Braced for Action Control:
Behavioral, EEG, and FMRI Evidence

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Abstract

Abstract

The present dissertation contains three studies that investigated the cognitive and neuronal basis underlying action control regulation prompted by prior conflicts, cues predicting conflict, as well as the state of arousal. These studies were based on inference paradigms involving trials that either induced response conflict (incompatible trials) or did not (compatible trials). Study 1 examined whether behavioral adjustments due to the trial sequence are equivalent to expectancy-based adjustments triggered by cues predicting compatibility. Behavioral and electroencephalographic (EEG) measures showed dissociation of these processes. The contingent negative variation (CNV), a pre-target EEG component indexing task anticipation, further indicated that sequence-related control adjustments already act in the intertrial interval. Study 2 focused on processes and neural substrates underlying cue-based anticipatory control. Cues predicting compatibility effectively benefitted behavioral performance, enhanced the pre-target CNV, and reduced post-target conflict-related processing, as indicated by the N2 component. In contrast to the control condition, indicators of response conflict were absent, a result pointing to conflict preemption strategies (a priori avoidance of conflict via transformation of condition-action rules). Functional neuroimaging fostered this conclusion by showing the involvement of neuronal networks associated with rule elaboration and maintenance rather than with conflict monitoring or resolution. Study 3 investigated the interrelation of action control and the state of arousal. Tone-induced arousal improved performance in both incompatible and compatible trials, whereas the latter ones were relatively more accelerated. N1 and N2 in EEG indicated that these effects are due to enhanced early perceptual discrimination and attentional allocation.

Zusammenfassung

Die vorliegende Dissertation beinhaltet drei Studien, welche die kognitiven und neuronalen Grundlagen der Kontrollregulation – ausgelöst durch vorherige Konflikte, konfliktankündigende Hinweise sowie Arousal – untersuchen. Jede Studie basierte auf Interferenzaufgaben mit Durchgängen, die Reaktionskonflikt auslösten (inkompatibel) oder nicht (kompatibel). Studie 1 untersuchte, ob Abfolge abhängigen Verhaltensanpassungen äquivalent sind mit erwartungsbasierten Kontrollprozessen, die durch Hinweise auf die Kompatibilität der nächsten Aufgabe ausgelöst werden. Behaviorale und elektroenzephalographische (EEG) Maße belegten, dass diese Prozesse dissoziieren. Die kontingente negative Variation (CNV), eine EEG Komponente, die Aufgabenantizipation indiziert, zeigte, dass von der Abfolge anhängige Kontrollanpassungen bereits zwischen den Durchgängen agieren. Studie 2 fokussierte auf Prozesse und neuronale Substrate der Kontrollantizipation durch Hinweise. Kompatibilitätshinweise begünstigten effektiv die Leistung, vergrößerten die CNV vor dem nächsten Durchgang und reduzierten konfliktbezogene Konfliktverarbeitung, wie sie durch die N2 Komponente indiziert wird. Im Gegensatz zur Kontrollbedingung gab es keine Anzeichen von Reaktionskonflikt, was auf präemptive Strategien hinweist (d.h. a priori Konfliktverhinderung durch Umschreibung von Bedingungs-Handlungs-Regeln). Funktionelle Bildgebung bestätigte dies, da sie Beteiligung neuronaler Netzwerke zeigte, die eher mit Regelelaboration und –aufrechterhaltung einhergehen als mit Konfliktüberwachung und –lösung. Studie 3 untersuchte das Verhältnis von Handlungskontrolle und Arousalniveau. Toninduziertes Arousal verbesserte Leistung in inkompatiblen und kompatiblen Durchgängen, wobei letztere stärker begünstigt wurden. N1 und N2 im EEG wiesen darauf hin, dass die Effekte auf bessere frühe perzeptuelle Diskriminierung und Aufmerksamkeitszuteilung zurückgehen.

1 Subject Definition and Research Objectives

"… free will is control of behavior by thought."

Donald O. Hebb

Imagine you have recently moved from Germany to America and bought a car. Distances are generally greater in America than in Germany, so you frequently have to drive your car on freeways. You may not think this is a problem because the traffic rules of both countries appear to be very similar. That is why you will be shocked when you try to take the next exit (because your GPS suddenly directs you) and do not see the black SUV that passes you on the right lane with incredible speed. You better brace yourself for such situations, since the SUV driver is completely justified in the United States, even if he would lose his driver license in Germany for such an undertaking. However, situations like these do not happen out of the blue in real life because you are usually prepared for the unexpected moves of other traffic participants when you are in a foreign county. In fact, you may have already experienced such difficulties. Thus, you might be generally more cautious. A friend who already lives in America may have even warned you in advance about the differences in traffic rules. Therefore, you will try to retrieve and utilize information you remember from this phone call before you hit the road. In short, our responsiveness to action affordances is subject to fluctuations depending on a variety of influencing factors of internal and external origin.

The term *cognitive control* generally refers to the ability to coordinate and guide cognitive subprocesses and their temporal structure in keeping with internal goals and/or external demands. However, it is important to recognize that this is a rather descriptive definition of cognitive control. Cognitive control is, in fact, exerted by a set of processes that are "easy to identify but hard to define" (Morton et al., 2011). One's ability to flexibly adapt to given subtle changes in context is critical for learning, coping, and everyday psychological functioning and can be easily observed. The definition, however, is a rather intricate affair because it is still an unresolved issue whether cognitive control is reducible to dedicated systems or neural circuits. A more conservative conception would be to conceive cognitive control functions as emergent functions that originate in a configuration of existing subordinate basic processes such as working memory, response inhibition, or response selection (Grindband et al., 2011).

The present work focuses on action control, which is a subset of cognitive control processes that are in demand when conflict arises; immediate response urge has to be coordinated with concurrent intentional or instructional response tendencies. However, most studies in this topic focus on instant mechanisms of action control like the online detection and resolution of response conflict. The former example, however, illustrates that most situations involving control in everyday life do not usually occur completely unexpectedly. The same applies for experimental settings in the neuroscience laboratory: Even if researchers intend to investigate ad-hoc action control, the participants will develop their own interpretation of task instructions and anticipate what will happen next on the basis of accumulating task knowledge. They will further learn from prior difficulties and adjust their performance. Richard Ridderinkhof et al. (2010) recently suggested a taxonomy of control processes. They distinguished *online action control* from its *anticipatory action regulation*, and further proposed that anticipation can be described by means of two orthogonal dimensions. It may be *prospective* if it is based on intentional preparation (i.e. after cues) or *reactive* if it is prompted by prior behavior or events (i.e. errors). Whether prospective or reactive, anticipatory action regulation may further be accomplished through *preemptive* adjustments (avoiding conflict; e.g. via selective attention towards task-relevant features) or *proactive* adjustments (anticipating conflict; e.g. preparing for inhibition). However, the conceptual assignment of processes to such categories remains somewhat arbitrary; not much is known about the neuro-cognitive processes and the interrelations that underlie such different types of anticipatory adjustments.

The present dissertation aims to investigate the underlying cognitive mechanisms and neuronal underpinnings of top-down and bottom-up influences on online action control. Using a neuro-cognitive approach I will show how sequence-related reactive regulation, cue-induced prospective regulation, and task-irrelevant lower-level stimuli impinge on online action control. In order to contribute to the conceptualizations of these processes, this paper will further investigate interrelations between these processes and evaluate the results from the perspectives of different theoretical frameworks. In the course of the theoretical and empirical outline, I will elaborate the three main research objectives of the present dissertation. The first research objective addresses the question of whether the processes underlying control adjustments induced by the prior experience of conflict differ from those induced by cues that predict conflict. The background of this question is that the origin of such reactive adjustments after conflicts is a much debated topic, with suggestions ranging from episodic memory to strategic control. Study 1 therefore compares these adjustments with clearly strategic cue-induced processes, taking account of electrophysiological markers of anticipation that occur prior to target-onset. The second objective in this dissertation is to gain a deeper understanding of the neuro-cognitive processes underlying prospective action regulation induced by cues predicting conflict. The particular interest here is whether such anticipation cancels out conflict by filtering out task-irrelevant stimulus features such that these fail to elicit strong conflict, or rather modulates basic processes like overall response readiness while leaving conflict unaltered. Study 2 addresses this question by investigating pre- and post-target processes in behavioral, electrophysiological and hemodynamic measures. The third research objective will focus on the influence of task-irrelevant tone stimulation on online action control as well as reactive adjustments after conflict. Study 3 investigates modulations induced by such bottom-up stimulation in behavioral and electrophysiological terms and addresses the question of which subprocesses it alters in the stream of information processing.

