outcome variables to adaptation signals are multiplexed in the EEG.

1. Introduction

Humans are capable of pursuing short- and long-term goals, to make the according decisions, to select the appropriate actions, to monitor the actions' outcomes and to adjust flexibly, if the context changes or the action fails. Thus, decision making and monitoring of own performance and the changeable environment are in a continuous mutual interaction: performance monitoring enables to verify whether a decision has yielded the expected and intended outcome and to update one's values and beliefs based on reinforcement learning mechanisms and/or inferential processes. Updated values and beliefs, in turn, as well as representations of their (un)certainty, guide future decisions. This can be sketched as a feedback loop of (e)valuation and decision making. If values and beliefs are clear and no (explicit) decisions about routine behavior are necessary, still errors in action execution can occur and require corrections and adaptations to avoid similar errors in the future. These adaptations are brought about by recruiting a broad range of mechanisms, mainly autonomic responses, cognitive control (such as adjustments in motor parameters, increased arousal, and focused selective attention) and modulations of affect and motivation. All these interactions of performance monitoring can be sketched in a simplified feedback loop, where performance monitoring drives a host of domain-general as well as domain-specific adjustments that can affect multiple cognitive and affective systems thereby optimizing either chosen actions or future decisions (Figure 1) (Ullsperger, 2017; Ullsperger, Danielmeier, & Jocham, 2014).

Neuroimaging, non-invasive and invasive electrophysiological recordings, and lesion studies strongly suggest that the posterior medial frontal cortex (pMFC) plays a key role in the monitoring – adaptation loop with its various effects on cognitive control and decision making (Kolling, et al., 2016; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Shenhav, Botvinick, & Cohen, 2013; Ullsperger, Danielmeier, & Jocham, 2014). The term pMFC is purely descriptive and mostly driven by neuroimaging findings often showing rather widespread activity on the medial wall affecting various cytoarchitecturally different cortices: anterior midcingulate cortex (aMCC), which in itself consists of several distinct cytoarchitectural areas (Vogt, 2009), pre-supplementary motor area (preSMA), and dorsomedial prefrontal cortex (dmPFC) adjacent to the preSMA. Most views on this region's function seem to converge on the notion that it signals the need for adaptation and encodes decision parameters in multiple hierarchies, but there has been a long-lasting, vivid and unresolved debate on the underlying computational and neuronal mechanisms (Behrens, Woolrich, Walton, & Rushworth, 2007; Brown & Braver, 2005; Holroyd & Coles, 2002; Holroyd & Verguts, 2021; Kolling, et al., 2016; Laubach, Caetano, & Narayanan, 2015; Meder, et al., 2017; Shenhav, Botvinick, & Cohen, 2013; Ullsperger, Danielmeier, & Jocham, 2014; Ullsperger, Fischer, Nigbur, & Endrass, 2014; Vassena, Deraeve, & Alexander, 2020). Monitoring outcomes, inferring the need for adaptation as well as encoding choice options, their values and costs and other decision parameters are highly dynamic, fast, and often overlapping processes, such that they are very difficult to disentangle with neuroimaging methods operating at a temporal resolution in the order of seconds. In contrast, EEG and MEG can provide very precise temporal information which enables inferring about the parameters represented in the cortex and building and testing hypotheses about the underlying computations. Of course, invasive recordings from multiple neurons show that the neural code is very complex (Fu, et al., 2022; Fu, et al., 2019) and many details are likely to get lost in the EEG/MEG signals summed up over large neuronal ensembles. But, as I will demonstrate in the following, the results from noninvasive EEG and MEG are highly informative and have the great advantage that they can be obtained easily

from diverse human populations. Particularly analysis approaches allowing to characterize single-trial and within-trial dynamics have significantly advanced the field.
In this review, I will first briefly recapitulate event-related potential (ERP) correlates of performance monitoring, cognitive control, and decision making. Then I will discuss methodological aspects of studying single-trial dynamics with EEG and MEG. Thereafter I will review the evidence for EEG/MEG representations of performance monitoring and decision variables and link them to current theoretical accounts. Most single-trial EEG work has been done in the subfield of feedback processing, such that I will mainly focus on this aspect. I will conclude the review by an outlook to open questions and novel methodological developments.

2. ERP correlates of performance monitoring and decision making

The seminal discovery of ERP "peaks and troughs" associated with errors in the early nineties has started a whole new field of cognitive neuroscience that has greatly expanded and later merged with research on cognitive control, decision making and learning. The error negativity (Ne) or error-related negativity (ERN) is a large frontocentrally distributed negative deflection peaking around 50-100 ms after erroneous responses in speeded reaction time tasks (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Gehring, Goss, Coles, Meyer, & Donchin, 1993). It is followed by an early, frontocentrally distributed positivity and a somewhat later, more sustained centroparietally distributed positivity called early and late, respectively, error positivity (Pe) (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990). Notably, the ERN-Pe complex is elicited by action slips and errors driven by prepotent responses where the error can be detected based information available to the agent at the time of the action. In contrast, errors made in uncertain situations when the agent cannot know whether or not the chosen action will be successful, performance monitoring must rely on external feedback. Negative and unexpected feedback is associated with a frontocentrally distributed negativity at 200 to 300 ms after feedback onset, the feedback-related negativity (FRN), also called feedback-ERN, feedback negativity or medial frontal negativity (Holroyd & Krigolson, 2007; Miltner, Braun, & Coles, 1997). The FRN is followed by a frontocentral P3a and a later, more sustained centroparietal P3b. Later it has been suggested that in this latency range two different deflections overlap: a surprise-driven frontocentral N200 shifting the waveform into the negative direction and a positive shift scaling with (positive) reward prediction errors. Therefore, the term reward positivity was coined (Holroyd, Pakzad-Vaezi, & Krigolson, 2008), but the term has been used differently by different authors. As reviewed by Krigolson (Krigolson, 2018), the term reward positivity is often used for the reversed difference wave: instead of subtracting waveforms to positive feedback from waveforms to negative feedback yielding a negative-going ΔFRN, the ERPs to negative feedback are subtracted from ERPs to positive feedback, yielding a positive-going difference wave (Proudfit, 2015). Overall, ERP research on the FRN and reward positivity suggests that in this latency range multiple performance monitoring variables are encoded in the EEG: reward prediction errors, salience, and surprise, and that the strength of encoding these parameters may be stronger for positive than for negative outcomes. This has also been supported by time-frequency decomposition (TF) analyses suggesting that positive and negative reward prediction errors as well as surprise signals are represented by different oscillations in the delta and theta band, respectively (Brown & Cavanagh, 2020; Cavanagh, 2015).
Invasive recordings in human and nonhuman primates suggest that different neurons in the pMFC encode positive reward prediction errors, negative reward prediction errors, and

unsigned prediction errors/surprise (Hayden, Heilbronner, Pearson, & Platt, 2011; Matsumoto, Matsumoto, Abe, & Tanaka, 2007) and that individual neurons and neuronal ensembles multiplex various performance monitoring variables (Fu, et al., 2022; Kennerley, Behrens, & Wallis, 2011).

