



How Conflict-Specific is Cognitive Control? Behavioral and Electrophysiological Indices

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Abstract

Cognitive control refers to a set of mental abilities that allow us goal-directed behavior in everyday life and to flexibly adapt to permanently changing environmental demands. The goal of the present dissertation was to investigate whether core functions in the area of conflict monitoring, conflict control, error processing and behavioral adjustments caused by these processes are enabled via a unitary control network or whether specific mechanisms that are possibly realized via independent control loops are responsible for the flexibility of our adaptability. I will approach this question from two different theoretical perspectives: Study 1 and 2 investigate general as well as specific aspects of conflict and error processing by using classic conflict paradigms and time-frequency-analytic methods. The focus of these analyses is on the one hand on the question, whether power differences in the theta band (4-8 Hz) can serve as a universal conflict measure and whether conflicts and errors are processed in a similar way. Study 1 compares the modulation of theta activity across 3 paradigms (Simon, NoGo, and Flanker task) and roughly situates it within medial frontal (MFC) cortex, a structure which has been characterized as crucial for conflict processing in manifold studies. Conflicts as well as errors led to robust theta power differences and had therefore been used in study 2, to observe dynamic network activations during processing of stimulus and response conflicts. Additional to power measures phase coupling between MFC related electrodes and other areas such as lateral prefrontal cortices (LPFC), motor and perceptual areas was analyzed. Data confirmed that a hypothesized network consisting of MFC, lateral PFCs and motor areas is involved in conflict resolution. Study 3 differs from the previous studies because it uses the evaluative functional properties that have been assigned to portions of the MFC as a modulatory variable to investigate the interdependencies of motivational and cognitive information processing involved in cognitive control functions. Using a Simon task which was executed either during a rewarding or a punishing context data revealed that conflict and error processing were influenced differentially by the context manipulation. While conflict processing was affected only marginally by reward and punishment, electrophysiological markers of error processing as well as behavioral adjustments were strongly influenced. In my opinion the present dissertation sheds light on the cognitive architecture of control functions in several ways: On the one hand it has been shown that by using theta dynamics general as well as specific network activity can be analyzed. Results confirm an involvement of MFC in these processes but also admit a response controlling function of MFC besides lateral frontal regions. Furthermore, the motivational manipulation suggests that systems for conflict and error processing are mostly independent. Against previous assumptions, several neuronal control systems seem to be engaged during conflict resolution and resulting behavioral adjustments. These can be analyzed using theta activity as well as dissociable sensitivities to motivational influences.

Zusammenfassung

Kognitive Kontrolle bezieht sich auf eine Vielzahl mentaler Fähigkeiten, die es uns erlauben im täglichen Leben zielgerichtete Entscheidungen zu treffen und sich flexibel an sich ständig ändernde Umweltanforderungen anzupassen. Das Ziel der vorliegenden Dissertation war es heraus zu finden, ob Kernfunktionen im Bereich der Konfliktüberwachung, Konfliktkontrolle, Fehlerverarbeitung und die daraus resultierenden Verhaltensanpassungen durch ein einheitliches Kontrollnetzwerk geleistet werden, oder ob spezifische Mechanismen die möglicherweise durch unabhängige neuronale Kontrollschleifen realisiert sind, die Flexibilität unserer Anpassungsfähigkeit steuern. Ich nähere mich dieser Frage von zwei theoretischen Ansätzen aus: Studie 1 und Studie 2 untersuchen sowohl generelle als auch spezifische Aspekte der Konflikt- und Fehlerverarbeitung mit Hilfe klassischer Konfliktparadigmen und dem Einsatz von Zeit-Frequenz-analytischen Auswertungsmethoden. Im Zentrum dieser Analysen steht zum einen die Frage, ob Powerunterschiede im Theta Band (4-8 Hz) als universelles Konfliktmaß dienen können und ob Fehler und Konflikte in ähnlicher Art und Weise verarbeitet werden. Studie 1 untersucht über 3 Paradigmen hinweg (Simon, NoGo und Flanker Aufgabe) die Modulation der Theta Aktivität und versucht diese grob innerhalb des medial frontalen Cortex zu verorten, einer Struktur die durch eine Vielzahl von Studien als entscheidend bei der Konfliktverarbeitung angesehen wird. Sowohl die verschiedenen Konflikte als auch die Fehlerverarbeitung führten zu robusten Theta Power Unterschieden und wurden in Studie 2 genutzt, um auch dynamische Netzwerkaktivierungen bei der Bearbeitung von Reiz- und Reaktionskonflikten zu beobachten. Zusätzlich zur Power wurde auch die Phasenkopplung zwischen medial frontalen Cortex (MFC) relatierten Elektroden und anderen Arealen wie lateral präfrontalen (LPFC), motorischen und perzeptuellen Arealen untersucht. Es konnte gezeigt werden, dass ein vermutetes Netzwerk bestehend aus MFC, lateralen PFCs und motorischen Arealen bei der Lösung von Reaktionskonflikten beteiligt ist. Studie 3 unterscheidet sich von den vorherigen Studien dadurch, dass hier die evaluative Funktion, die ebenfalls in Teilen des MFC verortet wird als modulierende Variable genutzt wird, um die Wechselwirkung motivationaler und kognitiver Verarbeitungsprozesse im Rahmen kognitiver Kontrollfunktionen zu untersuchen. Mithilfe einer Simon-Aufgabe, die innerhalb von belohnenden oder bestrafenden Kontexten durchgeführt wurde, konnte gezeigt werden, dass Konflikt- und Fehlerverarbeitung differentiell durch die Kontextmanipulation beeinflusst werden. Während Konfliktverarbeitung nur marginal durch Belohnung und Bestrafung beeinflusst wurde, zeigte sich, dass sowohl elektrophysiologische Marker als auch Verhaltensanpassungen der Fehlerverarbeitung deutlich stärker beeinflusst wurden. Meiner Meinung nach trägt die vorliegende Dissertation in mehrfacher Hinsicht dazu bei, die kognitive Architektur von Kontrollfunktionen zu charakterisieren: Zum einen kann gezeigt werden, dass mit Hilfe der Thetadynamik sowohl generelle als auch spezifische Netzwerkaktivitäten analysiert werden können. Die Ergebnisse bestätigen eine Beteiligung des MFC an diesen Prozessen, räumen ihm neben frontalen Arealen aber auch eine Handlungskontrollfunktion ein. Weiterhin kann mit Hilfe der motivationalen Manipulation nachgewiesen werden, dass es sich bei der Fehlerverarbeitung um ein von der Konfliktverarbeitung weitgehend unabhängiges System handelt. So scheinen entgegen voriger Annahmen mehrere neuronale Kontrollsysteme an der Lösung von Konflikten und daraus resultierenden Verhaltensanpassungen beteiligt zu sein. Diese können sowohl mit Hilfe von Thetaaktivität als auch dissoziierender Reaktionen auf motivationale Einflussfaktoren untersucht werden.

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1 Theoretical and Empirical Overview

“It is necessary to study not only parts and processes in isolation, but also to solve the decisive problems found in organization and order unifying them, resulting from dynamic interaction of parts, and making the behavior of the parts different when studied in isolation or within the whole...”