The theoretical and empirical outline (Chapter 2) will review relevant cognitive accounts and neuroscientific findings in order to develop the research questions. The next section (Chapter 3) will provide an overview of the studies that have been conducted in order to shed light on these questions. Chapter 4 constitutes an overall discussion of all studies. I will then discuss possible future research questions for the investigation of anticipatory regulation of action control in Chapter 5.

2 Theoretical and Empirical Outline

This chapter will first outline how online action control has been conceptualized and what is known about its neural implementation in the human brain. It will then introduce three different influencing factors that dynamically regulate online action control and discuss them from the viewpoints of different theoretical perspectives. First, it will introduce findings about how prior experience of action control impinges on subsequent control behavior. Second, it will outline what is known about the anticipatory regulation of action control. Finally, it will focus on how the state of arousal impacts action control. A resulting research question will be determined at the end of each of these three sections.

2.1 Online Action Control

Theoretical approaches. Online action control is needed whenever incorrect, inappropriate, or undesirable actions have to be suppressed and overcome in favor of intention-driven action selection. Different experimental paradigms elicit action control, such as the Stroop, the Eriksen flanker (Eriksen & Eriksen, 1974) or the Simon task (Simon, 1967). The common denominator of these tasks is that certain stimulus features prime an incorrect response because they overlap with task-relevant stimulus or response features. For instance, in a Simon task, a non-spatial stimulus feature (e.g. the stimulus figure) determines the response (e.g. right or left hand). Response conflict occurs when the spatial location of the response is incompatible with the task-irrelevant stimulus position. The underlying response-driving dynamics are often described in dual-route models (Kornblum et al., 1990). In these models, the identification of the stimulus activates a response via an indirect intention-driven route, and at the same time captivates activation of other correct or incorrect responses via a more direct processing route. The output of both routes converges at the level of response activation. This causes conflict if the activated responses are at odds (incompatible trial) and one of the activated motor programs has to be aborted in favor of the correct alternative. In case the output matches (compatible trial) response is facilitated, resulting in faster and more accurate responses. Incompatible trials are usually presented intermixed with compatible trials, and the difference in performance is regarded as a behavioral measure of response conflict.

Action selection is relatively more vulnerable to potent and possibly task-irrelevant action affordances during the early stages of processing. Analyses of behavioral accuracy as a function of response speed (conditional accuracy functions, CAF) show that fast responses tend to be more error-prone, especially in incompatible conditions (response capture, Ridderinkhof et al., 2010 for a review). Within the fastest portion of response times (RTs), accuracy usually starts low but improves quickly. Consequently, the slope between the first two bins in a CAF can be conceived as the amount of response capture (Ridderinkhof et al., 2010).

The suppression of unwanted response activation is indeed a core component of action control. However, it is inadequate to equal action control with response inhibition because successful performance requires additional processes, for example, task-set maintenance, attentional allocation, and goal-directed response selection. Furthermore, in some situations, it might be preferable to follow extraneous stimulus-driven associations rather than deliberate intention-driven action selection (for example, a child suddenly running out onto the street). In everyday life, one's cognitive system has to constantly re-evaluate the configuration of priorities on the basis of incoming information and changing internal goals and states. The broad scope of involved basic functions poses the (not yet conclusively answered) question of whether specific neural circuits accomplish action control in conflict situations.

Neural substrates. The conflict monitoring theory was the first prominent account that postulated such a dedicated neural circuit for conflict control (Botvinick et al., 2001; 2004). This account claims that the anterior cingulate cortex (ACC), a ventral brain region within the medial prefrontal cortex (mPFC), signals the occurrence of response competition, undetermined response selection, and the commission of errors. According to the authors, ACC activation modulates general responsiveness of the lateral prefrontal cortex (latPFC) through a performance monitoring mechanism that continuously indexes the need for top-down control. The latPFC is known to be involved in the maintenance of stimulus-action associations and to guide goal-directed action selection (Baddeley, 1998; Roberts et al., 1998; Smith & Jonides, 1999; Miller & Cohen, 2001). LatPFC biases the processing of posterior brain systems that store domain-specific knowledge (for example, action knowledge) in favor of intention or instruction-driven behavior (Bunge, 2004). The conflict monitoring account originates in a computational model of the loop between conflict detection (ACC) and conflict resolution (latPFC). Meanwhile, numerous functional imaging studies have verified mPFC activation in the presence of response conflict (Ridderinkhof et al., 2004, for a review). However, it is still contentious which of the many subareas of the mPFC are involved because the exact locus of activation varies from study to study (Krieghoff et al., 2011, for a review). Proponents of the conflict monitoring account still emphasize the importance of the ACC, although this ventral region is quite difficult to precisely localize due to high intersubject variability and its unusual shape and size (Vogt et al., 1995; Paus et al., 1996). In recent years, many authors have suggested that more dorsal parts of the mPFC, particularly the presupplementary motor area (pre-SMA), might be the critical region for action control. Neurochemical, neurophysiological and neuroimaging studies indicate that the pre-SMA is not a typical premotor area, but rather a prefrontal area involved in cognitive functions (for a review, see Krieghoff et al., 2011). Pre-SMA activation seems to be especially involved in endogenous initiation and intention (Lau et al., 2004; Kennerley et al., 2004; Sumner et al., 2007), or when stimulus-response (S-R) associations have to be re-learned or reversed (Nakamura et al., 1998), and when response competition is present (Milham et al., 2001; Derrfuss et al., 2004; Kennerley et al., 2004; Nachev et al., 2005; Taylor et al., 2007). In sum, it remains an open question whether mPFC activation is best characterized as conflict monitoring/detection or whether it is activated whenever responses have to be prepared or selected in the context of more complex stimulus-action associations (Rushworth et al., 2008).

In recent years, an event-related potential (ERP) in the electroencephalogram (EEG) has often been discussed in the context of action control and mPFC activation: The N2 is a negative wave that usually peaks between 200 and 350 ms after onset of the imperative stimulus. The amplitude of the anterior N2 is magnified by processes involving cognitive control (Kopp et al., 1996; Heil et al., 2000; Van Veen et al., 2002; Nieuwenhuis et al., 2003; Falkenstein, 2006). A second, different N2 family is rather attention–related and usually occurs (at least in the visual modality) more posterior (Folstein & van Petten, 2008). This N2 is reduced by the allocation of attention (Suwazono et al., 2000).

The effect of the misleading response priming can be measured as the initial incorrect hand activation in incompatible trials. This information can be assessed by means of the lateralized readiness potential (LRP), an electrophysiological correlate of motor preparation. The onset of the stimulus-locked LRP (S-LRP) indexes the duration of premotor processing stages (Leuthold et al., 1996; Masaki et al., 2004), whereas the onset of the response-locked LRP (LRP-R) indicates late motor-related processing (Hackley & Valle-Inclán, 1998). The calculation of the LRP holds for a certain side of the body, so that an activation of the incorrect response hand is reflected by an initial positive- instead of negative-going deflection.

2.2 Sequence-Related Reactive Regulation of Action Control

Theoretical approaches. Gratton et al. (1992) were the first to report that response conflict modulated subsequent action control performance in a flanker task (Eriksen & Eriksen, 1974). In this task, an imperative stimulus is flanked by task-irrelevant stimuli from the target stimulus set. Trials are incompatible if target and flankers indicate different responses and they are compatible if target and flankers match. Gratton et al. (1992) analyzed the effects of the trial sequence and found a reduced compatibility effect (difference between RTs for compatible and incompatible trials) after incompatible trials. To be precise, responses to incompatible events were faster after incompatible than compatible trials, whereas responses to compatible trials were faster after compatible than incompatible trials. Stoffels (1996) reported the same effect in a stimulus response compatibility (SRC) task, where stimulus and response locations are either spatially congruously mapped onto each other (compatible) or reversed (incompatible). Both Gratton et al. (1992) and Stoffels (1996) conducted additional experiments with cues that predicted compatibility and observed behavioral benefits derived from such cues. For example, compatible trials were accelerated by cue predicting compatible assignments. Based on the observation that both a preceding trial and cueing improved performance, they concluded that sequence- and cue-related effects are driven by equivalent control processes. Specifically, the authors proposed that sequence-related effects are an expression of a prospective process, namely, the strategic preparation for an expected stimulus. According to this view, participants harbor the *expectation* that the compatibility of the upcoming event will match with the preceding event.

