Exploring Neural Dynamics of Performance Monitoring: A Comprehensive Series of EEG Studies on Cognitive Control across Contexts

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General Abstract

Every human behavior bears the potential for a mistake. Sometimes it is hard to make the right decision. Sometimes it is difficult to perform an action correctly. Our everyday life involves a constant risk of performing a behavior more or less incorrectly, leading to negative consequences of varying severity. To err is human, but so is learning from our actions. In the course of evolution, humans have developed a complex neural system to detect errors, resolve cognitive conflict and adapt future behavior. As multifaceted the range of situations and behaviors we encounter in everyday life is, so are the neuroscientific studies and findings on this performance monitoring system.

Therefore, this dissertation aims to integrate different approaches to investigate performance monitoring with a particular focus on a neural indicator that consistently appears in the literature on performance monitoring research, namely frontomedial theta activity (FMT). In a series of four studies, FMT activity in the scalp-recorded electroencephalogram (EEG) was examined in different situations and settings, applying different analysis procedures and considering interpersonal differences and intraindividual temporal stability. Study 1 investigated fine-grained additive effects of FMT activity in response to multiple independent outcomes in a non-dynamic laboratory setting and their stability over time. In contrast to the distinctive feedback presentation in study 1, study 2 investigated the effects of continuously incoming information during the performance monitoring process in a dynamic shooting task within virtual reality. As in a wide variety of daily actions, this design allowed for the anticipation of an outcome before it occurs and thus “online” performance monitoring. Study 3 advances the dynamics of the setting even further by implementing a shooting task without virtual reality but in a Mobile Brain/Body Imaging (MoBI) setting (Makeig et al., 2009), using toy guns with foam darts to shoot a stationary target. This study investigated the characteristics of the oscillatory phase of the measured FMT signal. Study 4 investigated FMT activity in response to cognitive conflict rather than negative action outcomes. Using source separation analyses, individual sensitivities to different kinds of conflict are investigated to determine whether FMT has the same or different neural sources across different contexts.

The four studies are discussed to determine the functional role of FMT in performance monitoring and whether FMT may reflect a unitary signal for performance monitoring across diverse contexts and tasks.

1 Introduction

1.1 Why Performance Monitoring Matters

For many people driving a car is a common daily activity. Nevertheless, whether you enjoy driving or not, whether you've been driving for years or just recently got your license: As drivers, we need to pay attention to the road and constantly monitor our own behavior to ensure that we are driving safely and efficiently. This requires monitoring our speed, following traffic signals and adjusting our driving based on our environment and other driver’s actions. When we make a mistake while driving, such as missing a stop sign or accelerating too quickly, or when we make a wrong decision, such as speeding instead of breaking at a yellow traffic light, the consequences can be severe. Driving a car is a task that requires continuous performance monitoring, just as many other daily actions. By constantly monitoring and adjusting our behavior as needed, we can reduce the risk of accidents and improve our overall performance. Thus, performance monitoring is crucial in everyday life and helps us to achieve our goals and maintain a high level of performance in various tasks.

Performance monitoring can be described as the processes by which individuals evaluate the outcomes of their actions in real time and use this information to guide subsequent behavior (Reisberg, 2014). According to this definition, performance monitoring applies to the whole bandwidth of human behavior under all possible circumstances, whether we face behavioral errors, decision conflicts or motivational conflicts. The range of human behavior is vast and the number of possible errors in it seems endless. However, our performance monitoring system must be able to deal with (almost) all of them. This would require extraordinary versatility in order to be able to handle every single situation we might face in our lives and every conceivable error efficiently. This raises the question of whether there actually is one global, extremely versatile performance monitoring system that works across all contexts and tasks or whether what we call performance monitoring system might be a composite of several smaller systems or units that act in a more context-specific way. There could be different, independent systems all executing performance monitoring, but for example, one unit might be responsible for behavioral error, another for cognitive conflict and another for outcome processing.

Thus far, this question still needs to be answered. Representing an indication of a more context-specific mode of operation, some event-related potential (ERP) components in the scalp-recorded electroencephalogram (EEG) such as the error positivity (Pe) and the error-related negativity (ERN/Ne) are sensitive to behavioral errors and error detection (Debener et al., 2005; Falkenstein et al., 1991; Gehring et al., 1993; Gehring et al., 2011; Ullsperger, Fischer et al., 2014; Wessel et al., 2011). The feedback-related negativity (FRN) is a component that is sensitive to negative feedback (Nieuwenhuis et al., 2004; Sambrook & Goslin, 2015; Walsh & Anderson, 2012) and the N2 component is modulated by response conflict (Folstein & Van Petten, 2008; Nieuwenhuis et al., 2003)[1]. On the other hand, in the time-frequency domain, frontomedial theta (FMT) activity is associated with each of these ERP components (Cavanagh & Frank, 2014; Pezzetta et al., 2022) and thus might be less situationally specific than the ERP components aforementioned. FMT is characterized by an event-related power increase in the theta band (4Hz-8Hz) in response to behavioral errors, negative outcomes or action conflicts. While the functional role of FMT in the framework of performance monitoring is still unclear, it seems to reflect a common mechanism that acts across a broad range of contexts, speaking for a performance monitoring that, at least partially, works on a global level.

In order to identify how FMT functions in different contexts and whether there are contextual differences in FMT activity, an overarching integrative view is lacking. This dissertation aims to provide a comprehensive exploration of FMT from various perspectives. For this purpose, the present work will first discuss the concept of performance monitoring, including the neural structures and cognitive processes involved in this domain. Specifically, an overview of the most common theories related to performance monitoring will be provided to lay the foundation for the discussion of FMT, which will focus on FMT as a neural indicator of those performance monitoring processes as well as on different approaches to understanding its functional role. Against this background, the following four studies conducted in the framework of this dissertation will be discussed.

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[1] This dissertation focuses on FMT. For a review on frontocentral ERP components in the framework of performance monitoring, see Ullsperger, Fischer et al. (2014).

Study 1 assessed feedback-related FMT activity in a reinforcement learning task. Multiple feedback dimensions were utilized simultaneously to investigate whether additive effects in the "total feedback score" also have an additive effect on FMT activity or whether FMT activity is only sensitive to feedback valence independent of the feedback score. Further, this study assessed the temporal stability of individual FMT responsivities by performing a follow-up testing three months after the first testing.

Study 2 focused on the online process of performance monitoring. Instead of presenting feedback at distinctive time points, it implemented two shooting tasks in virtual reality where the projectile could either be observed or not. The ability to observe the projectile provides constantly incoming information that can be used to anticipate the most likely outcome of the shot even before it occurs. Integrating this information "online" can provide significant advantages for a time-critical system like the performance monitoring system.

Study 3 implemented another shooting task, but without virtual reality and in “real life” instead, using a toy gun and foam darts in a Mobile Brain/Body Imaging (MoBI) setting (Makeig et al., 2009). The purpose was to investigate whether such a dynamic setting elicits feedback-related FMT activity as well and how it is related to the phase of the signal, as it is not completely clear how FMT is linked to the error- and feedback-related ERP components mentioned above and whether some of them might originate from phase-locking of FMT (Luu et al., 2004; Pezzetta et al., 2018; Yeung et al., 2007).

The first three studies investigated performance- and outcome-related FMT activity and thus focus in particular on the first part of the definition of performance monitoring: "evaluate the outcome", either during the performance of the action or in response to the outcome. Therefore, Study 4 focuses on the second part of the definition: “guide subsequent behavior”, by investigating FMT during action selection, namely, in response to a cognitive conflict. Implementing a Flanker task and an approach-avoidance task, which are two different kinds of conflict tasks, conflict-related FMT activity was assessed. The two tasks were used to test for cross-task sensitivities of individual FMT responsivities, i.e., whether FMT responsivity in one task correlates with FMT responsivity in the other.

Further, recent studies indicate that there might be multiple independent neuronal sources of FMT (Beldzik et al., 2022; Töllner et al., 2017; Zuure et al., 2020). For this reason, source separation analyses were applied to separate multiple potential FMT sources and to test whether the extracted sources are the same or differ across the two tasks.

The findings of the four studies will be discussed to shed light on the question of whether FMT reflects a unitary signal that the performance monitoring system employs across various contexts and tasks. As the four studies conducted investigate performance monitoring at different stages of action performance and in diverse contexts, the results of these studies will be compared to elucidate the functional role of FMT in the performance monitoring process. It will be discussed how contextual, interindividual and intraindividual factors may initially affect the modulation of FMT activity, which can eventually be utilized as a global, unitary signal across different contexts and tasks.

1.2 Performance Monitoring

Performance monitoring is a fundamental cognitive function that allows for quickly detecting mistakes and adjusting our behavior in everyday life, whether we are driving a car or simply reaching for a glass of water (Desender et al., 2021). The performance monitoring system continuously scans for deviations between observed and predicted outcomes and communicates these to parts of the nervous system that can implement corrective measures. This ability is utilized in diverse ways, from simple motor reflexes to complex adjustments in cognitive and emotional processes, motivating learning effects, changes in motivational goals, re-evaluations of action outcome values and more (Ullsperger, Danielmeier & Jocham, 2014). This dissertation focuses on performance monitoring in goal-oriented behavior, with an emphasis on complex cognitive-affective adjustments rather than simple motor reflexes.

A crucial brain region driving performance monitoring-related neural activity is the medial prefrontal cortex (mPFC). Specifically, the anterior cingulate cortex (ACC) within the mPFC is suggested to be responsible for detecting errors and signaling the need for adjustments in cognition and behavior.

The mPFC is involved in the evaluation of the outcomes of actions, determining the success or failure of behavior and updating the behavior accordingly (Botvinick et al., 2004; Egner, 2017; Fidêncio et al., 2022; Fu et al., 2023; Holroyd & Coles, 2002; Kerns et al., 2004; Nee et al., 2011; Pezzetta et al., 2022; Ridderinkhof et al., 2004; Ullsperger, Danielmeier & Jocham, 2014; Ullsperger, Fischer et al., 2014; Wessel et al., 2011; Yeung & Cohen, 2006). Dysfunctions in the mPFC have been associated with impairments in performance monitoring and have been linked to various psychiatric disorders, such as posttraumatic stress disorder (Koenigs & Grafman, 2009; Shin et al., 2005), depression (Belleau et al., 2019; Murrough et al., 2016) attention-deficit/hyperactivity disorder (Hauser, Iannaccone, Ball et al., 2014), anxiety disorders (Marques et al., 2019; Xu et al., 2019) and schizophrenia (Chai et al., 2011; Pomarol-Clotet et al., 2010).

Theories suggest that the mPFC integrates information from various sources, including sensory inputs, memories and internal states, to evaluate the outcomes of our actions and make adaptive adjustments to our behavior (Friedman & Robbins, 2022; Ridderinkhof et al., 2004). However, the exact mechanisms underlying the role of the mPFC in performance monitoring and goal-oriented behavior are still being actively researched. The following section will outline different theories on how the mPFC helps us learn from mistakes and improve our decision-making.

1.2.1 Mismatch Theory

The mismatch theory proposes the existence of a comparator that compares the representation of the correct outcome of an action to the actual outcome. If the comparator detects a mismatch between the representations of the correct and the actual outcome, the brain generates a prediction error signal. This is reflected in the ERN/Ne and error-related ACC activity (Falkenstein et al., 2000; Folstein & Van Petten, 2008; Ullsperger, Danielmeier & Jocham, 2014; Wessel et al., 2011). In situations where a correct outcome cannot be identified without external feedback, the predicted outcome is compared to the outcome feedback. For instance, when driving a car, this can occur when attempting to accelerate but failing to provide sufficient gas, leading to the engine stalling instead of the car accelerating. The mismatch theory can provide explanations for error-related activity of the mPFC as well as feedback-related activity, which is, for example, reflected in the FRN. However, it cannot explain the modulations in mPFC activity that have been found related to correct actions that involve response competition (Ullsperger, Danielmeier & Jocham, 2014).