Also, during action planning and execution, performance monitoring is active. If unexpected difficulties occur, e.g., high response conflict arises or more effort than expected is needed, a frontocentral negativity with a latency depending on context and task is elicited. In many tasks it modulates the amplitude of the N2 (Danielmeier, Wessel, Steinhauser, & Ullsperger, 2009; Folstein & Van Petten, 2008; Yeung & Cohen, 2006), in the Stroop task or more complex task-switching situations the latency can be much longer (e.g., N450) (Brass, Ullsperger, Knoesche, von Cramon, & Phillips, 2005; Swick & Turken, 2002; West, 2003). Across all these different contexts of performance monitoring, a general pattern emerges (Ullsperger, Fischer, Nigbur, & Endrass, 2014): an ERP complex of a frontocentral negativity, immediately followed by a frontocentral positivity and a subsequent centroparietal positivity. This ERP complex arises from spatial and temporal overlap of electrophysiological activity in a multitude of (predominantly cortical) sources that are involved in performance monitoring, its inputs and its outputs. Source separation and localization as well as simultaneous EEG and fMRI consistently suggest that a major source of the frontocentral negativities is located in the pMFC (Debener, et al., 2005; Dehaene, Posner, & Tucker, 1994; Gruendler, Ullsperger, & Huster, 2011; Hauser, et al., 2014; Iannaccone, et al., 2015; Ullsperger & von Cramon, 2001; Wessel, Danielmeier, Morton, & Ullsperger, 2012); the sources of the positivities, particularly the more broadly distributed late Pe and P3b, are less easy to determine and comprise parietal and frontal cortices (Bledowski, et al., 2004; O'Connell, et al., 2007; Polich, 2007). Performance-monitoring-related ERPs, particularly the ERN, are rather easy to record also in patients and have, therefore, been studied extensively in clinical populations (de Bruijn & Ullsperger, 2011; Pezzetta, Wokke, Aglioti, & Ridderinkhof, 2021), where they have great potential as transdiagnostic markers for mental disorders (Endrass & Ullsperger, 2014; Hajcak, Klawohn, & Meyer, 2019; Riesel, 2019; Riesel, et al., 2019).

However, ERPs are not suited particularly well to study processes that change dynamically across and even within trials. Many current theories of performance monitoring, decision making, and cognitive control are mathematically formalized in computational models which make predictions on the temporal evolution of latent parameters across trials (and sometimes even within trials). These models can only be tested when trial-by-trial dynamics of brain activity is accessible. Binning trials and calculating separate ERPs can be used to address this problem, and I will report important ERP studies with this approach in this review. However, I will particularly focus on methods that enable analysis of single-trial EEG or MEG activity enable more fine-grained analyses and using the full power to reveal the representations of latent parameters varying from trial to trial (Debener, Ullsperger, Siegel, & Engel, 2007).

It should be noted that time-frequency decomposition also is a highly valuable approach to the analysis of trial-by-trial dynamics which can also reveal activity changes that are induced by events of interest but not strictly time-locked (Cohen, 2014). In particular, midfrontal theta power increases appear to be related to performance monitoring and cognitive control (Cavanagh & Frank, 2014; Cavanagh, Zambrano-Vazquez, & Allen, 2012; Duprez, Gulbinaite, & Cohen, 2020). To a large part, midfrontal theta reflects the processes encoded by the sequences of frontocentral ERP deflections (e.g., pre-ERN positivity – ERN – early Pe; P2-FRN/N2-P3a), but induced activity not phase-locked to the eliciting event is missed in ERPs. Midfrontal theta appears to be a mixture of activity in multiple sources (Zuure, Hinkley, Tiesinga, Nagarajan, & Cohen, 2020). Notably, theta increases induced by response conflict

seems to differ from error-related theta oscillations with respect to their main frequency, sources and function (Beldzik, Ullsperger, Domagalik, & Marek, 2022). Also the other frequency bands (alpha, beta, gamma, delta) have been studied in the context of cognitive control and decision making. However, a comprehensive review of time-frequency analyses and the interpretations of individual frequency bands would be beyond the scope of this work. In the following section I will discuss other methodological approaches that address trial-by-trial dynamics of EEG/MEG in the time domain. Note, that similar single-trial approaches are also applicable to time-frequency decomposed EEG/MEG data.