Today, the origination of such sequence-dependent effects is a very controversial topic. Nonetheless, numerous publications have replicated these effects in other conflict paradigms such as the Stroop (Kerns et al., 2005) and the Simon task (Ridderinkhof, 2002; Stürmer et al., 2002; Stürmer & Leuthold, 2003). The conflict monitoring account postulates that conflict in a prior trial leads to amplified conflict monitoring. This in turn increases the focus on task-relevant demands, resulting in better performance in the subsequent trial. Hence, this account highlights the *adaptation to conflict* and explains sequence-dependent effects with strategic top-down control regulation. Other researchers, however, have questioned the contribution of action control to sequential effects. They highlight that repetitions of compatibility conditions are confounded with repetitions of S-R features, and that mnemonic influence may account for the effect (Mayr et al., 2003; Hommel et al., 2004). While some studies report that sequence-dependent effects disappeared when repetitions were excluded (Niewenhuis et al., 2006; Wendt et al., 2006; Fernandez-Duque & Knight, 2008), others have found such effects, even in the absence of repetition priming (Kerns et al.,2004; Ullsperger et al., 2005; Akçay & Hazeltine, 2007; Freitas et al., 2007; Notebaert & Verguts, 2007). Ultimately, several studies provide evidence for the contribution of both strategic top-down and mnemonic bottom-up influence (Wühr, 2005; Wühr & Ansorge, 2005; Notebaert et al., 2006; Akcay & Hazeltine, 2007; Egner, 2007; Notebaert & Verguts, 2007; Bugg, 2008; Verguts & Notebaert, 2008; Chen and Melara, 2009; Davelaar and Stevens, 2009).

Utilizing cue information for subsequent behavioral optimization can clearly be regarded as a top-down executive process. Nevertheless, it remains an open question whether the control processes contributing to the sequence-related regulation of action control are equivalent. According to Ridderinkhof et al. (2010), cue-induced control can be labeled as prospective anticipatory regulation, whereas sequence-dependent adjustments can be regarded as the reactive anticipatory regulation of action control. However, to date, only one study has investigated whether these processes can be traced back to the same underlying control mechanisms. In a behavioral study, Fernandez-Duque and Knight (2008) found that cue-induced control generalized across different tasks, whereas sequence-related effects were task-specific.

Neural substrates. The neuroimaging studies of Kerns (2004, 2006) corroborated the conflict monitoring theory by presenting data that showed a linkage between mPFC/ACC activation in the previous trial, on the one hand, and subsequent behavioral adjustment and prefrontal cortex activation on the other. However, there is also evidence supporting the idea that sequence-dependent adjustments may be exerted by the prefrontal cortex and not by the mPFC (for a review, see Mansouri et al., 2009).

The temporal resolution of electrophysiological techniques makes them particularly suitable for the investigation of such transient trial-to-trial fluctuations. A study of Stürmer et al. (2002) showed an initial activation of the incorrect response hand in incompatible trials that followed compatible trials and no such effect subsequent to incompatible events. These findings were interpreted as a result of the anticipatory suppression of direct route processes. Among different ERPs, the contingent negative variation (CNV) is an especially predestinated candidate for shedding light on (prospective and reactive) anticipatory regulation processes before target onset. This slow negative component can be observed during the expectancy of an upcoming event after a warning signal or cue (Walter et al., 1994). The terminal phase of the CNV prior to target onset is assumed to reflect general preparation with sensory, motor and cognitive shares, depending on the particular task (Chwilla & Brunia, 1991; van Boxtel & Brunia, 1994; Lütke et al., 2009). In earlier years, the CNV was primarily associated with motor-related response preparation (see Leuthold et al., 2004, for an overview). However, early studies already showed its susceptibility for the overall informative value of a cue (Damen & Brunia, 1994). In a more recent study, Fan et al. (2007) showed that the CNV indicated general response readiness. The susceptibility of the CNV for sequence-induced reactive anticipatory regulation has not yet been examined.

The first research question aimed at elucidating whether the explicit cueing of compatibility, on the one hand, and the compatibility sequence, on the other, leads to equivalent expectancy-based strategic control regulation.

2.3 Cue-Induced Prospective Regulation of Action Control

Theoretical approaches. Online action control cannot only be biased by prior experiences. In everyday life, people usually try to avoid the costs of situations that are cognitively demanding by prospectively preparing for them. Any relevant information available in advance biases the processing of incoming stimuli in favor of goal-directed behavioral outcomes. Anticipatory regulation induced by cues has been shown to optimize performance in conflict paradigms (Fassbender et al., 2006; Luks et al., 2007; Sohn et al., 2007; Aarts et al., 2008; Donohue et al., 2008; Alpay et al., 2009). It is obvious to question whether specific systems prepare for action control. Following the conflict monitoring theory, some researchers have suggested that cues predicting conflict might activate conflict monitoring in an anticipatory manner (Sohn et al., 2007; Aarts et al., 2008, Hakun & Ravizza, 2012). They claim that the anticipatory activation of conflict monitoring reduces the need for conflict detection during subsequent task implementation.

Other studies point to the contribution of a variety of cognitive functions that are not necessarily linked to conflict control. For example, the active maintenance of information for the purpose of controlling further information processing has been traditionally discussed within the concept of working memory, a limited capacity system that temporarily stores information. In addition, information may not only be retrieved and held online, but may also be manipulated in light of incoming information in such a way that it is more effective for goal-directed behavior. One such strategy may be to prepare to increase the focus of selective attention on task-relevant stimuli or to filter out task-irrelevant stimuli such that cognitive conflict can be better managed, reduced, or even prevented.

Neural substrates. Only a few studies have investigated the processes underlying anticipation of conflict. However, Sohn et al. (2007) and Aarts et al. (2008) reported that activation of the ACC was enhanced by cues that informed about upcoming control demands. They also revealed that this activation was subsequently reduced after target onset. Sohn et al. (2007) additionally found higher ACC activation after cues that predicted high conflict rather than low conflict, while Aarts et al. (2008) could not find such a conflict-specific anticipation. In contrast, other studies did not find any preparatory ACC activation, but rather report anticipatory activation of the left latPFC and left inferior parietal lobe (IPL) during preparation for a Stroop (MacDonald et al., 2000; Donohue et al., 2008) or for a flanker task (Fassbender et al., 2006; Luks et al., 2007). The question of whether specific systems prepare for action control is linked to the question of whether there are dedicated systems for action control itself.

The CNV is an ideal candidate for examining cue-induced anticipatory regulation with electrophysiological measures. The relation of the CNV to successful task preparation has been demonstrated by studies showing enhancement of the CNV under more effortful task anticipation (Falkenstein et al., 2003), and lower individual error rates (Hohnsbein et al., 1998). However, few CNV studies have investigated the influence of higher-level processes like the anticipation of looming conflict. It has been shown that cues predicting trials with a response requirement enhanced the CNV as opposed to cues predicting a trial with no response requirement (Smith et al., 2006; Lütke et al., 2009; Hämmerer et al., 2010). Fan et al. (2007) further reported that an unspecific "ready" cue magnified the CNV amplitude compared to a "relax" cue in a flanker-like task. Another interesting question is how the anticipatory regulation of action control impacts subsequent task implementation. One study reported that cues predicting control demand reduced the N2 latency (Correa et al., 2009).

The second research question addressed the cognitive processes underlying cue-induced preparation in a Simon task. The aim was to identify the neural networks that contribute to the anticipation of cognitive conflict. Beyond medial prefrontal contribution, this work will identify the contribution of lateral prefrontal areas for reasons outlined in the next section.

