

# The time course of cognitive control: behavioral and EEG studies

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«GO FOR THE MESSES - THAT'S WHERE THE ACTION IS»

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# **CHAPTER 1**

## **INTRODUCTION**

Some of the things we do every day, such as singing, driving a car or reading on the train, are performed without much cognitive effort or without consciously making decisions about actions. However, in some conditions (when singing for a large audience, when a rabbit hops onto the road or when someone next to you is talking loudly on the phone) the task at hand becomes too important or too difficult for automatic processing and we need to take it up a notch. We need to focus attention on relevant stimuli while ignoring distracting information and we need to invest cognitive effort to take more control over our actions. To do this we rely on cognitive control. Cognitive control is a set of top-down mechanisms that can be implemented to coordinate more basic cognitive processes. Considering its importance for goal-oriented human actions, it is not surprising that cognitive control has been studied extensively over the past decades. Many important questions to do with cognitive control have been asked and studied in the field of experimental psychology and neuroscience. When and how is control implemented? What information is used to regulate control? What brain areas are involved in control, and how do these form networks to exercise control? Through which mechanisms and on what timescale can control be recruited?

In what follows, I will first give an overview of experimental methods and neural measures that have been used to study control empirically. Stalking

people who read on the train and starting loud phone conversations, or sacrificing rabbits on the road might not be the ideal scientific settings to study control. Psychologists and neuroscientists have therefore retreated to the lab to study cognitive control in more manageable conditions. Next, I will review several influential theoretical frameworks, that have been proposed to unify and explain empirical findings. I will also discuss how control poses a cost to the cognitive system, and how this cost is weighed against benefits in the decision to implement control. Finally, I will address one of the main research questions of this dissertation: what is the time course of cognitive control? Theoretical models disagree when it comes to how fast control can operate, and although neural processes involved in control become increasingly well known, their time course remains elusive. Why and how this dissertation intends to specify the time course of control will be explained near the end of this introduction. To conclude this chapter, I will sketch the outline of this dissertation and give an overview of the three empirical chapters.

## COGNITIVE CONTROL IN THE LAB

### **Congruency tasks offer a tool to study cognitive control experimentally**

In an experimental environment, *congruency tasks* are often used to study control. In these tasks, such as the flanker (Eriksen & Eriksen, 1974), Stroop (Stroop, 1935) or Simon (Simon, 1969) task, participants have to respond to a target stimulus (or stimulus feature) while ignoring distracting stimuli (or stimulus features). For instance in the flanker task, participants have to identify a stimulus presented in the center of a computer screen and are instructed to press the correct key on the keyboard. However, irrelevant,

possibly distracting stimuli are presented around the target stimulus. On incongruent trials, irrelevant stimuli trigger a different response than relevant stimuli, creating a response conflict. Participants are prompted by the target stimulus to push button one, but by the surrounding stimuli to push button two. On congruent trials no response conflict occurs since relevant and irrelevant stimuli are linked to the same response. The occurrence of response conflict makes a task more cognitively challenging and makes the response more difficult. This is reflected in slower response times (RTs) and a higher error likelihood for incongruent than for congruent trials (Hazeltine, Poldrack, & Gabrieli, 2000; MacLeod, 1991). The difference in RTs and error rates between congruent and incongruent trials is called the *congruency effect*, and serves as a marker for experienced response conflict and task difficulty. To maintain high task performance, more cognitive control is needed on incongruent trials than on congruent trials. Gratton, Coles, & Donchin (1992) show in their seminal paper that the congruency effect is reduced following incongruent trials, a phenomenon called the *sequential congruency effect*. This effect suggests that cognitive control is heightened as a result of conflict experienced on the previous trial.

Not only response conflict, but also response errors provide researchers with the opportunity to study control. For this reason, errors are often studied alongside response conflict in the field of cognitive control research (Holroyd & Coles, 2002; Steinhauser, Maier, & Hübner, 2008; Yeung, Botvinick, & Cohen, 2004). Since the current dissertation does not focus on post-error adaptations, this part of cognitive control research and theory will not be discussed in detail, but a limited overview of main findings is provided here. When participants make an error, this indicates poor performance and signifies that cognitive control should be increased in the future, e.g. in the

next trial (Steinhauser et al., 2012). Researchers have therefore also studied behavioral and neural responses following errors, probing the implementation of cognitive control. Following an error, RTs usually slow down (Dutilh et al., 2012; Rabbitt, 1966). This post-error slowing has previously been interpreted as a reflection of increased caution and controlled processing following an error. In line with this idea, response accuracy often increases following errors (Danielmeier & Ullsperger, 2011). However, accuracy decreases have also been observed, leading researchers to believe that perhaps errors do not only trigger increased control but might also disrupt processing (Jentsch & Dudschig, 2009; Notebaert et al., 2009; Van der Borgh, Braem, Stevens, & Notebaert, 2016). Directly following an error, processing is disrupted, but when more time to strategically adapt control is available, errors eventually lead to improved performance (Van der Borgh et al., 2016). Finally, it has been suggested that the congruency effect is diminished following errors, indicating that control has been implemented (Ridderinkhof, 2002). However, this finding has recently been challenged, again questioning control processes following errors (Van der Borgh, Braem, & Notebaert, 2014). Notwithstanding the seemingly contradictory findings and many unanswered questions in error research, it has become clear that errors are important events that almost certainly influence cognitive control.

In sum, congruency tasks provide an excellent tool to study cognitive control. By comparing behavioral and neural responses for congruent vs. incongruent trials and by monitoring processes following errors, researchers have learned a lot about cognitive control.



### **Measuring neural processes involved in cognitive control**

To study not only behavior, but also the neural underpinnings of cognitive control, researchers have relied on various brain recording techniques, including functional magnetic resonance imaging (fMRI) and electro-encephalography (EEG). fMRI can be used to measure the hemodynamic brain response (i.e. the BOLD response), revealing activation and deactivation in certain brain regions linked to events of interest. This technique offers high spatial resolution revealing activity in specific areas. Unfortunately, it offers only poor temporal resolution due to the slow nature of the BOLD response. On the other hand, EEG offers excellent, millisecond temporal resolution, but is much less spatially precise. One central aim of the current PhD was to gain insight into the neural time course of cognitive control and so I used EEG, exploiting its high temporal resolution.

When neurons fire, a change in electrical potential occurs, creating a small temporary electrical dipole with a positive and a negative end. Since neurons are spatially aligned, these small electrical dipoles all point in the same direction, summing up to one larger dipole which can be detected at the scalp. The occurrence of these dipoles can be determined very precisely in time, but since the electrical signal has to pass through several layers of tissue before reaching the scalp, volume conduction makes the electrical signal spatially diffuse. In search of consistent activation of neurons locked to a certain event (e.g. the presentation of a stimulus), the event of interest is repeated and the average EEG signal following the event is calculated. As noise is cancelled due to the averaging procedure, what remains is a series of positive and negative deflections in the signal, marking reliably generated dipoles and thus neuronal activity. This is called an *event-related potential*

(ERP). ERP deflections (or components) have been named in the literature on the basis of their sign (positive or negative) and timing. Reliably evoked components have also been linked to a wide variety of cognitive tasks and events (Kappenman & Luck, 2011). For cognitive control, a component known as the N2 (or N200) marks the detection of response conflict (Folstein & Van Petten, 2007). The N2 is a negative deflection peaking around 200-350 ms post stimulus onset. Although the sensitivity of the N2 is not limited to stimulus incongruency (the N2 also responds to stimulus novelty or mismatch) it is nevertheless a good marker for incongruency detection (Folstein & Van Petten, 2007). Another well-studied ERP component in cognitive control literature is the error-related negativity or error negativity (ERN or Ne), a component reliably evoked when an error is made (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Falkenstein, Hoormann, Christ, & Hohnsbein, 2000). The onset of the ERN occurs shortly before an erroneous response and the ERN peaks approximately 100 ms after the response. This component likely reflects awareness of an error. Also before stimulus onset, certain ERP components reflect attentional control. The contingent negative variation (CNV) and the stimulus preceding negativity (SPN) are slow going negative deflections in the ERP, with a central or centro-parietal scalp distribution (Brunia & van Boxtel, 2001; Tecce, 1972; van Boxtel & Böcker, 2004). These components occur when participants are attentively anticipating an upcoming stimulus. This stimulus might be an imperative stimulus requiring a response (CNV) or an informative stimulus, such as a feedback stimulus (SPN).

ERP analysis provides only one possible way to look at the EEG signal. The EEG signal can be considered as a weighted sum of many sinusoidal signals oscillating at different frequencies. The contribution of each frequency to the total EEG signal varies over time. Time-frequency (TF) analysis of EEG

data identifies how certain events reliably change the strength or power of certain frequencies over time (Cohen, 2014). The variations of power over time of a range of frequencies are calculated and averaged over trials, locked to an event of interest. As in ERPs, averaging cancels noise and leaves only consistent power changes that can be mapped in time and frequency space. One advantage of TF analysis is that it captures both phase-locked and non-phase-locked signals in the EEG, whereas ERPs only capture phase-locked signals (Cohen, 2014). When the phase of an oscillation is not fixed at the event of interest (e.g. because it is not reset by the event), the magnitude and sign of the signal amplitude following the event will differ over trials, and averaging will result in cancelling out this signal. Consequently, non-phase-locked signals will not show up in the ERP. Whether or not the ERP captures only phase-reset oscillatory signals or also encompasses other evoked signals is under continuous debate (Fell et al., 2004; Makeig, 2002).

Power in certain frequency bands has been linked to cortical activation or deactivation and to several cognitive processes. For instance, power in the alpha frequency band (8-14 Hz) is negatively correlated with BOLD activity measured by fMRI (Laufs et al., 2003, 2006; Ritter, Moosmann, & Villringer, 2009; Zumer, Scheeringa, Schoffelen, Norris, & Jensen, 2014). In monkeys, neuronal firing is locked to the trough of alpha oscillations, and alpha power decreases in areas involved in the task at hand (Haegens, Nacher, Luna, Romo, & Jensen, 2011). Initially alpha oscillations were attributed to states of cortical idling (Pfurtscheller, Stancák, & Neuper, 1996), but later a more active inhibitory role was discovered for alpha oscillations (Cooper, Croft, Dominey, Burgess, & Gruzelier, 2003; Klimesch, Sauseng, & Hanslmayr, 2007; Palva & Palva, 2007). The *gating by inhibition* theory states that alpha oscillations reflect inhibition of irrelevant input and can be strategically adjusted to admit

relevant information into processing (Jensen & Mazaheri, 2010). In visual attention tasks, decreases in alpha power occur in cortical occipital regions that are actively involved in task performance (Foxe, Simpson, & Ahlfors, 1998; Kelly, Lalor, Reilly, & Foxe, 2006; Worden, Foxe, Wang, & Simpson, 2000). Moreover, alpha power modulations in these areas are predictive of target detection (Händel, Haarmeier, & Jensen, 2011; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). In working memory tasks, alpha power is increased when distracting information is presented, and alpha modulations are again predictive of task performance (Bonnefond & Jensen, 2012, 2013). Also in cognitive control tasks, alpha power before task onset predicts performance and can be strategically adjusted, e.g. following errors, to increase cognitive control (Mazaheri, Nieuwenhuis, Van Dijk, & Jensen, 2009). These findings all support the idea that alpha oscillations can serve as an active inhibitory mechanism.