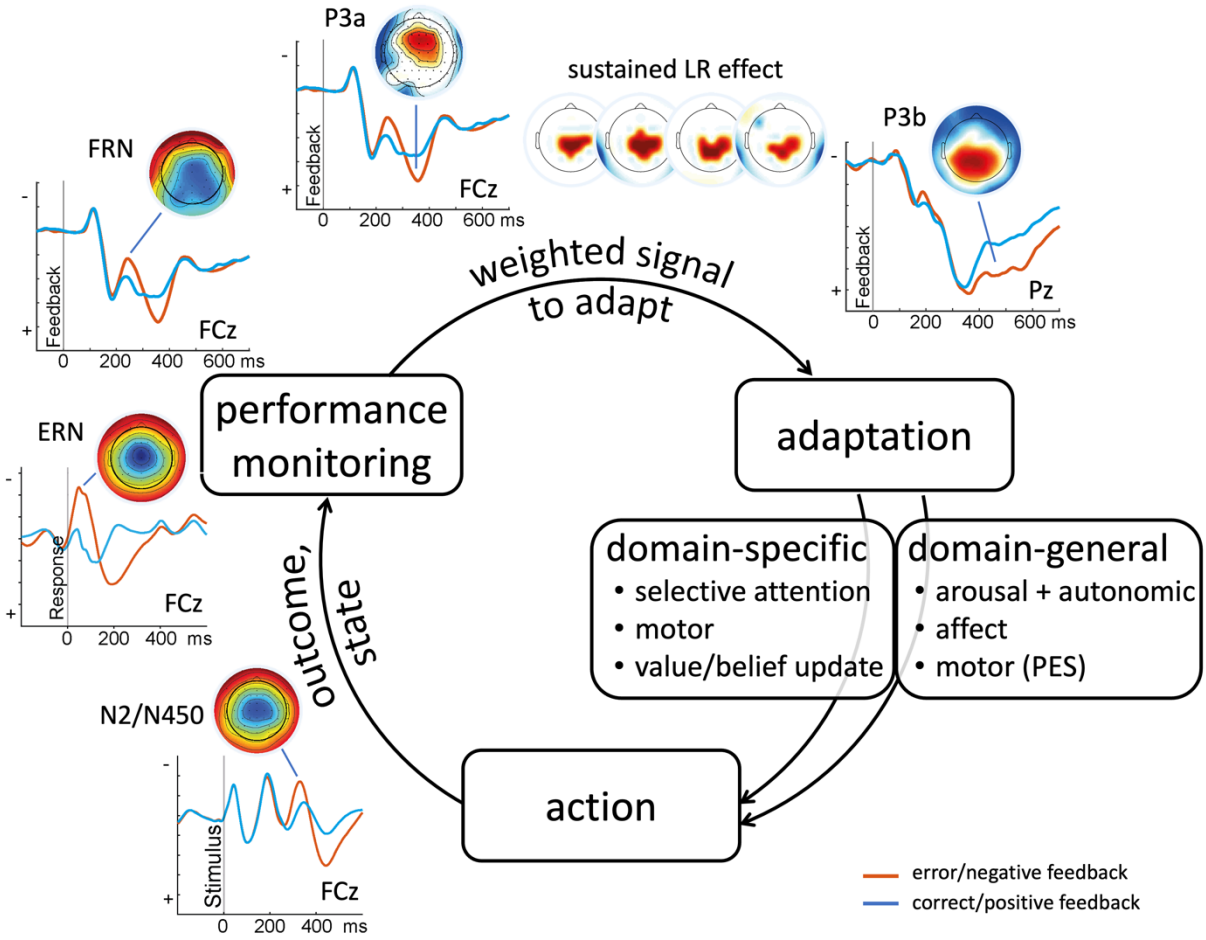

Figure 1. Cognitive control loop and associated EEG correlates. Actions and external factors result in outcomes and state changes. These, reflected in various salient events, are monitored by the human performance monitoring system. It weights, transforms and biases the monitored information into an adaptation signal encoding the need and magnitude of adaptations needed to compensate the performance problem and/or to improve future behavior. The adaptation signal is conveyed to other brain regions implementing domain-general and domain-specific adjustments acting at multiple levels with different time courses. The figure shows schematic prototypical time courses and scalp topographies of EEG correlates of performance monitoring and adaptation. Note: ERN, error-related negativity; FRN, feedback-related negativity; PES, post-error slowing. The schematics of EEG correlates were created based on data from Gruendler, Ullsperger, and Huster (2011); Humann, Fischer, and Ullsperger (2020); and Kirschner, Fischer, and Ullsperger (2022).

3. Methodological approaches to single-trial dynamics

Various methods have been developed to study single-trial dynamics in EEG and MEG data. Here I focus on those that have been used to study performance monitoring, cognitive control and decision making and give a brief overview on their main principles. In single-trial data signal-to-noise ratio (SNR) is often very poor which explains the great success of ERPs, where averaging increases the SNR of EEG activity time-locked to the eliciting event (at the cost of obscuring systematic changes of this activity across trials). Single-trial analyses aim at elucidating activity that is common for an event or process of interest while enabling to study variations of its magnitude and latency.

3.1. Source separation

Under the assumption that, under similar conditions, a neuronal computation or representation is carried out by a highly similar set of neuronal ensembles, a potential way of quantifying amplitude and latency variations is to select and isolate the associated sources, remove all other EEG activity, and measure the time course of the source activity. While it may be interesting to identify the localization of the sources, it is not necessary for studying the temporal dynamics of the activity.

The blind source separation technique independent component analysis (ICA) has been used successfully to characterize the trial-by-trial variability of error-related brain activity (Debener, et al., 2005). Temporal ICA separates EEG data into independent components (ICs), characterized by a constant scalp topography and a activity time course, such that the components, from an information-theoretic perspective, are maximally independent (Makeig, Debener, Onton, & Delorme, 2004). Individual ICs can be interpreted as spatial filters enabling to isolate the activity time course of the underlying selected sources. ICA is a blind source separation technique, such that, in a second step, meaningful ICs putatively representing the process or parameter of interest need to be identified. This can be based on an *a priori* template or other spatio-temporal characteristics (Debener, et al., 2005; Wessel & Ullsperger, 2011). For example, EEG data from a flanker paradigm was subjected to ICA and, based on scalp topography, within-epoch time course and time-frequency analysis, ICs contributing to a "prototypical" ERN were identified. Removing all other ICs and backprojecting the activity of the selected ICs to sensor space yielded the individual time courses of ERN source activity at a much higher signal-to-noise ratio. In other words, the backprojected signal that was clean enough to quantify single-trial ERN peak amplitudes. This analysis revealed a rather large trial-by-trial variability of the ERN. Furthermore, the vector of single-trial ERN amplitudes was used to inform a parametric analysis of simultaneously recorded fMRI data and to identify brain regions whose hemodynamic response covaried with the EEG correlate of error processing. This approach yielded a region in the aMCC (Debener, et al., 2005). In a similar study, ICA was mainly used to remove clearly identifiable artifacts which was sufficient for single-trial quantification of the ERN and the stimulus-locked N2, replicating and extending the findings: single-trial ERN and N2 amplitudes co-varied with the fMRI signal in partly overlapping subregions of the pMFC (Iannaccone, et al., 2015). An equivalent approach was also applied to the FRN obtained in a reversal learning task, revealing that single-trial FRN amplitudes covaried with fMRI activity in the pMFC (Hauser, et al., 2014).

Furthermore, separating their sources using ICA has been used to test whether certain ERPs arise from overlapping sources: if the time course of activity of ICs identified as sources of one ERP can also explain the time course of another ERP, this suggests substantial overlap of the ERPs' sources. This way, overlap of the sources of the ERN, the correct-related negativity (CRN), the FRN, surprise-related N2 and motor-inhibition-related N2 was demonstrated

(Gentsch, Ullsperger, & Ullsperger, 2009; Roger, Benar, Vidal, Hasbroucq, & Burle, 2010; Wessel & Aron, 2013; Wessel, Danielmeier, Morton, & Ullsperger, 2012). A potential disadvantage of ICA at the individual level is that solutions may differ substantially between participants and that it may be difficult to unequivocally identify ICs reflecting the process or parameter of interest. It appears to work robustly for processes associated with clearly identifiable, large ERPs such as the ERN and N2 but has been less successful for processes associated with small and variable ERPs. Moreover, as selected ICs reflect the activity within a constant set of sources, interactions between subsets of these sources or shifts in activity between different sources are not straightforward to reveal.
Other methods that have been used (but less so in cognitive control and decision making research) are, for example, principal component analysis (PCA) (Dien, 2010), wavelet denoising (Freeman & Quiroga, 2003) or mapping the time course of source activity of dipoles or distributed sources determined by various source localization techniques (e.g., Brass, Ullsperger, Knoesche, von Cramon, & Phillips, 2005; Wibral, Bledowski, & Turi, 2010).

3.2. Single-trial regression and deconvolution

Model-based analyses of EEG data is particularly useful, if variables of interest that vary from trial to trial (e.g., reward prediction errors estimated in a reinforcement learning model fitted to behavioral data) can be related to EEG phenomena that vary from trial to trial. The simplest and most-used approach to explore such a relationship has been the classic mass univariate general linear model (GLM) applied to epoched EEG data. Here, similarly as in neuroimaging analyses, parameters of a GLM are estimated for each participant at each time point and each electrode independently across all epochs (first level analyses). Estimated parameters from the first level analyses are then integrated across subjects in a second level analysis (Pernet, Chauveau, Gaspar, & Rousselet, 2011). Thus, in the first-level analysis, single-trial (i.e., epoch) EEG data are regressed at the within-subject level against parametric predictors (e.g., the reward prediction error varying from trial to trial), such that this mass univariate GLM approach also has been called – perhaps somewhat imprecisely – single-trial regression (Fischer & Ullsperger, 2013). This approach allows to model the contributions of multiple factors to the EEG dynamics time-locked to an eliciting event. It can disentangle factors leading to variations in EEG amplitude and, at the same time, control for potential confounds. This enables highly informative model-based EEG/MEG analyses in well-controlled experiments. If the latency of the process of interest varies across time, this GLM approach is not optimal: similarly as in averaged ERPs, it can result in weaker effects smeared across time or even yield spurious findings. These problems, that occur particularly in more natural, less controlled experiments, can be addressed with deconvolution analyses which correct for overlap (Ehinger & Dimigen, 2019; Hassall, Harley, Kolling, & Hunt, 2022). However, deconvolution approaches have rarely been applied in studies focusing on decision making and cognitive control so far.