2.3.1 The Neural Networks of Rule Use

Effective task preparation requires the retrieval and maintenance of previously learned task rules. Such processes are embedded within a broad neural network that serves various aspects of rule use, ranging from acquisition and long-term storage to implementation (Bunge & Wallis, 2008). Here, I will briefly outline the neural networks that underlie rule use for the purpose of an overview beyond mPFC activation. Research on the neural underpinnings of rule representation has primarily focused on latPFC, a region that can be subdivided into the ventrolateral prefrontal cortex (vlPFC, Brodmann areas [BA] 44, 45, 47) and the dorsolateral prefrontal cortex (dlPFC; BA 9, 46). The type of rule seems to be a critical factor in determining which subregions within the PFC are involved (White & Wise, 1999; Asaad et al., 2000; Hoshi et al., 2000; Wallis et al., 2001). Neuroimaging studies show that learned associations can be retrieved by the anterior vlPFC (BA 47; Poldrack et al., 1999; Wagner et al., 2001). DlPFC activation is particularly associated with response selection based on more complex or inhibitory task rules (MacDonald et al., 2000; Hester et al., 2004, Bunge & Souza, 2008). Corroborating a recent hypothesis regarding a possible posterior-to-anterior control hierarchy within the prefrontal cortex, some studies show rostral prefrontal cortex (rPFC, BA 10) activation whenever rules have to be elaborated on a superordinated level, such as changing between instructions (Sakai & Passingham, 2003, 2006; for a review, see Badre, 2008).

However, latPFC is not likely to be the long-term repository of rule memory, since neuropsychological studies report difficulties in flexible rule implementation, while knowledge about the rules often remains sound after its damage (Shallice & Burgess, 1991; Cohen & Servan-Schreiber, 1992; Miller & Cohen, 2001; Braver & Barch, 2002). The posterior middle temporal gyrus (postMTG, BA 21) has been shown to act as a long-term storage for action-related semantic knowledge (such as tool use), while the inferior parietal cortex (IPL, BA 40) is associated with action knowledge and motor attention (Goodale & Milner, 1992; Snyder et al., 2000, Anderson, & Buneo, 2002; Johnson & Grafton, 2003; Kellenbach et al., 2003; Rushworth et al., 2003; Johnson-Frey, 2004). In her review, Bunge (2004) presents the schematic of a hypothetical framework of rule use that graphically summarizes the aforementioned processes (Figure 1).

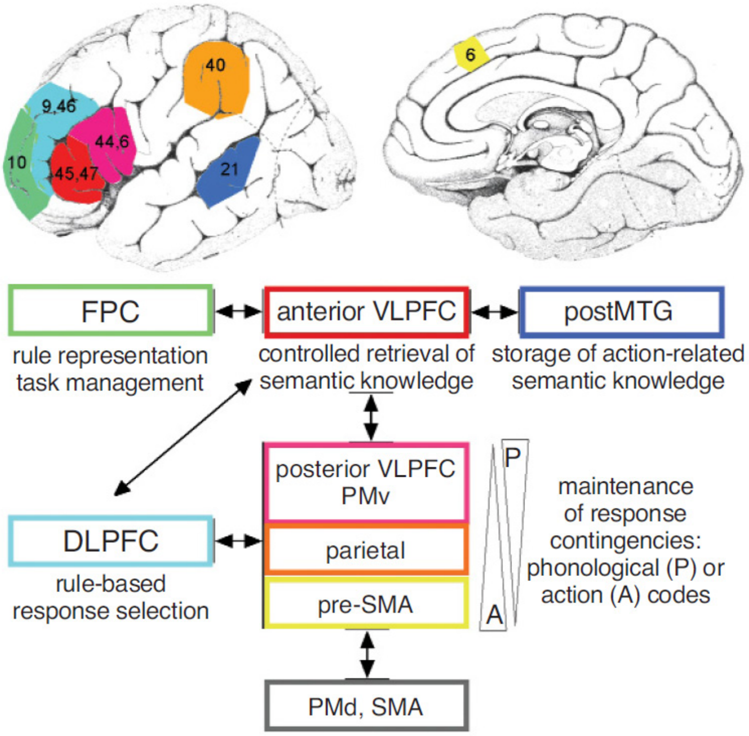

Figure 1. Schematic of the neural structures subserving rule use according to Bunge (2004).

The centered part of this schematic is important for the present purpose. According to Bunge (2004), relevant response contingencies can be maintained online over a delay through interactions between the pre-SMA (BA 6), posterior vlPFC (BA 44), ventral premotor cortex and IPL (see Figure 1). More precisely, rule maintenance can be based on phonological rehearsal and involve the left posterior vlPFC (Smith & Jonides, 1999; Bunge et al., 2003; Wagner et al., 2004) and/or it can be based on abstract representations of possible responses and involve the pre-SMA (Hazeltine et al., 2000).

2.4 Arousal and Action Control

Theoretical approaches. Up to now, this paper has discussed task-related influencing factors. This section will examine an influencing factor that is not related to the task, but also modulates responsiveness to action affordances. Arousal is a physiological and psychological state of being reactive to stimuli and is thus vital for regulating consciousness, attention, and information processing. However, how does arousal interrelate with action control?

The influential attentional networks account postulates a hierarchical relation among arousal, orienting, and executive control (Posner & Boies, 1971; Fan et al., 2002). The orienting network is defined as responsible for the selection of information from sensory input, whereas the executive control network is thought to be active when the cognitive system faces situations that involve planning, decision-making, error detection, or response conflict. Thus, both arousal and action control are conceived as attentional networks. Fan et al. (2002) measured the efficiency and interrelations of the networks within a cued flanker-like task. They found the flanker effect (as a measure of executive control) to be enhanced after alerting signals (visual cues) and inferred that arousal inhibits executive control. More importantly, Fan et al. (2002) did not elaborate how this conclusion can be integrated with the fact that arousing stimuli accelerated RTs in their study. Callejas et al. (2005) replicated the enhanced interference effect with auditory stimuli and came to the same conclusion. Just as in the study of Fan et al.

(2002), the behavioral output was actually improved by arousing stimuli. The interference effect was also greater because compatible trials benefited relatively more than incompatible trials.

An alternative explanation was recently suggested by Fischer et al. (2010), who replicated accelerated performance and greater interference in a Simon task with accessory tones. Referring to dual-route frameworks (Kornblum et al., 1990), they proposed that the general speed-up of RTs in trials with auditory stimuli points to a facilitation of deliberate response selection (indirect route). The simultaneous increase of the Simon effect was seen as a consequence of enhanced response priming (direct route). Thus, Fischer and collaborators assumed a boost of both routes. In short, the interpretation of this rather consistent results pattern within these different theoretical frameworks led to contradictory claims.

The salient point is whether arousal actually modifies action control. If so, it can be regarded as a form of reactive anticipatory control regulation and should then originate in processes that are equivalent to sequence-related adjustments. The relation between tone-induced and sequence-related effects has only once been investigated (Fischer et al., 2010). They found that exact repetitions of compatibility conditions benefitted from accessory tones. This finding is in line with an alternative explanation that arousal facilitates basic perceptual processes that are not necessarily related to control-specific information processing.

Neural substrates. Fan et al. (2007) reported in an fMRI study that arousal was associated with a broad fronto-parietal network, including thalamic contribution. Although thalamic contribution has often been reported, the specific neural substrates of arousal are naturally very dependent on the type of stimulation (modality) and task. For instance, arousal in a visuo-spatial task may be associated with occipital activation (Thiel et al., 2004), while arousing stimuli that have a warning character (alerting) may activate the ACC and pre-SMA (Yanaka et al., 2011).

By means of electrophysiological measures, the N1 has been linked to the state of arousal (Nash et al., 1982; Neuhaus et al., 2010) and selective attention (Hillyard et al., 1973; Griffin et al., 2002). This large, negative-going ERP peaks between 80 ms and 120 ms after the stimulus onset. It has been shown to reflect mostly preattentive early perceptual processes (Mangun & Hillyerd, 1995). An enhancement of the N1 is related to the facilitation of perceptual processes (Jepma et al., 2008). The N1 is, therefore, an appropriate candidate to examine whether arousal modulates early perception within a task that requires action control. However, no study has investigated the effect of arousal on conflict-related ERPs such as the N2 or incorrect LRP activation.

The third research question of the present dissertation is focused on clarifying the origin and processes underlying both the overall improved performance and the increased difference between compatibility conditions caused by accessory tones. In particular, it aims to find out whether accessory tones hamper/boost action control (Fan et al., 2002; Fischer et al., 2010) or whether they facilitate early perceptual processes independently of conflict-specific processing.