Ludwig von Bertalanffy, General System Theory

1.1 Introduction and Research Questions

Every day of our lives is determined by manifold choices and decisions that most of the time sum up to certain goal-directed behaviors. Imagine yourself on a rainy day driving a car during rush hour in the city: permanently you will have to monitor for other cars, street signs, traffic lights, a sudden rerouting, observe kids playing on the pavement and yelling seniors on their bikes. Furthermore, due to an inspiring social gathering yesterday you woke up too late knowing that in case you don't hurry up you will be delayed to a very important meeting with your boss. Due to this the emotional pressure your reaction to sudden changes in the traffic might be improved, but at the same time you might be susceptible to driving a bit too fast and risk an accident...

In cognitive terms you are confronted with a stream of dynamic information which you have to monitor continuously. You have to register environmental cues, your own behavior as well as behaviors of others according to your set goal. You will permanently adjust your attentional resources in a moment-to-moment fashion to the salient and expedient events and you will be influenced by your current mood and motivations. Although these higher-level functions have been studied intensively for the past decades, also regarding their break-down in certain neuropsychiatric disorders such as ADHD, Schizophrenia, Parkinson's disease and many others, not much is known about the neuronal realization of these processes

that allow us to adapt flexibly to an unpredictably changing environment. While describing such higher control functions, a demon of cognitive neuroscience - the so-called “homunculus” - has repeatedly had his comeback, especially when conceptual considerations failed to incorporate the emergent and reciprocal organization of the cognitive system (Thompson and Varela, 2001). However, recent approaches try to avoid such notions and use also computational models besides other neuroscience methods to characterize our cognitive capabilities underlying executive functions (Hazy et al., 2007).

The present work investigated the properties of an assumed modular executive control system which consists according to latest theories of several functional-neuro-cognitive mechanisms. These dissociable mechanisms are responsible for the detection of and adaptation to conflicts, the regulation and evaluation of behavioral outcomes and presumably are influenced by low-level motivational and emotional systems. I have chosen a very broad scope to characterize the different functional properties of the cognitive system which can be subsumed under two perspectives: The first perspective will relate to within-trial adaptation which is basically measuring online-adjustments and respective brain mechanisms engaged during processing and resolution of a conflict. To deepen the understanding of neuronal aspects of conflict processing I will use conflicts at different levels of processing to prove that different neuronal pathways are activated during different conflicts. The second perspective looks at the modulatory influences of affective states on across-trial adaptation processes. I will use a motivational manipulation to figure out how error and conflict processing are affected by these manipulations and which conclusions can be drawn from these dissociable effects. In my view, although the two perspectives arise from very different theoretical approaches the interplay of affective states and cognitive processes can help to elucidate how our control systems are organized.

Along the introductory part of this thesis I will develop three main research questions that comprise different aspects of cognitive control functions: The first ques-

tion of interest is how general or specific conflict control can be engaged: therefore I will compare on-line adjustments in cognitive control in different paradigms within trials and distill a new measure which reflects conflict processing in the brain. Another notion here regards the question, whether errors are treated such a conflicts or whether they only share some certain processes with conflicts. The second question deepens the connection between cognitive conflicts and underlying neuronal mechanisms by asking how different types of conflict, namely perceptual and response conflict, can be characterized by the time-frequency dynamics within the theta range and inter-areal communication. The third question is concerned with the influence of motivational incentives on conflict adaptation processes as well as error monitoring. Here, I will focus on inter-trial adaptation and error processing and how these mechanisms can be modulated by motivational incentives.

In the upcoming chapters I will (1) outline the development of theoretical frameworks for cognitive control functions also by reviewing their assumed neuronal counterparts, (2) explain which methodological approaches we used to address the question of general and specific properties of control, and (3) report the results and main conclusions of the performed studies. Finally, I will give (4) a general discussion of the studies and (5) propose future directions to close the gap between the perspectives of cognitive conflict resolution processes and its reciprocal connections with affective and motivational processing.

1.2 Conflict Processing and its Control

From an evolutionary perspective brains are constructed to predict the environment. To do so, learning mechanisms that code whether an external event predicts positive or negative outcomes are crucial. Despite these humans developed a set of mental abilities that have previously been labeled by terms such as executive functions or cognitive control. These labels comprise interconnected functions that can usually be classified in one of the following functional categories such as,

goal representations (Bunge, 2004; Miller and Cohen, 2001), on-line maintenance / working memory (Baddeley, 1998; Braver and Cohen, 1999; Goldman-Rakic, 1996), top-down biasing (Desimone and Duncan, 1995; Norman and Shallice, 1980; Schneider and Shiffrin, 1977) and interference / conflict management (Botvinick et al., 2004; Carter et al., 1998). In general, these abilities in humans constitute the basis for a very powerful repertoire of goal-directed behaviors including overcoming automatic behavior, inhibition of pre-potent responses, planning and cognitive flexibility. One could roughly say that humans are hyper-adaptive organisms and perfect in predicting contingencies between observations from the outside and expectations from past experience by these means optimizing their behavior.

1.2.1 Functional Perspectives on within-trial Control

Imagine you are crossing a street in the UK: residing on continental Europe you are used to look to the left whenever you cross the street. Therefore, you will be confronted with a new environment you will have to adapt to by establishing new behaviors according to the incoming stimuli and goals. During your stay you will learn to inhibit the learned impulsive urge to look to the left and you will overcome this by a top-down controlled sight to the right. This learning process can be advanced via additional task-relevant information (as written on the pavement) or sudden aversive events that will motivate you to foster the new behavior (i.e. almost getting hit by a horn blowing bus coming from the right). Comparable, imagine you are looking for your favorite toothpaste in the supermarket. All the features of the dozens of products seem similar but you will focus your attention to one of the features (maybe a combination of colors) and you will have to ignore all other features like words or shape.

As can be seen in the examples, conflict – the concurrent presence of stimuli or action plans - can occur at different stages. Whereas in the street example one has to overcome a learned tendency to respond with a look to the left, in the super-

market example one just has to focus on the relevant features and ignore the irrelevant features. In cognitive science several stages have become commonly accepted, starting from stimulus perception and evaluation, to response selection and preparation and finally response execution. Cognitive control therefore can be studied via a wide range of paradigms, but for the present purpose I will focus on stimulus-response compatibility tasks. The prominent Eriksen Flanker paradigm (Eriksen, 1974) uses target items that are surrounded by distracting items which are either identical to the target (compatible), are different but code for the same response (stimulus conflict, because conflict arises only at the perceptual level) or are different and code for another response (stimulus and response conflict, because the flanker indicate a response with the other hand). The stable finding here is that people take more time and make more errors during the conflict conditions.

However, the source or stage of conflict can differ, as for example in the Simon task, where the irrelevant location leads to conflict at the response level, or in the Stroop task, where the semantic content of the word can lead both to stimulus and response conflict. I will refer in the following to compatible conditions when no feature of the stimulus introduces conflict and to incompatible conditions when either at the perceptual level or later in information processing such as the response level conflict is elicited. The assumption here is that all these types of within the lab induced conflicts tax higher demands on the control functions compared to situations where no conflicting information occurs. In the past, mainly dual-route models were used to account for such interference effects and assumed a direct route, which is primed by visuo-motor integration processes and an indirect route which is guided by task instructions (Kornblum et al., 1990). In a "buffer" somehow these two activations are weighted and in a "the-winner-takes-it-all" fashion the correct response is selected. Later accounts which will be outlined in the next section assigned neuronal counterparts of these processes within different portions of the prefrontal cortex.