3.3. Multivariate pattern analysis

Multivariate pattern analyses (MVPA) comprise a set of statistical analyses aimed to decode information from patterns in the neural data, to predict data from encoding models, and to compare multivariate representations of information in neural activity (Haynes, 2015; Kriegeskorte & Kievit, 2013). Decoding has become very popular in fMRI analyses and is increasingly used in EEG and MEG (Grootswagers, Wardle, & Carlson, 2017). For example, time-resolved decoding of visual perception, selective attention, and working memory have

been reported, e.g., (Bae & Luck, 2018; Bae & Luck, 2019; Ort, Fahrenfort, Ten Cate, Eimer, & Olivers, 2019; van Ede, Chekroud, Stokes, & Nobre, 2018). However, in performance monitoring research MVPA has been used only rarely (e.g., (Bode & Stahl, 2014; Fischer, Danielmeier, Villringer, Klein, & Ullsperger, 2016; Kirschner, Fischer, & Ullsperger, 2022; Kirschner, Humann, Derrfuss, Danielmeier, & Ullsperger, 2021)). This may result from the fact that latent variables of performance monitoring are more difficult to determine and to use for classifier training. Steinhauser and colleagues have successfully built classifiers discriminating errors from correct trials based on response-locked ERPs. They used the classifiers to extract error-related EEG dynamics and thus enabled detailed analyses at the single-trial level (e.g., (Maier & Steinhauser, 2013; Maier, Yeung, & Steinhauser, 2011; Steinhauser & Yeung, 2010; Steinhauser, Maier, & Steinhauser, 2017)).

4. Representations of performance-monitoring, control and decision-making variables

Performance-monitoring and decision-making research using single-trial analysis can pursue multiple goals. A number of studies focus on characterizing the "classical" ERP deflections known from conventional ERP approaches and aim at investigating the trial-by-trial variability of these prototypical waveforms and understanding what processes they reflect. Emphasis on a functional interpretation is weighted more strongly in studies that aim at extracting any EEG activity reflecting an observable, clearly defined variable such as error vs. correct or gain vs. loss. Model-based analyses aim at elucidating representations of latent constructs. That means, variables not directly observable in behavior are estimated by fitting computational models to the behavioral data. Representations of these latent variables, that vary across contexts, trial types, or trials are then revealed in the EEG dynamics. If features of the EEG covary with these model-derived variables, inferences on possible underlying computational mechanisms can be drawn. Notably, models are always a simplification and need not reflect the actual computational mechanism implemented in the brain. Still, they can advance mechanistic understanding by analogy, help to elucidate neural representations and their geometry, and bridge between micro-, meso- and macroscales of observation. Furthermore, they can help identifying EEG correlates and markers of latent variables and interpreting differences between (clinical) populations at a mechanistic level.

In the following paragraphs, I will discuss results from single-trial analyses elucidating the representations of behavioral phenomena, such as errors, error signaling, and post-error adjustments, as well as of latent variables estimated by computational modeling based on current theories of performance monitoring.

4.1. Errors in speeded reaction time tasks

Action slips, i.e., errors of action execution result from factors such as wrong motor programming under time pressure, the "automatic" execution of highly overlearned, prepotent responses that are often repetitively carried out in fast succession, or the interference from conflicting responses that are driven by distracting stimulus features and misguided selective attention. Information needed to detect the error is available to the agent at the time of action execution; external feedback is not necessary. The ERN, followed by the (early and late) Pe, appear to represent the difference in performance monitoring between incorrect and correct responses. In order to extract prototypical ERN activity, various methods briefly described above have been applied. ICA was used to remove all non-ERN EEG activity

and then find covarying, simultaneously recorded fMRI activity in the aMCC (Debener, et al., 2005). ICA was also applied to demonstrate that ERN source activity underlies, to a substantial extent, the FRN, N2, and correct-related negativity (Gentsch, Ullsperger, & Ullsperger, 2009; Roger, Benar, Vidal, Hasbroucq, & Burle, 2010; Wessel & Aron, 2013; Wessel, Danielmeier, Morton, & Ullsperger, 2012). Using multiple robust regression across trials, response-locked EEG activity covarying with response type (error/correct) was cleaned from other trial-wise varying potentially confounding effects reflecting stimulus conflict and response speed, thereby revealing robust sex differences in the electrophysiological response to errors (Fischer, Danielmeier, Villringer, Klein, & Ullsperger, 2016). This difference was also reflected, though with a lower effect size as no control of confounds was possible, in the averaged ERPs, i.e., the ERN amplitude is, on average larger in males than in females. Interestingly, no sex difference in response-locked EEG dynamics related to stimulus features giving rise to response conflict was found. Also, the within-subjects regressions revealing that larger, more negative single-trial ERN amplitudes predict longer reaction times on subsequent trials (post-error slowing, cf. Section 4.4) did not differ between women and men.

A study addressing conscious awareness of errors again used the GLM approach to disentangle various factors that may have influenced the response-locked ERPs: accuracy, error awareness (i.e., whether participants classified their response as correct or incorrect in a judgment immediately after each trial), confidence of the error-awareness judgment (operationalized via the reaction time of the response classification response), and the interaction of the latter both factors (Kirschner, Humann, Derrfuss, Danielmeier, & Ullsperger, 2020). Error awareness was represented as a central positive-going effect in the latency range of the Pe, supporting previous reports that the Pe is robustly increased on errors that entered consciousness (e.g., Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001; Wessel, Danielmeier, & Ullsperger, 2011). Accordingly, an MVPA analysis revealed that a central positivity around 250 ms indicated error awareness with >60% decoding accuracy (Kirschner, Humann, Derrfuss, Danielmeier, & Ullsperger, 2020). A further analysis suggested that the increased Pe on aware errors at least in part resulted from increased intertrial phase clustering, i.e., reduced jitter of the positive-going EEG deflection.

Errors in speeded reaction time tasks can lead to adjustments of future behavior, such as post-error slowing (PES), post-error reduction of interference (PERI), and post-error improvement of accuracy (PIA) (Danielmeier & Ullsperger, 2011). Most studies on post-error adjustments have linked error-related EEG dynamics to PES. There has been a debate whether PES is adaptive or maladaptive and evidence for both views has been reported (Danielmeier & Ullsperger, 2011; Fischer, Nigbur, Klein, Danielmeier, & Ullsperger, 2018; Notebaert, et al., 2009; Purcell & Kiani, 2016; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Wessel, 2018). Already in 1993, by means of trial binning it has been shown that within-subject variations of the ERN were predictive of PES (Gehring, Goss, Coles, Meyer, & Donchin, 1993). This was supported by several studies using multiple regression showing that larger (more negative) single-trial ERN amplitudes and larger (more positive) single-trial amplitudes of the early frontocentral Pe were associated with longer reaction times on the subsequent trial (Debener, et al., 2005; Fischer, Danielmeier, Villringer, Klein, & Ullsperger, 2016; Fischer, Endrass, Reuter, Kubisch, & Ullsperger, 2015; Wessel & Ullsperger, 2011). Importantly, a large study in more than 800 participants showed that, in contrast to intraindividual amplitude fluctuations, interindividual differences in ERN or Pe amplitudes are not predictive for interindividual differences in PES (Fischer, Danielmeier, Villringer, Klein, & Ullsperger, 2016).