Another frequency band that plays an interesting role in cognitive control is the theta frequency band (4-8 Hz). Theta power measured at frontal electrodes is increased in many cognitive control tasks, both following response conflict and errors (Cavanagh, Zambrano-Vazquez, & Allen, 2012; Cohen, van Gaal, Ridderinkhof, & Lamme, 2009). It has therefore been proposed that mid-frontal theta indicates situations where control is required. Furthermore, mid-frontal theta oscillations may entrain other brain areas involved in implementing cognitive control (Cavanagh & Frank, 2014). Oscillatory synchronization, has indeed been shown as an important mechanism for (long-distance) communication between brain regions (Bressler, 1995; Fries, 2005; Uhlhaas, Roux, Rodriguez, Rotarska-Jagiela, & Singer, 2010; Varela, Lachaux, Rodriguez, & Martinerie, 2001). Not only synchronization within one frequency, but also synchronization across

frequencies plays an important role in neural communication (Canolty & Knight, 2010). In monkeys, synchronization of neuronal spiking in distinct areas has been shown during attentional control (Phillips, Vinck, Everling, & Womelsdorf, 2014; Voloh, Valiante, Everling, & Womelsdorf, 2015; Womelsdorf, Ardid, Everling, & Valiante, 2014). In humans, increased theta synchronization between mid-frontal cortex and other cognitive control areas has been shown following response conflict (Cohen & Cavanagh, 2011; Hanslmayr et al., 2008; Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012) or errors (Cavanagh, Cohen, & Allen, 2009; Cohen et al., 2009). Interestingly, frontal theta power has also been linked to occipital alpha power modulations: following errors, a correlation was observed between frontal theta power increases and occipital alpha power decreases (Mazaheri et al., 2009), suggesting that frontal theta can influence alpha oscillations. In sum, there is compelling evidence that cognitive control is a complex process, operating through several dynamic brain networks, where distant brain areas communicate through oscillations of varying frequencies, including frontal theta and posterior alpha oscillations (Cohen & Ridderinkhof, 2013).

### **COGNITIVE CONTROL – THEORETICAL FRAMEWORKS**

Experiments using congruency tasks, regularly in combination with diverse neuro-measurements, such as fMRI or EEG, have provided researchers with a very rich and intricate picture of cognitive control and its neural substrates and mechanisms. To unify and explain empirical findings, several theoretical frameworks on cognitive control have been proposed. These in turn provide new hypotheses that can guide future research.

**The conflict monitoring theory**

The *conflict monitoring theory* (CMT; Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004), one of the most influential cognitive control accounts, states that response conflict or a response error is detected in the brain by a conflict detection unit. This unit is located in the anterior cingulate cortex (ACC). When activated, the conflict monitoring unit triggers cognitive control implementation in a general fronto-parietal attentional control network, including the dorsolateral prefrontal cortex (PFC) and posterior parietal cortex (including the intraparietal sulcus: IPS) (Corbetta & Shulman, 2002; Dosenbach et al., 2007; MacDonald, Cohen, Stenger, & Carter, 2000; Nobre et al., 1997). The CMT offers a valuable theoretical framework in the form of a computational model that can explain important empirical reaction time (RT) and error rate findings. The sequential congruency effect (Gratton, Coles, & Donchin, 1992) provides evidence for control updating following response conflict: cognitive control on the current trial has been heightened as a result of conflict experienced on the previous trial. This is in line with how the CMT conceptualizes the control implementation process. The neural substrates for conflict detection and control implementation proposed by the CMT are also supported by fMRI studies (Carter et al., 1998; Kerns, 2004; MacDonald et al., 2000). These studies show that on incongruent trials ACC activation is increased, reflecting activation of the conflict monitoring unit. Sequential effects also appear in the fMRI signal: when an incongruent trial is encountered, control is increased and less conflict is experienced on the next trial, resulting in less ACC activation following incongruent trials than following congruent trials (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999).

In ERP research, source modelling revealed the ACC as the neural generator of classical response conflict related components such as the N2 and ERN/Ne component (Yeung et al., 2004). Conflict and error detection are also reflected in an increase of mid-frontal theta oscillations (Cavanagh et al., 2012). The source for these theta oscillations was again estimated in the ACC (Debener et al., 2005). These source modelling studies provide compelling evidence that typical conflict detection EEG signals reflect ACC activation. Beyond conflict detection, EEG studies also support the idea that conflict detected in the ACC triggers a fronto-parietal control network. In monkeys, highly spatially precise neural measures have shown how frontal and parietal areas form a communicating network during attentional control. Synchronization of neuronal spiking in the beta and gamma band has revealed increased communication between the ACC and lateral PFC in attentional tasks (Womelsdorf et al., 2014). Communication between these two areas is further supported by increased cross-frequency coupling between theta and gamma oscillations (Voloh et al., 2015). Finally, also synchronization between frontal and parietal areas was observed during attention in monkeys (Phillips et al., 2014). Scalp EEG measures have revealed similar network dynamics in humans. The theta power increase generated by the ACC is followed by increased synchronization in the theta frequency band between ACC and lateral PFC (Cavanagh et al., 2009; Cohen & Cavanagh, 2011; Cohen et al., 2009; Hanslmayr et al., 2008; Nigbur et al., 2012). Also, cross-frequency coupling between ACC and posterior parietal cortex was observed (Cohen & Ridderinkhof, 2013). These findings show how the conflict monitoring unit communicates with the control network through oscillatory synchronization.

### **The dual mechanisms of control framework**

The focus of the CMT rests heavily on control implementation triggered by response conflict. However, control can also be implemented strategically, before task onset. According to the *dual mechanisms of control framework* (DMC; Braver, 2012), control can be implemented in two ways: reactively and proactively. Reactive control acts when a challenging situation occurs, and is only implemented at the time it is needed. Proactive control on the other hand is exerted in anticipation of a cognitively demanding task, and is a sustained mode of goal-driven attentional selection. When response conflict is highly expected, either because it has been cued (Aarts & Roelofs, 2011; Aarts, Roelofs, & van Turennout, 2008) or in a context where a large proportion of trials are incongruent, a smaller congruency effect is observed (known as the proportion congruency effect: Gratton et al., 1992; Logan & Zbrodoff, 1979). This shows that when conflict is expected, proactive control is effectively implemented in preparation for the task. Like reactive control, proactive top-down control uses the fronto-parietal control network to focus attention and prepare for upcoming conflict (Braver, Paxton, Locke, & Barch, 2009; Corbetta & Shulman, 2002; Locke & Braver, 2008).

### **Associative models of control**

Together, the CMT and DMC framework provide an idea of when control is implemented: when conflict is experienced or expected. To also answer the question how control is implemented, *associative models of control* were proposed (Abrahamse, Braem, Notebaert, & Verguts, 2016; Egner, 2014; Verguts & Notebaert, 2008, 2009). According to the associative control models, control is implemented via associations between perceptual, motor, and control representations. When response conflict occurs or is



expected, perceptual and/or motor input activates associated control representations. These representations initiate a boost in arousal that leads to increased binding between cortical areas that are active at the moment of the arousal boost, i.e. task-relevant cortical areas (Verguts & Notebaert, 2009). Control is thus automatically implemented in the areas that play an important role specifically in the task at hand, since these areas are active when control is triggered.

The involvement of task-specific areas in control is supported by the fact that sequential control effects only occur within the same task, showing that control acts locally to task-specific information (Notebaert & Verguts, 2008). This idea is further supported by fMRI research, showing activation consistent with control implementation in sensory areas processing relevant and irrelevant stimulus material (Egner & Hirsch, 2005; Polk, Drake, Jonides, Smith, & Smith, 2008; Weissman, Warner, & Woldorff, 2004). For instance, in a Stroop-like task using pictures of faces as relevant stimuli, activation in the fusiform face area processing these relevant stimuli was affected by stimulus congruency (Egner & Hirsch, 2005). Similarly, incongruency was reflected in auditory or visual processing areas when auditory or visual stimuli respectively were relevant to task performance (Weissman et al., 2004). Finally, in addition to increased processing in relevant areas, also suppression of processing in irrelevant areas has been found (Polk et al., 2008). EEG research shows that the ACC triggers control in distant specific sensory areas through oscillatory synchronization (Cohen & Van Gaal, 2013; Cohen et al., 2009). For example, cross-frequency coupling between MFC and occipital areas processing stimuli increases following errors (Cohen et al., 2009). Finally, BOLD activity in the fronto-parietal control network is also correlated to modulations in alpha oscillations in specific visual areas processing relevant

or irrelevant stimuli. Higher alpha power is observed in areas processing irrelevant stimuli and lower alpha power is observed in areas processing relevant stimuli (Zumer et al., 2014). In conclusion, research suggests that control is implemented not only through a general fronto-parietal control network, but also acts locally, in areas specific to the task (Slagter et al., 2007; Weissman et al., 2004).

### THE COST OF COGNITIVE CONTROL

Cognitive control improves task performance, reducing errors and speeding RTs for challenging tasks. So why would control ever *not* be implemented? This is because control or mental effort, much like physical effort, also carries a cost (Kool, McGuire, Rosen, & Botvinick, 2010). So when making a decision about how much cognitive control to implement, potential benefits have to be weighed against the cost of control (Botvinick & Braver, 2015; Shenhav, Botvinick, & Cohen, 2013; Westbrook & Braver, 2015). The *expected value of control model* (EVC model; Shenhav et al., 2013) states that a decision about control is based on the expected value of control (EVC). This EVC is the net value of control: benefits minus cost. The EVC can be calculated for different control settings (types and levels of control) to select the most optimal setting. In the EVC calculation, the benefits of a certain control setting are determined by two types of information: (1) the probability of successful task performance given the control setting and (2) the profit of successful task performance. This means that cognitive control will be implemented if this will increase the probability of success and if this success is valuable. To decide if this is the case, two types of information are especially relevant, namely information about task difficulty and information

about potential reward. Cognitive control is only implemented when needed (for a difficult task), because only then control can increase the probability of success. Control is also only implemented when good performance pays off (when high reward is likely).