1.2.2 Neuronal Underpinnings I: Conflict Processing and Control

Recent approaches highlight a crucial role of different portions of the prefrontal cortex in all control related functions (Miller and Cohen, 2001) and especially the medial frontal cortex (MFC) has been acknowledged as a nexus between sensory, motoric, subcortical and prefrontal areas (Paus, 2001). In their meta-analysis Ridderinkhof et al. (2004) present current perspectives on MFC functioning and emphasize its role during pre-response conflict, decision uncertainty, response errors, and negative feedback. Especially the conflict monitoring account has led to an immense amount of research regarding the cognitive processes that are realized within this area. Botvinick et al. (2004) propose that a “cortical response to conflict” within the MFC, namely anterior cingulate cortex (ACC) can be associated with one of three behavioral contexts: during tasks that require overriding of pre-potent responses, undetermined responding or during the commission of errors. Supported by computational modeling work and numerous imaging studies the claim is that ACC signals the occurrence of conflicts in information processing and at the same time recruits control from other, mostly lateral prefrontal areas, which has been shown by interconnected activation patterns (MacDonald et al., 2000).

One set of data supporting this ideas stems from electrophysiological approaches that used N2 or N2c measures of the event-related brain potential in order to characterize brain activity during conflict tasks (Heil et al., 2000; Kopp et al., 1996). The N2 can be observed as a negative shift over fronto-central scalp locations, with a peak between 250 and 350 ms following a No-Go stimulus but also following incompatible trials in conflict tasks. Although several studies emphasize an exclusive role for N2 enhancements during response conflict (Van Veen and Carter, 2002) according to others there is yet no conclusive agreement on which processes are reflected in this component family. Folstein and Van Petten (2008) point out that the N2 effects typically elicited during cognitive control paradigms should be understood as a compound of separate control- and mismatch related

subcomponents. Until now, however, no study has directly compared N2 measures across different conflict paradigms.

Additional to other critical voices questioning the essential role of ACC in conflict processing (Fellows and Farah, 2005; Grinband et al., 2011) alternative accounts propose that the ACC itself can act as a top-down controlling unit that is activated whenever incongruent information is entering the system either on stimulus but also on response side (Posner and Di Girolamo, 1998). I will follow both outlined ideas speculating that different portions of the MFC are activated whenever divergent information enters or emerges within the cognitive system.

A side question but nevertheless of high importance has been developed already in the 60ies by Rabbitt (1966). He observed that people tend to make a speed-accuracy tradeoff after errors. Since the discovery of the error-related negativity (ERN), a negative component with a medial frontal distribution occurring approximately 50-100 ms after making an error (Falkenstein et al., 2000; Gehring et al., 1993), the research on error processing has been enlarged extensively.

On the one hand it was important to know whether the ERN is just another conflict that is similarly processed compared to cognitive conflicts (Carter et al., 1998). Yeung et al. (2004b) tried to explain the properties of the ERN compatible to the N2 with a connectionist model concluding that the ERN displays response conflict and that monitoring provides a simple mechanism for detecting errors. On the other hand also here subsequent behavioral adjustments such as post error slowing (PES) could be observed. In their review Danielmeier and Ullsperger (2011) point out that PES, post reduction of interference (PERI) and post error improvement in accuracy (PIA) can be explained by several accounts. The cognitive control account (Botvinick et al., 2004; Carter et al., 1998; Gehring et al., 1993), the orienting account (Notebaert et al., 2009), and the inhibitory account (Aron, 2007; Ridderinkhof, 2002) provide complementary accounts on these phenomena.

Within this scenery of possible functional MFC properties, the similarity of electrophysiological control indices and theoretical assumptions regarding underlying systems my first research issue tries to shed light on the following question: Can we extract a common mechanism underlying all interference paradigms and will this measure help us to determine whether all conflicts are processed in the same way?

1.3 Conflict Adaptation and Specificity

Up to now, numerous studies have chosen several pathways to investigate whether cognitive control is realized as a unitary mechanism that spans over different domains or whether it consists of several modules / networks that are recruited during these operations.

1.3.1 Functional Perspectives on Conflict Adaptation

An elegant way to show the temporal variability of control usage was presented by Gratton et al. (1992). In a flanker task they showed that control dynamics are not only active within a trial but change in a trial-by-trial fashion. They divided reactions depending on their direct preceding trial which led to four possible trial combinations (cC, cI, iC and iI) and presented a pattern with very strong conflict effects following compatible trials and a strong reduction of this effects following incompatible trials (i.e. the conflict adaptation effect). They interpreted this context driven strategic adjustments as the result of expectancies about the relative utility of the information extracted (in this case use of the flankers) to activate responses. Although others pointed out that also other processes like feature-overlap and direct repetitions (Hommel et al., 2004; Mayr et al., 2003) contribute to this pattern it is commonly accepted that the inter-trial adjustments mirror partly changes in cognitive control engagement (Ullsperger et al., 2005).

In numerous follow-up studies regarding the question whether such adaptations occur also when two conflict types are intermixed empirical findings leave an

inconclusive picture: Whereas some groups report such overlays (Freitas et al., 2007) others do not find any evidence for cross-conflict transfer of control (Runger et al., 2010). However, several studies presented evidence for a multiple process view one of them suggesting that different types of conflict are resolved via distinct cognitive control loops, implying that conflict-driven cognitive control processes should not be thought of as emanating from a single, central resource but, rather from a collection of conflict-specific regulatory loops that may operate in parallel (Egner, 2008).

1.3.2 Neuronal Underpinnings II: Adaptation and Networks

Kerns et al. (2004) and (2006) presented data that supported the interdependency between the ACC as a conflict monitoring device and the engagement of the dorsolateral prefrontal cortex (dlPFC) during cognitive control and behavioral adjustments in the upcoming trial. Although a previously assigned role of dlPFC has been linked to preparatory activity (MacDonald et al., 2000) and biasing of incoming stimuli information (Miller and Cohen, 2001) ambiguous results exist whether subsequent behavioral adaptations are caused by MFC or dlPFC structures (Mansouri et al., 2009).

In a meta-analysis by Nee et al. (2007) different conflict paradigms such as Stroop, flanker, NoGo, stimulus-response compatibility, Simon and stop signal tasks engaged a network comprising ACC, dlPFC, inferior frontal gyrus, posterior parietal cortex and anterior insula which has been identified during all tasks. Interestingly, individual task analyses showed differential patterns of activation among tasks. They concluded that interference might be resolved among several processing stages namely stimulus encoding, response selection and response execution and these processes therefore should recruit different neural regions. Similarly, Egner et al. (2007) proposed that several areas serve as independent controlling units. Again a compelling question here arises, namely, how these networks are organized and whether they interact or not.