Studies on PERI and PIA are generally sparse and mostly used fMRI rendering it difficult to assess the exact time course of error-related brain activity predicting these adjustments (e.g.,

Danielmeier, et al., 2015; Danielmeier, Eichele, Forstmann, Tittgemeyer, & Ullsperger, 2011; King, Korb, von Cramon, & Ullsperger, 2010). A study using steady-state visual evoked potentials (SSVEP) found that attentional selectivity for relevant stimuli was increased after the error very rapidly – within less than 200 ms (Steinhauser & Andersen, 2019). Moreover, larger ERN amplitudes as well as larger late, parietal Pe amplitudes were associated with post-error attentional adjustments.

4.2. Learning: expected values, outcome, reward prediction errors

When the success of actions is monitored and evaluated, discrepancies of the observed outcome and the intended goal state are highly informative. This notion was already the basis of the first theoretical account of the ERN and FRN, the mismatch theory (Coles, Scheffers, & Holroyd, 2001; Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Gehring, Goss, Coles, Meyer, & Donchin, 1993). Clay Holroyd and Mike Coles (Holroyd & Coles, 2002) were the first to link performance monitoring with reinforcement learning theory (Sutton & Barto, 1998) and proposed that the ERN and FRN reflect representations of the signed reward prediction error (RPE). Briefly, Holroyd and Coles built an actor-critic temporal difference error learning model in which any event indicating a change in outcome prediction yields an RPE that, weighted by a learning rate (LR) parameter, serves as a teaching signal and updates future outcome predictions and, at the same time, may signal the need for adaptations, such as remedial actions and adjustments in the case of an error. Put simply, a positive RPE indicates that an outcome is better than expected and the reward prediction, i.e., the expected value of a stimulus or an action, is updated in the positive direction. A negative RPE indicates that an outcome is worse than expected and that the reward prediction is updated by reducing the expected value. While RPE signals have been found in many structures in the primate brain, such as the ventral striatum and the dopaminergic nuclei in the midbrain, the theory by Holroyd and Coles (2002) suggests that they are also represented in the pMFC and thus reflected in the ERPs ERN and FRN/RewP. As reward predictions are updated at any informative event (outcomes, predictive cues etc.) and variable RPEs occur at any of these events, ERPs averaged across trials cannot easily prove or disprove hypotheses on the representation of learning signals in the EEG correlates of performance monitoring. Model-based analysis of EEG or MEG data can address the question whether learning signals such as RPEs are represented in noninvasively accessible electrophysiological activity of the human cortex. Usually, parameters of suitable reinforcement learning models are fitted to the behavioral data reflecting participants' choices. The models are then used to estimate the RPE for each event. The vector representing RPEs across the course of the experiment is then used as a predictor for the M/EEG amplitude in each epoch thereby revealing amplitude changes related to RPE variability. In simple reinforcement learning models, RPE is the difference of expected reward (predicted value of an event) and the obtained reward (outcome). A neural signal can be interpreted as reflecting an RPE when it meets a number of axiomatic requirements (Caplin & Dean, 2008; Rutledge, Dean, Caplin, & Glimcher, 2010). Specifically, it should not only correlate positively with the outcome (this would also hold for a pure representation of the outcome), but it should, at the same time, correlate negatively with the expected reward. In a combined EEG/MEG study, Talmi, Fuentemilla, Litvak, Duzel, and Dolan (2012) applied a GLM analysis and found that the feedback-locked MEG sensor activity around 320 ms complied with the requirements of an axiomatic test for an RPE signature. In the EEG data, an FRN was found in this time range, but it did not fully correspond to an RPE signal. Notably, they had used a decision-making task without a learning component, such that no

reinforcement learning model could be applied. Fischer and Ullsperger (2013) used a probabilistic learning task to search for RPE signatures in the human EEG. Participants were presented with individual stimuli from a set of three stimuli, which were associated with high (70-80%), medium (50%), or low (20-30%) reward probabilities, and had to indicate whether they would like to gamble with the presented stimulus or not. Choosing to gamble was followed by a real outcome, represented by factual feedback, according to the stimulus' reward probability. A positive outcome was indicated by a smiley and yielded a gain of 10 points. A negative outcome was indicated by a frowny and was associated with a loss of 10 points. Participants could also decide not to gamble which then yielded no gain or loss. However, they were presented with counterfactual feedback showing the fictive outcome they would have received had they chosen to gamble instead. A counterfactual smiley thus indicated that they missed a reward and a counterfactual frowny showed that they had forgone a loss. Participants were able to learn stimulus reward probabilities from both factual and counterfactual feedback to an equivalent extent. Fischer and Ullsperger (2013) fitted a Rescorla-Wagner type reinforcement learning model with an exponentially decaying learning rate to the behavioral data and, thus, estimated trial-by-trial expected values and RPEs. For real outcomes, they found that feedback-locked EEG covaried with single-trial RPEs at multiple latency ranges. In the time range of the FRN, between 250 and 300 ms after feedback, the EEG correlated positively with the EEG amplitude at central electrodes. In other words, negative RPEs are associated with a more negative-going EEG, which fits the FRN. This is followed by a frontocentral negative correlation in the time range of the P3a (around 400 ms) and a centroparietal negative correlation overlapping with the P3b (420 – 600 ms). As an axiomatic test a second GLM was conducted, in which the constituents of the RPE term, expected value and outcome, served as separate regressors at the within-subjects level. This revealed that only in the time range of the FRN the EEG contains a real signature of the RPE according to axiomatic testing: both predictors had opposite effects, outcome correlated positively with the EEG amplitude and expected value negatively. In the time range of the P3a and P3b the effect of expected value quickly returned to zero and the outcome effect reversed its sign, suggesting that only an outcome signal but not an RPE signature contributes to these ERPs. These findings were replicated in further studies using similar probabilistic learning tasks (Burnside, Fischer, & Ullsperger, 2019; Humann, Fischer, & Ullsperger, 2020; Kirschner, Fischer, & Ullsperger, 2022; Schuller, et al., 2020). Furthermore, Collins and Frank (2018) showed that the representation of the expected value at choice (a negative-going frontocentral effect roughly 250 to 450 ms after stimulus onset) negatively affected the representation of the feedback-locked RPE effect in the time range of the FRN, again providing an axiomatic test of an RPE signal in the feedback-related EEG dynamics. Together, these findings provide strong support for the hypothesis that an RPE signature substantially contributes to the feedback-locked EEG dynamics in the time range of the FRN.