The importance of difficulty and reward information in the decision to implement control was formalized in the *adaptive effort model* (Verguts, Vassena, & Silvetti, 2015). This model states that the ACC and ventral striatum integrate information about difficulty and reward to allocate cognitive effort to cortical stimulus-action pathways, effectively implementing control and improving task performance. The model is able to explain a wide range of empirical findings, including classical cognitive control findings such as the sequential congruency effect and the proportion congruency effect. Importantly, this shows that the model exerts reactive as well as proactive control. It is therefore compatible with the DMC framework proposed by Braver (2012). fMRI research supports the interaction between reward and difficulty information and cognitive control, showing that reward and difficulty expectation trigger an overlapping brain network that contains areas of the fronto-parietal control network as well as subcortical areas likely involved in processing saliency (Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Vassena et al., 2014).

The experience or expectancy of response conflict leads to increased cognitive control (Aarts & Roelofs, 2011; Aarts et al., 2008; Gratton et al., 1992). Since we can view response conflict as a specific case of task difficulty, this provides evidence for the role of difficulty information in motivating control. Also reward plays an influential role in cognitive control. Reward has beneficial effects on control (Bijleveld, Custers, & Aarts, 2010; Botvinick &

Braver, 2015; Padmala & Pessoa, 2010, 2011) strongly suggesting that reward can provide the necessary motivation to implement control. In blocks of trials where reward is linked to task performance, control is increased (Leotti & Wager, 2010; Padmala & Pessoa, 2010) and also when a cue before a trial informs participants that a reward can be obtained, control is implemented (Aarts et al., 2014; Bijleveld et al., 2010; Knutson, 2005; Krebs et al., 2012; Padmala & Pessoa, 2011; Schevernels, Krebs, Santens, Woldorff, & Boehler, 2014).

In conclusion, because cognitive control poses a cost on mental resources, it has to be motivated. Both task difficulty and reward play an important and interacting role in motivational cognitive control.

### **THE TIME COURSE OF COGNITIVE CONTROL**

Although cognitive control has been ardently studied in the past decades, and solid theoretical frameworks have provided clarity and structural insights into control, some aspects of control and neural control processes remain relatively unknown. The time course of control is such an aspect. Although the brain areas involved in control have been thoroughly studied, the timescale on which they operate has received less attention. Also, typical control experiments are not designed to investigate the (fast) timing of control. Consequently, there is not yet a theoretical agreement on the time course of control. To improve control frameworks, this dissertation aimed to determine on what timescale control can be implemented, and to define the time course of neural processes involved in control.

Classical models of attentional control conceptualize control as a serial and thus relatively slow process (Posner & Presti, 1987; Shiffrin & Schneider, 1977). Consistently, the CMT typically predicts relatively slow reactive cognitive control adaptations, measured on a trial-by-trial basis. Within the DMC framework, proactive control is again conceptualized as rather slow. The CMT and DMC framework have inspired experiments exploring relatively slow control, such as the investigation of between-trial adaptation to response conflict (Gratton et al., 1992) or post-error adaptations for the next trial (Steinhauser et al., 2008). In contrast, associative models for control argue that control is implemented via associations between perceptual, motor, and control representations (Abrahamse et al., 2016; Egner, 2014; Verguts & Notebaert, 2008, 2009). A stimulus (for instance a conflicting stimulus) can trigger a control representation, which subsequently improves the signal-to-noise ratio of current processing pathways and influences activation in areas relevant to the task. This perspective on control predicts that control might be implemented associatively. Depending on the type and exact connectivity structure of the associations, cognitive control can thus be implemented rapidly, perhaps even during task execution.

To study the time course of cognitive control, EEG has proven very valuable due to its excellent temporal resolution. The timing of the N2 ERP component (Folstein & Van Petten, 2007) and of the peak of the frontal theta burst (Cavanagh et al., 2012) strongly suggest that conflict detection usually occurs around 200 to 300 ms post stimulus onset. It must be noted that this is also task-dependent: in the Stroop task conflict detection might occur later (Coderre, Conklin, & van Heuven, 2011; Rebai, Bernard, & Lannou, 1997). The timing of the ensuing control processes, and especially how fast these can occur is however less clear. Even ERP studies are usually not designed to

focus on fast within-trial control implementation (Larson, Clayson, & Baldwin, 2012; Van Veen & Carter, 2002). However, there is some evidence that fast control implementation can indeed occur. Fast control implementation was shown in an EEG frequency tagging experiment. On incongruent trials control was adaptively adjusted as attention towards task-relevant information increased continuously throughout the trial (Scherbaum, Fischer, Dshemuchadse, & Goschke, 2011). Also following errors, fast control implementation has been reported. Increases in oscillatory synchrony between the ACC and visual areas during the trial were observed as soon as 400 ms post stimulus onset (Cohen et al., 2009). Finally, it has also been suggested that reward can initiate fast within-trial cognitive control (Boehler, Hopf, Stoppel, & Krebs, 2012; Krebs, Boehler, & Woldorff, 2010).

One of the main aims of this dissertation is therefore to further specify the time course of cognitive control, and to test the hypothesis of associative control models that control can occur very rapidly, within the trial.

### **OUTLINE OF THIS DISSERTATION**

Based on the theoretical frameworks on cognitive control and the role of reward and difficulty information in motivating control, I hypothesized during my PhD that reward and difficulty information would influence cognitive control, both reactively and proactively. This created four possible research questions in a two by two structure: how will (1) reward and (2) difficulty information influence (1) reactive and (2) proactive control. As discussed above, the effect of reward on proactive control has been studied thoroughly in the past (Aarts et al., 2014; Bijleveld et al., 2010; Knutson,

2005; Krebs et al., 2012; Padmala & Pessoa, 2011; Schevernels et al., 2014), so this question will not be discussed in this dissertation. The three remaining questions in the two by two structure make up the three empirical chapters of this dissertation.

A second question is how cognitive control processes occur in time. Classical control theories, such as the CMT, conceptualize control as a rather slow process, occurring between trials, whereas recent associative models hypothesize that control can also occur very rapidly, since it relies on associations between stimulus and control representations. The time course of cognitive control processes thus makes another important focus of this dissertation and is assessed in every empirical chapter.

	Reward	Difficulty
Reactive control	Chapter 2	Chapter 3
Proactive control	see previous research	Chapter 4

*Figure 1.* Outline of this dissertation. Theoretical models on control predict that both reward and difficulty information will influence reactive and proactive control, providing four possible research questions. Three of these questions are addressed in the three empirical chapters of this dissertation. In Chapter 2, the effect of reward on reactive control was investigated. In Chapter 3, the effect of difficulty information, again on reactive control was investigated. In Chapter 4, the effect of difficulty information on proactive control was assessed.

## Chapter 2

In Chapter 2, the effects of *reward* information on *reactive control* were studied. In this behavioral study, the primary goal was to reveal the fast time course of control, triggered by reward information. Participants performed a visual discrimination task, requiring controlled attention. To test the prediction of fast control proposed by associative control models, reward information was presented either 200ms before, at the same time as, or 200ms after stimulus presentation. We investigated how a reward cue influences cognitive control in each timing condition, thus revealing the fast time course of control. Importantly, the reward manipulation was orthogonal to the response, ensuring that reward effects are not due to automatic activation of rewarded stimulus-response associations but truly reflect fast cognitive control implementation.

## Chapter 3

In Chapter 3, I studied the effects of *difficulty* information, again on *reactive control*. I show how the experience of difficulty triggers control. In this study, the experience of difficulty was manipulated through stimulus and response incongruency of the stimuli. Cognitive control frameworks state that the need for control is detected by mid-frontal brain areas and is implemented through a fronto-parietal network and sensory areas specific to the task. Associative control models further predict that this control implementation can occur on a fast timescale. In this chapter I used the temporal precision of EEG to investigate the time-course of control processes, with a focus on fast, within-trial control processes in sensory areas. Both an ERP and TF approached were used. A lateralized flanker task was applied to separate task-relevant from task-irrelevant visual areas by containing these to separate



hemispheres. Mid-frontal theta power and the difference in alpha power between task-relevant and task-irrelevant areas were investigated to show how fast control is implemented in specific sensory areas following stimulus and response conflict.

## Chapter 4

Finally, in Chapter 4 I again studied the effect of *difficulty* information, but this time one *proactive control*. Control theories state that difficulty information can serve as a cue for motivated control, implemented through a fronto-parietal control network. In this chapter a cued mental calculation task was used, where the cue provided participants with information about the difficulty of the upcoming calculation. Crucially, no motor preparation occurred in the cue-task interval, since the task did not require an immediate motor response. To identify a detailed and clear-cut (motor-free) electrophysiological signature of proactive control, EEG was recorded and I used both an ERP and TF approach. The effects of difficulty information on the stimulus preceding negativity (SPN) and power in the alpha frequency band during the cue-task interval were studied. These electrophysiological markers show the evolution of proactive control throughout this interval. In addition, intracranial local field potential recordings from a patient diagnosed with epilepsy were investigated. These recordings from cortical and subcortical areas, including posterior parietal cortex and striatum, provide electrophysiological data with both high spatial and temporal resolution. Hence these recordings presented an excellent opportunity to study the fronto-parietal network and subcortical areas underlying motivated proactive control.

### **General discussion**

In the general discussion the results of the three empirical chapters are reviewed and their relevance for cognitive control theories is evaluated. What these chapters have taught us about the time course and nature of cognitive control processes, and about the relevance of reward and difficulty information in triggering proactive and reactive control is also discussed.

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## CHAPTER 2

### THE TIME COURSE OF COGNITIVE CONTROL IMPLEMENTATION<sup>1</sup>

*Optimally recruiting cognitive control is a key factor in efficient task performance. In line with influential cognitive control theories, earlier work assumed that control is relatively slow. We challenge this notion and test whether control can also be implemented more rapidly by investigating the time course of cognitive control. In two experiments a visual discrimination paradigm was applied. A reward cue was presented with variable intervals to target onset. The results showed that reward cues can rapidly improve performance. Importantly, the reward manipulation was orthogonal to the response, ensuring that the reward effect was due to fast cognitive control implementation rather than to automatic activation of rewarded S-R associations. We also empirically specify the temporal limits of cognitive control, since the reward cue had no effect when it was presented shortly after target onset, during task execution.*

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<sup>1</sup> Janssens, C., De Loof, E., Pourtois, G., & Verguts, T. (2016). The time course of cognitive control implementation. *PSYCHONOMIC BULLETIN & REVIEW*, 22(6).

## INTRODUCTION

Humans are cognitive beings with intentions and goals. To achieve those goals, they monitor actions and their outcomes to adjust attention and effort levels to suit the situation (Botvinick, Cohen, & Carter, 2004). This set of top-down processes is referred to as ‘cognitive control’ as it allows controlling basic cognitive processes. Control improves task performance, but carries a cost (Kool, McGuire, Rosen, & Botvinick, 2010). To decide if enhancing control is useful, humans integrate cues for difficulty and reward. Evidence for cue integration has been reported in several fMRI studies (Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Vassena et al., 2014) and their influence on control implementation was formalized in computational reinforcement learning models (Verguts, Vassena, & Silvetti, 2015).