3 Summary of Studies

The objective of the following studies was to investigate the nature of deliberate and automatic regulation of action control after the occurrence of different influencing events. Study 1 compares control regulation prompted by the trial sequence, with prospective anticipatory regulation released by cues predicting conflict in a SRC and Simon task. Study 2 further enlarges upon the investigation of the exact processes underlying cue-induced anticipatory regulation in a Simon task. Finally, Study 3 broadens the perspective by focusing on bottom-up automatic influence, thereby investigating the impact on online action control.

3. 1 Study 1: Sequence-Related Reactive Regulation of Action Control

Research question. Study 1 addresses the question whether the processes underlying sequence-dependent performance are based on equivalent control adjustments to those induced by cueing. The notion that these processes may hark back to the same expectancy-based strategic control process stems from the first publications that reported sequence-dependent effects (Gratton et al., 1992; Stoffels, 1996). If based on comparable control mechanisms, expectancy/strategic control triggered by a preceding trial should be nullified by a subsequent cue that predicts the next trial compatibility with full reliability. In order to test this hypothesis, cueing was applied to a spatial stimulus-response compatibility task (SRC; Experiment 1) and a Simon task (Experiment 2). In both experiments, cues either indicated the upcoming compatibility (rule cues) or only the target position (position cues). That is, rule cues explicitly manipulated the expectancy of the upcoming trial compatibility, whereas position cues were used as a control condition. The latter decreased the response alternatives to the same extent but did not provide any compatibility information. Additionally, cue reliability was varied blockwise in such a manner that cues were either completely (100%) or predominantly (75% or 80%) valid. The last manipulation assessed insight into whether cue-induced control strategies depend on completely reliable information (Posner et al., 1980; Gratton et al., 1992; Braver et al., 2007). In Experiment 2, we additionally added a third No-go stimulus to force participants to select responses on the base of the stimulus figure and not based on stimulus position (e.g. rule cue *compatible* could mean “push the button on the same side as the stimulus appears”). The electrophysiological data was then recorded and analyzed in order to investigate whether cue-induced and sequence-related effects are reflected in the contingent negative variation (CNV). The CNV is an event-related potential (ERP) in the cue-target interval that functions as a marker of pre-target preparation (see Leuthold et al., 2004).

Results. Rule cues improved performance against the position cues in both the SRC and the Simon task. While in the SRC task both compatibility conditions benefitted, only compatible cues were accelerated by rule cues in the Simon task. These effects occurred only with 100 percent reliable cues. Independently of these cueing benefits, sequence-dependent performance was observed in both experiments. Even 100 percent reliable rule cueing did not cancel out the adaptation processes caused by previous trial compatibility. Cue conditions that achieved the largest behavioral benefit were not subjected to the trial sequence. No-gos in Experiment 2 that served control reasons did not modulate the result pattern and thus were not further analyzed. The CNV amplitude was enhanced with 100 percent reliable cueing, indicating the susceptibility of this ERP for cue utilization. This result is in line with studies that relate the CNV to the overall informative value of a cue (Damen & Brunia, 1994), since only fully valid cues allowed for the preselection of two out of four S-R assignments. The CNV was additionally magnified when the preceding trial was compatible, pointing to its’ susceptibility for sequence-dependent effects. A higher overall response readiness after compatible trials or a curbed response readiness after incompatible trials (Botvinick et al., 2001, 2004) may account for this finding (Fan et al., 2007). However, like in the behavioral results, the cue-induced and sequence-related effects were additive.

Discussion. The behavioral results of Study 1 show that even reliable cueing of the compatibility assignment does not override the effects of sequential adaptation in either the SRC task or the Simon paradigm. The electrophysiological results further corroborate this data pattern, since the CNV was additively modulated by both general cue utilization and trial sequence. These findings contradict the idea that sequence-dependent and cue-induced adjustments recruit similar strategic control processes. Whereas cueing can definitely be seen as prospective anticipatory regulation, the processes underlying sequential effects are still debatable. A contribution of mnemonic processes to the overall sequential effect cannot be ruled out, since exact but not partial repetitions were excluded in the present study. More importantly, the fact that the CNV shows sequence-related effects prior to the target presentation suggests the existence of some anticipatory control process beyond episodic memory.

Knowledge gain. The results of Study 1 cast doubt on the idea of one single control mechanism because they indicate that the processes underlying sequence-related effects differ from cue-induced strategic processes. Furthermore, the electrophysiological data indicate that sequence-related effects were already present in the intertrial interval and are therefore not solely based on episodic memory. The findings of Study 1 support the idea that there might be different types of anticipatory control outlined as “reactive anticipatory regulation” and “prospective anticipatory regulation” (Ridderinkhof et al., 2010).

3.2 Study 2: Cue-Induced Prospective Regulation of Action Control

Research question. Study 2 takes up Study 1 and expands on the neural networks of prospective anticipatory regulation of action control in pre-target processes. Just as in Study 1, rule cues and position cues were presented in a Simon task and a non-informative cue condition was added. No-gos were again employed in order to force the participants to pay attention to the stimulus figure. Behavioral, electrophysiological and fMRI measures of anticipatory control were collected in two within-subjects experimental sessions. The aim was to gain a deeper understanding of the exact processes underlying rule cue-induced anticipatory regulation. Besides behavioral performance, we sought to investigate the influence of rule cues on the electrophysiological markers of anticipatory regulation (pre-target CNV) and of online conflict control (post-target N2; Folstein & Van Petten, 2008). Furthermore, we were interested in hemodynamic changes indicating brain networks that contribute to anticipatory control regulation. We were not only interested in activations of the mPFC that were brought into prominence by the conflict monitoring account; under the assumption that anticipation may involve networks described for rule maintenance, we were also interested in changes in the prefrontal cortex.

Results. Both the rule and position cues benefitted responses for compatible and incompatible events. Compatible trials were thereby accomplished more quickly than incompatible trials in all cue conditions. In sum, the results of Study 2 showed effective anticipatory regulation of action control: rule cues elicited the shortest RTs with the lowest error rate, while they enhanced the CNV amplitude and subsequently reduced the N2. FMRI results revealed the activation of a broad rule cue-induced fronto-posterior brain network during anticipation. Frontal cortex activation within this network involved the left lateral rPFC (BA 10), left vlPFC (BA 44), bilateral pre-SMA (BA 6), and primarily left lateral IPL (BA 40). Among the latter frontal structures, only the pre-SMA correlated with the behavioral rule cue benefit. This points to the importance of this region for the preparation of specific response contingencies. No difference was found within rule cues between the anticipation of an incompatible and a compatible event, neither in fMRI nor in the CNV amplitude. Position cues yielded a smaller RT benefit and exhibited a different result pattern, since they entailed no CNV effect and failed to reduce the N2 significantly (compared to non-informative cues). In contrast to rule cues, position cues induced a more posterior anticipatory network without any prefrontal or pre-SMA contribution. Conjunctive activation of rule and position cue-related processes was found in this posterior network, not in the prefrontal areas. In contrast, non-informatively cued trials showed the slowest RTs and a typical pattern of compatibility effects in the N2 and accuracy data. This suggests the presence of cognitive conflict. In addition, analyses of accuracy as a function of response speed revealed a bigger impact of the misleading stimulus position (response capture, LIT) in non-informatively cued incompatible trials. Such indicators of cognitive conflict were absent after both rule cues and position cues.