1.2.2 Response Conflict Theory

The response conflict theory assumes that the performance monitoring system does not scan for deviations of predicted and observed actions, i.e., errors, but rather for conflicting response tendencies. If there are several conflicting response tendencies before an action is performed (e.g., evoked by distracting stimuli or braking vs. maintaining speed upon detecting a yellow traffic light), this induces pre-response conflict (Yeung & Nieuwenhuis, 2009). The performance monitoring system then needs to enforce that one of the behavioral tendencies is executed. Furthermore, whether or not multiple tendencies were present prior to the response, an implemented behavioral tendency may result in a negative outcome. In that case, further response tendencies may arise even after the response. These response tendencies are based on the newly gathered information and represent corrective response tendencies that conflict with the error response tendency. So, in this case, response conflict arises after the action, and thus negative outcomes are associated with increased post-response conflict (Botvinick, 2007; Kerns, 2006). However, this theory strongly focuses on situations that involve motor responses. It lacks to explain performance monitoring-related activity when no active responses are involved (Ullsperger, Danielmeier & Jocham, 2014).

1.2.3 Reinforcement Learning Theory

The reinforcement learning (RL) theory (Holroyd & Coles, 2002) posits that the midbrain dopamine system plays a key role in performance monitoring. Specifically, the dopamine system signals the difference between a given action's predicted and actual outcomes, referred to as reward prediction error (RPE). Unsigned and signed RPEs are distinguished, where the former reflects the absolute magnitude of the difference between the predicted and actual outcomes, while the latter conveys both the direction and magnitude of the deviation. Outcomes that are better than predicted lead to positive (signed) RPEs and worse outcomes lead to negative (signed) RPEs. The size of the RPE increases as the discrepancy between the predicted and actual outcomes increases (Sutton & Barto, 2018). The striatum in the basal ganglia acts as the comparator, which is called critic in the RL theory. It codes the signed RPE signal via a phasic adjustment in dopamine release. Positive RPEs lead to an increase in dopamine release, and negative RPEs lead to a decrease. This change in dopamine levels is thought to modulate neuronal activity in the ACC and thus generate the ERN/Ne response measured in the EEG (Ullsperger, Danielmeier & Jocham, 2014). The ACC acts as a control filter that initiates adjustments based on the RPE signal it receives. Also, its signal is used to improve outcome prediction in the striatum, thus closing the feedback loop of the reinforcement learning model (Ullsperger, Fischer et al., 2014).

The RPE has been shown to be related to mPFC activity (Daw et al., 2006; Gläscher et al., 2010; Rutledge et al., 2010; Talmi et al., 2012) as well as the ERN/Ne and the FRN (Cohen & Ranganath, 2007; Fischer & Ullsperger, 2013; Frank et al., 2005; Hajcak et al., 2006; Holroyd & Coles, 2002; Walsh & Anderson, 2012; Yeung & Sanfey, 2004). The RL theory has proven to be a valuable framework for understanding how the brain processes information about action outcomes in order to optimize behavior.

1.2.4 Predicted Response-Outcome Model

The predicted response-outcome model is a recently emerging theory that can be seen as a specific instantiation of the broader RL theory. Its key aspect is the “predicted response-outcome” (PRO), as the name says (Alexander & Brown, 2011). According to the PRO model, the PRO signal reflects a prediction the brain makes about the expected outcome of a given action. It is based on individual neuron assemblies that code the expected probability of various possible outcomes of that action. When a predicted outcome actually occurs, the corresponding prediction signal is inhibited.

Thus, when a completely unexpected outcome occurs, no prediction signal is inhibited, resulting in maximal mPFC activity (Ullsperger, Danielmeier & Jocham, 2014; Ullsperger, Fischer et al., 2014). Similarly to the RL theory, the PRO signal is thought to be represented by the activity of dopamine neurons in the midbrain that provide a prediction error signal that updates the value of each action based on the difference between the predicted and actual outcomes. In contrast to the RL theory, the PRO signal is considered an unsigned value signal. Accordingly, studies found correlations between mPFC activity and unsigned prediction errors as well as surprise (Ferdinand et al., 2012; Hayden et al., 2011; Pessiglione et al., 2006), ERN/Ne (Cohen & Ranganath, 2007; Wessel et al., 2011) and FRN (Amiez et al., 2012; Hauser, Iannaccone, Stämpfli et al., 2014; Talmi et al., 2012).

1.2.5 Synthesizing the Theories of Performance Monitoring: An Integrative Perspective

While each of these theories has contributed to our understanding of performance monitoring, they also have their limitations. The mismatch theory, for example, focuses on the detection of errors but does not explain how the brain evaluates the significance of those errors or how it decides to adjust behavior in response to them. Conversely, the response conflict theory emphasizes the role of conflicting information in performance monitoring but does not provide a clear account of how the brain resolves such conflicts. The RL theory and the PRO model, which are based on computational models of reinforcement learning, provide a more detailed account of how the brain learns from feedback. However, they do not fully account for all aspects of performance monitoring, such as detecting errors and evaluating their significance. Given these limitations, an integrative approach that combines the strengths of these theories may provide a more comprehensive account of performance monitoring.

The following section aims to integrate the different theories of performance monitoring into a comprehensive model (see Figure 1) based on the framework suggested by Ullsperger, Danielmeier and Jocham (2014). The presented model extends this framework by further differentiating an action execution and feedback delay phase and by revising the role of the performance monitoring system across the various stages of the process of performing an action[2]. The sequential process of performing an action from the very beginning will be illustrated first. Afterward, the role of the performance monitoring system in each step will be elaborated.

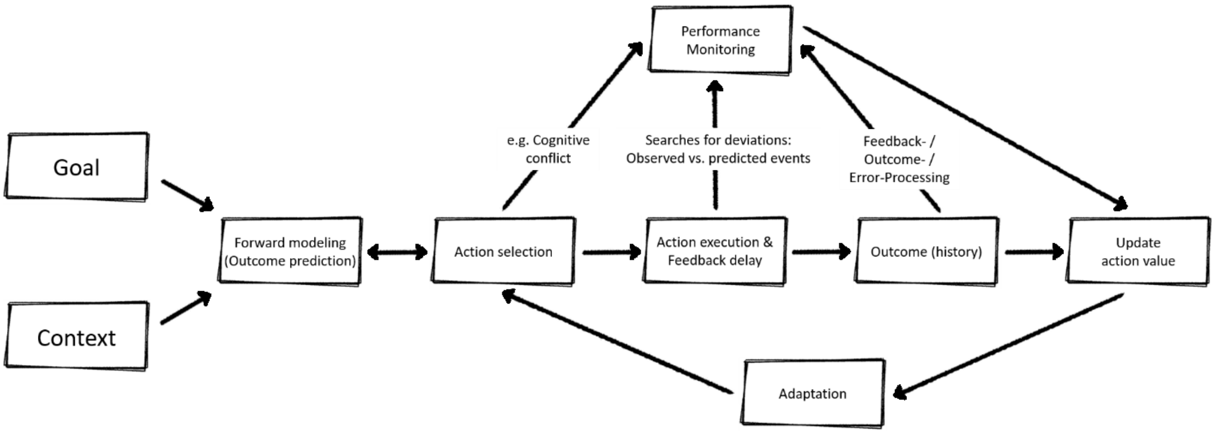

Figure 1: Integrative procedural model of action performance

The process of performing an action starts identifying a goal within a given context. During this stage, the organism predicts the outcome probabilities of various possible actions in a forward modeling manner. The selection of an appropriate action is made based on this exchange of information. Once an action is selected, it is executed, resulting in a specific (potentially multidimensional) outcome. Depending on the action at hand, the final outcome may be perceivable immediately after action execution or after a feedback delay phase, which can range from a few milliseconds to several days. This delay phase can be leveraged for anticipatory processes, depending on the nature of the action. Upon perceiving the outcome, it is incorporated into the history of outcomes. The value of the performed action is then updated based on the outcome relative to the initial expectations. Finally, the updated value of the action is used as feedback for adapting the action selection process and improving the precision of future outcome predictions.

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[2] Following, the term "performing an action" will be utilized in reference to the entire process that encompasses action execution and performance. This process commences with goal identification and encompasses action selection, execution, outcome evaluation and resulting adaptation processes. Therefore, the term encompasses all phases of the process and is not limited to the execution of the motor act alone.

In the initial stage of goal identification and action selection, the performance monitoring system plays a critical role in monitoring the context, the organism's internal state and predicting the outcome probabilities of different actions. This information is used to aid in the selection of an appropriate action. In the example of driving a car, we might encounter a yellow traffic light, and we then have to decide whether to brake or maintain speed, reflecting two conflicting response options. The response conflict theory posits that the performance monitoring system is responsible for resolving conflicts between different response options. Particularly in situations with high levels of decision conflict or response conflict, performance monitoring functions become increasingly engaged during this stage. Thus, one aspect that increases the need for the performance monitoring system is increased cognitive conflict during the action selection phase. This aspect is particularly investigated in study 4, which focuses on the impact of cognitive conflict during the action selection phase.

During action execution, the performance monitoring system continuously searches for deviations between the intended behavior and outcome from the executed behavior and probable outcomes, for example, after deciding to break upon the yellow traffic light. We need to monitor whether our speed adjustment leads to the desired effect or deviates from it. Detecting any deviations as quickly as possible enables a timely adaptation before negative consequences occur[3]. Study 2 explores the continuous adaptation of cognitive control during the action execution and feedback delay phase.

The performance monitoring system also plays a crucial role in creating a history of outcomes. This history is essential for updating the value of the performed action accurately. By tracking the past outcomes of a particular action, the performance monitoring system can better estimate its value and improve the accuracy of future outcome predictions. All of the previously mentioned theories make statements about how a deviation of an expected outcome from an actual outcome leads to increased activity of the performance monitoring system, e.g., according to the mismatch theory, a comparator

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[3] It should be noted that this is not possible for every action. Some actions may directly lead to an outcome or cannot be permanently monitored and adapted. For this subset of actions, this step of performance monitoring has less significance or does not apply.

detects a mismatch and the brain generates a prediction error signal. The RL theory states that the striatum computes an RPE after the occurrence and perception of an unexpected outcome. Based on the RPE, the action value is updated and adaptations in action selection and outcome prediction are initiated accordingly. According to the PRO model, a PRO signal is already computed during action selection and outcome prediction. When an outcome occurs, the corresponding neuron assemblies that code the predicted outcome are inhibited, while the others are not. Studies 1 and 3 focus on this outcome processing stage of performance monitoring.

In summary, the performance monitoring system plays a vital role in multiple stages of action selection and performance. By monitoring the environment, predicting outcomes, tracking history, providing feedback and resolving conflicts, the performance monitoring system helps the organism to select appropriate actions and improve its performance in complex environments. Due to the complexity of this process, there are many different theories and neuropsychological approaches. However, this integrative perspective has also revealed some similarities. Therefore, in the following, this dissertation will focus on a neural indicator that recurs across different contexts and tasks in the framework of performance monitoring and could represent a unifying element, namely frontomedial theta activity.