Surprisingly, a completely different picture was seen for counterfactual feedback. The RPE regressor showed a short early occipitoparietal effect around 200 ms and a similar centroparietal effect in the time range of the P3b as for real outcomes. Both these effects did not comply with the axiomatic test for an RPE signature. Most surprisingly, however, there was no RPE signal whatsoever in the EEG between 250 and 400 ms (Fischer & Ullsperger, 2013). Again, this absence of cortical RPE signals in the time range of the FRN and P3a has been replicated several times since (Humann, Fischer, & Ullsperger, 2020; Kirschner, Fischer, & Ullsperger, 2022; Schuller, et al., 2020). Similarly, in an observational learning study in which two participants either actively made decisions in a three-armed bandit task or observed the partner's choices and outcomes and swapped their roles every few trials an axiomatic test

revealed frontocentral RPE coding in the time range of the FRN for own outcomes but no RPE coding in this time range for observed outcomes (Burnside, Fischer, & Ullsperger, 2019). Based on these observations it can be speculated that the representation of the RPE in posterior medial frontal cortex areas (which include motor areas such as the preSMA and the human homologues of the cingulate motor areas) critically depends on agency. Choosing to gamble with a stimulus or making a choice in a bandit task should be associated with a stronger sense of agency than avoiding the gamble or observing another person's choice. Indeed, research suggests interactions between performance monitoring, post-error adaptation, and the preventability of outcomes with the sense of agency (Di Costa, Thero, Chambon, & Haggard, 2018; Kulakova, Khalighinejad, & Haggard, 2017; Majchrowicz, Kulakova, Di Costa, & Haggard, 2020). However, future research should directly address whether and how the sense of agency influences representations of RPEs in the pMFC and scalp-recorded EEG. Interestingly, in a recent study, schizophrenia patients performing the above-described probabilistic learning task showed significant coding of counterfactual outcomes in the FRN latency range (Kirschner, et al., 2023). One is tempted to speculate that this finding results from the disturbed sense of agency often observed in this mental disorder.

The first reports of the FRN were based on results from a time-estimation task, in which participants have to press a button a predetermined time after an imperative stimulus (Miltner, Braun, & Coles, 1997). An adaptive response time window ensures that negative feedback occurs with a predetermined frequency (50% in the original version). A task variant with asymmetric adaptation of the response time window, blocks with high (75%) and low (25%) frequencies of negative feedback were applied allows to disentangle the effects of outcome expectedness and valence (Holroyd & Krigolson, 2007). Outcome expectedness here equals $1 - |\mathrm{RPE}|$; thus, it is low when the outcome is surprising and vice versa. An EEG measure covarying with the interaction of outcome expectedness and valence reflects an RPE signal. Data from 1000 participants performing this task variant was subjected to a GLM analysis, which revealed that outcome valence and expectedness are both represented by dissociable EEG patterns between 200 and 400 ms. Most importantly, feedback-locked EEG-dynamics covaried with the interaction term of valence and expectedness at frontocentral electrodes between 250 and 330 ms and, thereafter until 400 ms, at centroparietal electrodes (Kirsch, Kirschner, Fischer, Klein, & Ullsperger, 2022). Thus, also in a time-estimation task an RPE signal is coded in feedback-locked EEG dynamics with a similar temporospatial pattern as in the learning tasks discussed above.

4.3. Learning rate

In reinforcement learning theory the expected value is updated by the weighted RPE. The weighting factor is called learning rate in Rescorla-Wagner type learning algorithms. In the simplest versions, it is a constant estimated across all available choice data of an individual. However, it has been shown that subjects dynamically adjust the learning rate depending on the statistical features of the environment such as its volatility (Behrens, Woolrich, Walton, & Rushworth, 2007). In stable environments with constant rules, the learning rate is low such that decisions are based on the integrated experience over a long time range. In contrast, when rules change often, learning rate must be higher to quickly adapt learned values to the changed environment. Generally, high uncertainty, be it driven by volatile rules or by high stochasticity of the outcomes should increase the learning rate. In probabilistic learning tasks where outcomes may be misleading, e.g., when the choice of an option with a general reward rate of 80% leads to a loss, the learner needs to distinguish whether the outcome is informative and should be used to update the expected values or not. For example, in the

probabilistic learning task used by Fischer and Ullsperger (2013) this can be achieved by a decaying learning rate. In the early phase, all outcomes need to be taken into account to quickly update the expected values to ensure fast learning. In later stages, when the learnt expected values of the stimulus have approached an asymptote close to the real stimulus values, misleading probabilistic feedback should have a small impact on learning such that it cannot drive wrong decisions anymore. This can be achieved by a small learning rate downweighing the RPE. Fischer and Ullsperger fitted such an exponential decay of the learning rate to the learning performance and used the trial-by-trial values of the learning rate as an additional regressor in the within-subjects GLM analysis of the feedback-locked EEG data. This revealed a sustained central-to-centroparietal positive shift of the EEG dynamics from 200 to 550 ms which reached its maximum around 300 to 400 ms. This effect was present for both, factual and counterfactual feedback. The higher the learning rate, i.e., the more impact a single outcome had on learning, the more positive-going was the EEG. However, given the design of the study this effect was potentially confounded with other factors covarying with learning progress, e.g., time on task. Therefore, follow-up studies were conducted in which the learning paradigm was changed into a reversal learning task. After a variable number of trials, good, bad, and neutral stimulus could change their values without notice and participants had to infer from the accumulation of unexpected feedback that they should adjust their choice behavior accordingly. To capture the behavior in such reversal learning tasks with reinforcement learning models, a dynamic learning rate should be modeled that is high immediately after a rule shift and decays until the next reversal. This can be achieved by means of a hybrid Pearce-Hall – Rescorla Wagner model (Li, Schiller, Schoenbaum, Phelps, & Daw, 2011; Roesch, Esber, Li, Daw, & Schoenbaum, 2012). Here, the learning rate (associability) changes from trial to trial and reflects the weighted sum of the learning rate from the previous trial and the surprise associated with the outcome, i.e., the absolute RPE. The weighting factor κ is estimated by fitting the model to the behavioral data. A high κ indicates strong dynamics of the learning rate depending on surprise, a very low κ renders the learning rate nearly constant. Applying this hybrid model to data from a reversal learning task data yielded a trial-by-trial estimate of the learning rate that varied independently from time on task. Again, a sustained central positive effect between 300 and 550 ms was found (Humann, Fischer, & Ullsperger, 2020). Interestingly, the dynamics of the learning rate varied with participants' working memory capacity. High-span individuals showed stronger dynamics of their learning rates leading to lower learning rates at the end of a block of trials with the same stimulus value and a higher relative increase of the learning rates after a reversal. Recently, two clinical samples, patients with schizophrenia and major depressive disorder, respectively, underwent EEG recording while they performed a (non-reversal) version of the probabilistic learning task (Kirschner, et al., 2023). Both groups performed worse than healthy controls. Computational modeling revealed a transdiagnostic inflexibility of their learning rates. In contrast to healthy controls and a normative model they were less able to reduce the learning rate with learning progress which rendered them more susceptible to misleading probabilistic feedback. Similarly as in the previous studies with healthy participants, the learning rate was represented in the EEG between 300 and 500 ms as a positive shift. The maximum of this effect was somewhat more posterior than in previous studies - at parietal electrodes.