Discussion. The behavioral and electrophysiological results clearly demonstrate the benefits of anticipatory regulation of action control induced by rule cues. FMRI revealed the activation of a network consisting of the lateral rPFC, posterior vlPFC, pre-SMA and lateral IPL. This network has been previously described for rule maintenance and rule elaboration on an instructional level (Bunge, 2004; Bunge & Wallis, 2008). Specifically, the lateral rPFC is associated with higher order rule management on the instructional level (Bunge et al., 2003; Sakai & Passingham, 2003, 2006; Crone et al., 2005), whereas the posterior vlPFC serves phonological rehearsal and the pre-SMA maintains action representations (Cohen & Servan-Schreiber, 1992; MacDonald et al. 2000; Miller & Cohen, 2001; Braver et al., 2002; O'Reilly et al., 2002). Despite these overall rule cue effects, the anticipation of incompatible and compatible trials did not differ in the fMRI or the CNV (same accounts for Study 1). In addition, no conflict-specific effects were observed in error rates and in the N2. Such effects were also absent in the behavioral and ERP findings in trials with position cues. These results cast doubt on whether the behavioral difference between compatibility conditions in rule and position cues can be considered a consequence of cognitive conflict. Rule and position cues apparently caused processes that prevented or at least greatly reduced the occurrence of conflict. In particular, with rule cues, the participants may have translated or remapped the instruction into more effective condition-action rules (e.g. cue “incompatible” means a crossed S-R mapping). Since rule cues reduced the task set from four to two possible S-R assignments, it might have been easier to shift attention towards more relevant perceptual/conceptual task features. Thus, the participants used rule cues for preemptive anticipatory regulation (avoiding conflict) instead of proactive anticipatory regulation (preparing for conflict; Ridderinkhof, 2010). The RT difference between the compatibility conditions may thus not be a consequence of response priming, but rather the result of an ideomotor effect in incompatible trials. Predicted compatible assignments were particularly easy to accomplish and therefore exhibited considerably shorter RTs. This led to an enhanced difference between the compatibility conditions. In contrast to rule cues, position cues induced no CNV effect and exhibited no prefrontal or pre-SMA contributions in the fMRI. The attentional shift to the relevant visual half-field thus prevented spatial conflict without involving rule transformation and maintenance.

Knowledge gain. The anticipation of action control is an up-and-coming research field. The majority of the few existing studies investigated anticipatory high-conflict versus low-conflict effects focused on predictions based on the conflict monitoring account. They came to inconclusive results regarding ACC or PFC contribution (Luks et al., 2007; Sohn et al., 2007; Aarts et al., 2008; Donohue et al., 2008). Study 2 suggests that this might be due to the existence of different types of anticipatory mechanisms. In his taxonomy, Ridderinkhof (2010) conceptually subdivided anticipatory regulation of action control into preemptive anticipation (avoiding conflict) and proactive anticipation (preparing for conflict). When elaborating rules, we usually try to break their implications down into action rules that are easier to handle. This especially accounts for situations that imply cognitive demand (Kool et al., 2010). The present study shows how preemptive anticipatory regulation of action control modulates behavioral, electrophysiological, and fMRI correlates. At least in this paradigm, preemptive anticipatory regulation did not involve ACC, but rather prefrontal and premotor regions that accomplish rule elaboration/translation and rule maintenance.

3.3 Study 3: Arousal and Action Control

Research question. Accessory tones have been shown to lead to faster overall responses and to increase interference effects (Fan et al., 2002; Callejas et al., 2005; Fischer et al., 2010). Researchers referring to the attentional networks account (Posner & Peterson, 1990) assumed that the arousal network inhibits the executive attention network, resulting in more conflict (Fan et al., 2002; Callejas et al., 2005). Other researchers referring to dual-route frameworks proposed that either the instruction-based indirect as well as the concurrent priming-based direct route is boosted by tones (Fischer et al., 2010). Study 3 was designed to clarify the processes underlying both the general performance improvement and the increased interference effect. Using electrophysiological measures we addressed the question of whether accessory stimuli in interference tasks alter early processes that initiate conflict or later reactive processes of conflict resolution. Two tone conditions with different SOAs (200 and 500 ms before target onset) and one condition without tones were employed in a Simon task. Accessory tones were assumed to enhance the N1 amplitude if they facilitate early perceptual stimulus processing (Mangun & Hillyard, 1995). Tone-induced enhanced allocation of attention to the visual target should reduce the attention-related overall N2 amplitude (Folstein & Van Petten, 2008). We also investigated the LRP-R and the S-LRP in order to localize the effect in the stream of information processing (Leuthold et al., 1996; Hackley & Valle-Inclán, 1998) as well as the S-LRP activation of the incorrect response hand in incompatible trials (Stürmer et al., 2000). If tones hamper executive control, they may diminish sequence-dependent adaptation as well as the conflict-related N2 difference between incompatible and compatible trials.

Results. Study 3 replicates the previously reported behavioral findings. Accessory stimuli improved behavioral performance in compatible and incompatible trials and resulted in a larger difference between compatibility conditions. The ERP results indicate that accessory tones function before or during response selection and might affect the perceptual processing of stimuli, since they caused an earlier onset of the stimulus-locked S-LRP and enhanced the N1 amplitude. Overall reduced N2 amplitudes can be seen as further evidence that accessory signals potentiated attentional allocation. The early incorrect LRP was magnified by accessory tones only in the short SOA condition. Neither the conflict-related N2 nor sequential adaptation was affected by accessory tones.

Discussion. The results of Study 3 are in line with the assumption that accessory tones amplified early perceptual discrimination and attentional allocation. In contrast, there were no effects on the electrophysiological markers of conflict-specific processes like the compatibility effect in the N2 or on sequence-related adjustments. The latter result and performance improvement clearly contradict the interpretations of enlarged interference effects as a result of hampered action control by arousal (Fan et al., 2007). It is plausible that deepened perceptual processing and enhanced attentional allocation aid in task accomplishment. The speeding-up of both incompatible and compatible events and the lower error rates foster this conclusion. However, incompatible trials might benefit less because the conflicting feature is tied to the visual stimulus whose initial processing stages are at the same time boosted so that the perceptual benefit cannot fully evolve. The latter effect caused the greater RT difference between compatible and incompatible trials. Like Fischer et al. (2010), we suggest an interpretation within a dual-route framework. The overall improvement of performance indicates boosting of the indirect route, while the increased Simon effect points to a boost of response priming in the direct route.

In general, a caveat needs to be issued in this study regarding an ancillary effect of the auditory stimulus. Since the temporal presentation was fixed in time, one may argue that the effect found may originate in a reduction of temporal uncertainty. This argument cannot be ruled out in the present study and may thus pose an alternative explanation. However, in unpublished follow-up experiments of this study, temporal uncertainty was reduced to the same extent in tone and no-tone conditions by a color change of the fixation cross. The results were comparable to Study 3 and showed that the effects varied as a function of tone intensity. Thus, they unequivocally demonstrate an arousal effect.

Knowledge gain. The interrelation between arousal as an influencing factor that modulates responsiveness to environmental stimuli and action control is pivotal for the conceptualizations of action control and attention. Study 3 extends previous behavioral findings in the existing literature by electrophysiological evidence to evaluate explanations made by different theoretical frameworks. The results clearly show that arousal does not directly influence conflict-specific information processing, but rather boosts early stages of the visual processing stream. This enhances perceptual discrimination and attentional allocation. Moreover, arousal did not alter sequence-dependent adjustments. It can therefore not be conceived as a form of a reactive control anticipatory process.

4 General Discussion

Action control cannot be considered an isolated process. Rather, it is a set of cognitive functions that are constantly subjected to a variety of top-down and bottom-up influencing factors of intrinsic and extrinsic origin. In the scope of this dissertation I investigated three research questions. Each of these questions examined the influence of at least one of the following influencing factors: cue-induced preparation, sequence-related adjustments, and task-irrelevant state of arousal.

These factors have been discussed in previous literature within different frameworks such as the conflict monitoring theory, dual-route models, rule-guided behavior or the attentional networks account. However, none of these frameworks provide a universally valid neuro-cognitive concept of all control modulations; nonetheless, each framework offers valid explanations for some of the adjustments described in this dissertation. The nomenclature defined by Ridderinkhof et al. (2010) turned out to be very applicable for the purpose of this dissertation. The authors emphasize the importance of differentiating action control from the processes that regulate it in an anticipatory manner. They further refer to cue-induced anticipation as prospective anticipatory regulation of action control. Moreover, anticipatory control regulation can be subdivided in proactive and preemptive adjustments: Proactive adjustments involve the strengthening of action control, for instance via the a priori amplification of inhibitory mechanisms. Alternatively, the need for online action control can be preempted, for instance by increasing the focus of selective attention on task-relevant stimuli or by filtering out task-irrelevant stimuli such that these fail to elicit strong response capture. Thus, the taxonomy provides working titles in order to categorize sequence-related adjustments as reactive control anticipation, cue-induced adjustments as prospective anticipation, and the avoidance of conflict as a preemptive mechanism. These labels are used in the knowledge that they are as arbitrary as the assignment of processes to these categories, as long as less is known about the nature and interrelation of these factors that regulate online action control.