Despite the interference tasks I presented in the previous section also other functions like motor inhibition have been linked to cognitive control. In his review Aron (2007) poses the question whether motor inhibition is fundamentally different from other forms of inhibition such as selective attention, memory, or emotion. Although he advocates a careful use of this concept he describes motor inhibition as a robust member of cognitive control functions. (Nieuwenhuis et al., 2003) used a NoGo-paradigm and confronted subjects with 3 different NoGo probabilities (20, 50 and 80%). They found larger N200 amplitudes for NoGos in all three probabilities but also a frequency effect with greater N2 amplitudes also for rare Go signals. Additionally, using dipole modeling they suggest a similar mechanism underlying error and conflict detection.

In a series of experiments we also tested the idea of inter-trial conflict adaptation across different paradigms. For this purpose we used a combined Simon-Go-NoGo-experiment with different amounts of NoGos ranging from 17, 33 to 50% per experiment. Our hypotheses following the conflict monitoring account by (Botvinick et al., 2004) were that each type of conflict (Simon interference, NoGos and errors) should lead to enhancements of cognitive control in the upcoming trial. The conflict adaptation effect depending on predecessor event, N2 measures, as well as the lateralized readiness potential (LRP) should mirror the engagement of cognitive control following incompatible Simon trials and NoGo trials. Surprisingly, we found that only after incompatible Simon trials but not after inhibition or erroneous trials a reduction of interference at the behavioral level occurred. Furthermore, the wrong hand LRP reduction was visible only after incompatible trials, while following NoGos and Errors only a general slowdown in RT was observed affecting mainly compatible trials. Again, these results question a unified control instance equally responsible for different conflict resolution processes and subsequent behavioral adjustments.

My second research question builds upon these pilot studies and focuses on network interactions among different types of cognitive conflict. To standardize the

induced conflicts the flanker paradigm with its stimulus and response conflicts was suited ideally for the time-frequency analyses which will be introduced below.

1.4 “Warm” Perspectives on Control: Conflict Adaptation, Errors, and Dopamine

Besides confronting the brain with different conflicts to answer the yet unresolved question how multiple mechanisms work in parallel to allow conflict resolution and adaptation another approach could be to ask whether these subsystems are influenced differentially by other modulatory influences like emotions or motivation.

Ashby et al. (1999) proposed that positive affect leads to temporary increase in of DA in mid-brain DA-generation centers which is propagated to prefrontal cortex and striatum. They proposed further that increased DA levels enhance the ability to overcome dominant responses and increase cognitive flexibility in various tasks. The evaluative function of MFC subareas has further been investigated within the theoretical framework of reinforcement learning, especially the error-processing system as a learning mechanism: Holroyd and Coles (2002) highlight the close interactions between MFC and Basal Ganglia (BG) via an interlaced mesencephalic dopamine system which enables phasic as well as tonic changes in dopamine (DA) levels (Schultz, 1998; 2007; 2010). Bush et al. (2000) proposed a similar view emphasizing cognitive as well as emotional influences in anterior cingulate cortex. He highlights the role of ACC as part of the limbic system therefore receiving input from several sources and puts forward the idea that the ACC is a part of a circuit involved in a form of attention that serves to regulate both cognitive and emotional processing. Whereas the cognitive division encapsulates dorsal portions of the MFC, the affective division is situated in the more rostral-ventral portions of MFC. He further raises the question, where in this subdivision error processing has to be situated and more importantly, how interactions be-

tween cognitive and emotional processes are realized. (Botvinick, 2007) integrated the conflict monitoring and the reinforcement learning account by claiming that conflicts are perceived as aversive themselves and should therefore lead to similar adaptation as errors or aversive events.

In our laboratory we tested this prediction in a project where NoGo tasks were combined with emotional measurements (Schacht et al., 2009). Against previous hypotheses results indicated that conflicts are not experienced as aversive but inhibition might be appraised as goal-obstructive, which was further substantiated in a follow-up study (Schacht et al., 2010). If the conflicts themselves are not necessarily experienced aversive one could therefore ask, which other factors influence conflict processing and with respect to the assumed overlap of error and conflict processing whether positive or negative affect improve control / error monitoring. A study by van Steenbergen et al. (2009) followed also the idea of aversive perceived conflicts and induced unpredictable gains or losses in a flanker task. This lottery-like procedure affected conflict adaptation such that after monetary rewards the conflict adaptation effect decreased compared to neutral or negative events. In their view the reward neutralized the aversive quality of conflict and led to a down-regulation of control.

Besides conflict processing several researchers have investigated if and how error processing can also be altered by induction of affective moods and motivation. Studies focusing on ERN modulations have come to inconclusive results, either resulting in decreased ERN amplitudes following negative feedback (Ogawa et al., 2011) or increased ERNs (Wiswede et al., 2009a). Furthermore pleasant moods led to either larger ERNs (Larson et al., 2006), but unconscious smiling on the other hand led to smaller ERNs (Wiswede et al., 2009b). As can be seen from these exemplary studies the induction of mood, emotion, or motivation is still not standardized and much more experimental protocols have to be established in order to investigate cognition-emotion interdependencies. Despite the ERN another component, the feedback-related negativity (FRN), has been a valuable tool to

measure the appraisal of the motivational impact of certain outcome events. The FRN is a relatively negative deflection in the ERP and has been widely used in reinforcement-learning tasks (Gehring and Willoughby, 2002; Holroyd et al., 2003) or in the framework of reinforcement learning regarding the reward prediction error (Hajcak et al., 2005).

In my third study, I approached the affective influence on conflict adaptation by combining a Simon task with two feedback regimes that were either unpredictable or performance-dependent. Study 3 will address the issues regarding the effects of induced motivational “contexts” on conflict and error processing as well as adaptations.

2 Approaches to Dynamics in Cognitive Control

Up to now I have presented mainly results from studies using functional imaging or electrophysiological methods that try to assign functional roles to certain brain areas. Besides such findings with a functional localization character, in recent years the call for network descriptions enabling certain cognitive functions has received more and more attention. An important goal here is to use techniques that do not only provide information about an assumed location of a certain process but to integrate this location as a node into a distributed network: To get information about the networks underlying conflict resolution I chose a dynamic approach which will be shortly outlined in this section.

2.1 Additional information from time frequency transformed data

To understand the cognitive architecture of the human mind and also to measure brain activity with an emphasis on high temporal resolution event-related potentials (ERPs) have provided a tremendously exciting amount of empirical data from all cognitive domains. In the area of cognitive control mainly the already mentioned N200 family as well as the ERN and FRN have been used extensively to characterize the interplay of processes and mechanism related to performance monitoring, response evaluation and conflict processing.

In contrast to the averaged ERP time-frequency transformed data offers another perspective on brain function. Makeig et al. (2004) oppose two “views” on brain activity - the ERP and the dynamic view - that focus on different aspects of the EEG data and complement each other. One of the main assumptions when analyzing ERPs is that they are understood in a sequential, bottom up fashion irrespective of the as non-relevant rated background activity. Furthermore, it is assumed that brief, monophasic potentials contribute similarly to the evoked potential and therefore can be seen in the averaged potential only. However, these assumptions have some drawbacks mainly in regard to the notion that background activity can-

not tell anything about the current status of the system and that processes underlying cognitive phenomena are always time-locked to the stimulus or the response. It has been shown for example that alpha activity in the pre-stimulus interval predicts whether or not a visual cue will be perceived or not (Hanslmayr et al., 2007). However, the most significant disadvantage of conventional ERP average technique is that the signal traces from changes in power, which reflect partly phasic synchronous activity of neuronal populations will be deleted. In contrast, time-frequency representations preserve such local synchronous activity.