Bayesian inference models enable to disentangle the factors driving the learning rate, i.e., the strength of the belief update in response to a new observation (Behrens, Woolrich, Walton, & Rushworth, 2007; McGuire, Nassar, Gold, & Kable, 2014; Nassar, et al., 2012; Nassar, Wilson, Heasly, & Gold, 2010; Yu, Wilson, & Nassar, 2021). Using a change-point detection task that

allowed to quantify behavioral adaptation reflecting individual belief updates on a trial-by-trial level McGuire, Nassar, Gold, and Kable (2014) showed that normative factors such as the change-point probability, which is transiently elevated upon surprising outcomes, and the relative uncertainty, i.e., the uncertainty in one's belief about the state of the environment, as well as incidental factors such as reward value influence the learning rate (Fischer & Ullsperger, 2014). The learning rate integrating these factors was represented in the pMFC, anterior insula and parietal cortex, which appears compatible with the finding of a sustained central learning-rate effect on the EEG.

4.4. Factors biasing learning and decision making

In the study by McGuire, Nassar, Gold, and Kable (2014) it remained unclear whether the suboptimal boosting effect of reward value resulted from the occasionally increased value itself or from the relative rareness of the value increase, i.e., task-irrelevant surprise. To follow up on this question, Kirschner, Fischer, and Ullsperger (2022) modified the probabilistic task from Fischer and Ullsperger (2013) by changing it into a reversal-learning (more precisely a change-point detection) task and adding task-irrelevant features to the feedback. First, the magnitude of the outcome was varied randomly between high and low independently from the valence of the outcomes (real or fictive gain or loss). Thus, the outcome magnitude did not convey any information on the stimulus value, which was only determined by the reward probability (good = 80%, neutral = 50%, bad = 20%). Therefore, an optimal learner should ignore the outcome magnitude and base value updates only based on the outcome valence. Second, in 20% of the trials, the black background of the feedback screen changes into red for negative and green for positive feedback (congruent to the color of the feedback itself). While this surprising color change did not convey any additional information, it could act on learning in two ways. Either it could enhance feedback salience due to the color congruence and increase the learning rate on these trials, or it could distract participants from feedback processing and decrease the learning rate. Analyses of the behavioral data showed that both, high outcome magnitudes and increased feedback salience, slowed down choice reaction times on the directly subsequent trial. High outcome magnitudes furthermore influenced choices on the next trial with the same stimulus (on average 2-3 trials later) in a complex way reminiscent of an enhanced win-stay/lose-shift strategy. Computational modeling with an extended reinforcement-learning model showed that (a) learning rates were increased after high outcome magnitudes and (b) many participants were distracted by visual surprise during feedback (learning rate reduction) while some participants showed a minor increase in learning rate. Model-based analysis of the EEG again revealed multiplexed representations of the parameters underlying learning and resulting adaptations of choice behavior. The same differential RPE effects as in previous studies – a frontocentral positive effect in the time-range of the FRN for factual feedback and no RPE effect for counterfactual feedback – were found. Outcome magnitude had a small frontal positive effect in the FRN time range and a pronounced parietal positive effect in the time range of the P3b for real and fictive outcomes, supporting an early finding of magnitude effects on the P3b (Yeung & Sanfey, 2004). Visual surprise during feedback influenced visual ERPs at frontocentral and occipital sites, slightly enhanced the FRN, and had a strong frontocentral positive-going effect at the latency of the P3a. Again, these surprise effects did not differ between factual and counterfactual feedback. Thus, both normative (RPE) and biasing (magnitude, visual surprise) factors influencing learning and guiding future decisions were represented and multiplexed in the EEG dynamics between 200 and 600 ms after feedback onset.

4.5. Adaptation of future choice behavior

If, as discussed above, variables relevant for value learning and belief updating are represented in the feedback-locked EEG, is it possible to predict future decisions from these EEG data as well? This was addressed by Fischer and Ullsperger (2013) and in follow-up studies. A regressor coding whether participants would stay with their previous choice or change it (from choosing to avoiding the stimulus or vice versa) at the next encounter with the same stimulus showed a centrally to centroparietally distributed positive effect between 300 and 550 ms for upcoming behavioral shifts. This was the case when this switch regressor was added to the entire GLM thereby covering all behavior that was not explained by the reinforcement learning model (Fischer & Ullsperger, 2013) and also when the switch regressor was the only predictor in the model (Humann, Fischer, & Ullsperger, 2020). A multivariate pattern classification analysis (MVPA) applied to feedback-locked EEG data decoded switch vs. stay behavior at the next encounter with the stimulus with above-chance accuracy in a latency range from 110 ms until 790 ms after feedback onset (Kirschner, Fischer, & Ullsperger, 2022). A search-light algorithm again revealed a centroparietal distribution at the latency of maximal decoding accuracy (nearly 70% around 490 ms). A regression analysis furthermore revealed that longer choice reaction times of the immediately subsequent trial were also predicted by a central positive-going effect at a latency around 300 ms. Thus, P3b-like EEG activity predicted later adaptations. This pertains to slowing of subsequent reactions, predicted by a centroparietal positivity at 380 ms, and to future choices when the same stimulus is encountered, best predicted by a centroparietal positivity roughly 100 ms later (Kirschner, Fischer, & Ullsperger, 2022). Similar results were found in a study with patients suffering from schizophrenia and major depression, respectively (Kirschner, et al., 2023). Surprisingly, even in schizophrenia patients where, as expected, no feedback-related P300-like response was found (Ford, 1999; Jeon & Polich, 2003), the choice at the next encounter with the same stimulus could be predicted with an accuracy above 70% based on the feedback-locked EEG in the latency range of the P3b.

Based on these findings, we suggested that centroparietal P3b-like activity in feedback-related EEG dynamics represents a common final pathway of value or belief updating in memory which later results in behavioral adaptation (Fischer & Ullsperger, 2013; Kirschner, Fischer, & Ullsperger, 2022; Ullsperger, Fischer, Nigbur, & Endrass, 2014). However, the association between P300-like activity and learning is context-dependent. Nassar and colleagues (Nassar, Bruckner, & Frank, 2019) compared feedback-related activity between two conditions, one in which the environment changed in a blockwise fashion requiring belief update at change points indicated by a significant deviation of the feedback compared to preceding trials and one with a stable environment with interspersed oddball feedback stimuli requiring no adaptation. In both conditions, frontocentral P3a-like activity (350-650 ms) and centroparietal P3b-like activity (400-700 ms) scaled with the surprise associated with the deviant stimulus (the prediction error). However, in the changing environment change-point-related P3-like activity was positively associated with subsequent adaptation whereas in the oddball condition higher P3-like activity was associated with lower behavioral changes. One potential interpretation could be that P3-like feedback-related activity indicates the magnitude of the needed adaptation, but the type of adaptation is determined by context and not encoded in the P3: in the change-point condition, stronger deviation of the feedback should lead to stronger adaptation (via larger belief-updates) whereas for oddballs the previous model-based belief should be strengthened and any behavioral change should be inhibited. Such a context-dependent implementation of an adaptation signal reflected in the P3 could also explain the findings in a time-estimation task where feedback provides no indication how to

adapt future behavior (Kirsch, Kirschner, Fischer, Klein, & Ullsperger, 2022): feedback-related centroparietal P3b-like activity correlated negatively with subsequent changes in reaction time (RT) and there was an interaction of RT change and feedback valence spatiotemporally overlapping with the P3a. This indicates that the putative adaptation signal was used differently depending on context. Upon positive feedback, when time estimation was correct, RT changes should be maximally inhibited, whereas upon negative feedback RT changes should be larger but not too large to avoid overshooting. In sum, feedback-related centroparietal EEG activity with spatiotemporal features of the P3 seem to reflect an adaptation signal that, depending on context, may drive reaction-time changes as well as appropriate updates of values and beliefs which guide future decisions.