The ensuing sections will evaluate the results of this dissertation work and discuss them in a broader context.

Sequence-related reactive control anticipation

Different accounts have been proposed about the processes underlying sequence-related adjustments in the current literature. Empirical studies that aim at disentangling the proposed sources have generally fostered the conclusion that both mnemonic and attentional influences contribute to sequence-related effects (for a review, see Egner, 2007). The two main accounts for attentional/strategic control influences are an expectancy-based account (Gratton et al., 1992; Stoffels, 1996) and a conflict-driven account (Botvinick et al., 2004). The first account regards sequence-related effects as an expression of a prospective process equal to cue-induced strategic preparation for an expected stimulus. The second account views post-conflict effects as a result of strategic task set reinforcement released by prior conflict detection. The first research question aimed to clarify whether the source of expectancy-based strategic control is also responsible for sequence-related modulations. The third research question further investigated the interrelation between the state of arousal and sequence-related control adjustments. More importantly, while the present work focuses on the top-down sources of sequence-related effects, it does not rule out that mnemonic processes may contribute to the overall pattern.

The results of Study 1 results demonstrated that explicit cueing of compatibility, on the one hand, and compatibility sequence, on the other, generate additive effects in performance and in the CNV. This casts substantial doubt on the validity of the expectancy-based account (Gratton et al., 1992; Stoffels, 1996). Meanwhile, another study tested the role of expectancy in sequence-related adjustments and came to the same conclusion. Egner et al. (2010) ruled out expectancy-based accounts, since they found sequence-related effects to decay very quickly. Therefore, if not expectancy, what is the source of this effect? Accounts claiming that sequence-related effects are caused by mnemonic processes would have predicted such an additive effect of sequence- and cue-induced adjustments. However, the fact that the compatibility of the preceding trial already modulated the CNV contradicts the notion that mnemonic processes are the only source of this effect. Moreover, enhanced arousal after the experience of conflict may also not account for these effects, since Study 3 revealed no relationship between arousal and sequence-related adjustments.

Study 1 was not designed and is thus not suitable to test assumptions of the conflict monitoring account. However, it is worth considering whether the present results support the claims made by this account. Unlike the early accounts mentioned above, the conflict monitoring account does not use the term *expectancy*. However, conflict-triggered reinforcement of top-down attention (as proposed by the conflict monitoring) would presumably enhance the CNV (Tecce, 2010) and not reduce its amplitude, as found in Study 1. Consequently, sequence-related adjustments may be best conceived as a reactive control regulation that operates via proactive adjustments according to the terminology of Ridderinkhof et al. (2010). Proactive adjustments means that participants may a priori amplify those processes that help keep their horses in check when strong response competition is anticipated. The pre-target CNV modulation that exhibits reduced amplitudes subsequent to conflict fosters this notion. Fan et al. (2007) showed that the CNV amplitude is magnified by enhanced response readiness. One can also speculate that if sequence-related adjustments are of a preemptive nature, an interrelation to cue-induced control regulation would have been found (since Study 2 shows the latter process to be preemptive).

This notion, however, poses one potential caveat for the conclusion that sequence- and cue-induced adjustments differ regarding expectancy, since the difference between underlying proactive and preemptive processes may have also caused additive effects. It is furthermore notable that only compatible events were accelerated by the compatibility predictions in Study 1. Interestingly, Study 2, using almost the same task design, exhibited sound behavioral benefits for both compatibility conditions. Basically, only two relevant differences between the task designs of Study 1 and Study 2. First, the cue-target interval was shorter in Study 1 (1.5 s) than in Study 2 (6 s). Second, Study 1 used a vertical Simon task, whereas Study 2 used a horizontal Simon task (since vertical S-R assignments would have been ambiguous in horizontal body position during the fMRI). Both more time as well as a more pre-wired horizontal assignment may account for better cue utilization in incompatible trials (Vallesi et al., 2005). The fact that the CNV did not exhibit overall differences between the cue types in Study 1 whereas Study 2 revealed such effects is probably due to the same reasons.

In sum, the results of the present work suggest that sequence-related adjustments differ from cue-induced adjustments. Control adjustments triggered by prior trial compatibility can be conceived as reactive control regulation that is already active in the anticipatory period. Moreover, the results of the present indicate a reduction of response readiness (rather than prospective enhancement of attentional processes) after the experience of conflict.

Cue-induced prospective control anticipation

The investigation of anticipatory mechanisms in action control is an up-and-coming research domain. Not much is known about anticipatory mechanisms, since the vast majority of prior studies have focused on online action control. From a theoretical perspective, there are two major notions about the nature of anticipatory control. First, the same neuro-cognitive systems carrying out online action control may be activated in a preparatory manner. Second, other basic functions such as attention, memory, or response readiness may be geared to the upcoming task demand. Some researchers have seized the first notion and postulated that cues informing about upcoming conflict lead to anticipatory activation of the conflict monitoring ACC-dlPFC loop (Sohn et al., 2007; Aarts et al., 2008). This claim poses the question whether there is a difference between anticipatory mechanisms triggered by cues and prior conflicts (see section above). Then again, if basic functions rather than a conflict-specific circuit prepare for action control, which functions are these and how do they modulate information processing? The second research question regarded this question and asked how anticipatory control regulation impinges online action control.

Both the electrophysiological and functional imaging data in Study 2 provide evidence that cues informing about upcoming compatibility resulted in rule transformation and the avoidance of conflict. Behavioral and electrophysiological indicators of conflict control were only present in trials with non-informative cues. The left rPFC, vlPFC as well as the pre-SMA were involved in anticipatory neural networks that carried out rule transformation and rule maintenance. Neither mPFC nor dlPFC activation was present in Study 2. This pattern of results does not match with postulations that conflict-specific neural circuits prepare for conflict via the anticipatory activation of these structures. Rather, it suggests the involvement of a network that is associated with the use of task rules (Bunge, 2004). Previous research has led to the identification of a set of brain regions that mediate rule-guided behavior. The rPFC has been shown to be associated with higher-level rule elaboration, for example, when instructions have to be elaborated (Sakai & Passingham, 2003; 2006). The vlPFC is known to be involved in the verbal rehearsal of rules (Smith & Jonides, 1999; Bunge et al., 2003; Wagner et al., 2004), while abstract action representation involves the pre-SMA (Hazeltine et al., 2000).

In Study 2, pre-SMA seems to play a particularly important role for effective rule implementation, since its activation correlated with the behavioral benefit derived from the cues. In fact, some researchers claim a key role for the pre-SMA in anticipatory control regulation. Hikosaka and Isoda (2010) concluded in their review that pre-SMA activation occurs when cues indicate a switch (anticipatory processes in task-switching), whereas ACC activation occurs after error feedback (reactive processes in task-switching). Ullsperger and King (2010) seized this idea, proposing that not only task-switching but rather all processes of online action control can be more or less regulated by anticipation, and that the underlying processes might be associated with pre-SMA activation (King & Ullsperger, 2010). In addition, Rushworth et al. (2005) concluded that the pre-SMA appears to be activated whenever responses have to be prepared for the context of more complex stimulus-action associations (Rushworth et al., 2005). Moreover, Rushworth et al. (Mars et al., 2009; Neuhaus et al., 2010) also assume that pre-SMA rather than ACC activation is associated with situations involving the direct competition (Ullsperger & Von Cramon, 2001), inhibition (Nachev et al., 2007), updating (Shima et al., 1996), or reprogramming (Isoda & Hikosaka, 2007) of actions.

The present work cannot provide a conclusive answer to the overall significance of pre-SMA activation for online action control and its anticipatory regulation. However, at least in the paradigm employed in Study 2, pre-SMA and not ACC activation contributed to anticipatory control regulation. At this point, it is not possible to determine whether this pattern of results can be generally associated with anticipatory control regulation or whether it is specific to the processes underlying conflict preemption. In other words, it is possible that other networks involving the ACC may play a crucial role in proactive anticipatory adjustments. Different underlying networks might also explain why prior studies that cued conflict came to inconclusive results regarding ACC and prefrontal contribution. A closer look into the experimental designs of these studies suggests this explanation. Future research has to directly compare the neuro-cognitive systems involved in preemptive and proactive anticipatory control.