But, how can we measure such power changes? As proven by Fourier any periodic function (signal) can be described in terms of an infinite sum of sine and cosine functions with (harmonic) frequencies. Therefore spectral analyses have also been used in EEG research. As an extension of (short-term) Fourier transformation, which calculates the frequency and phase content of local sections of a signal as it changes over time, wavelets are continuously shifted (convoluted) along the signal and calculate the spectrum for every single time point. Then this process is repeated many times with a slightly shorter or longer wavelet (daughter wavelets) formed by translation and contraction. In the end the result will be a collection of time-frequency representations of the signal that can be averaged together.

Physiologically, two possible reasons can be responsible for an increase in the amplitude / power of a certain frequency component of the EEG: First, although the amount of neuronal activity stays the same, more precise synchronization can lead to less loss during summation. Second, although the precision of synchronization stays the same more neuronal activity is induced by a larger locally synchronizing population. Therefore, time-frequency analysis of power is mainly sensitive to changes in oscillatory neuronal activity and/ or synchronization at the local level (see Yeung et al. (2004a) for a discussion of the methodological caveats of such analyses).

Since the discovery of the alpha rhythm described by Berger (1929) many researchers have tried to assign specific functional roles to certain somewhat arbitrarily defined bands. For example, hippocampal theta has been assigned to such a range of different cognitive functions across species ranging from arousal, over orienting, memory consolidation, positive emotions and motivation, voluntary movements and many more (see Buzsaki (2005) for an extensive review) that it seems unreasonable to think of certain bands reserved for only one functional process. However, a precise assignment of possible functional roles to oscillatory phenomena remains to be developed.

Although several taxonomies for these phenomena exist, such as evoked versus induced activity, (Pfurtscheller and Lopes da Silva, 1999), event-related synchronization and desynchronization (Klimesch et al., 2007) or event-related spectral perturbations (Makeig et al., 2004) all approaches assume coherent local or distributed neuronal oscillations as generators for the power changes that can be observed in the scalp EEG.

To elucidate cognitive control functions most studies have used the theta band (4-8 Hz) in order to investigate error processing (Luu and Tucker, 2001; Yordanova et al., 2004). However, until now no one has looked at theta power changes in humans during conflict processing or across several conflict paradigms. Given its involvement in performance monitoring functions it should therefore also be sensitive to cognitive demands during correct responses. Study 1 of this dissertation therefore aimed at testing whether theta activity can be used as a general measure of conflict processing.

2.2 Synchrony measures of EEG

Additional to pure power representations of the EEG signal there is more relevant information provided by the phase characteristics of the signal. A very intriguing idea regards the claim that different brain areas responsible for different mental

processes such as perceptual processing, stimulus evaluation and response programming are realized in distributed networks (Basar et al., 2001; Klimesch et al., 2007). Pfurtscheller and Lopes da Silva (1999) describe two main factors that determine the properties of EEG oscillations: First, the intrinsic membrane properties of the neurons and the dynamics of synaptic processes, and second the strength and extent of the interconnections between network elements, most often formed by feedback loops. They argue that different kinds of feedback loops can be distinguished, namely involving thalamo-cortical or cortico-cortical loops either at short or at long distances. As a third factor they mention the modulating influences from general or local neurotransmitter systems. To summarize, local and large scale integration networks seem to operate via specific frequency bands and these transient processes can be characterized by their spatial, temporal and frequency specific properties. Several computational approaches and theoretical accounts (Dehaene et al. (1998) with a global workspace model or Lamme and Roelfsema (2000) in their consciousness definitions) therefore assume that recurrent networks can hold information exactly via these distributed networks of activity.

To embed cognitive control functions within such networks Engel et al. (2001) suggest that several levels of top-down control work in parallel. In their view top-down factors can lead to states of ‘expectancy’ or ‘anticipation’ that can be expressed in the temporal structure of activity patterns before the appearance of stimuli. Additionally, Varela et al. (2001) suggest that information coding in the brain depends on concurrent activation of neurons distributed across different brain areas that are transiently linked by reciprocal dynamic connections. Top-down and bottom-up processes are therefore heuristic terms for a large-scale network that integrates (top-down) endogenous activity from frontal and limbic areas and (bottom-up) incoming sensoric activity. In this view, phase synchronization is the integration mechanism that organizes this large-scale brain network.

To investigate such cognitive control synchronizations the theta band has been used in the area of error processing (Cavanagh et al., 2009; Luu et al., 2004), conflict processing (Cohen and Cavanagh, 2011; Hanslmayr et al., 2008) and also in memory related top-down functions (Sauseng et al., 2010). Theta activity is primarily associated with top-down processes, such as response controlling or (Basar et al., 2001) but seems to act also in broader integration mechanism via cross-frequency coupling (Jensen and Colgin, 2007).

In order to use phase characteristics to describe such mechanisms, one has to calculate some measure of coherence. Coherence is a measure of neuronal synchronization between two signals. It is normalized for the amplitude of the two signals. Thus, amplitude changes of the EEG signals do not affect coherence. The coherence measure avoids the confound between the precision of synchronization and the amount of activity that is unavoidable when neuronal synchronization is indirectly measured as the amplitude of EEG oscillations.

Following these methodological approaches, study 2 investigated specific neuronal networks underlying the resolution of stimulus and response conflict in terms of “inter-channel-phase-synchrony” (ICPS). These networks were previously defined according to neuro-anatomical considerations derived from recent theoretical frameworks.

3 Summary of studies

Based on the state of the art research outlined above, the following studies aimed at shedding light on the question of conflict specificity from different perspectives: Study 1 and 2 concentrate on the basic functional aspects of conflict processing, namely theta activity as a general marker for cognitive conflict (study 1) and theta synchrony as the means of coordinated activity in order to overcome response conflict in a flanker task (study 2). Study 3 then takes a much broader perspective since here differential modulations of conflict and error adaptation processes are investigated to test whether the processes belong to the same system or not.

3.1 Study 1 - Conflict Control: Common Cognitive Mechanisms

Research Question: Study 1 aimed at testing for a common mechanism underlying any conflict resolution processes as assumed in three classical interference paradigms. Therefore we applied a within-subject design to compare performance and neural correlates along a Simon task, a Go-NoGo task and a flanker task. Both the Simon and the flanker task are known to induce behavioral conflicts at the level of response programming. Additionally, we used a Go-NoGo paradigm with 33% NoGos which seem to be sufficient to induce a prepotent response tendency in every trial which has to be withheld in one third of all cases. Although many studies reported bigger N2 amplitudes during such interference tasks (Heil et al., 2000; Kopp et al., 1996) no one ever compared these tasks and the elicited brain activity in a within-subject design. We concentrated on the theta band because some theories, especially the conflict monitoring account by Botvinick et al. (2001) assume a close link between response evaluation and conflict detection processes when not even equate them. Since many studies have shown an involvement of theta in ERN generation the rationale behind the study was that similarly during conflict detection and response execution processes theta should

play an important functional role. As an approximation of the loci of these activities dipole modeling was used to confirm tentative sources of the theta power differences.