1.3 Frontomedial Theta Activity

Frontomedial theta (FMT) activity is a neural indicator observed in various contexts and tasks related to performance monitoring. FMT is often associated with cognitive control processes, including error detection, conflict monitoring and attentional allocation (Cavanagh & Frank, 2014; Cohen & Donner, 2013; Hsieh & Ranganath, 2014; Luu et al., 2004). Given its widespread occurrence in different domains, FMT activity has been suggested as a potential unifying element that underlies performance monitoring across different cognitive processes and tasks (Cavanagh et al., 2012). Following, the neural mechanisms and functional significance of FMT activity in the context of performance monitoring will be outlined.

1.3.1 Exploring Frontomedial Theta Activity: Occurrence, Modulation and Influential Factors

FMT is a frontomedial event-related oscillatory activity in the theta frequency range (4Hz – 8Hz). There is compelling evidence from fMRI, combined EEG and fMRI, PET studies, invasive recordings and EEG source localization that FMT is generated in the mPFC (Botvinick et al., 2004; Cavanagh & Frank, 2014; Debener et al., 2005; Kerns et al., 2004; MacDonald et al., 2000; Nee et al., 2011; Ridderinkhof et al., 2004), more specifically the ACC (Cavanagh & Shackman, 2015; Cohen & Cavanagh, 2011; Hanslmayr et al., 2008; Hauser, Iannaccone, Stämpfli et al., 2014; Holroyd & Umemoto, 2016; Wang et al., 2005; Wessel et al., 2012; Womelsdorf et al., 2010) but also in the pre-supplementary motor area (pre-SMA; Nachev et al., 2007; Rushworth et al., 2002) which is involved in motor planning and control.

FMT is found across various contexts but has shown to be sensitive to a range of task and environmental factors. FMT amplitude is typically larger following the commission of an error than following correct responses (Cavanagh et al., 2009; Cohen & Ranganath, 2007; Debener et al., 2005; Wessel et al., 2012). The strength of this effect varies depending on the task and the level of error likelihood (Cohen & Cavanagh, 2011; Huster et al., 2013). FMT is also found in response conflict paradigms, with higher conflict leading to larger FMT amplitudes (Cavanagh et al., 2012; Cohen & Cavanagh, 2011). Furthermore, FMT is sensitive to feedback on performance outcomes. For example, FMT amplitude is larger when participants receive negative feedback than when they receive positive feedback (Cavanagh et al., 2010; Cohen & Ranganath, 2007; Osinsky et al., 2016; Paul et al., 2020; van de Vijver et al., 2011). Some studies have shown that FMT is sensitive to cognitive load, with larger amplitudes observed under conditions of high cognitive demand (Hanslmayr et al., 2007; Hauser, Iannaccone, Ball et al., 2014). Overall, these results clearly indicate the central role that FMT plays in cognitive effort and attentional control.

1.3.2 Theta – Lingua Franca?

Several theories try to explain the functional role of FMT in performance monitoring. One is the conflict monitoring theory proposed by Botvinick et al. (2001). According to this theory, the ACC acts as a conflict monitoring system that detects conflicts between different response options and initiates adjustments in behavior to resolve those conflicts. The theory assumes that the FMT activity reflects the degree of conflict experienced, with larger FMT amplitudes reflecting greater levels of conflict (Botvinick, 2007; Kerns et al., 2004). This theory overlaps with the response-conflict theory of performance monitoring, which also suggests that the strength of response conflict modulates the conflict-related activity.

While the conflict monitoring theory provides a compelling explanation for the role of FMT in detecting conflicts and errors, it does not fully explain other vital aspects of performance monitoring, such as the evaluation of feedback or the allocation of attentional resources. It does not address why FMT amplitude is larger when participants receive negative feedback compared to positive feedback (Gehring & Willoughby, 2002; Paul et al., 2020; van de Vijver et al., 2011) or why FMT is sensitive to cognitive load and shows larger amplitudes under conditions of high cognitive demand (Brzezicka et al., 2019; Gärtner et al., 2015). These aspects of performance monitoring suggest that FMT plays a more general role in regulating cognitive effort and attentional resources rather than just being a conflict detection mechanism.

Cavanagh et al. (2012) propose that FMT serves as a "need for control" signal to initiate top-down cognitive control in the face of unexpected or novel events, such as errors, response and decision conflict or changing task demands. The FMT signal is thought to be an early warning system that triggers the recruitment of additional cognitive resources to cope with the demands of the current task (Cavanagh & Shackman, 2015). In this view it is as a global, neutral “alarm bell” that signals the need for increased cognitive control in response to a wide range of task demands and context – acting as a “lingua franca” (Cavanagh et al., 2012). This means that FMT is not specific to any particular type of task or cognitive process but instead reflects a generic alert signal that indicates the need for greater attentional and cognitive resources to be allocated toward the task at hand. The idea is that when FMT is triggered, it sends a signal to other brain regions that are involved in cognitive control and attention, including the prefrontal cortex and the parietal cortex, to increase their level of activity and coordinate their processing to handle the task demands better. In this way, FMT serves as a mechanism for regulating cognitive effort and attentional resources, allowing the brain to respond adaptively to changing task demands (Cavanagh & Frank, 2014).

Overall, Cavanagh's hypothesis suggests that FMT is a critical component of the brain's performance monitoring system, serving as a general alarm signal that helps to regulate and optimize cognitive control and attentional resources across a wide range of task contexts. It provides a more general framework for understanding the role of FMT in performance monitoring and has gained support from numerous studies that have shown that FMT is sensitive to a range of task and environmental factors, including response conflict, feedback about performance outcomes and cognitive load (for a detailed review, see Cavanagh & Frank, 2014).

1.4 A Multiperspective View on Frontomedial Theta Activity

The presented findings collectively demonstrate that FMT is a complex and multidimensional neural signal that is involved in a range of cognitive processes related to performance monitoring. While FMT is commonly investigated within a specific context, the assumption of FMT as a need for control signal provides a useful framework for understanding how FMT operates across these different contexts as a global, neutral signal that indicates the need for increased cognitive control. It seems to serve as a means of regulating cognitive effort and attentional resources, allowing the brain to respond adaptively to changing task demands.

Following, an overview will be provided of how each of the four studies used in this dissertation offers a unique perspective on FMT, shedding light on different aspects of its functioning in performance monitoring. By examining FMT from various perspectives, this dissertation aims to provide a comprehensive view of its complex and multidimensional nature and to contribute to a better understanding of how it serves as a key component of the brain's performance monitoring system. In addition to exploring the functional role of FMT in performance monitoring, each study employs a unique approach to analyze FMT as a neural indicator, utilizing different analysis methods that may enhance our understanding of the generation of FMT.

1.4.1 Study 1: The Role of Frontomedial Theta in Complex Outcome Integration & Temporal Stability of Individual Frontomedial Theta Responsivities

FMT has been linked to the detection and processing of negative feedback. As outlined before, FMT activity increases in response to negative feedback (Cavanagh et al., 2010; Cohen & Ranganath, 2007; Osinsky et al., 2016; Paul et al., 2020; van de Vijver et al., 2011). The RL theory suggests that when an action leads to negative feedback, the striatum computes an RPE, as the predicted outcome deviates from the actual outcome. This induces an increased need for cognitive control, which is presumably being communicated via increased FMT activity (Cavanagh & Frank, 2014). The size of the RPE resembles the difference of the predicted and the actual outcome. Larger RPEs have been associated with larger amplitudes of FMT (Cavanagh et al., 2010; Cohen & Ranganath, 2007) and other feedback-sensitive event-related potentials, i.e., the FRN (Gehring & Willoughby, 2002; Hajcak et al., 2006). As larger RPEs require greater cognitive control, those lead to enhanced increases in FMT activity.

However, many actions involve complex outcomes with multiple independent consequences, some of which may be positive and others negative. The RPE should be sensitive to an integrated value of all of these consequences and the FMT activity should reflect this as well. Study 1 investigated this relationship between the fine-grained integration of action outcome values and FMT activity using a reinforcement learning design. Each decision was associated with a three-dimensional outcome, thus leading to three consequences that could vary independently. The most positive overall outcome value, and thus the smallest RPE, should arise when there is a positive outcome in all three individual dimensions. The most negative overall outcome value should arise when there is a negative outcome in all individual outcome dimensions. Accordingly, this combination should generate the largest RPE. The outcome combinations in between should evoke an RPE, scaled according to the overall outcome value. If FMT reflects cognitive control evoked by the deviation of the predicted and the observed outcome, the feedback-related FMT activity should also be scaled according to the size of the RPE.

Further, such a global function of signaling need for control, as suggested by Cavanagh and Frank (2014), might show trait-like characteristics (Roberts & DelVecchio, 2000). Therefore, some degree of temporal stability in the interindividual differences in FMT responsivity over time would be necessary. This is also investigated in study 1, utilizing a retest session after three months.

1.4.2 Study 2: Continuous “Online” Performance Monitoring: Trial Level Effects

The adapted integrative procedural model allows for “online” performance monitoring during action execution and the feedback delay phase. Many daily actions allow for anticipating an outcome before it occurs. Thus, it would be more efficient for the performance monitoring system to use this real-time information than to wait for the outcome before getting engaged. The RL theory suggests that negative feedback elicits an RPE signal when the observed outcome (negative feedback) does not match the predicted outcome (positive feedback). This discrepancy triggers a need for cognitive control, which is signaled by increased FMT activity (Holroyd & Coles, 2002). However, when an action leads to an expected negative outcome, which can be anticipated during the feedback delay phase, the predicted outcome should be adjusted accordingly, even before the outcome occurs. In this case, the new predicted outcome would be negative feedback. Upon feedback presentation, this prediction then matches the actual outcome. Consequently, no RPE (or at least a reduced RPE) would arise, attenuating the feedback-related increase in need for control and in FMT activity.

To test this assumption, study 2 employed two shooting tasks in virtual reality (VR). Participants shot at balloons with a virtual pistol in a virtual environment. In one experiment, they were able to observe and visually track the projectiles during the flight. Therefore, this experiment contains a feedback delay phase between aiming/pulling the trigger of the gun and the moment when the projectile hits the balloon or flies past it. While the motor action itself (firing a gun) is less of an everyday action, the situational factors of the performance monitoring involved more closely resemble those of common performance monitoring tasks, namely tracking and estimating the trajectory of a moving object in a three-dimensional space. In a second experiment, participants again shot at balloons within a virtual environment but were not able to observe the projectile. Thus, they were not able to anticipate the outcome. Comparing the two experiments, missing shots in the second experiment should evoke RPEs and thus increased FMT activity in response to the outcome feedback. In the first experiment, negative feedback can be anticipated, as the projectile can be tracked. Continuous online performance monitoring should draw on this information and adjust the expectations of the outcome. Therefore, missing shots should evoke smaller RPEs and attenuated increases in FMT activity in this experiment.

While study 1 assessed FMT in response to complex multidimensional feedback, study 2 further expands the dynamics and richness of the feedback information. The use of VR as a methodological tool offers several advantages here, with, above all, complete information about the situation at any moment. Thus, for example, the information about the position of the subject, the target and the projectile was available at every time point during a trial. While this information can also be obtained in a real-life setting, it would have to be acquired via additional external sensor systems, whereas it is directly available within the VR setup (Jungnickel et al., 2019). This steady flow of information allows to overcome limitations of common condition-average based EEG analysis (Cavanagh et al., 2010; Cohen & Cavanagh, 2011; Cooper et al., 2019). By employing single-trial regression analyses, using the VR-provided information as predictors at every time point, regression-based event-related spectral perturbations (rERSP; Smith & Kutas, 2015) were computed, allowing for the investigation of trial-level variance in FMT activity (Gehrke & Gramann, 2021). This approach can provide a more nuanced understanding of FMT, as it allows for the assessment of trial-level effects in addition to the more common condition-level and task-level effects.