Classical models of cognitive control conceptualize control as a serial and thus relatively slow process (Posner & Presti, 1987; Shiffrin & Schneider, 1977), as do more recent models where reactive control is updated between-trials in response to experienced task difficulty (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick et al., 2004). Also proactive control (in response to cues before task onset) is conceptualized as rather slow (Braver, 2012). These models have inspired experimental designs exploring relatively slow control, such as the investigation of between-trial adaptation (Gratton, Coles, & Donchin, 1992). Conversely, recent associative models argue that control is implemented via associations between perceptual, motor, and control representations (Egner, 2014; Verguts & Notebaert, 2008, 2009). In this view, a difficult or potentially rewarding stimulus triggers a control representation, which subsequently improves the signal-to-noise ratio of current processing pathways. From such a point of view, control might be implemented more rapidly, perhaps even during



task execution. Yet, its exact time course was not clearly specified in such models, perhaps due to lack of empirical specification of this time course.

Research has recently started to look at the time course of control. Evidence for fast control implementation was reported in an EEG frequency tagging experiment (Scherbaum, Fischer, Dshemuchadse, & Goschke, 2011) showing that on difficult, incongruent trials, attention towards task-relevant information increases continuously throughout the trial. A large literature shows that cues that are directly relevant for task execution are processed more efficiently (e.g. Kunde, Kiesel, & Hoffmann, 2003; Spruyt, De Houwer, Everaert, & Hermans, 2012). Item congruency (as in Scherbaum et al., 2011) is in this sense directly relevant for task execution and can thus be expected to be processed efficiently. However it remains unclear to what extent also task-irrelevant cues – such as reward cues, which are uninformative about the upcoming task – can induce control enhancements on a faster time-scale, as predicted by associative models.

The influence of reward on performance has been extensively studied. Beneficial effects of reward on cognitive control were found consistently (Bijleveld, Custers, & Aarts, 2010; Botvinick & Braver, 2015; Padmala & Pessoa, 2010, 2011) strongly suggesting that reward motivates participants to intensify control. This earlier work mostly demonstrated relatively slow adjustments. In many studies reward was manipulated between subjects (Huebner & Schloesser, 2010) or between blocks (Leotti & Wager, 2010; Padmala & Pessoa, 2010). This allows participants to deliberately increase control, but its time scale remains unknown. Another common procedure is to present cues indicating upcoming reward before task onset. Here also, there is ample time for cue processing as it is always presented with a long interval (several seconds) before task onset (Aarts

et al., 2014; Bijleveld et al., 2010; Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; Krebs et al., 2012; Padmala & Pessoa, 2011; Schevernels, Krebs, Santens, Woldorff, & Boehler, 2014).

Studies investigating faster reward-based control implementation are scarce. Krebs et al. (2010) used a Stroop task in which trials with certain ink colors were rewarded and showed that responses were faster for those trials than non-rewarded ones. Since reward information was presented only at task onset, this suggests control can be implemented on a very short time scale. A similar fast reward effect was shown for response inhibition (Boehler, Hopf, Stoppel, & Krebs, 2012). In both studies however, specific rewarded stimuli were linked to specific responses. Hence, when a stimulus and subsequent response were rewarded, the S-R link was possibly strengthened. When the rewarded stimulus was then presented again, the associated response was automatically activated, possibly speeding task performance (Damian, 2001). Studies avoiding this issue by using an orthogonal S-R mapping are scarce and only report evidence for slow control (Neely, 1977). The latter priming study concluded that control implementation takes at least 400 ms.

As mentioned above, associative models theoretically allow fast control but as the literature review illustrates, an empirical specification of its time course is currently lacking. Filling this gap is the aim of the current study. A visual discrimination task was used in combination with symbolic reward cues unrelated to the target stimulus and response. Three different fast cue timings allowed investigating the time course of cognitive control implementation. The reward cue was presented either 200 ms before, simultaneous to, or 200 ms after target onset. This third condition was included to study ultra-rapid control enhancement during a trial, when task execution has already been initiated. Note

that for all timing conditions, the cue-target interval was considerably shorter than in the reward studies discussed above (Aarts et al., 2014; Bijleveld et al., 2010; Krebs et al., 2012; Schevernels et al., 2014). Crucially, the cues were uncorrelated with responses so no S-R learning could occur for the cue. This ensures we measured control rather than automatic S-R effects.

## EXPERIMENT 1

### Method

18 paid subjects participated. Reward consisted of points linked to winning a gift voucher. Stimuli were presented centrally on a black background in 18 blocks of 48 trials. A trial (Figure 1) consisted of a full grey circle (1000 ms), the target, being an opening in the top and bottom of the grey circle (400 ms), a fixation cross (600 ms) and feedback (600 ms). Participants indicated the larger of the two openings with a button press. There were two difficulty levels, determined by the size difference in the openings. A reward cue was presented, indicating no information (+# in white, 50% of trials), reward (+4 in green, 25% of trials) or no reward (+0 in red, 25% of trials). Cue timing was variable: 200 ms before (pre), simultaneous to (at) or 200 ms after (post) target onset (all timings equally probable). Feedback depended on the reward manipulation and the response (+4 or +0 in green for correct and -4 or -0 for error trials). 50% of all trials were rewarded (if correct). All trial types were presented randomly intermixed.

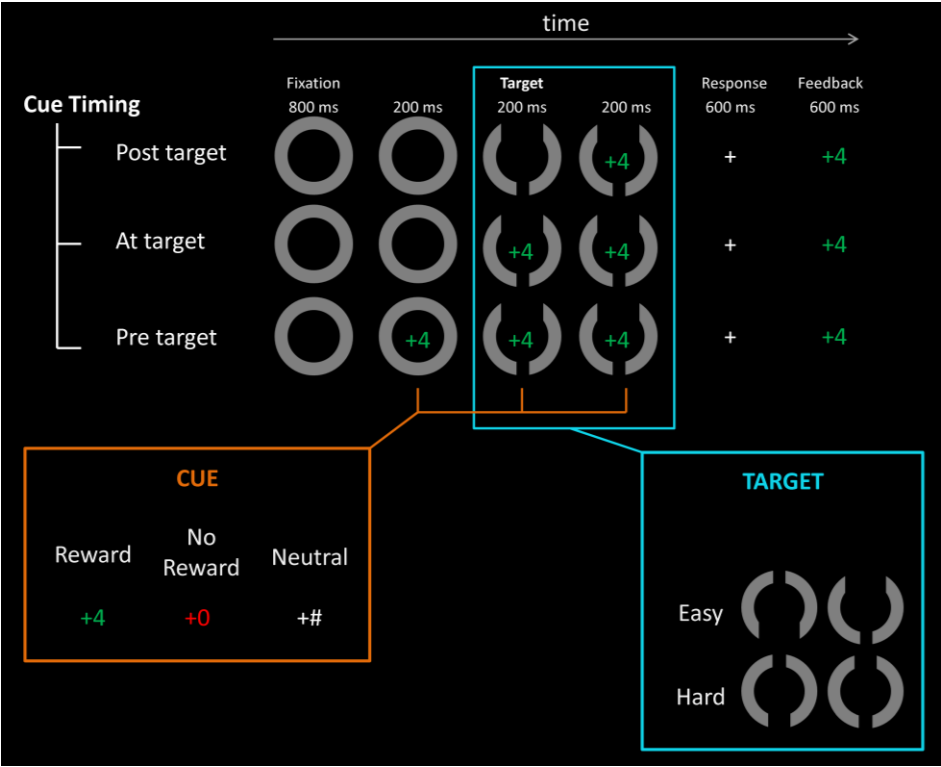


Figure 1. Experimental paradigm. Participants made a visual target discrimination. A reward cue was presented with different timing relative to the target, either post, at or pre target onset. Cues could be informative (indicating reward or no reward) or neutral.

A linear mixed effects (LME) model was fitted for reaction times (RTs) with several predictors: reward (reward vs. no reward vs. neutral), cue timing (pre vs. at vs. post target onset), location of the largest opening (location; top vs. bottom) and difficulty (easy vs. hard). Also, a random intercept across subjects was modeled. Although a maximal random effects structure has been proposed as optimal (Barr, Levy, Scheepers, & Tily, 2013), it has recently been argued that this often results in overparameterized models that fail to converge (Bates, Kliegl,

Vasishth, & Baayen, 2015). Therefore a model building strategy was applied. The added value of a random slope per subject was tested by comparing the basic model to a model with a random slope for one of the predictors. This was then repeated for every predictor. Significant random slopes were obtained for location and difficulty, which were added to the final model. Effects in this final model were tested by ANOVA type III; F-statistics were calculated with Kenward-Roger adjustment of the degrees of freedom (Kenward & Roger, 1997).

A generalized linear mixed effects (GLME) model for binary data was fitted for accuracy with the same predictors and model selection procedure as for RT analysis. The final model included a random slope for location. Since no small-sample adjustments of the degrees of freedom for binary responses have been proposed in the literature, chi-square statistics rather than F-statistics are reported.

## Results

### RT

Results showed a main effect of difficulty,  $F(1, 17) = 127.66, p < 0.001$  (slower RTs for difficult trials), and cue timing,  $F(1, 13336) = 22.36, p < 0.001$ . RTs were slowest in the at condition (compared to post:  $t(1, 17) = 6.00, p < 0.001$ ; compared to pre:  $t(1, 17) = 5.17, p < 0.001$ ) and fastest in the pre condition (compared to post:  $t(1, 17) = 2.46, p = 0.03$ ). Crucially, there was a significant main effect of reward information,  $F(1, 13335) = 4.04, p = 0.02$  which interacted with cue timing,  $F(2, 13335) = 7.20, p < 0.001$  (Figure 2a). To investigate this interaction, the effect of reward was tested for each cue timing separately. This revealed no significant effect for the post condition,  $F(2, 16) = 0.43, p = 0.66$ , a marginally significant effect for the at condition,  $F(2, 16) = 2.77, p = 0.09$  and a

significant effect in the pre condition,  $F(2, 16) = 6.54, p = 0.008$ . To further qualify the effect of reward in the pre condition, paired t-tests were performed, revealing a difference between reward and no-reward cues,  $t(1, 17) = 4.52, p < 0.001$ , and between reward cues and neutral cues,  $t(1, 17) = 2.30, p = 0.03$  but not between no-reward cues and neutral cues,  $t(1, 17) = 1.76, p = 0.10$ .