Results: Strong evidence for consistent theta enhancement was found in all three paradigms. As visible in the time frequency plots within the theta band a prominent burst was visible in all three paradigms. This burst ranged from 200-400 ms in the Simon and Go-NoGo paradigm, in the flanker time the onset started around the target presentation (note that flankers in this task were presented 150 ms before the target). Comparing the theta activity differences strongest amplitude differences within theta power were visible in the NoGo and the flanker paradigm compared to the Simon task. Dipole modeling suggested pre-SMA and motor areas or errors, false alarms, Simon as well as response conflict in the flanker task.

Discussion: To conclude, we could show that conflicts lead to a consistent theta power enhancement across different interference paradigms, but the possible sources might be distributed differentially. Theta, therefore, might act as in integration mechanism of a broader distributed network which engages stronger the more conflicting information enters the stream of information processing. The more response output related these conflict arise the closer to motor areas these mechanism might engage.

Gain in knowledge: Theta power seems to reflect a unitary mechanism underlying conflict control in all used conflict paradigms situated within MFC. Nevertheless, the present findings do not hint to a local restricted phenomenon but instead suggest a general mechanism possibly acting as a functional integration-loop thereby also influenced by other brain structures.

3.2 Study 2 - Conflict Control: Specific Types of Conflict Resolution

Research Questions: The aim of study 2 was to use theta synchrony measures to test the hypothesized recruiting mechanism between left lateral PFC and MFC (Kerns et al., 2004; MacDonald et al., 2000). Furthermore, since some researchers assume an involvement of right prefrontal cortex in general inhibition processes we also tested this connection (Aron, 2007). Additionally, following ideas that assume a direct involvement in motor control of MFC we checked whether ipsi- and/or contra-lateral motor cortices engage differently during a paradigm which is ideally suited for comparing different types of conflict: In the flanker task two types of conflict are realized namely response conflict (which is occurring whenever two response alternatives are activated at the same time) and perceptual conflict (which occurs whenever the surrounding flankers differ from the target stimulus, but indicate the same response). We used continuous wavelet transformations in order to extract power and phase information of the EEG signal in the theta band (4-8 Hz) and calculated inter-channel-phase-coherence and inter-trial phase coherence according to the MFC connections as pointed out above.

Results: We found that inter-channel-phase-synchrony was enhanced following our predictions: synchrony between medial frontal and lateral prefrontal electrode sites was enhanced only during the more demanding response conflict condition. Similarly, synchrony between medial frontal and motor sites contra-lateral to the respective response hand was enhanced in response conflict situations. In contrast, stimulus conflict did not lead to enhancements of inter-channel-phase-synchrony but nevertheless to an increase in theta power.

Discussion: The present findings speak against the claim that MFC activation is only enhanced during response conflict (van Veen et al., 2001) but supports accounts assuming that MFC itself can exert a response controlling function (Posner and Di Girolamo, 1998). While theta power was enhanced in both conflict situations, prefrontal-medial-lateral couplings were only observed during response

conflict. Furthermore, couplings between MFC and motor sites contra-lateral to the response hand were also observed. MFC coupling with early perceptual areas were rare and more likely due to sensory-motor integration processes during response execution. Follow-up analyses showed that also lateral prefrontal areas were connected to motor execution areas.

Gain in knowledge: By using time-frequency transformed EEG data we could provide evidence for a condition dependent change in brain connectivity as measured via inter-channel-phase-synchrony. Following previous reports of MFC-LPFC coupling from functional magnetic imaging (fMRI) literature our results support the idea of enhanced communication in cognitive demanding situations. Interestingly, theta power and theta synchrony measures dissociated between stimulus and response conflict, suggesting a highly sensitive network with a unitary conflict detection unit (theta power) and a specific network configuration to resolve response conflicts (theta synchrony).

3.3 Study 3 - Conflict Adaptation: Modulatory Influences of Affect

Research question: Study 3 consists of two interconnected experiments that aim to test modulatory influences of motivational contexts on conflict adaptation. The first experiment has a replicatory character regarding the finding by van Steenbergen et al. (2009) that reward and positive affect diminish behavioral conflict adaptation. Following the claim by Botvinick (2007) that every conflict has an aversive quality, aversive events themselves should also induce adjustments in subsequent processing and should therefore also lead to conflict adaptation. However, a positive unexpected event in this view should then counteract conflict adaptation and should therefore lead to a smaller conflict adaptation compared to neutral or negative outcomes. Even brief affective states should modulate cognitive control and especially reward and punishment should due to their close linkage to dopamine levels (Schultz, 2010) alter conflict processing. In a first experiment we combined a Simon task with a lottery algorithm so that participants

could either win or lose a certain amount of money following every trial. As a baseline condition also neutral feedbacks were introduced and finally conflict adaptation effects could be compared due to their preceding feedback. We also used EEG recording to check whether feedback is processed according to our hypotheses. In a second experiment we used performance-dependent feedback in two separate blocks. In one block participants were rewarded for their fastest 25% RTs (reward block) whereas in another block they were punished in their slowest 25% of RTs (punishment block). An adaptive staircase algorithm secured that each participant received in 25% of all trials a gain or loss feedback, during the other 75% they received a neutral “blank” feedback indicating that they neither won nor lost anything. Additionally, we were interested in whether error and conflict processing would be influenced differentially by these contexts and analyzed besides feedback-related components also the ERN and behavioral post-error slowing (PES). If reward would suppress conflict adaptation (CA) it should also suppress error adaptation, assuming that both processes are dependent. If PES would be influenced differently compared to CA this would be another hint to a relative independence of these systems.

Results: We could not replicate the finding by (van Steenbergen et al., 2009) in our Simon task, conflict adaptation was not influenced at all by the motivational state caused by previous feedback although FRN measures confirmed feedback processing according to our hypotheses. In our second experiment performance-contingent feedback influenced conflict adaptation only in the reward block, where conflict adaptation was increased after gain signals compared to blank feedback. No such changes were found in the punishment block. Furthermore, error adaptation was strongly influenced by our motivational context manipulation and ERN as well PES measures were significantly enhanced in the reward block.

Discussion: We found that not conflict adaptation per se but error adaptation is influenced by the motivational contexts set in the used tasks. Behavioral data as well as the ERN measures suggest that mainly error processing and error adapta-

tion were influenced by motivational context. Feedback that was not contingent to performance did not alter conflict adaptation. Present findings show that modulatory influences on conflict and error adaptation dissociate and, therefore, underline the claim of distinguishable adaptation mechanisms probably not sharing common neural substrates.

Gain in knowledge: Surprisingly, the Simon conflict and its adaptation are only marginally influenced by manipulations induced by reward and punishment. The claim that affects generally influence cognitive functions seems therefore overextended at least for our experimental paradigm. It remains an open question why flanker and Simon conflicts differ in this respect. However, robust effects were found in the domain of error processing. A preliminary account could propose that if strategic adjustments following errors are propagated via dopaminergic projections from limbic to neocortical areas, the DA changes induced by reward and punishment feedbacks seem not to stretch out to areas responsible for motor conflict resolution. This can be understood as another hint to the idea that conflict adaptation and error processing are realized via two independent networks that are differentially affected by long- and short-term changes in outcomes.