1.4.3 Study 3: Phase Coherence of Frontomedial Theta Activity

Pushing the dynamics of the experimental task to its limits, Study 3 investigated the role of FMT in a physical setting without the use of VR. In this study, participants engaged in a shooting task using a toy gun and foam darts. By assessing FMT in a dynamic situation and dynamic action, the study aimed to shed further light on the global need for control signal proposed by the need for control theory.

However, despite the growing body of research on FMT, there is an ongoing debate about its neural origin (Cavanagh & Frank, 2014). There is a complex relationship between the spectral power of an EEG signal in the time-frequency domain and electrical activity in the time domain. Especially considering the phase of oscillatory activity, a stimulus-locked phase resetting response may generate an ERP effect in the time domain representation. Conversely, adding a fixed polarity and phase ERP to every single trial of a signal can induce phase-locking of the observed spectral activity (Makeig et al., 2004). FMT activity has been associated with several ERPs, such as the ERN/Ne, Pe, N2 and the FRN (Cavanagh et al., 2012; Cavanagh & Frank, 2014; Pezzetta et al., 2022), which reflect evoked and thus phase-locked neural activity by their definition. However, recent evidence suggests that the non-phase-locked portion of the FMT signal is more sensitive to the performance monitoring-related processes than the phase-locked portion (Duprez et al., 2020). This suggests that FMT as a need for control signal is affected by modulations of ongoing theta oscillations and is thus not phase-locked to the eliciting event (Cohen & Donner, 2013). To assess this characteristic of FMT, study 3 further evaluated inter-trial phase coherence (ITPC) and differentiated phase-locked and non-phase-locked FMT activity.

1.4.4 Study 4: Frontomedial Theta Activity in Action Selection: Task-Dependence & Multiple Sources?

All of the previous studies focus on feedback-related FMT activity in performance monitoring. However, as outlined in the adapted integrative procedural model, the performance monitoring system is also engaged in action selection processes. Different situations can cause more or less difficulties in action selection. One potential issue during this phase is cognitive conflict. It arises when there are two or more conflicting response options, which is also the focus of the response-conflict theory. Several studies have demonstrated increased FMT activity in response to simple stimulus response conflicts (Cavanagh et al., 2012; Cavanagh & Castellanos, 2016; Cohen & Ridderinkhof, 2013; Duprez et al., 2020; Gulbinaite et al., 2014; McDermott et al., 2017; Nigbur et al., 2012; Oehrn et al., 2014; Pastötter et al., 2013; Töllner et al., 2017; van Driel et al., 2015; Zuure et al., 2020). As soon as a response conflict arises, FMT activity increases, signaling the increased need for control. Accordingly, this increase in FMT should also occur in response to other types of conflicts. Therefore, study 4 implemented a design that induces an approach-avoidance conflict, which is a different type of conflict that arises when a stimulus possesses appetitive and aversive motivational qualities simultaneously. Further, participants performed two tasks in study 4. An approach-avoidance task was used to induce an approach-avoidance conflict and a Flanker task was used to induce a simple stimulus response conflict. Employing both types of conflict-inducing tasks allows investigation of any cross-task relationship of FMT activity. If FMT acts as a global, context-independent need for control signal, there should be strong cross-task interrelations of FMT activity.

However, recent studies found evidence for multiple neural sources of FMT (Beldzik et al., 2022; Töllner et al., 2017; Zuure et al., 2020). This contradicts the assumption of a global, unitary need for control signal. In order to pursue this question, study 4 employed source separation analyses to differentiate multiple possible FMT components. Based on the dual-task study design, different FMT components for each task would indicate a more fine-grained basis of FMT activity. In contrast, finding the same components across tasks would indicate a rather task-independent operation of FMT.

1.5 Summary and Outlook

This dissertation seeks to investigate performance monitoring by evaluating the role of one of its neural indicators, FMT activity. It explores the nature and characteristics of FMT and its relationship to cognitive control from various perspectives. To this end, four studies were conducted. Every study investigates FMT activity in the context of performance monitoring but in regard to different functional stages of action performance, which are displayed in the integrative procedural model of action performance. Therefore, integrating the results from the four studies provides an overview of the various functionalities of FMT in the performance monitoring system. Further, every study applies different analysis methods to explore different characteristics of FMT as a neural signal.

The different perspectives on FMT that the results of the four studies provide will be discussed to shed light on the functional role of FMT in performance monitoring and whether it reflects a global, unitary need for control signal or how it is affected by contextual factors and intra- and interindividual characteristics.

2 Empirical Publications

Study 1

Rommerskirchen, L.*, **Lange, L.***, Osinsky, R. (2021). The reward positivity reflects the integrated value of temporally threefold-layered decision outcomes. *Psychophysiology*, 58(5).

Study 2

Lange, L., Kisker, J. & Osinsky, R. (*under review*). Midfrontal signaling of need for control continuously adapts to incoming information during outcome anticipation. *NeuroImage: Reports*.

Study 3

Lange, L. & Osinsky, R. (2020). Aiming at ecological validity—Midfrontal theta oscillations in a toy gun shooting task. *European Journal of Neuroscience*, 54(12), 8214-8224.

Study 4

Lange, L.*, Rommerskirchen, L.* & Osinsky, R. (2022). Midfrontal Theta Activity Is Sensitive to Approach–Avoidance Conflict. *Journal of Neuroscience*, *42*(41), 7799-7808.

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2.1 Study 1: The reward positivity reflects the integrated value of temporally threefold-layered decision outcomes

Abstract:

In reinforcement learning, adaptive behavior depends on the ability to predict future outcomes based on previous decisions. The Reward Positivity (RewP) is thought to encode reward prediction errors in the anterior midcingulate cortex (aMCC) whenever these predictions are violated. Although the RewP has been extensively studied in the context of simple binary (win vs. loss) reward processing, recent studies suggest that the RewP scales complex feedback in a fine graded fashion. The aim of this study was to replicate and extend previous findings that the RewP reflects the integrated sum of instantaneous and delayed consequences of a singular outcome by increasing the feedback information content by a third temporal dimension. We used a complex reinforcement-learning task where each option was associated with an immediate, intermediate and delayed monetary outcome and analyzed the RewP in the time domain as well as frontomedial theta power in the time-frequency domain. To test if the RewP sensitivity to the three outcome dimensions reflect stable trait-like individual differences in reward processing, a retesting session took place 3 months later. The results confirm that the RewP reflects the integrated value of complex temporally extended consequences in a stable manner, albeit there was no relation to behavioral choice. Our findings indicate that the medial frontal cortex receives fine graded information about complex action outcomes that, however, may not necessarily translate to cognitive or behavioral control processes.

Rommerskirchen, L., **Lange, L.** & Osinsky, R. (2021). The reward positivity reflects the integrated value of temporally threefold-layered decision outcomes. *Psychophysiology*, 58(5).

Open access via the publisher’s website: https://doi.org/10.1111/psyp.13789

2.2 Study 2: Midfrontal signaling of need for control continuously adapts to incoming information during outcome anticipation

Abstract:

Performance monitoring is essential for successful action execution and previous studies have suggested that frontomedial theta (FMT) activity in scalp-recorded EEG reflects need for control signaling in response to negative outcomes. However, these studies have overlooked the fact that the most likely outcome can be anticipated during outcome anticipation. To optimize action execution, it is necessary for the time-critical performance monitoring system to utilize continuously updated information to adjust actions in time. This study used a combination of mobile EEG and virtual reality to investigate how the performance monitoring system adapts to continuously updated information during brief phases of outcome evaluation that follow action execution. In two virtual shooting tasks, participants were either able to observe the projectile and hence anticipate the outcome or not. We found that FMT power increased in response to missing shots in both tasks, but this effect was suppressed when participants were able to anticipate the outcome. Specifically, the suppression was linearly related to the duration of the anticipatory phase. Our results suggest that the performance monitoring system dynamically integrates incoming information to evaluate the most likely outcome of an action as quickly as possible. This dynamic mode of performance monitoring provides significant advantages over idly waiting for an action outcome before getting engaged. Early and adaptive performance monitoring not only helps prevent negative outcomes but also improves overall performance. Our findings highlight the crucial role of dynamic integration of incoming information in the performance monitoring system, providing insights for real-time decision-making and action control.

Lange, L., Kisker, J. & Osinsky, R. (*under review*). Midfrontal signaling of need for control continuously adapts to incoming information during outcome anticipation. *NeuroImage: Reports*.

2.3 Study 3: Aiming at ecological validity — Midfrontal theta oscillations in a toy gun shooting task

Abstract:

Laboratory electroencephalography (EEG) studies have already provided important insights into the neuronal mechanisms of performance monitoring. However, to our knowledge no study so far has examined neuronal correlates of performance monitoring using an ecologically valid task outside a typical laboratory setting. Therefore, we examined midfrontal theta and the feedback-related negativity (FRN) using mobile EEG in a physical shooting task within an ecologically valid environment with highly dynamical visual feedback. Participants shot a target using a toy gun while moving and looking around freely. Shots that missed the target evoked stronger midfrontal theta activity than hits and this response was rather phase-unlocked. There was no difference between misses and hits in the FRN. The results raise the question whether the absence of certain ERP components like the FRN could be due to methodological reasons or to the fact that partially different neuronal processes may be activated in the laboratory as compared to more ecologically valid tasks. Overall, our results indicate that crucial neurocognitive processes of performance monitoring can be assessed in highly dynamic and ecologically valid settings by mobile EEG.

Lange, L. & Osinsky, R. (2020). Aiming at ecological validity—Midfrontal theta oscillations in a toy gun shooting task. *European Journal of Neuroscience*, 54(12), 8214-8224.

Open access via the publisher’s website: https://doi.org/10.1111/ejn.14977

2.4 Study 4: Midfrontal Theta Activity Is Sensitive to Approach–Avoidance Conflict

Abstract:

Midfrontal theta (FMθ) in the human EEG is commonly viewed as a generic and homogeneous mechanism of cognitive control in general and conflict processing in particular. However, the role of FMθ in approach–avoidance conflicts and its cross-task relationship to simpler stimulus-response conflicts remain to be examined more closely. Therefore, we recorded EEG data while 59 healthy participants (49 female, 10 male) completed both an approach–avoidance task and a flanker task. Participants showed significant increases in FMθ power in response to conflicts in both tasks. To our knowledge, this is the first study to show a direct relationship between FMθ and approach–avoidance conflicts. Crucially, FMθ activity was task dependent and showed no cross-task correlation. To assess the possibility of multiple FMθ sources, we applied source separation [generalized eigendecomposition (GED)] to distinguish independent FMθ generators. The activity of the components showed a similar pattern and was again task specific. However, our results did not yield a clear differentiation between task-specific FMθ sources for each of the participants. Overall, our results show FMθ increases in approach–avoidance conflicts, as has been established only for more simple response conflict paradigms so far. The independence of task-specific FMθ increases suggests differential sensitivity of FMθ to different forms of behavioral conflict.

Lange, L., Rommerskirchen, L. & Osinsky, R. (2022). Midfrontal Theta Activity Is Sensitive to Approach–Avoidance Conflict. *Journal of Neuroscience*, *42*(41), 7799-7808.

Open access via the publisher’s website: https://doi.org/10.1523/JNEUROSCI.2499-21.2022

3 General Discussion

The aim of this dissertation is to explore the role of frontomedial theta (FMT) activity in performance monitoring. In particular, to advance understanding of the mechanisms that underlie FMT activity and whether it represents the global need for control signal, it is thought to be. The dissertation comprises four studies that employed a variety of experimental paradigms to examine different facets of FMT activity within the framework of performance monitoring. Investigating FMT activity has the potential to enhance our understanding of how the brain adapts to changing task demands and environmental conditions, which is crucial for everyday actions such as driving a car.