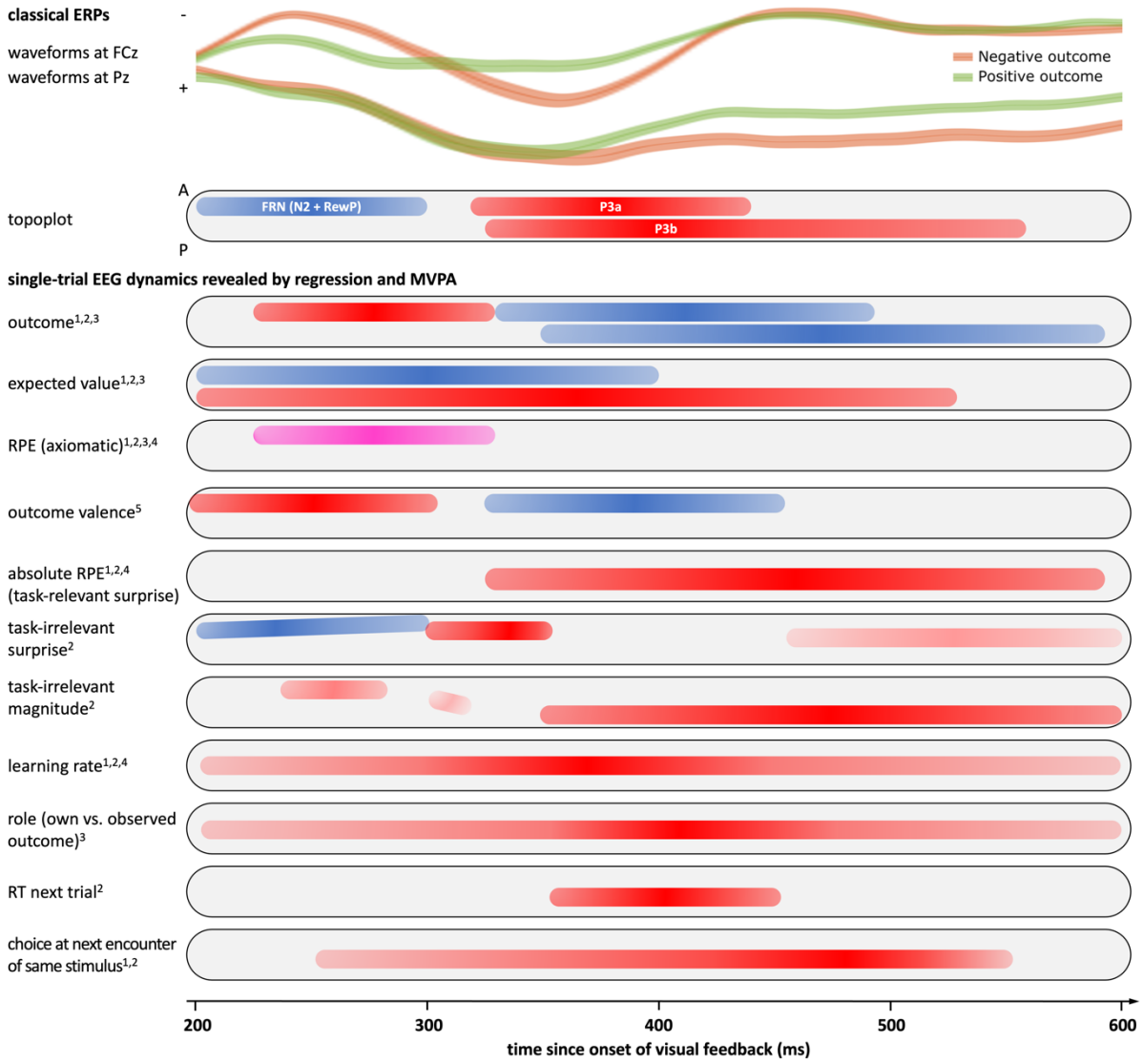

Figure 2. Multiplexed performance monitoring signals. Schematic of time courses and scalp distributions of feedback-locked event-related potentials (ERPs) and EEG dynamics representing individual monitoring and decision-making variables as well as future adjustments. Note: A, anterior; P, posterior; superscripts refer to references on which the schematic spatiotemporal distribution of the representations is based. [1]Fischer and Ullsperger (2013); [2]Kirschner et al. (2022); [3]Burnside et al. (2019); Humann et al. (2020); [4]Kirschner et al. (2024); [5]Kirsch et al. (2022).

5. Conclusion

The evidence reviewed above demonstrates convincingly that analyses of single-trial EEG dynamics enable to reveal neural representations of performance monitoring and decision-making variables in a fine-grained fashion and to test specific hypotheses derived with the help of computational models. At all stages of the cognitive control loop EEG signatures of these variables can be found (Fig. 1). While many of those overlap with the peaks and troughs in the prototypical ERP waveforms (e.g., ERN, early Pe, late Pe, or FRN/RewP, P3a, P3b), the maximal representations do not need to coincide with the peaks and other representations may have a more sustained time-course over hundreds of milliseconds (e.g., learning rate). In other words, while classical ERPs may help describing the latency and topography of the representations, it may be misleading to directly associate individual performance monitoring or decision-making variables to individual ERPs in a one-to-one fashion. The results of single-trial analyses rather suggest that the representations of these variables are multiplexed reflected in complex and overlapping spatiotemporal patterns. Fig. 2 shows the representations of various variables underlying normative as well as biased learning and decision making in the first 600 ms after feedback presentation. This is consistent with the mixed selectivity of neurons in pMFC and other frontal regions found in invasive recordings (Fu, et al., 2022; Fu, et al., 2019; Kennerley, Behrens, & Wallis, 2011; Parthasarathy, et al., 2017). Population code analyses can extract domain-general and domain-specific variables from these multiplexed neuronal signals. This is, to some extent, also possible with scalp-recorded EEG, even though the inverse problem precludes the localization of the underlying sources with the same precision as invasive recordings. Still, model-based single-trial and within-trial analyses of event-related EEG dynamics are valuable tools to gain a mechanistic understanding of higher cognitive functions such as performance monitoring, cognitive control, and decision making. Taking into account within-subject and between-subjects variance is particularly useful to understand interindividual differences and to reveal transdiagnostic markers and mechanisms in mental disorders.

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