### Accuracy

There was a main effect of difficulty,  $\chi^2(1, N = 18) = 74.76, p < .001$  (more errors for difficult trials) and of cue timing,  $\chi^2(1, N = 18) = 20.82, p < 0.001$ . Fewest errors were made in the post condition (compared to at:  $t(1, 17) = 3.18, p < 0.01$ ; compared to pre:  $t(1, 17) = 3.61, p < 0.01$ ). There was no difference between the at and pre condition,  $t(1, 17) = 1.28, p = 0.22$ . There was no main effect of reward,  $\chi^2(2, N = 18) = 2.46, p = 0.29$ , but there was an interaction of reward and cue timing,  $\chi^2(4, N = 18) = 10.02, p = 0.04$  (Figure 2b). To investigate this interaction, the reward effect was modeled for each cue timing separately. There was no significant reward effect in the post and at conditions,  $\chi^2(2, N = 18) = 1.32, p = 0.52$  and  $\chi^2(2, N = 18) = 1.04, p = 0.60$  respectively, but there was a reward effect in the pre condition,  $\chi^2(2, N = 18) = 15.37, p < 0.001$ .

### Discussion

We investigated how rapidly reward prospect can modulate task performance. The beneficial reward effect was clear when the cue preceded target onset, both for RTs and accuracy, indicating truly enhanced processing efficiency rather than a shift in speed-accuracy tradeoff. The reward effect was less clear when cue and target appeared simultaneously, with only a marginally significant

effect for RTs and no effect for accuracy, and disappeared altogether when the cue followed target onset.

To explore the marginally significant effect in the simultaneous condition and to push the timing limits of the fast control adjustments observed in Experiment 1, cue processing was reduced to its simplest form in Experiment 2. In Experiment 1 participants distinguished between three intermixed cue types (neutral, reward and no-reward). In Experiment 2 we confined neutral cues and informative cues (reward or no-reward) to separate, alternating blocks, thus reducing the number of cues and making distinction easier. Further, we increased power by testing a larger number of subjects.

## EXPERIMENT 2

### Method

27 paid subjects participated. The method was nearly identical to that of Experiment 1 (Figure 1), except that trials with neutral cues and trials with informative cues appeared in separate alternating blocks. The predictors and model selection procedure were identical to that of Experiment 1. Both the model for RTs and accuracy included random slopes for location and difficulty.

### Results

In a preliminary analysis, neutral blocks were compared to informative blocks by fitting an LME model for RTs with block type (neutral vs. informative) as the fixed factor and a random slope for block type. Results showed an effect of block type, with faster RTs in neutral blocks compared to informative blocks,  $F(1, 26) = 7.49$ ,  $p = 0.01$ . There was no block difference for error rates (tested

with a GLME model for binary responses),  $\chi^2(1, N = 27) = 2.48, p = 0.11$ . Because of this block effect, neutral trials cannot be straightforwardly compared to reward and no-reward trials. Hence in the remainder of the results we focus on informative blocks only.

### RT

A main effect was observed of difficulty,  $F(1, 26) = 115, p < 0.001$  (slower RTs for difficult trials) and of cue timing,  $F(1, 26) = 74.24, p < 0.001$ . RTs were slowest in the at condition (compared to post:  $t(1, 26) = 5.16, p < 0.001$ ; compared to pre:  $t(1, 26) = 7.68, p < 0.001$ ) and fastest in the pre condition (compared to post:  $t(1, 26) = 3.15, p < 0.01$ ). There was a main effect of reward,  $F(1, 9871) = 14.88, p < 0.001$ . The interaction of reward and cue timing was marginally significant,  $F(1, 9872) = 3.65, p = 0.056$  (Figure 2c; note that an F-statistic is by definition two-sided). To investigate the interaction further, separate models were fitted for each timing condition. These revealed no effect of reward in the post condition,  $F(1, 3372) = 0.56, p = 0.46$ , but did show an effect in the pre and at condition,  $F(1, 3250) = 11.69, p < 0.001$ , and  $F(1, 3260) = 4.72, p = 0.03$ , respectively.

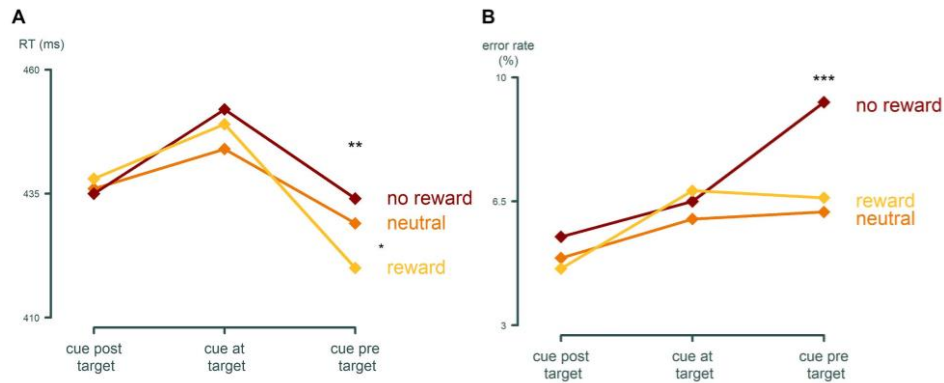
### Accuracy

There was a main effect of difficulty,  $\chi^2(1, N = 27) = 133.87, p < .0001$  (more errors for difficult trials), and of cue timing,  $\chi^2(1, N = 27) = 29.37, p < 0.001$ . Fewest errors were made in the post condition (compared to at:  $t(1, 26) = 3.37, p < 0.01$ ; compared to pre:  $t(1, 26) = 2.20, p = 0.04$ ). There was no difference between the at and pre condition,  $t(1, 26) = 0.22, p = 0.82$ . There was a main effect of reward,  $\chi^2(2, N = 27) = 6.35, p = 0.01$ , and an interaction of reward and cue timing,  $\chi^2(4, N = 27) = 7.93, p < 0.01$  (Figure 2d). Tests for each cue timing

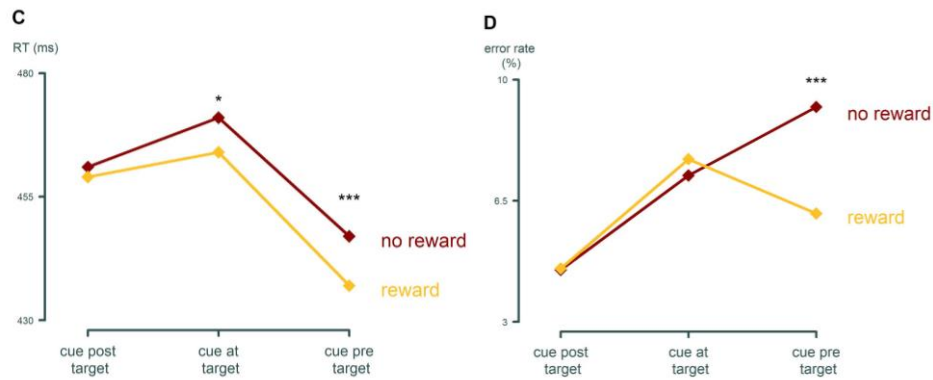


separately revealed no significant reward effect for the post or at condition,  $\chi^2(2, N = 27) = 0.005, p = 0.94$  and  $\chi^2(2, N = 27) = 0.34, p = 0.56$  respectively, but there was an effect for the pre condition,  $\chi^2(2, N = 27) = 15.37, p < 0.001$

## Experiment 1



## Experiment 2



*Figure 2.* Experiment 1: RTs (A) and error rates (B) were significantly influenced by reward in the pre condition. The reward effect is mainly driven by response speeding for reward trials relative to neutral trials (plotted in yellow and orange, A) and by an increase in error rate for no-reward trials compared to neutral trials (plotted in red and orange, B). Experiment 2: RTs (C) were significantly influenced by reward in the pre and at condition, error rates (D) were only influenced by reward in the pre condition. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$

## GENERAL DISCUSSION

In two experiments we demonstrated that control can be rapidly enhanced in response to reward. The use of three timing conditions also provides novel insights into the nature and time course of cognitive control implementation. When a reward-predictive cue was presented 200 ms before target onset, it improved processing efficiency. The effect of reward diminished as less time was available for cue processing, with smaller effects for simultaneous cue and target presentation, and no effect for cues presented after target onset.

One might argue that difficulty was unmatched across timing conditions: the less time there was to process the cue, the more difficult the task might have become. Since reward and difficulty cues are weighted in the decision to increase control, increased difficulty might eliminate a reward effect. However, RTs were faster and fewer errors were made in the post condition than in the simultaneous condition, indicating that, if anything, the task was more difficult in the simultaneous condition, where we did find a reward effect.

A broad research effort is uncovering the fast and far-reaching influences of reward on cognition. Visual attention research has extensively shown that rewarded stimuli capture attention automatically, even when this is counterproductive (Hickey & van Zoest, 2012; Pearson, Donkin, Tran, Most, & Le Pelley, 2015). Interestingly this might imply that the currently reported reward effects are an underestimation of enhanced control. Reward cues automatically attracted attention away from the actual discrimination task stimulus, which would cause a slowing of responses rather than the observed speeding.

Our findings challenge models that conceptualize cognitive control as a slow process (Botvinick et al., 2001, 2004; Braver, 2012; Posner & Presti, 1987;

Shiffrin & Schneider, 1977). Such models have been challenged before in congruency tasks. There, the magnitude of the congruency effect depends on the proportion of incongruent trials in the task. This proportion congruency effect (PCE) is typically ascribed to a slow process that tonically enhances control in the context of high proportions of incongruency (Braver, 2012). In contrast, Crump et al. (2006) showed that the PCE also occurs if the proportion congruency only becomes apparent at stimulus onset, suggesting a fast, stimulus-driven control enhancement. Our research shows that also task-irrelevant reward cues (i.e., which are uninformative for the task) can induce such rapid adjustments.

The current research supports more recent accounts that conceptualize cognitive control from an associative learning viewpoint (Egner, 2014; Verguts & Notebaert, 2008, 2009) and adds to these models by specifying the time constraints of cognitive control. We emphasized that we were careful to exclude stimulus-response learning; however, what then is learned in the associative learning point of view? We argue that subjects learn associations between perceptual (in this case, reward cue) and *control* (rather than motor) representations, which are automatically activated with the next cue appearance (e.g., in event files: Hommel, 1998; Waszak, Hommel, & Allport, 2004) and quickly trigger appropriate levels of control. Future research is needed to determine whether such cueing requires training at all (instruction-based control implementation) and whether its timing changes with extensive training.