Study 1 investigated FMT activity in response to complex multidimensional feedback in a reinforcement learning task and the long-term stability of the individual FMT responsivities. The results showed increased FMT activity in response to negative feedback and partial scaling of feedback-related FMT amplitude according to the quantity of negative outcomes, even though this effect was not as straightforward as for the feedback-related negativity (FRN). While the difference scores comparing condition-wise FMT power showed small temporal stability, this was to be expected, as the reliability of difference scores of highly correlated variables is biased towards zero (Thomas & Zumbo, 2012). The absolute amplitude of condition-wise FMT power, which is not affected by this attenuation, showed good to excellent scores for temporal stability. Overall, this study showed that FMT activity is partially sensitive to the graded value of action outcomes. Further, the modulation of FMT activity as a nuanced teaching signal may be subject to stable interindividual differences, highlighting the potential relevance of FMT activity in individual differences in performance monitoring and learning.

Study 2 investigated the continuous adaptation of FMT activity to constantly incoming information, employing regression analyses to explore trial-level effects. The results of the shooting tasks in virtual reality (VR) showed that feedback-related FMT activity is attenuated when the most likely outcome of an action can be anticipated beforehand, in a linear relationship between FMT attenuation and duration of the anticipatory phase. The results suggest that the performance monitoring system can quickly and efficiently adapt to available information, thus reducing the resulting reward prediction error (RPE) and the need for control upon feedback presentation.

Study 3 investigated FMT activity in a dynamic action and context, aiming to shed further light on the global need for control signal proposed by the need for control theory (Cavanagh & Frank, 2014). The study used a shooting task with a toy gun and foam darts and examined phase-locking of FMT by differentiating phase-locked and non-phase-locked FMT activity. The results showed that non-phase-locked FMT activity is sensitive to negative outcomes, suggesting that FMT as a need for control signal is affected by modulations of ongoing theta oscillations that are not phase-locked to the outcome event.

Study 4 investigated the role of FMT in different types of conflicts during action selection processes, using an approach-avoidance task and a Flanker task. The study aimed to examine the assumption of a global, context-independent need for control signal by assessing cross-task relationships of FMT activity. The results showed that approach-avoidance conflicts induce similar FMT increases as simple response conflicts. However, individual FMT responsivities to the two types of conflict were independent from each other, suggesting no global and unitary sensitivity of FMT to different forms of behavioral conflict. However, source separation analyses revealed no clear pattern of conflict-specific FMT sources but pointed to individual differences in the configuration of conflict-sensitive FMT generators.

The individual studies and their respective findings have been discussed in detail in their corresponding publications. The following discussion will therefore focus on integrating the results of the four studies into a comprehensive framework of FMT activity in performance monitoring. Specifically, it will address when FMT occurs in the process of action performance, i.e., the action selection phase, action execution and feedback delay phase and outcome evaluation, in order to clarify its functional role within this process. Next, the different contexts in which performance monitoring-related FMT activity increases will be discussed regarding the contextual role of FMT. The discussion will then delve into the characteristics of FMT as an indicator of neural activity from a methodological point of view and finally addresses the question of whether FMT represents a global need for control signal of the performance monitoring system in the sense of a "lingua franca".

3.1 The Role of Frontomedial Theta Activity within the Process of Action Performance

The integrative procedural model adapted by Ullsperger, Danielmeier and Jocham (2014) proposes that the performance monitoring system is engaged in several phases during the execution of an action, including action selection, action execution and feedback delay phase, as well as evaluation of the outcome and related adaptive processes. Study 4 specifically examined conflict-related FMT activity during action selection, while the first three studies explored feedback-related FMT activity. In particular, study 2 focused on the feedback delay phase and the impact of anticipatory information during this phase, whereas studies 1 and 3 concentrated on the phase of outcome evaluation and related feedback-related FMT activity.

Study 1 implemented a reinforcement learning task where decisions could lead to negative outcomes that were indicated by visual feedback following the decision. In study 3, participants shot at targets using a toy gun. The visual feedback in this experiment consisted of the foam dart and its flight path that could be observed, including the crucial moment of hitting the target. In both studies, FMT activity was increased in response to negative feedback compared to positive feedback, consistent with previous findings of feedback-related FMT (Gehring & Willoughby, 2002; Paul et al., 2020; van de Vijver et al., 2011).

The reinforcement learning perspective suggests that during outcome evaluation, the increase in feedback-related FMT activity reflects the receipt of negative RPEs by the brain (Holroyd & Coles, 2002). According to the RL theory, negative feedback elicits a signed RPE signal which represents the discrepancy between the expected and the actual outcome. The dopaminergic RPE signal is generated in the striatum and is used to modulate the activity of the anterior cingulate cortex (ACC; Ullsperger, Danielmeier & Jocham, 2014). Based on the incoming RPE signal, an increased need for cognitive control is triggered in the ACC in order to initiate adjustments. In this process, FMT reflects the signaling of this increased need for control but is not related to the following adjustments. FMT signals the need for action but not the specific action required (Cavanagh & Frank, 2014).

Therefore, studies 1 and 3 demonstrate that FMT signals an increased need for control during the outcome evaluation phase. It functions as an alarm signal in response to negative feedback, indicating that an adjustment is necessary to avoid repeating the behavior that led to the negative outcome. This process is consistent with the RL theory, which suggests that FMT reflects the ACC receiving negative RPEs during outcome evaluation, eliciting increased need for cognitive control to initiate appropriate adjustments. While the exact nature of these adjustments seems not to be reflected in the modulation of FMT activity, its increase is a crucial indicator of the need for intervention.

Study 2 examined feedback-related FMT activity as well. However, study 2 aimed to investigate the feedback delay phase, using virtual reality shooting tasks in two experiments. In one experiment, the projectile was visually trackable and the most likely outcome could be anticipated, while in the other experiment, there was no observable projectile. In both experiments, participants shot a virtual target in the form of a balloon. Upon hitting it, this balloon popped into green fragments and red fragments upon missing it. So, in both experiments, there was visual outcome feedback for both possible outcomes.

The results showed a significant increase in FMT activity in response to negative outcome feedback compared to positive outcome feedback in both experiments. But importantly, this effect was attenuated when the projectile was observable and the most likely outcome could be anticipated during the feedback delay phase. According to the previously described adapted integrative procedural model and the RL theory, an outcome prediction is formed before action execution (Holroyd & Coles, 2002; Ullsperger, Danielmeier & Jocham, 2014). When the projectile is not observable, this outcome prediction persists until the moment that the outcome feedback appears, as it immediately follows the action execution. Comparing the predicted and the actual outcome, an RPE arises upon the feedback of missing the shot, inducing increased need for control, as outlined before. However, when the projectile is observable, the most likely outcome can be anticipated during the feedback delay phase, using the permanently incoming information about its trajectory. Based on this constantly updated anticipation, the initial outcome prediction can be adapted during the feedback delay phase. If a negative outcome is anticipated at some point, the outcome prediction can be updated to a negative one. Then upon receiving the final outcome feedback, the updated negative outcome prediction matches the actual negative outcome, thus inducing a reduced RPE, less increase in need for control and less increase in FMT activity. This is also in line with results of attenuated ACC activity in cued conflict paradigms. If a cue informs about an upcoming conflict, the conflict-related ACC activity in response to the actual conflicting stimuli is attenuated, as the conflicting stimuli do not evoke such a sudden increase in need for control anymore (Aarts et al., 2008; Asanowicz et al., 2022; Ide et al., 2013; Luks et al., 2007).

The finding of attenuated feedback-related FMT activity based on the information incoming during the anticipatory phase has several implications. Firstly, it is consistent with the theory that FMT activity reflects a need for control signal (Cavanagh & Frank, 2014). This means that FMT is only observed when there is an increase in the need for cognitive control, and when this is not the case, there is no significant change in FMT activity. Secondly any need for control signal should be one of the first steps in response to deviations from a desired outcome. By definition, the signaling of need for control must happen before the initiation of adjustments, which is why FMT should be sensitive to early, anticipatory information. The fact that FMT activity is affected by the earliest information, even before an outcome occurs, supports this idea. Initiating cognitive control as soon as possible during the feedback delay phase could minimize the potential for errors and reduce the need for later adjustments.

However, this finding also raises some questions. Since the tasks implemented in study 2 and study 3 were similar, one would expect a similar effect of FMT attenuation in study 3, where participants could observe the foam darts. While study 3 does not allow to investigate the effect of the feedback delay phase directly, the results showed significantly increased FMT activity in response to the negative outcome feedback (while the projectile was observable in every shot). Thus, if there was an attenuating effect on FMT activity in study 3, the FMT increasing effect seems to be stronger than the attenuation. The same applies to the one experiment in study 2, where the projectile was also observable. The feedback-related FMT activity does not get fully suppressed, it just gets attenuated. This might imply that the negative outcomes still induce RPEs when the outcome can be anticipated, but smaller RPEs, which evoke less FMT activity.

This is an interesting finding that corresponds well to the findings from study 1: The size of the RPE seems to be associated with the amplitude of the FMT activity. Other studies found a similar relationship of graded FMT activity depending on the size of an error (Arrighi et al., 2016; Jonker et al., 2021; Spinelli et al., 2018). Such a sensitivity of FMT power to the size of the RPE would be essential to reflect the magnitude of the discrepancy between expected and actual outcomes. This way, the FMT activity would already code whether the brain needs to make minor adjustments to improve performance monitoring or if more substantial changes are required. This is also in line with the PRO model, according to which the unsigned PRO signal indicates the expectedness of an outcome (Alexander & Brown, 2011). In contrast to the signed RPE signal, the unsigned PRO signal does not contain information about the directionality of expectation deviation (better/worse than expected). Consequently, the primary component of the PRO signal is to communicate the magnitude of expectation deviation and evidence suggests that FMT activity is highly correlated with this information (Arrighi et al., 2016; Cavanagh et al., 2010; Hanslmayr et al., 2007; Hauser, Iannaccone, Ball et al., 2014; Huster et al., 2013; Jonker et al., 2021; Osinsky et al., 2016; Spinelli et al., 2018).

However, the results of study 1 showed a modulation of the increase in feedback-related FMT activity depending on the quantity of negative outcomes to some degree but did not show a clear linear relationship between FMT activity and integrated outcome value. Furthermore, study 2 found a significant negative linear relationship between FMT activity and error size. Thus, larger errors were associated with less FMT activity, contrary to previous findings (Arrighi et al., 2016; Jonker et al., 2021; Spinelli et al., 2018). These results suggest a limitation that needs to be addressed. Although the so far discussed results have shown that FMT is increased in response to negative feedback and that anticipation of the feedback can attenuate this effect, it is unclear how this anticipation is built and evaluated. In the VR shooting task in study 2, it can be assumed that anticipating a negative outcome is easier the farther the projectile is off the target. In other words, a missing shot can be identified easier and earlier as such when the target is missed by several meters compared to just a few centimeters, either based on the observation of the projectile or on motoric representations during aiming. Therefore, the outcome can be anticipated with less effort and greater confidence in more poorly executed actions with larger error sizes. The error size would have an effect not only on the size of the RPE, with larger errors leading to increased RPEs (Holroyd & Coles, 2002), but at the same time on the anticipation formed, with larger errors leading to improved anticipations (Frömer et al., 2021). These error-size-dependent differences in the anticipations may also affect the attenuation of FMT power with an enhanced attenuation of FMT power simply because the anticipation is improved. In this case, the amplitude of FMT activity would stand in a positive relation with error size, mediated by the size of the RPE, but at the same time in a negative relation with error size, mediated by the quality of the anticipation. If the latter relationship dominates, increasing error size would in total have a decreasing effect on FMT activity, as found in study 2.