4 General Discussion

In the framework of this dissertation I aimed at investigating various aspects of cognitive control functions and their neural counterparts as measured by different electrophysiological indices. The presented studies started from two theoretical accounts that have recently progressively been incorporated (Botvinick, 2007).

The first approach is driven by ideas from conflict monitoring theory which is based on the assumption that a conflict-control loop constantly adapts according to changing environmental demands. In theory, this loop consists of a conflict detection device that is situated within (dorsal) medial frontal cortex and interacts with (left) lateral prefrontal cortex. This, in turn can modulate information processing by biasing incoming stimuli according to its utility for goal-directed behavior (Botvinick et al., 2004; Carter et al., 1998). Furthermore, it has been stated that once the MFC has been activated it triggers several other phenomena which can be observed as behavioral adaptations, namely increased control in the upcoming trial and post-error slowing (Debener et al., 2005; Kerns, 2006; 2004; MacDonald et al., 2000).

The second approach is derived from approaches emphasizing “warm” emotional and motivational aspects of cognitive control that are linked to outcome evaluation functions and also situated within of (rostral / ventral) MFC. Due to its proximity to limbic cortex traversed by dopaminergic projections from basal ganglia structures some authors suggested that the lower parts of MFC (in close proximity to orbitofrontal cortex) are involved in calculations of reward prediction errors and cost-benefit decision making (Bush et al., 2000; Holroyd and Coles, 2008; Rushworth et al., 2004).

Similarities in conflict processing via ERPs and time-frequency transformations

Therefore, my research questions are located between the conceptual gap of cognitive and emotional processing and their respective neuronal correlates. The first two studies aim at resolving the question to what extent conflict processing within a trial is accompanied by a unitary mechanism. The functional role of this mechanism might be related to detection processes but also to regulatory activity over motor output structures. In detail, the second study tries to elucidate the embedding of this mechanism within a neural network dynamics that are differentially engaged depending on the domain where conflict has to be resolved. In contrast, the third study had a twofold question of interest and used motivational contexts as an independent variable. First, we were interested whether positive or negative outcomes would improve conflict processing and adaptation. Second, keeping in mind the proposed overlap of conflict and error processing we examined whether these processes were influenced similarly or differentially by motivational incentives.

Study 1 and 2 shed light on the question how general these mechanisms are by comparing conflict resolution processes stemming from different sources. Regarding the question how general MFC involvement in such conflict tasks is present data of study 1 provides clear evidence that N2 measures as well as theta activity seem to be sensitive to all different kinds of conflict. Dipole-modeling suggested a more fine grained subdivision of MFC with theta activity centers in motor preparation areas during conflicts at the response level but also during errors. In contrast, during stimulus conflict the center of activity was shifted towards ventral portions of the MFC.

Specificities in conflict resolution and error processing

Study 2 extends the use of theta power to investigate dynamic changes in network activity during stimulus and response conflict in the flanker task. Surprisingly, we

found robust dissociations of theta power and theta synchrony during both types of conflict. Whereas theta power over medial frontal sites was enhanced in both conflict conditions, an increase in synchrony between MFC and LPFCs was only observed in response conflict situations. Furthermore, comparable activity patterns of synchrony between MFC, LPFCs and motor areas seem to suggest, that these structures form a network that is activated during response conflict. Against previous assumptions, that MFC is exclusively active during response conflict our data show that also a conflict in stimulus encoding leads to theta enhancement.

There are several limitations which should be accounted for in future experiments and analyses: The theta power results in study 1 have to be interpreted carefully for several reasons. On the one hand, since power is a measure of squared theta activity it cannot be disentangled to what proportion “by proxy” ERP components (P2, N2 or P3) in each individual trial might be associated with power changes. To circumvent this interpretation difficulties one has to check also the non-squared activity pattern in order to determine whether positive or negative deflections are responsible for the observed effects. On the other hand, several researchers have pointed out that there exist differences in inter-trial phase coherence (Yordanova et al., 2004) and although we have ruled out that this influences our results in study 2, study 1 did not provide data for this possible confound. Finally, some authors have proposed that there exist individual band borders which have to be aligned to an alpha peak recorded independent of the experimental data (Klimesch, 1999). A further point regards the synchrony effect maps of study 2, which although strictly hypothesized previously regarding its analyzed electrode pairs show somewhat diffuse scalp distributions, broadly distributed over several prefrontal areas. A more advanced analyses scheme could analyze synchrony across all possible electrode pairs and then determine which statistical boundaries could be used to extract meaningful network activity.

Study 3 then takes again a more general perspective on conflict adaptation effects using behavioral effects and ERPs. We established two experimental environments

in which participants either could gain or lose money, performance independent and contingent. Contrary to expectations, conflict adaptation was only marginally influenced by motivational contexts. Neither the short term effects of feedback in the upcoming trial nor the block effects resulted in a coherent pattern of control-motivation interactions. However, we found strong effects in ERN measures as well as behavioral adjustments following errors which corroborate the suggestion that two complementary modes of cognitive control, namely proactive and retroactive are situated within different portions of MFC (Hikosaka and Isoda, 2010; Isoda and Hikosaka, 2011; Ullsperger and King, 2010). Therefore, it can be speculated that re-(tro)-active control, accompanied by alterations of midbrain DA release, is susceptible to changes in DA level caused by reward and punishment and results in direct strategic adjustments of response thresholds. In contrast, proactive control, associated with improvements in performance monitoring is not susceptible to such modulations since the responsible brain areas (pre-SMA) are not directly connected to the midbrain DA system.

Although our experiment did not detect any evidence for modulations of conflict adaptation one has to be careful to jump to conclusion regarding the interplay of emotion and motivation and cognitive processing: As mentioned in the introduction mood inductions can be performed via many different stimuli ranging from pictures, videos, music, face expressions, verbal admonishments and monetary gains and losses, related to performance or not. It remains unclear, which feedback form works on which emotional system or neural pathway. To pose the question from the neuronal perspective we know that reward and punishment are unlikely to be processed via the same pathways (Berridge and Robinson, 2003; Haber and Knutson, 2010) and also are influenced by other factors like arousal or endocrinal factors. Hence, a precise hypothesis of the effect of certain external feedback stimuli should be able to predict a) where in the neural system a change in DA levels should lead to b) which processing benefits or difficulties over c) which time-course.

A final interesting unreported finding from study one relates to the correlations of PES and conflict adaptation across paradigms. While conflict adaptation measures as well as interference effects seem to be uncorrelated across paradigms, there is a strong correlation regarding the PES effects. On the one hand, this again speaks for a dissociation of conflict and error adjustments as mentioned before. On the other hand the reliability of PES (Danielmeier and Ullsperger, 2011) has also been related to structural differences in white matter tracts (Segalowitz et al., 2010) which might be relatively stable over time. An interesting question would be to compare post conflict slowing with PES in order to find out whether the assumed neuroanatomical basis, consisting of pre-supplementary motor area (pre-SMA), lateral inferior frontal cortex (IFC) and right nucleus subthalamicus (STN) (Aron, 2007) is involved in both slowing processes.