It is also worth mentioning that the absence of anticipatory ACC activation in Study 2 does not necessarily mean that the ACC does not play a role in anticipatory networks. In conventional analysis, it means that no significant effect is present across subjects. In recent years, more and more researchers have attempted to access individual variability by incorporating individual indices from behavioral or electrophysiological measures into fMRI multiple regression analyses (Forstmann, 2008; Jamadar et al., 2010; King & Ullsperger, 2010). Specifically, parameters that quantify theoretical cognitive constructs are incorporated as covariates in correlational analyses. In this manner, it can be determined which brain area covaries with these parameters. Such an analysis revealed that ACC and vlPFC activation covaried with the behavioral benefit derived from cues predicting compatibility in Study 2. These effects were however weak, since they were only present for a low threshold (uncorrected, $p < 0.001$) and were thus not reported.

The state of arousal in online action control

The question of how arousal interrelates with online action control is of interest because arousal is considered a low-level attentional process that modulates responsiveness to external stimuli. It is thus theoretically possible that arousal modulates the processes of online action control and should thus be regarded as a form of reactive anticipatory control regulation. Posner (1994) assumed that a shutdown of control activity is advantageous when the brain has to concentrate on the detection of external signals ("clearing of consciousness"). The attentional networks account postulated that enhanced arousal leads to the inhibition of action control (Posner & Boies, 1971). The finding that arousing auditory stimuli enhanced the conflict effect was regarded as evidence of this notion (Fan et al., 2002; Callejas et al., 2005). However, an alternative explanation is that arousal rather facilitates early perceptual processes that are not specifically related to control-specific information processing, thereby benefitting performance. One hint fostering this view is that despite increased conflict, all previous studies reported better overall performance. This idea was seized by Fischer et al. (2010), who referred to a dual-route framework and assumed that tones boost processing in both the indirect (leading to better performance) and direct (resulting in more conflict) route.

The results of Study 3 demonstrated that tones benefitted RTs and accuracy. Both compatible and incompatible assignments were accelerated. The fact that compatible events were relatively more speeded up than incompatible events resulted in an increased Simon effect. The ERPs revealed that auditory stimuli improved early stages of the visual processing stream and amplified perceptual discrimination as well as attentional allocation, although they did not alter the conflict-specific N2. Moreover, arousal did not interact with sequence-related reactive control adjustments. Thus, one can conclude that arousal improved the early processing stages and did not directly affect the actual processing of action control. In particular, it can be inferred that the Simon effect increased because compatible assignments were relatively more facilitated. Incompatible trials were less accelerated, since the conflicting feature is tied to the visual stimulus whose initial processing stages are at the same time boosted.

Expressed in the terminology of the dual-route framework, we suggest that the overall improvement of performance indicates boosting of the indirect route. On the other hand, the increased Simon effect was associated with a boost of response priming in the direct route. Meanwhile, another study reported N1 enhancement after auditory stimuli in the flanker task and concluded the arousal-induced amplification of perceptual discrimination (Neuhaus et al., 2010).

It is an interesting outcome that auditory stimuli in Study 3 did not result in the hampering of executive control (“clearing of consciousness”), as proposed by Posner (1994). From a theoretical perspective, Posner’s notion makes particular sense in the context of warning stimuli. Future studies have to investigate whether warning stimuli that enhance attention towards external stimuli (alerting) impact action control differentially than stimuli enhancing unspecific intrinsic arousal.

Conclusion

Online action control is subjected to fluctuations depending on a variety of influencing factors of internal and external origin. The aim of the present work was to investigate the nature of different types of adjustments that brace our cognitive system for demands of action control. The scope of the underlying processes ranged from reactive to prospective anticipatory action control, which involved preemptive as well as proactive adjustments. Reactive regulation of action control is triggered by the prior experience of action control. The present results indicate that this regulation already starts before the next demand arises.

However, the nature of this process differs from expectancy-based control and seems to proactively reduce response readiness. Prospective regulation of action control released by explicit information about the degree of an upcoming control demand can lead to a re-mapping of task rules so that conflict can be preempted. The networks carrying out such anticipatory control regulation involve task-general structures associated with the transformation and maintenance of task rules and are not necessarily specific for action control. The overall state of arousal does not engage anticipatory control regulation, and therefore differs from the other factors investigated in this dissertation. It rather facilitates early perceptual processes that are not directly related to control-specific information processing. Future research has to accept the challenge to further understand and systemize such influencing factors and their interrelations in order to include them in dynamic models of action control.

5 Future Directions

Here, I will discuss future directions on two more general levels. On the one hand, there are specific questions resulting from the studies in the present work. On the other hand, conceptual and methodological challenges have to be met.

The studies included in this dissertation can only provide a brief insight into some excerpts of the processes that regulate action control. Research is about to start investigating how action control is regulated. The generalizability of the present results can and should be questioned, as long as they have not been replicated in other tasks or with different or cue stimuli. Some future research questions have already been suggested in the sections above. In my view, the differentiation of anticipatory processes regarding their preemptive or proactive nature seems to be of particular importance. I speculated that sequence-dependent reactive control might be driven by proactive adjustments in terms of a reduction of response readiness after conflicts. However, more studies have to address the questions of whether, when, and which processes are enhanced (e.g. selective attention) or curbed (e.g. response readiness) after conflict. Regarding prospective anticipatory control, future studies do not only have to carefully control for such strategies. Rather, preemptive control adjustments have to be explicitly included into the understanding of anticipatory control, since they might be the preferred strategy in the presence of looming conflict. Future studies also have to separate conflict-specific information processing from other general processes underlying rule use or low-level attentional processes like arousal.

Neuroimaging research has led to the identification of a set of brain networks that are associated with different aspects of action control. An important next step will be to characterize temporal dynamics between involved regions. Accordingly, studies involving simultaneous EGG/fMRI would prove useful. However, since we are investigating higher-order cognition, we are trying to capture complex, dynamic, context-dependent and volatile processes with a fragile alliance of cognitive psychology and the technological possibilities of neuroscience. We might be able to measure the where and when of brain activity but we still do not know whether we really capture the concepts we created. The regulation of higher cognition in the service of goal-directed behavior has been historically conceptualized as a set of control functions that may include response selection, inhibition, and task-maintenance. This approach has been continued in research domains investigating rule-guided behavior. However, the term *cognitive control* has increasingly replaced the collective of control functions. This conceptual transition bears the fundamental problem of bridging psychology and neuroscience. Does the cognitive construct of *cognitive control* necessarily capture a basic mental function as implemented in the brain? Or is cognitive control an emergent function composed of task-general processes such as working memory and response selection? More studies are needed that test the assumptions of the conflict monitoring account against a null hypothesis that claims that conflict is resolved by task-general processes (Grinband et al., 2010; Lenartowicz et al., 2010; Grinband et al., 2011). The validity of the conflict monitoring account is of particular interest for future research about anticipatory control regulation that naturally has to face the same issues. Eventually, the question of whether specific circuits accomplish anticipatory control is closely tied to the question of whether specific circuits exist for cognitive control.

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6 Submitted Publications/ Manuscripts

Study 1: Alpay, G., Goerke, M., and Stürmer, B. (2009). Precueing imminent conflict does not override sequence-dependent interference adaptation. *Psychological Re*search 73(6), 803-816.
DOI: 10.1007/s00426-008-0196-9

Study 2: Strack G, Kaufmann C, Kehrer S, Brandt S and Stürmer B (2013). Anticipatory regulation of action control in a Simon task: behavioral, electrophysiological, and fMRI correlates. *Front. Psychology* **4**:47.
DOI: 10.3389/fpsyg.2013.00047

Study 3: Böckler, A., Alpay, G., Stürmer, B. (2011). Accessory stimuli affect the emergence of conflict, not conflict control: A Simon-task ERP study. *Experimental Psychology,* 58(2), 102-109.
DOI: 10.1027/1618-3169/a000073

7 Supplement

Hiermit erkläre ich an Eides statt,

- dass ich die vorliegende Arbeit selbständig und ohne unerlaubte Hilfe verfasst habe,

- dass ich die Dissertation an keiner anderen Universität eingereicht habe und keinen Doktorgrad in dem Promotionsfach Psychologie besitze,

- dass mit 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.

Gamze Strack