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## CHAPTER 3

### OCCIPITAL ALPHA POWER REVEALS FAST ATTENTIONAL INHIBITION OF INCONGRUENT DISTRACTORS <sup>1</sup>

*Recent associative models of cognitive control hypothesize that cognitive control can be learned (optimized) for task-specific settings, via associations between perceptual, motor, and control representations; and once learned, can be implemented rapidly. Mid-frontal brain areas signal the need for control, and control is subsequently implemented by biasing sensory representations, boosting or suppressing activity in brain areas processing task-relevant or task-irrelevant information. To assess the timescale of these processes, we employed EEG. In order to achieve the spatial specificity needed to pinpoint control implementation in specific sensory areas, we used a flanker task with incongruent flankers in only one hemifield (congruent flankers in the other hemifield). Event-related potentials (ERPs) revealed modulations specifically in visual processing areas contralateral to the incongruent flankers. To test whether these modulations reflect increased or decreased processing of incongruent flankers, we investigated alpha power, a marker for attentional inhibition. Importantly, we show increased alpha power over visual areas processing incongruent flankers from 300 to 500 ms post-stimulus onset. This suggests fast cognitive control by attentional inhibition for*

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<sup>1</sup> Janssens, C., De Loof, E., Boehler, C. N., Pourtois, G., & Verguts, T. (submitted). Occipital alpha power reveals fast attentional inhibition of incongruent distractors.

*information disrupting goal-oriented actions. Additionally, we show that mid-frontal theta earlier in the trial is also modulated by incongruency, and that theta power predicts subsequent control implementation. This supports the hypothesis that mid-frontal conflict detection leads to control implementation, and reveals that these mechanisms take place on a fast, within-trial timescale. Notably, we show conflict detection and attentional inhibition for both stimulus-incongruent (SI) and response-incongruent (RI) trials, showing that response conflict is not a prerequisite for control implementation.*

## INTRODUCTION

Routine activities, such as driving a car, are often performed automatically, without consciously deciding which actions to perform. However, when a cyclist suddenly crosses the street, the flow of automatic functioning is broken and we are forced to focus attention on relevant stimuli in the environment to guide deliberate actions. Such goal-directed behavior relies on cognitive control, a set of top-down mechanisms employed to regulate more basic processes (Botvinick, Cohen, & Carter, 2004). Since cognitive control is vital for everyday functioning, it has been extensively studied in psychology, often with congruency tasks (Eriksen & Eriksen, 1974; Hazeltine, Poldrack, & Gabrieli, 2000; MacLeod, 1991; Stroop, 1935). In such tasks a response conflict is induced between a target stimulus and distracting stimuli in order to manipulate cognitive control.

Classical theoretical models assume cognitive control to be a rather slow process (Posner & Presti, 1987; Shiffrin & Schneider, 1977). Consistently, computational models (e.g., conflict monitoring theory, Botvinick, Braver, Barch, Carter, & Cohen, 2001) have typically implemented relatively slow (trial-to-trial) cognitive control. In contrast, recent associative models of control do predict that control adaptation can occur rapidly, within trials. Such models state that control is implemented via associations between perceptual, motor, and control representations (Abrahamse, Braem, Notebaert, & Verguts, 2016; Egner, 2014; Verguts & Notebaert, 2008, 2009). Perceptual or motor input quickly activates associated control representations, which in turn influence perceptual or motor processes. Also reward representations are known to trigger or enhance control (Stürmer, Nigbur, Schacht, & Sommer, 2011). In a behavioral study, Janssens, De Loof, Pourtois, & Verguts (2016) already show the fast associative nature of this by showing rapid control implementation in response to a reward cue.

On the neural level, conflict is thought to trigger control representations in mid-frontal brain areas (e.g., anterior cingulate cortex (ACC)). These representations in turn activate sensory cortical areas responsible for stimulus processing (Botvinick et al., 2001). This purported pathway has gained some support from fMRI, where congruency boosts activity in task-relevant sensory areas (Egner & Hirsch, 2005; Weissman, Warner, & Woldorff, 2004) or suppresses activity in irrelevant sensory areas (Polk, Drake, Jonides, Smith, & Smith, 2008). However, due to the slow resolution of the BOLD signal, these studies cannot reveal the timescale of these sensory adaptations and thus cannot directly show the fast associative nature of these modulations. EEG is a temporally much more precise technique and has been used to investigate fast control processes. Scherbaum, Fischer, Dshemuchadse, & Goschke (2011) applied EEG with frequency tagging and showed that attention focused on the target stimulus increased during stimulus processing, whereas attention to distractors decreased. Importantly these changes occurred continuously throughout the trial, demonstrating the fast dynamics of the control system.

To localize sensory control processes in both time and specific sensory regions, Appelbaum, Smith, Boehler, Chen and Woldorff (2011) used ERPs to study distractor processing in sensory brain areas during a trial. They administered a lateralized Eriksen flanker task, in which incongruent flanker letters appeared in only one visual hemifield (congruent flankers always appeared in the other hemifield). When comparing occipital activation for left vs. right hemifield incongruent flanker trials, they obtained a lateralized incongruency difference (LID), showing differential ERP activity to incongruent versus congruent flankers. However, it remains to be tested whether the LID is caused by the visual discrepancy between target and flankers, or by the response conflict. In other words, it is unclear whether this processing reflects bottom-up attentional capture

by visually distinct flankers or instead an active control process downregulating attention for response-conflicting flankers. Since this study only included congruent (CON) and response incongruent (RI) trials, differences cannot be unambiguously attributed to the response incongruency. Moreover, it remains unclear how to interpret the sign of an ERP voltage difference.

To address these issues, we introduced stimulus incongruent (SI) stimuli, in which there is a visual discrepancy between target and flanker, but no response incongruency. This allows an unambiguous attribution of the effects of differences between flankers and targets. More broadly, the importance of the distinction between RI and SI is illustrated by fMRI and EEG research demonstrating ACC activation for RI but not for SI trials (Van Veen & Carter, 2002; Van Veen, Cohen, Botvinick, Stenger, & Carter, 2001, but see Wendt, Heldmann, Münte, & Kluwe, 2007).

A second important feature of our study is a time-frequency decomposition of the EEG data. Time-frequency analysis of EEG data allows to study changes in power over time in separate frequency bands. Unlike the polarity of an ERP component, which cannot be linked in a straightforward manner to increases or decreases in neural activity, changes in power in specific frequency bands allow for relatively clear interpretations of the underlying cognitive process. In particular, power in the alpha range (approximately 8 to 12 Hz) is increased in sensory areas processing distracting stimuli in sustained attention tasks (Kelly, Lalor, Reilly, & Foxe, 2006; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000). It is thought that such alpha power enhancements are used for active inhibition of cortical areas (Jensen, Bonnefond, & VanRullen, 2012; Jensen & Mazaheri, 2010). Furthermore, alpha power is negatively correlated with brain activity (Haegens, Nacher, Luna, Romo, & Jensen, 2011; Laufs et al., 2003; Ritter,

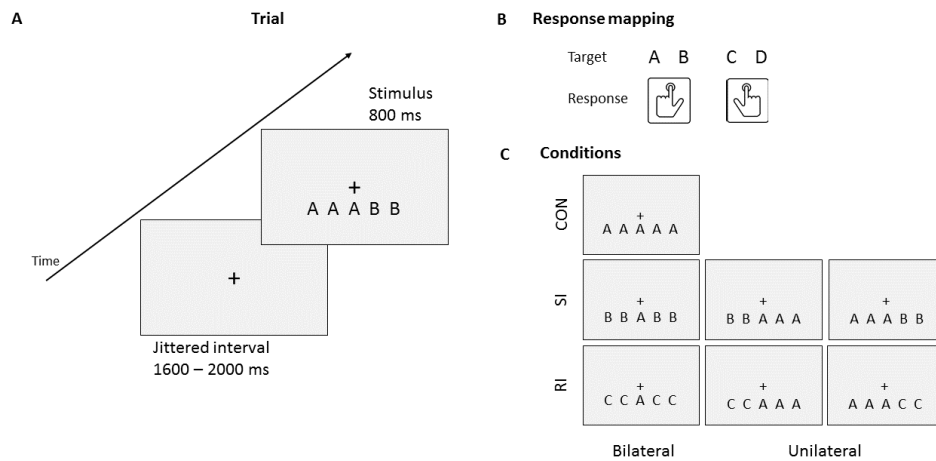
Moosmann, & Villringer, 2009). In general, changes in alpha power are a well-established empirical index of attentional modulation and thus offer a powerful tool to investigate fast sensory-specific cognitive control. In addition, power in the theta band (approximately 4 to 8 Hz) has been coupled with conflict and error detection processes, since frontal theta power is increased in a wide variety of cognitive control tasks (Cavanagh, Zambrano-Vazquez, & Allen, 2012; Cohen, van Gaal, Ridderinkhof, & Lamme, 2009). We therefore also investigated the time course of mid-frontal theta power.

The current study combined lateralized incongruency (both SI and RI) with time-frequency analysis to investigate the time course of control in visual sensory areas. The LID ERP (Appelbaum et al., 2011) shows that incongruent flankers are rapidly processed. If flankers visually distinct from the target draw attention, we predicted less alpha power (more attention) in areas processing these flankers than in areas processing flankers identical to the target. Also, we predicted that this modulation of alpha would be observed both in SI and RI conditions. On the other hand, if cognitive control operates by inhibiting attention for response-conflicting flankers, we predicted the opposite, namely more alpha power (less attention) in areas processing incongruent flankers. Moreover, we predicted that this active control process would be triggered by response conflict, and thus would only appear in the RI condition, but not in the SI condition. In this study, alpha power was compared across CON, SI, and RI conditions to pit these predictions against one another. Finally, we also investigated the relation of sensory modulations with activity in frontal conflict detection areas by linking alpha power to frontal theta power, a likely neural marker for ACC conflict processing.

## METHODS

### Experimental design

Twenty paid subjects participated to this experiment. Participants performed a flanker task similar to the one used by Appelbaum et al. (2011). An overview of the paradigm and stimuli is presented in Figure 1. A total of 384 trials were presented in 16 blocks of 24 trials, interspersed by self-paced breaks. Stimuli consisting of five letters were presented for 800 ms, mixed with jittered interstimulus intervals sampled from a uniform distribution (1600-2000 ms). The presented stimulus consisted of one central target letter and four flanker letters, two to the left and two to the right of the central target (see Figure 1A). Stimulus letters came from a set of four letters. There were two possible sets of letters (set 1 = ABCD, set 2 = WXYZ). Sets were counterbalanced across participants, so each participant only received letters from one set. Participants were instructed to respond to the identity of the central target letter with a button press as soon as possible. Two letters mapped onto one response (see Figure 1B). Since the experiment took place following another similar experiment (same experiment for each participant; outside the scope of this paper) with the same response mapping, this mapping was well-learned by the beginning of the experiment. Stimuli were congruent (50%), stimulus incongruent (SI, 25%), or response incongruent (RI, 25%). For both types of incongruent stimuli, incongruent flankers were presented on both sides of the central target (33%) or on only one side of the central target (33% only left and 33% only right). If incongruent flankers were presented on one side of the target, congruent flankers were presented on the opposite side (see Figure 1C).