Theta networks in the service of cognitive control

MFC theta activity was increased during stimulus and response conflict. We found specific theta inter-channel-phase-synchrony patterns along relevant brain areas, supporting the idea that IPFC-MFC-communication is enhanced during response conflicts. However, MFC-motor-couplings can be interpreted as involvement of MFC in response controlling processes. According to Luu et al. (2003) theta appears to index the adaptive adjustments required for the ongoing regulation of action and also be incorporated in the Papez circuit. In our analyses theta power was obviously concentrated over medial frontal cortex in all paradigms and seemed to be a major rhythm in frontal areas during performance monitoring and action selection. I speculate that theta activity although possibly generated in hippocampal areas, forms a coordinating activity net / loop that reacts whenever certain changes in the level of entropy in information processing is reached. It is highly predestinated to incorporate signals from other brain areas which might be coded in faster oscillations and could also pre-activate motor responses. In a global workspace model theta nodes could be the frame-frequency for integrating information from different areas.

Control is enabled via several such recurrent networks. From a dynamic brain perspective it is likely that neuronal activity codes via different frequency bands information with fast oscillations predominantly in sensory cortices (gamma) and slower oscillations in slower band like alpha or theta. The described Papez circuit seems to be the candidate because it is known that theta is generated in the mammillary bodies / septum in rats. Furthermore it is perfectly suited for the online-monitoring of behavioral outputs as well as environmental events and feedback. Functionally, the different portions of the MFC are responsible for detecting any deviation ranging from rare unexpected stimulus input, motor activations, as well as deviations from predicted external outcome and errors.

Towards a building block model of cognitive control and adaptations

Although using a broad approach to investigate control functions can have disadvantages regarding the interpretation of results within qualitatively different theoretical perspectives, considering both cognitive and motivational aspects can help understanding the assumed processes and mechanisms.

Considering the evidence from the different data sets of this experimental series we can conclude that the assumed parcellation of MFC into regions responsible for either more evaluative functions or more conflict resolution processes fits surprisingly well our results. Although we used motivational contexts only as a modulatory manipulation our results support the idea that error processing and conflict resolution seem to be realized via mainly independent neuronal systems. Whereas motivational context affects ERN and PES measures, conflict adaptation is largely unaffected. Furthermore, the theta activity observed during errors was located very close to pre-motor areas instead of the usually reported locations from fMRI studies. Considering the inconsistency of measures from BOLD activity, ERPs and band specific power changes much more research is needed to account for such differences.

However, in order to link results of the first two studies with the last study much more research is needed: When talking about building blocks of cognitive control we have to keep in mind that possibly several mechanisms lead to observable adjustments: Candidate mechanism for such constituents involve (1) a basic response threshold modulation (possibly realized via sub-cortical dependent DA pathways resulting in changes in tonic motor excitability), (2) specific conflict adaptation mechanisms (stemming from domain specific top-down biasing mechanisms) and (3) low level influences (elicited by arousal, orienting, emotional valence and motivational manipulations).

Conclusion

The goal of this dissertation was to advance knowledge about different cognitive control functions and their relations within the cognitive domain as well with motivational modules. Both systems seem inseparable from each other in terms of cognitive processing as well as neural realization to enable any goal-directed behavior. The main question of my thesis, namely how conflict-specific cognitive control works can naturally not be answered with a yes or no: While we find several hints for a general involvement of MFC activity in all applied conflict paradigms the much more interesting questions arise when taking into account the manifold dissociations either in neural activity related to different conflicts or the dissociable impacts of motivational factors on conflict and error processing. To deconstruct the homunculus in cognitive control a much more fine-grained approach to the in parallel working systems, their main “hubs” and the involved neurotransmitter system is needed. New analyses techniques such as time-frequency and coherence analyses open a wide landscape of fascinating future studies that might help to explain the complex strategies we use to adapt to our environment.

5 Future Directions

In my dissertation I focused mainly on theta power and synchrony measures. A challenge for future studies will regard the relation of certain “frequency-band–location combinations” to event-related potentials and fMRI signals. To follow their different time-courses combined measurements would help to understand their interactions. For example, a systematic search for other markers that can be related to certain functions, such as beta- and μ -oscillations over motor areas (Pfurtscheller et al., 2006), alpha power over posterior areas (Romei et al., 2008) or theta and gamma power over prefrontal and parietal areas (Sederberg et al., 2003) could help to investigate the dynamic brain activity during preparatory, executive and evaluative processes in various tasks.

Related to further identification of cognitive control networks there can be thought of several approaches: First, confronting subjects with other control related demands such as working memory or task switching could help to elucidate the role of theta power, which in the area of memory related control has been investigated intensively already (Sauseng et al., 2010). Second, since we only can measure roughly what happens under the surface of the scalp, more advanced analyses techniques should be helpful to investigate intrinsic properties of brain organization. These include cross frequency couplings, such as theta-gamma couplings and especially phase-phase and phase-power relations during information processing (Cohen, 2011; Jensen and Colgin, 2007).

Additionally, the emotional side of the control coin raises also the question, how emotions and affects themselves can be controlled. Here the mechanisms of self regulation, emotion regulation (Ochsner and Gross, 2005) and their relation to known inhibitory mechanisms can possibly help to unite emotional theories with cognitive control ideas.

Furthermore, a pending task in my project has been the use of transcranial-magnetic stimulation (TMS). Once certain spectral markers have been identified, one could use disturbing as well as supporting TMS-protocols either to change motor thresholds or to disturb other regulatory control centers. Candidate areas would be lateral prefrontal cortices as well as sensory-motor integration areas in posterior parietal cortices.

To summarize, the mentioned in parallel working systems can possibly be described as connected networks that are can be measured via different means (phase coherence, transmitter interactions, white matter connectivity, genetic and individual variability, and many others). The insight in these system interactions can provide a more fine-grained understanding of cognitive control functions.

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6 Submitted Manuscripts

Study 1:

Nigbur R, Ivanova G, Stürmer B. (in press). Theta power as a marker for cognitive interference. *Clinical Neurophysiology* 122 (2011), pp. 2185-2194 doi: information: 10.1016/j.clinph.2011.03.030

Study 2:

Nigbur R, Cohen MX, Ridderinkhof KR, Stürmer B. (in press). Theta Dynamics Reveal Domain-specific Control over Stimulus and Response Conflict. *J Cogn Neurosci*. 2011 Aug 23. doi:10.1162/jocn_a_00128

Study 3:

Stürmer B, Nigbur R, Schacht A and Sommer W (2011) Reward and punishment effects on error processing and conflict control. *Front. Psychology* 2:335. doi: 10.3389/fpsyg.2011.00335

7 Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt,

- dass ich die vorliegende Arbeit selbstständig und ohne unerlaubte Hilfe verfasst habe,
- dass ich die Dissertation an keiner anderen Universität eingereicht habe und keinen Doktorgrad in dem Promotionsfach Psychologie besitze und,
- dass mir die Promotionsordnung der Mathematisch-Naturwissenschaftlichen Fakultät II vom 17.01.2005, zuletzt geändert am 13.02.2006, veröffentlicht im Amtlichen Mitteilungsblatt Nr. 34/2006 bekannt ist.

Berlin, den 24.09.2011

Roland Nigbur