Consequently, the relationship between FMT activity and error size might reflect a different effect in this shooting task compared to tasks where the error size is not linked to the quality of the anticipation (Arrighi et al., 2016; Jonker et al., 2021; Spinelli et al., 2018). Further studies are necessary to clarify the effects on the built anticipations and their relationship with FMT activity. Specifically, it is possible that increased FMT activity already occurs during anticipation, as cognitive control may become necessary in response to updating the expectation rather than in response to the outcome feedback. The timing of such an effect would depend on the exact moment the anticipation is built or evaluated, which can vary each time a particular action is performed. Although the applied regression analyses in study 2 are able to reflect temporally varying effects (Cohen & Cavanagh, 2011), the results did not show an effect of increased FMT activity during the anticipatory phase. Therefore, the nature of the anticipation of the upcoming feedback remains unclear and deserves dedicated investigation in future studies.

Overall, studies 1 to 3 provide evidence that feedback-related FMT activity serves as an early need for control signal during action performance. Depending on the nature of the task, this can be affected by the anticipatory phase, facilitating the timely initiation of adaptive or corrective processes, or arise after outcome occurrence, laying the foundation for learning processes and adjustments of future behavior via adapting outcome prediction and action selection.

Study 4, on the other hand, focused on a third phase of the action performance process, namely action selection, which occurs before action execution and outcome evaluation. In an approach-avoidance task, participants needed to decide whether they wanted to engage in a behavior that is associated with the chance of a reward and the chance of a punishment at the same time or whether they wanted to refrain from it. The two contrary consequences associated with the engaging behavior induced two conflicting motivations simultaneously, namely an approach motivation toward the potential reward and an avoidance motivation toward the potential punishment. Therefore, a cognitive conflict is expected already during the action selection phase. In study 4, a colored cue was used to indicate the graded chances of a reward and punishment. The results showed increased FMT activity in response to this conflict inducing cue. Thus, FMT activity is also sensitive to approach-avoidance conflict during the action selection phase.

The response conflict theory suggests that FMT activity during action selection reflects the competition between the potential responses. It proposes that the ACC monitors response competition and signals the need for control to other brain regions when conflict is detected (Botvinick et al., 2001). Accordingly, FMT would again act as a need for control signal, but evoked in the action selection phase, which differs from the phases investigated in the first three studies. In this phase, a cognitive conflict arises and the brain needs to inhibit differing response tendencies instead of processing negative feedback. Nonetheless, this conflict requires increased cognitive control to be resolved and to engage appropriate reactions, which is indexed by increases in FMT activity. This is consistent with several findings on increased FMT activity and activity in the ACC in different response conflict paradigms, such as Flanker tasks (Cohen et al., 2008; Nigbur et al., 2011; Nigbur et al., 2012), simon tasks (Nigbur et al., 2011), go/no-go tasks (Jiang et al., 2015a; Nigbur et al., 2011) or stroop tasks (Ergen et al., 2014; Jiang et al., 2015b; Kerns et al., 2004), which all involve response conflict during the action selection phase.

Furthermore, the response conflict theory posits that the FMT activity is modulated by the level of response competition, with increased conflict resulting in increased FMT activity (Ullsperger, Danielmeier & Jocham, 2014). The results of study 4 show a strong positive relationship between the amplitude of FMT activity and the graded level of approach-avoidance conflict, with stronger conflict evoking enhanced increases in FMT activity. Interestingly, the FMT activity was the strongest in the condition where the strongest intraindividual conflict was perceived, indicated by the most ambivalent behavioral reactions (condition with response ratio close to 50% approach/50% avoidance). Therefore, the level of individually perceived conflict had a greater impact on the modulation of FMT activity than the objectively measurable levels of conflict (e.g., 50%/50% chance of reward/punishment vs. 25%/75% chance of reward/punishment). This modulation of FMT activity is also in line with the results mentioned above of studies 1 to 3, in which the amplitude of FMT activity also reflects the magnitude of the need for control.

In summary, the so far discussed results of all four studies indicate that FMT reflects a need for control signal that is dynamically scaled to the magnitude of the increase in need for control. The fact that FMT is increased during various stages of action performance supports the idea that it functions as an alarm signal that alerts the brain of the need for intervention without specifying what type of intervention is required. Accordingly, FMT acts as a content-independent signal of the performance monitoring system, allowing for the necessary flexibility to operate during the various, very different stages of action performance. We can imagine a similar alarm signal in everyday life, such as a beeping sound in a car that signals a problem without indicating its exact nature, whether it is the need to refill the oil or the loss of tire pressure. Nonetheless, the signal prompts us to identify the problem and find a solution. Further, we have learned to respond to alarm signals like beeping tones and sirens at all times, not just when driving a car. So, while FMT seems to be content-independent within the process of performance monitoring, the question that arises is how FMT operates across different situations and contexts.

3.2 Frontomedial Theta Activity across Contexts

To examine the way in which need for control is elicited across different contexts and situations, the four studies employed within this dissertation implemented different tasks that all evoked increased FMT activity.

Study 3 utilized a shooting task in a stimulus-rich physical environment. As the task involved aiming at the target, which required motoric components, one factor the performance monitoring system needed to address was motor behavior. The visual feedback involved observing the projectile hitting or missing the target. Study 2 utilized a similar shooting task within VR. The visual input for the participants was more controlled than in study 3 but still stimulus-rich compared to traditional laboratory settings. The task again focused on motoric behavior. In both experiments of study 2, participants received visual feedback upon hitting or missing the target balloon, with the color of the fragment depending on the outcome of the shot. Additionally, in one experiment, the projectile could be visually tracked throughout its flight, while in the other experiment this was not possible. Summing it up, both study 2 and study 3 employed shooting tasks that required motoric actions, with participants receiving visual feedback on the outcome of their actions. Study 1, on the other hand, employed a more traditional, highly standardized lab setting. The reinforcement learning task implemented required decision making and enabled trial-to-trial learning of action values based on visual feedback of the action outcome. Therefore, the task included motor behavior only for indicating the decision via a button press and instead solely focused on cognitive processes.

Comparing the different tasks of studies 1 to 3, the action monitored by the performance monitoring system differs fundamentally between the studies. Study 1 investigated a cognitive decision and learning task, while studies 2 and 3 employed a motor action. Furthermore, study 1 utilized a laboratory setting, study 2 a VR setting and study 3 a “physical” setting without any virtual or digital components. Despite those differences in the type of action and the context, all tasks elicited increased feedback-related FMT activity, signaling increased need for control. Therefore, FMT activity seems not to be specific to certain kinds of actions and modulations of FMT activity are found in response to other tasks as well, such as response conflict tasks (Cavanagh et al., 2012; Cohen & Donner, 2013; Cohen & Ridderinkhof, 2013; Duprez et al., 2020; Pastötter et al., 2013) or gambling tasks (Cohen & Ranganath, 2007; Gheza et al., 2018; Mueller, Panitz et al., 2015). Since FMT arises across different types of actions, these findings provide further support for FMT as a content-independent need for control signal. This implies that FMT is not only content-independent within its role within the process of performing an action but also in regard to the action itself. Such independency would provide a high degree of flexibility for its general function in performance monitoring, enabling it to be used as a global signal, a lingua franca (Cavanagh et al., 2012), in any situation.

The approach-avoidance task implemented in study 4 involved decision making, while the Flanker task focused on response conflict in a speeded reaction time paradigm. Both tasks elicited increased FMT activity in response to an increased need for cognitive control, consistent with the abovementioned results on FMT across different tasks. However, study 4 specifically investigated the cross-task relationship of FMT activity and interestingly, the results do not show any correlations of individual FMT responsivity in the approach-avoidance task and the Flanker task. This means that participants that showed high FMT activity in response to conflict inducing stimuli in one task did not do so in the other task, suggesting that the different types of conflict did not trigger similar increases in FMT activity across tasks.

This finding challenges the previously proposed idea that FMT acts task- and context-independent and uniformly modulates cognitive control in any situation. If FMT activity was to be this highly dynamical, global function that modulates cognitive control in any situation, such a universal, highly relevant function could be expected to show trait-like characteristics with intraindividual consistency in its responsivity over time and across measures (Corr & Matthews, 2020). Instead, FMT may have more task-specific characteristics that require further attention to better understand its properties as a neuropsychological variable and therefore will be discussed in the following.

3.3 Intraindividual Consistency of Frontomedial Theta Responsivity

In the field of personality psychology, the extent to which a variable displays rank-order consistency over time is a crucial characteristic to be taken into account when considering it as a stable trait (Roberts & DelVecchio, 2000). To examine the temporal stability of individual FMT responsivities, study 1 conducted a retest session three months after the first EEG session. The study primarily focused on differences in FMT activity in response to negative and positive feedback. However, it is worth noting that the amplitudes of individual neural responses to positive and negative feedback generally tend to be highly correlated (Meyer et al., 2017), which is also the case in study 1. Difference scores of highly correlated variables have the characteristic of being biased towards low reliability scores since those two variables share a large amount of common variance, which can be canceled out by subtracting one variable from the other (Thomas & Zumbo, 2012; Trafimow, 2015). Therefore, the temporal stability scores can only be interpreted to a limited extent. The correlation coefficients of differential FMT activity in study 1 indicate poor temporal stability and coefficients corrected for this attenuation still suggest only small temporal stability for two of the three feedback dimensions. However, the differential activity in response to one dimension and the absolute amplitudes of FMT activity in response to each dimension show strong temporal stability. Thus, the condition-wise FMT responses provide some evidence for the temporal stability of individual FMT responses but do not conclusively prove a consistent pattern of a trait-like, stable FMT responsivity. In light of the ambiguous results from study 1, it is particularly intriguing to relate these to further results of study 4 before drawing a conclusion about whether there is something like a "universal FMT".

As previously stated, study 4 found increased conflict-related FMT activity in both an approach-avoidance task and a Flanker task but no cross-task relationship of individual FMT responsivity. These results suggest that FMT is sensitive to various types of conflict but the distinct conflict types may elicit increases in FMT activity differently and independently from each other. To clarify these things, source separation analyses were conducted utilizing generalized eigendecompositions (GED), which were designed to compute spatial filters that aim to isolate sources of theta-band activity (Cohen, 2022).

Accordingly, those extracted components exhibiting frontomedial component topography are indicative of FMT activity modulation and thus were used to compute component time courses. These were subsequently analyzed in addition to sensor-level analyses on FMT (Zuure & Cohen, 2021).

The component-level results of Study 4 mirrored the sensor-level findings. Specifically, no cross-task relationships of FMT component activity were observed between the approach-avoidance task and the Flanker task. Further GEDs that specifically compared the two tasks against each other yielded inconclusive results, as some components differentiated between the two tasks only for a portion of participants. Overall, the GED results of study 4 did not establish a clear pattern of conflict specific FMT activity.

The absence of cross-task relationships in FMT activity and FMT component activity suggests that there might be either one global FMT source that is active across tasks but responds differentially to various conflict types or multiple FMT modules that operate independently depending on the specific type of conflict in the task at hand, which would be consistent with findings from other studies that indicate multiple independent neuronal sources of FMT activity (Beldzik et al., 2022; Töllner et al., 2017; Zuure et al., 2020). However, the results of study 4 do not allow to map a particular component to a specific task, indicating a lack of task-specific differentiation of the components, which would serve as strong evidence for multiple task-specific FMT sources.