*Figure 1.* Overview of the flanker paradigm. (A) A stimulus was presented (800 ms) consisting of one central target letter and two flanker letters on each side of the target. Stimuli were interspersed with a jittered interval (1600-2000 ms). (B) There were four possible targets, linked to only two responses. (C) There were congruent (CON, 50 %), stimulus-incongruent (SI, 25%) and response-incongruent (RI, 25%) trials in the experiment. SI and RI trials could have bilaterally incongruent flankers (33%) or unilaterally incongruent flankers (left or right hemifield, both 33%).

### EEG data acquisition, processing and analysis

Continuous EEG activity was acquired at 512 Hz using a 64-channel (pin-type) Biosemi Active Two system (<http://www.biosemi.com>) referenced to the CMS-DRL ground and positioned according to the extended 10/20 international EEG system. Six additional electrodes were attached to the head: left and right mastoids, two electrodes for vertical and horizontal electro-oculogram.



EEG data were analyzed using EEGLAB (Delorme & Makeig, 2004) and ERPLAB (<http://erpinfo.org/erplab>) software, running on MATLAB. The data were re-referenced offline to linked mastoids. Independent component analysis (ICA) was performed on continuous data to identify and remove components associated with eye blink and horizontal eye movement artifacts. Epochs of -200 to +1000 ms locked to stimulus onset were selected. Semi-automatic artifact rejection was applied to the data using a 200  $\mu$ V threshold for initial artifact marking and visual inspection for final artifact removal.

For ERP analysis the epochs were baseline corrected to the pre-stimulus period. Next, the epochs were averaged per condition per participant and a grand average across participants was created resulting in one average ERP per condition. To enhance spatial resolution, these averages were transformed using the CSD toolbox for Laplacian transformation (Kayser & Tenke, 2006; <http://psychophysiology.cpmc.columbia.edu/software/CSDtoolbox>). Current source densities (CSDs) were calculated according to the spherical spline algorithm of Perrin, Pernier, Bertrand, & Echallier (1989), using a 10 cm head radius and a smoothing constant of 1–5.

Previous research by Appelbaum et al. (2011) used the LID to show activity specific to incongruent flankers. The LID was computed by subtracting the signal for trials with incongruent flankers in the right hemifield (e.g., AAA\*\*); here, \* can be any SI or RI flanker in the stimulus set, e.g., AAABB or AAACC) from the signal for trials with incongruent flankers in the left hemifield (\*\*AAA). Note that the LID shown by Appelbaum et al. (2011) in Figure 3C is defined as contra – ipsilateral flanker presentation, resulting in a symmetrical difference by definition, whereas the LID here is defined as left – right flanker presentation, resulting in a typically non-symmetrical difference. The LID was quantified at electrodes PO7

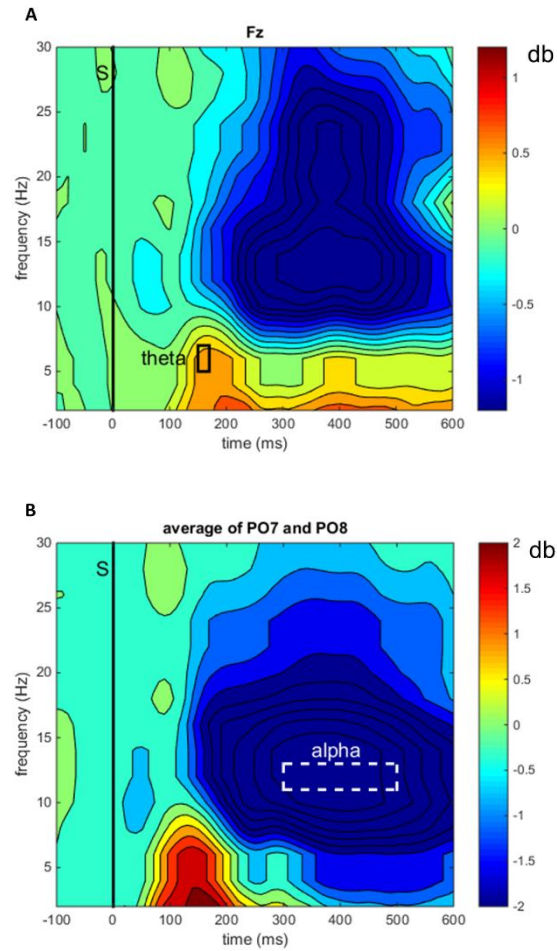
(left hemisphere) and PO8 (right hemisphere) for further analysis. These electrode sites were selected based on Appelbaum et al. (2011) and on previous literature showing that these electrode locations index lateralized visual attention processes (Eimer, 1996; Hickey, Di Lollo, & McDonald, 2009). To investigate the LID, the interaction of electrode site (left vs. right hemisphere) and side of the incongruent flankers (left vs. right visual hemifield) was tested. To determine differences in LID for SI vs. RI conditions, congruency type was also added to the analysis, resulting in a repeated-measures ANOVA performed for ERP amplitudes with three factors: (1) congruency (RI vs SI), (2) electrode site (left hemisphere vs right hemisphere) and (3) incongruent flanker side (left hemifield vs right hemifield). This analysis was done for a number of different time windows, ranging from 100 to 600 ms post stimulus onset in steps of 50 ms (selected times based on Appelbaum et al., 2011).

For the time-frequency analysis, Fast-Fourier Transform (FFT) was applied to the selected epochs in a moving window (width: 250 time points/488 ms, with Hann tapering), resulting in power estimates ranging from -100 ms to 600 ms (step 10 ms) locked to stimulus onset. Single trial event-related spectral perturbation (ERSP; i.e., power) estimates were acquired using the *newtimef* function from EEGLAB. Estimates were obtained for 15 uniformly distributed frequencies ranging from 2 to 30 Hz. Obtained output of the function was baseline corrected to the pre-stimulus period (baseline per subject, frequency, electrode and condition), and then converted to decibel. Note that due to decibel conversion, the sum of the baseline is not necessarily zero and there may appear to be differences between conditions at stimulus onset (approach based on Cohen, 2014).

We defined our time-frequency ROIs (TF-ROIs) based on the grand-average time-frequency analysis (as in Cavanagh et al., 2012, see Figure 2), and hence

independent of the specific research question. This revealed a power increase in the theta band (4-8 Hz) followed by a power decrease in the alpha band (8-14 Hz). For the purpose of the research question, we selected occipital regions: PO7 for the left hemisphere, PO8 for the right hemisphere. These same electrodes were used to determine the LID and are commonly used when investigating occipital alpha (e.g. Kelly et al., 2006). For frontal regions electrode Fz was selected. This electrode has a location similar to that used by Appelbaum et al. (2011).

Both occipital alpha and frontal theta power were analyzed. Based on the TF-ROIs (see Figure 2) occipital alpha power was defined as mean power at 12 Hz in the interval 300-500 ms post stimulus onset, representing the observed alpha power decrease. Frontal theta was defined as the peak amplitude of the initial theta power increase (power at 6 Hz at 160 ms post stimulus onset). Power estimates were standardized per subject, and outliers were removed (more than four standard deviations from mean) prior to statistical analyses.



*Figure 2.* ERSP (power) locked to stimulus presentation (at time 0) at frontal (Fz, panel A) and occipital (average of PO7 and PO8, panel B) sites. A power increase in the theta band (3 – 8 Hz) peaking around 160 ms was followed by a power decrease in the alpha band (8 – 14 Hz) peaking between 300 and 500 ms. TF-ROIs were based on this pattern of power changes.

## RESULTS

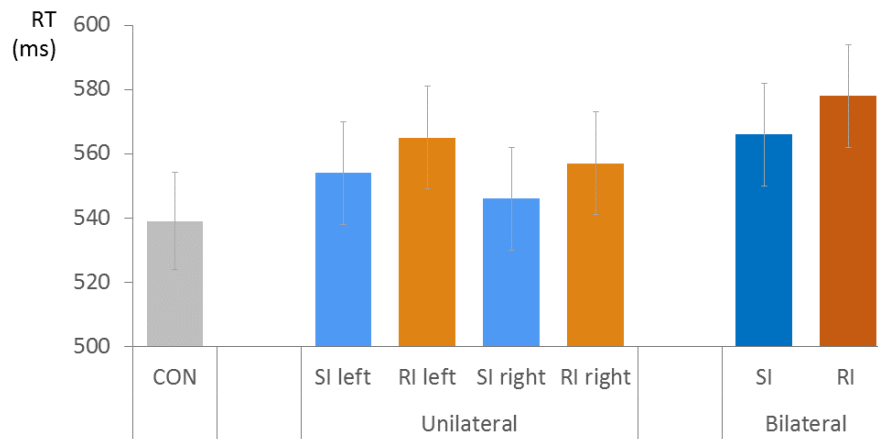
### Behavioral results

For RT analysis (see Figure 3), error trials and post-error trials were removed. First, a linear mixed effects (LME) model was fitted for RTs with congruency (CON vs. SI vs. RI) as a fixed factor and a random intercept per subject. Results show a main effect of congruency,  $F(1, 6573) = 26.8, p < 0.001$ . Follow-up contrasts revealed that RTs on CON trials (in grey) were significantly faster than on SI trials (in blue),  $t(6573) = 4.16, p < 0.001$ , and faster than on RI trials (in orange),  $t(6573) = 7.06, p < 0.001$ . Also RTs on SI trials were faster than on RI trials,  $t(6573) = 2.52, p = 0.01$ .

Second, to investigate the effect of laterality of the incongruent flankers, congruent trials were excluded from the analysis, since laterality is not defined for congruent trials. A LME model was fitted for RTs with congruency (SI vs. RI) and laterality of the incongruent flankers (unilateral vs. bilateral) as fixed factors and a random intercept per subject. This revealed a main effect of congruency,  $F(1, 3265) = 5.95, p = 0.01$ , with again faster RTs for SI than for RI trials, and a main effect of laterality,  $F(1, 3265) = 5.29, p = 0.02$ , with faster RTs for unilateral compared to bilateral incongruent flankers. There was no significant interaction of congruency and laterality,  $F(1, 3265) = 0.02, p > 0.05$ , indicating an SI vs. RI difference both with unilateral and bilateral incongruent flankers.

Mean accuracy was 92.5%. First, a generalized LME model for binary responses was fitted for accuracy with congruency (congruent vs. SI vs. RI) as a fixed factor and a random intercept per subject. There was no effect of congruency,  $\chi^2(2, N = 20) = 0.42, p > 0.05$ . Second, to investigate the effect of laterality of the incongruent flankers, congruent trials were excluded from the analysis, since for

congruent trials laterality is not defined. A model was fitted with congruency (SI vs. RI) and laterality of the incongruent flankers (unilateral vs. bilateral) as fixed factors and a random intercept per subject. This revealed no effect of congruency  $\chi^2(1, N = 20) = 0.97, p > 0.05$ , no main effect of laterality,  $\chi^2(1, N = 20) = 0.91, p > 0.05$ , and also no interaction,  $\chi^2(1, N = 20) = 1.34, p > 0.05$ .