While the results of study 4 do not provide such clear evidence for the existence of multiple FMT sources, they still challenge the assumption of FMT as a unitary need for control signal. The absence of cross-task relationships in FMT activity suggests the presence of conflict-specific effects in FMT generation. One potential explanation for the absence of cross-task relationships in FMT activity is individual differences in sensitivity to different types of conflicts. For example, some individuals may perceive the approach-avoidance conflict as more intense than the Flanker conflict, potentially leading to a stronger increase in FMT activity or vice versa. Thus, the lack of cross-task relationships may be due to differences in conflict perception rather than specific FMT-related processes. To test this explanation, further research would need to clarify the role of intraindividual conflict perception in the generation of universal FMT activity. Another explanation for the absence of cross-task relationships in FMT activity is the existence of multiple independent FMT sources, which will be discussed in the following.

3.4 Context-Specific Generators, Universal Signal?

The four studies conducted in this dissertation provide evidence supporting the theory of FMT as a universally utilized need for control signal, on the one hand, as increased FMT activity was found across various tasks and contexts. On the other hand, the relatively small temporal stability observed in study 1 and the lack of any cross-task relationships in FMT activity and underlying components in study 4 challenge this idea. While these findings could be due to inter- and intraindividual differences in the perception and evaluation of relevant stimuli, such as conflict stimuli or feedback, another potential explanation is the existence of multiple FMT modules that are differentially engaged based on intraindividual and situational factors. These modules would work independently from each other but share the same characteristic: They identify increased need for control and communicate this need to other brain areas via modulations in FMT activity. Thus, the generation of FMT would take context-specific factors into account but FMT itself depicts a generic signal that can be received universally.

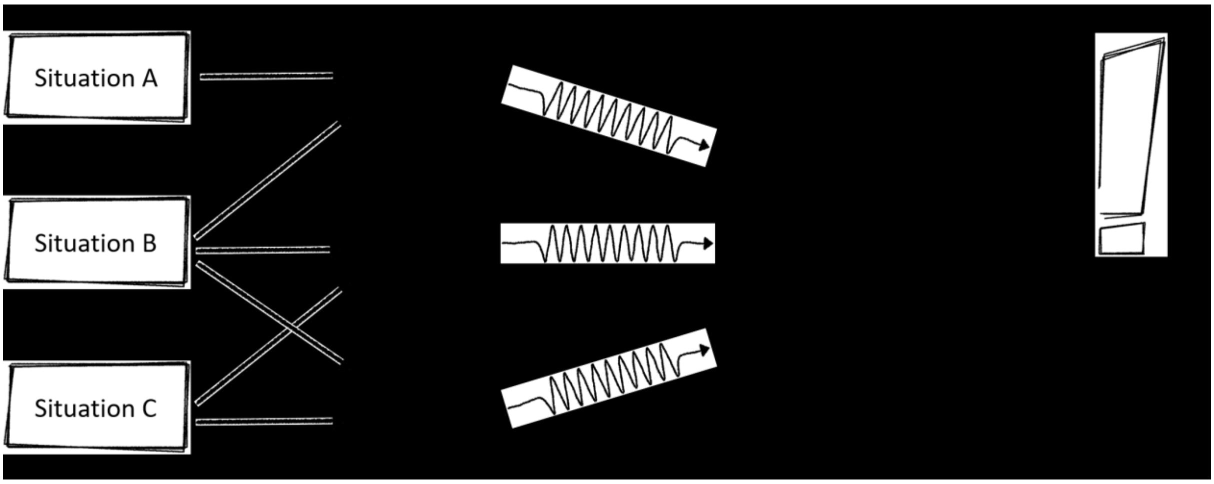

Figure 2: Illustration of frontomedial theta as a uniquely generated but universally received need for control signal

Figure 2 depicts a model of how FMT might act as a universal signal whose generation is sensitive to situational and individual factors. Central to this model is the assumption of multiple independent FMT modules that are responsible for generating increases in FMT activity. These modules may represent the independent sources of FMT activity found in previous research (Beldzik et al., 2022; Töllner et al., 2017; Zuure et al., 2020). Different FMT modules are activated in response to different inputs, such as receiving an RPE signal, a PRO signal or detecting a mismatch or response conflict, relating to the previously outlined theoretical approaches to performance monitoring (Botvinick et al., 2001; Holroyd & Coles, 2002; Ullsperger, Danielmeier & Jocham, 2014).

An exemplary situation might involve negative feedback and thus an RPE signal generated by dopaminergic neurons in the striatum. One FMT module *A* may be responsible for processing RPE signals. Upon detecting this RPE-related modulation in dopamine level, FMT module *A* would then initiate an increase in FMT activity to signal increased need for control. Similarly, another exemplary situation might involve decision conflict, for which another FMT module *B* would be responsible. This module then increases FMT activity triggered by the decision conflict. Thus, different situations engage different FMT modules but ultimately result in an increase in FMT activity.

Furthermore, some situations may be related to multiple FMT modules. For instance, a situation that involves decision conflict and feedback processing in terms of an RPE signal would activate both FMT module *A* and FMT module *B*. This would result in additive levels of FMT increases, where the overall increase in FMT activity would be the (weighted) combined result of the individual increases generated by each module. Depending on situational characteristics, both modules can be engaged to the same degree or one module may be activated stronger than the other. A situation that, by its nature, involves a proportionally “larger” decision conflict than RPE would activate FMT module *B* stronger than FMT module *A*.

Additionally, this model allows for the connections between situational factors and FMT modules to be modulated by individual traits and states. For instance, individuals with high sensitivity to decision conflict may exhibit stronger connections between situational factors that involve decision conflict and FMT modules. This could manifest in either strong activation of the associated FMT modules or activation of a greater number of FMT modules in response to decision conflict. Studies have shown correlations between response-/feedback-related FMT activity and individual traits, such as dispositional anxiety (for an overview, see Cavanagh & Shackman, 2015), which can be modulated by situational threat (Osinsky et al., 2017), as well as anhedonia and depression (Mueller, Panitz et al., 2015; Mueller, Pechtel et al., 2015), highlighting the link between individual traits and FMT activity.

The results of study 1 suggest that individual states can also affect the connections between situational factors and FMT modules. Given the low temporal stability of FMT responses found in study 1, some state variables may vary from the first EEG session to the second EEG session three months later. This can lead to changes in the weighting of the relationships to FMT modules and thus reduced temporal stability in the measurements of individual FMT responsivity.

Furthermore, the individual configurations of associations with FMT modules may explain the absence of cross-task relationships found in study 4. The associations of different conflict types with specific FMT modules are independent of each other, as they may relate to different FMT modules. Individuals with high general conflict sensitivity may exhibit strong associations of any conflict type with FMT modules. Individuals more sensitive to one type of conflict than the other may exhibit a more varied network of associations with FMT modules, resulting in differential degrees of activation across FMT modules. This can lead to different levels of overall FMT increases based on the type of conflict, where the FMT response is stronger for the type of conflict that is more salient for the individual. In other words, the individual's sensitivity to different types of conflict can shape their pattern of FMT module activation, resulting in different levels of FMT increase depending on the type of conflict experienced.

Overall, this model can account for inter- and intraindividual differences and context-dependent factors in the generation of FMT. These factors can affect the amplitude of FMT increase, while the resulting FMT signal serves as a generic, universal signal that signals the need for control. This approach has several advantages for the performance monitoring system, as it first considers differential factors in the generation of the need for control signal and then translates it into a universal signal.

As outlined in the introduction, the scope of the performance monitoring system encompasses a wide range of behavior and cognitive processes. The performance monitoring system has diverse responsibilities, which can be effectively managed by dividing them into smaller, highly specialized subsystems. The existence of several FMT modules enables a solution where each module is responsible for a specific task. This divides the "larger" performance monitoring system into multiple smaller, highly specific subsystems. Each of these subsystems only needs to fulfill one task, which is much simpler than being able to react to all possible challenges.

The essential feature in this regard is that all of these subsystems use the modulation of FMT activity as output. Thus, every deviation from expectations, decision conflict, behavioral error and everything else that requires intervention in terms of cognitive control leads to a modulation of FMT activity. Therefore, any receiving functional network in the brain associated with cognitive control only needs to pay attention to one signal, namely FMT activity. It can be addressed by any of the FMT modules and the output of the independent FMT modules is integrated and coded through the sum of increases in FMT activity.

The division of the performance monitoring system into smaller, highly specialized subsystems creates a high degree of flexibility, enabling FMT to be utilized as a signal during various stages of action performance. The origin of the increased need for control during cognitive conflict in the action selection phase, as implemented in study 4, is very different from the origin of increased need for control during the feedback delay phase, as implemented in study 2, or outcome evaluation, as implemented in study 1 and study 3. Under the assumption of multiple FMT modules, the event-related increases in FMT activity found in all four studies would be due to the fact that different FMT modules are engaged in different tasks, with each module being active during its own associated task and not necessarily the others. Therefore, the multiple FMT modules provide the basis for FMT to be involved in different stages of action performance and paradoxically, the subdivision in several unique FMT generators allows FMT to be used as a unitary need for control signal.

If the individual modules of the performance monitoring system work in a task-specific manner, the question arises as to why the differentiated task-specific information that these modules could provide is abandoned in favor of a uniform signal. While the studies conducted in the context of this dissertation cannot provide a direct answer to this question, it is possible to hypothesize that it is more feasible for the performance monitoring system to work with this kind of universal signal. If each FMT module were to communicate a specific signal or specific information about the underlying problem, it would exponentially increase the complexity in this communication phase. If the submodules had to derive and communicate appropriate response options or similar, beyond merely recognizing and communicating an increased need for cognitive control, it would significantly increase the demands placed on each submodule. This would likely increase the need for cognitive resources and prolong the duration of the involved cognitive processes. Therefore, it appears simply more economical for the brain to bundle these cognitive processes in another, more global functional network that is activated by signaling an increased need for cognitive control.

The efficiency of context-independent warning signals becomes apparent when we consider everyday warning signals that we might hear, from a beeping tone while driving a car to a loud siren. Simply hearing or seeing the warning signal is enough to alert us and prompt us to look for a solution. In the first moment, the signal does not need to provide a detailed description of the error. This could even be counterproductive for a rapid response.

Overall, the performance monitoring system utilizes FMT to signal an increased need for cognitive control in various situations. This occurs across contexts and tasks during different phases of the process of performing an action. However, individual differences in FMT responsivity suggest that it is affected by the individual evaluation of the eliciting situations. These differences can be explained, in part, by the existence of different FMT generating modules that are influenced by situational and individual factors. Nevertheless, their output would be a modulation of FMT activity, which serves as a global signal, effectively acting as a "lingua franca”. While this type of lingua franca may differ slightly from Cavanagh’s original proposal, as the generators would be highly specific, they essentially translate the circumstances that require an increased need for control into a unified language.

While this explanation provides a plausible account of the findings of the four studies conducted in the framework of this dissertation and is consistent with previous research on FMT, it is important to note that these four studies alone cannot fully substantiate the theory. Further research is needed to confirm the assumptions derived from these findings. For instance, high-density EEG studies with more sensors could enhance the power of source separation analyses by extracting an increased number of potential sources of neural activity. Such studies could provide a more detailed understanding of the neural sources underlying FMT. Additionally, it would be valuable to specifically examine the timing of FMT activity during the different phases of action performance, i.e., modulations of FMT activity during the pre-response phase, feedback delay phase and post-outcome phase. Future studies could build upon the findings of this dissertation and provide an opportunity to explore the assumptions derived from the current research, ultimately leading to a more comprehensive understanding of FMT and its role in performance monitoring.

3.5 Thoughts on Neural Origin, Temporal Constraints and Clinical Implications

In addition to the findings mentioned above, there are considerations regarding the neural origin of FMT that should be acknowledged. First, the neural origin of FMT is not yet fully understood. While there is compelling evidence that the ACC is the primary source of FMT activity (Asada et al., 1999; Berger et al., 2015; Botvinick et al., 2004; Cavanagh & Frank, 2014; Cavanagh & Shackman, 2015; Cohen et al., 2008; Cohen & Cavanagh, 2011; Debener et al., 2005; Gevins, 1997; Hanslmayr et al., 2008; Hauser, Iannaccone, Stämpfli et al., 2014; Holroyd & Umemoto, 2016; Ishii et al., 1999; Ishii et al., 2014; Kerns et al., 2004; MacDonald et al., 2000; Nee et al., 2011; Nigbur et al., 2011; Onton et al., 2005; Ridderinkhof et al., 2004; Sauseng et al., 2007; Wang et al., 2005; Wessel et al., 2012; Womelsdorf et al., 2010) other brain regions, such as the pre-SMA (Nachev et al., 2007; Rushworth et al., 2002) may also contribute to FMT activity.

FMT seems to be closely linked to ongoing neural activity in the brain. Study 3 differentiated phase-locked and non-phase-locked FMT activity and found that both types of FMT activity showed a significant increase in response to negative outcomes. However, in study 3, the increase in non-phase-locked FMT activity showed a much larger effect size than the increase in phase-locked FMT activity.

Further, inter-trial phase coherence estimates (ITPC) differed only marginally between positive and negative outcomes and were generally small, indicating only a small amount of phase-locking of outcome-related FMT activity. Cohen and Donner (2013) found similar results in a speeded Flanker task and proposed that modulations in FMT power reflect non-phase-locked oscillations in the ACC.

This pattern of phase-locking of FMT activity may reflect communication of the need for control to other brain areas. Studies found increased theta phase coupling between frontomedial and lateral frontal electrode sites during error commission (Cavanagh et al., 2009) and during response conflict (Nigbur et al., 2012) in Flanker tasks and in stroop tasks (Hanslmayr et al., 2008). Accordingly, the ACC might be responsible for the detection of an increased need for control, e.g., error detection and conflict detection, and then signals increased need for control to the lateral prefrontal cortex, which would be responsible for the implementation of cognitive control (Botvinick et al., 2004; Gable et al., 2022; Nigbur et al., 2012).

Beyond the question of the neural basis of FMT as a need for control signal, it is also important to consider that different contexts and situations may require different amounts of cognitive control. For example, some tasks may have a higher baseline level of cognitive control needed due to their inherent complexity, such as tasks that require multitasking or tasks that involve decision-making under high levels of uncertainty. Moreover, if FMT is to serve as an early warning signal for the need for cognitive control, this would be particularly relevant in contexts where fast and accurate responses are required, such as in high-stress environments or in response to sudden changes in the environment. Many studies that assess FMT activity utilize Flanker tasks, simon tasks, go/no-go tasks or stroop tasks (for an overview, see e.g., Ullsperger, Danielmeier & Jocham, 2014; Cavanagh & Frank, 2014; Pezzetta et al., 2022), which all reflect speeded response or decision tasks. Pastötter et al. (2012) found significantly higher pre-response FMT activity in trials where participants were instructed to prioritize response accuracy than in trials in which they were instructed to prioritize response speed. The signaling of increased need for pre-response cognitive control seems to depend on the relevance of accurate responses. Therefore, the demands on speed and accuracy of an action seem to be relevant in modulating FMT activity. However, contexts that elicit, for example, outcome-related FMT activity often do not involve the same time pressure or need to respond quickly, contradicting the assumption that FMT primarily arises in contexts where speed and accuracy are critical. Thus, further research needs to clarify the factors that modulate this phenomenon.

Lastly, it should also be noted that FMT may operate differently in different populations, such as individuals with psychiatric or neurological conditions. For example, individuals with anxiety disorders may show a higher baseline level of FMT activity due to increased need for cognitive control in response to anxiety-provoking stimuli. Individuals with attention-deficit/hyperactivity disorder (ADHD) have been found to exhibit reduced FMT activity and phase consistency during tasks requiring cognitive control (Bluschke et al., 2016; Cowley et al., 2022), which may contribute to the difficulties with attention and impulse control. In individuals with schizophrenia, impaired FMT responses have been observed during tasks involving working memory and attention (Cooper & Hughes, 2018; Reinhart et al., 2015; Ryman et al., 2018), while anxiety disorders are associated with increased FMT activity (Cavanagh & Shackman, 2015). FMT might have the potential to serve as a biomarker for a range of psychiatric and neurological conditions, providing insights into the underlying neural mechanisms of these disorders (McLoughlin et al., 2022). However, to fully realize the clinical potential of FMT as a diagnostic or prognostic tool, further research is needed to elucidate its clinical relevance and develop standardized methods for measuring and interpreting FMT activity. By advancing our understanding of the neural mechanisms underlying cognitive control processes, FMT may also inform the development of new interventions for psychiatric and neurological disorders characterized by cognitive control deficits.

3.6 Concluding Remarks

The goal of this dissertation was to explore the neural mechanisms that underlie performance monitoring, with a particular focus on the role of FMT in signaling an increased need for cognitive control across diverse contexts and tasks. To achieve this, four distinct studies were conducted, each employing different measures and tasks to probe the relationship between FMT activity and cognitive control.

The findings of this dissertation highlight the central role of FMT in performance monitoring across different contexts and tasks. All four studies conducted in this dissertation found modulations of FMT activity at different phases during the process of performing an action, indicating that FMT is involved during various stages of action performance. The results suggest that FMT signals an increased need for cognitive control without specifying potential interventions, making it a content-independent alarm signal that can be utilized throughout the entire process of action performance.

Furthermore, FMT modulations were found across different types of actions, indicating its content-independency in not only its role within the process of performing an action but also in regard to contextual characteristics and the action itself. This flexibility allows FMT to be utilized as a global signal in any situation, providing further support for its role as a content-independent signal. Together, these findings suggest that FMT is a vital component in performance monitoring that signals the brain that something needs to be done without specifying the exact course of action required.

However, the findings of the studies conducted within this dissertation also show up limitations to the flexibility of FMT. The low intraindividual stability of FMT responsivity across time and tasks suggests that FMT is not just “one global signal” but requires a more fine-grained differentiation. While FMT modulations are found across different tasks, there seem to be intraindividual differences in FMT responses to different tasks. One promising explanation would be multiple FMT modules that are differentially sensitive to different inputs, such as tasks or contexts, and can vary in their intra- and interindividual configurations. In this way, the origin of FMT modulations would lie in highly specific submodules, but they translate their input into one generic output, namely FMT activity.

In conclusion, the findings of this dissertation support the view that FMT is a versatile signal utilized by the performance monitoring system to modulate the need for control across different tasks, contexts and stages of action performance. It appears to be a unitary and unidimensional signal that signals an increased need for control. However, the generation of FMT seems to be more complex and differentiated, being sensitive to both intra- and interindividual factors. This allows for a fast, efficient and accurate modulation of cognitive control whenever necessary, enabling individuals to execute actions as optimally as possible.

This dissertation provides important insights into the neural mechanisms underlying performance monitoring and the role of FMT in signaling an increased need for cognitive control under various circumstances. The findings have implications for our understanding of how the brain regulates behavior and adapts to changing environmental demands and may have important implications for the development of interventions to improve cognitive control in individuals with impairments in this area.

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5 Appendix

5.1 Erklärung über die Eigenständigkeit der erbrachten wissenschaftlichen Leistung

Ich erkläre hiermit, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus anderen Quellen direkt oder indirekt übernommenen Daten und Konzepte sind unter Angabe der Quelle gekennzeichnet.

Bei der Auswahl und Auswertung folgenden Materials haben mir die nachstehend aufgeführten Personen in der jeweils beschriebenen Weise unentgeltlich geholfen.

Study 1: Rommerskirchen, L., **Lange, L.** & Osinsky, R. (2021). The reward positivity reflects the integrated value of temporally threefold-layered decision outcomes. *Psychophysiology*, 58(5).

Konzeptualisierung: Roman Osinsky (RO)

Datenerhebung: Anke Bavendam-Kreib (ABK) mit studentischen Hilfskräften der Differentiellen Psychologie und Persönlichkeitsforschung und Psychologie-Studierenden der Universität Osnabrück

Datenanalyse: Leon Lange (**LL)**, Lena Rommerskirchen (LR), Feedback von RO

Schreiben: RO (Einleitung), **LL** (Methoden & Ergebnisse), LR (Diskussion), Feedback und Einverständnis aller Koautor:innen; **LL** und LR teilen die Erstautorenschaft

Study 2: Lange, L., Kisker, J. & Osinsky, R. (*under review*). Midfrontal signaling of need for control continuously adapts to incoming information during outcome anticipation. *NeuroImage: Reports*.

Konzeptualisierung: **LL**, RO, Joanna Kisker (JK)

Datenerhebung: **LL**, JK mit studentischen Hilfskräften der Differentiellen Psychologie und Persönlichkeitsforschung und Psychologie-Studierenden der Universität Osnabrück

Datenanalyse: **LL**, Feedback von RO

Schreiben: **LL**, Feedback und Einverständnis aller Koautor:innen

Study 3: Lange, L. & Osinsky, R. (2020). Aiming at ecological validity—Midfrontal theta oscillations in a toy gun shooting task. *European Journal of Neuroscience*, 54(12), 8214-8224.

Konzeptualisierung: **LL**, Feedback von RO

Datenerhebung: **LL** mit studentischen Hilfskräften der Differentiellen Psychologie und Persönlichkeitsforschung und Psychologie-Studierenden der Universität Osnabrück

Datenanalyse: **LL**, Feedback von RO

Schreiben: **LL**, Feedback und Einverständnis von RO

Study 4: Lange, L., Rommerskirchen, L. & Osinsky, R. (2022). Midfrontal Theta Activity Is Sensitive to Approach–Avoidance Conflict. *Journal of Neuroscience*, *42*(41), 7799-7808.

Konzeptualisierung: RO

Datenerhebung: LR mit studentischen Hilfskräften der Differentiellen Psychologie und Persönlichkeitsforschung und Psychologie-Studierenden der Universität Osnabrück

Datenanalyse: **LL**, LR, Feedback von RO

Schreiben: **LL**, Feedback und Einverständnis aller Koautor:innen; **LL** und LR teilen die Erstautorenschaft

Verena Gottlieb & Joanna Kisker haben auf Rechtschreibung und Grammatik bezogenes Feedback zum Rahmentext dieser Dissertation gegeben.

Weitere Personen waren an der inhaltlichen materiellen Erstellung der vorliegenden Arbeit nicht beteiligt. Insbesondere habe ich hierfür nicht die entgeltliche Hilfe von Vermittlungs- bzw. Beratungsdiensten (Promotionsberater oder andere Personen) in Anspruch genommen. Niemand hat von mir unmittelbar oder mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Die Arbeit wurde bisher weder im In- noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt.

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(Ort. Datum) (Unterschrift)

5.2 List of Abbreviations

ACC	Anterior cingulate cortex
aMCC	Anterior midcingulate cortex
EEG	Electroencephalogram
ERN/Ne	Error-related negativity
ERP	Event-related potential
FMT	Frontomedial theta
FRN	Feedback-related negativity
GED	Generalized eigendecomposition
ITPC	Inter-trial phase coherence
MoBI	Mobile Brain/Body Imaging
mPFC	Medial prefrontal cortex
Pe	Error positivity
Pre-SMA	Pre-supplementary motor area
PRO	Predicted response-outcome
rERSP	Regression-based event-related spectral perturbations
RewP	Reward positivity
RL	Reinforcement learning
RPE	Reward prediction error
VR	Virtual reality