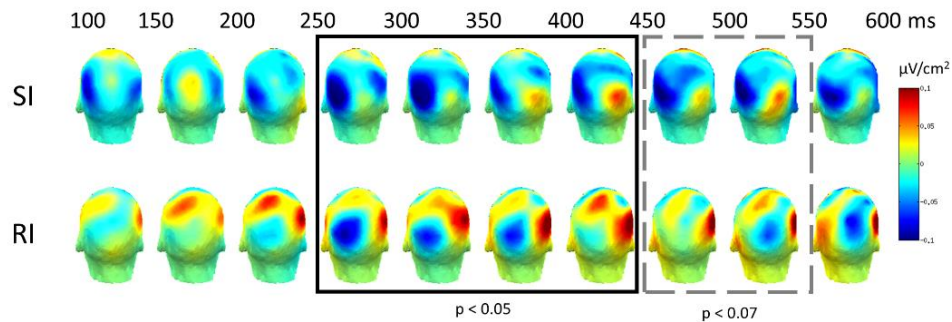
*Figure 3.* Behavioral results for reaction times (RTs). Error bars reflect standard errors. There was a significant effect of congruency on RTs with fastest RTs for congruent, slowest for RI and intermediate for SI trials. This congruency effect did not interact with laterality of the incongruent flankers (uni- or bilateral).

## EEG results

### Lateralized incongruency difference

To investigate the LID and the effect of congruency type, a repeated measures ANOVA for mean amplitudes was performed with three factors: (1)

congruency (RI vs SI), (2) electrode site (left hemisphere vs right hemisphere) and (3) incongruent flanker side (left hemifield vs right hemifield). The LID (interaction of electrode site and flanker side) was significant in all 50 ms windows from 250 to 450 ms ( $p < 0.05$ , indicated in Figure 4 by black rectangle) and was marginally significant in windows from 450 to 550 ms ( $p < 0.07$ , indicated in Figure 4 by grey dashed square). In all other time windows it was not significant ( $p > 0.10$ ). The LID did not differ for SI vs. RI conditions in any of the tested time windows, as was shown by a non-significant three-way interaction of electrode site, flanker side and congruency type ( $p > 0.10$ ).



*Figure 4.* Lateralized incongruity difference (LID): ERP topographical plots for the difference between left hemifield incongruent-flanker trials (\*\*AAA) and right hemifield incongruent-flanker trials (AAA\*\*) are shown. Mean amplitude in a 50 ms time window is plotted ranging from 100 to 600 ms post stimulus onset. A lateralized pattern of activation (negative difference in the left hemisphere, positive in the right hemisphere) shows that incongruent flankers are processed differently from congruent flankers. This is the case for both SI and RI conditions.

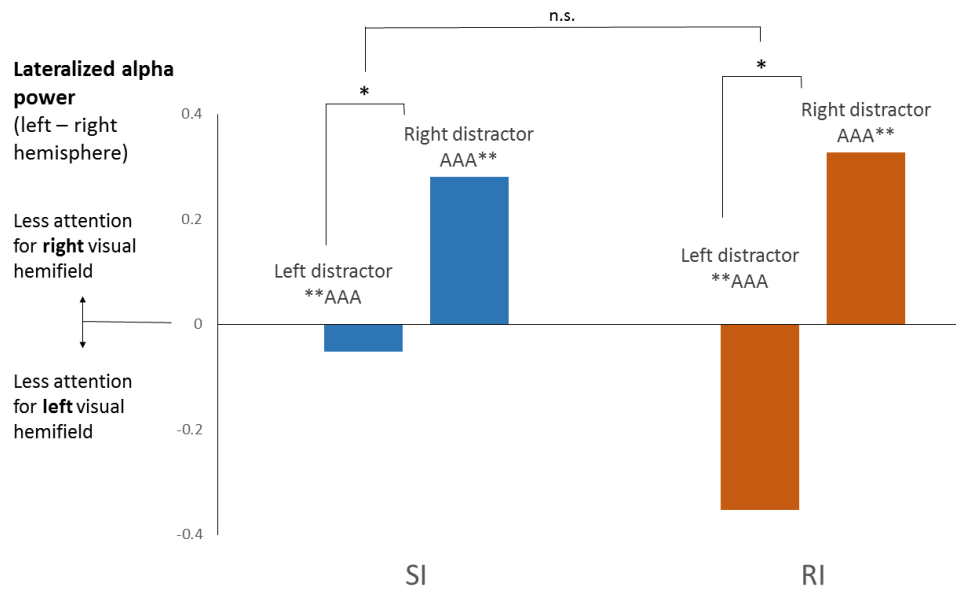
### Occipital alpha power is increased for irrelevant flankers

The effect of incongruent flankers on alpha power in lateral occipital electrodes was tested. Lateralized alpha power, the difference in alpha power for left vs. right hemisphere (power at PO7 minus power at PO8), was determined on every trial. A LME model was fitted for this hemispheric difference in alpha power with presentation side of the incongruent flankers (left vs. right hemifield) as a fixed factor and a random intercept per subject. Importantly, this revealed a significant effect of incongruent flanker side on alpha power lateralization,  $\chi^2(1, N = 20) = 6.47, p = 0.01$ . Figure 5 shows lateralized alpha power in the interval 300-500 ms post stimulus onset, with negative values indicating more alpha in right hemisphere (so more attention for the left visual hemifield) and positive values indicating more alpha power in the left hemisphere (so more attention for the right visual hemifield). Trials with left incongruent distractors (\*\*AAA) elicited more alpha power in the right hemisphere than in the left hemisphere (negative value in Figure 5), suggesting more attention directed to the right hemifield, away from the distractors. Trials with right incongruent distractors (AAA\*\*) reversely elicited more alpha power in the left hemisphere than in the right hemisphere (positive value in Figure 5), suggesting more attention directed to the left hemifield, again away from the distractors. This pattern of results is similar for SI and RI trials; the interaction of distractor hemifield and congruency type (SI vs. RI) was not significant,  $\chi^2(1, N = 20) = 0.78, p = 0.38$ . There was also no main effect of congruency type  $\chi^2(1, N = 20) = 1.15, p = 0.28$ .

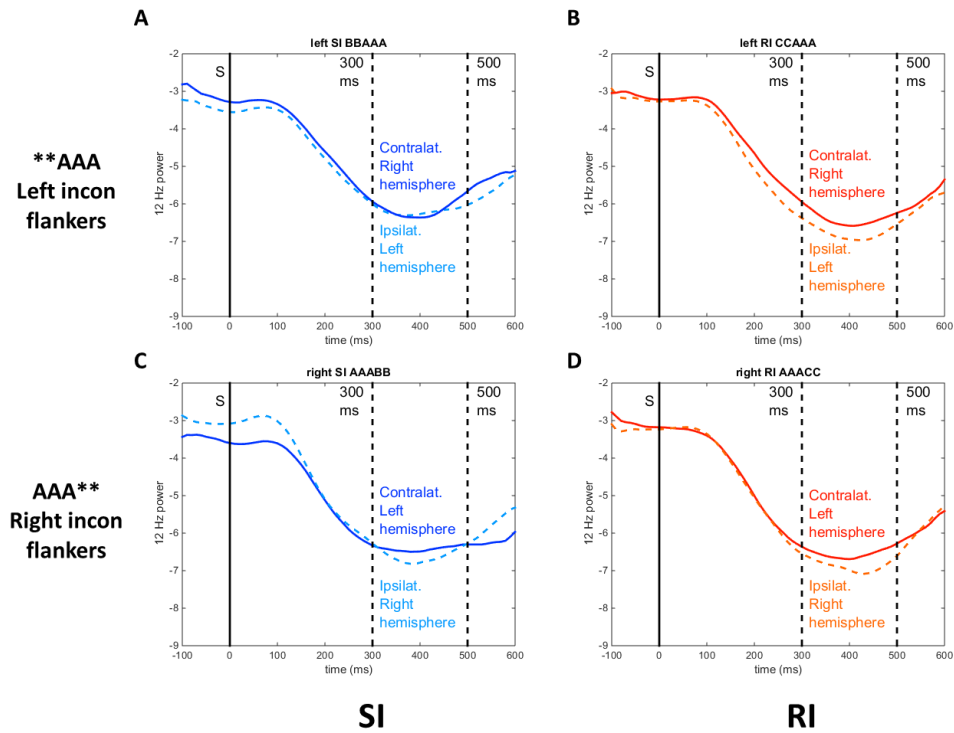
Figure 6 shows the time course of alpha power in more detail. It again shows more alpha power in the hemisphere contralateral to incongruent flankers, and shows that this difference in alpha power occurs between 300 and 500 ms post stimulus onset.



To test if the observed alpha power modulations predict behavior, an LME model was fitted for RTs with alpha lateralization (alpha contralateral minus alpha ipsilateral to incongruent flankers) as a predictor and a random intercept per subject. Lateralized alpha power was not significantly predictive of RTs,  $\chi^2(1, N = 20) = 0.01, p = 0.97$ .



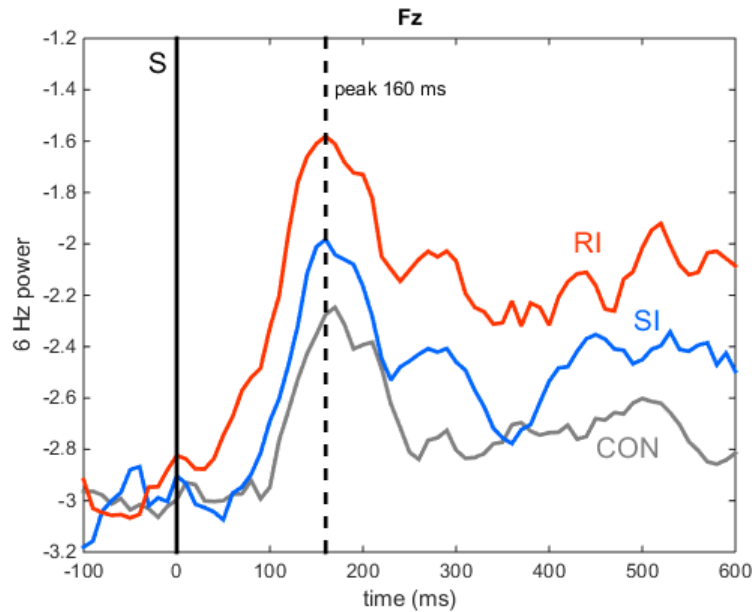
*Figure 5.* Lateralized alpha power (alpha power at PO7 – alpha power at PO8) in the interval 300-500 ms post stimulus onset. Positive values indicate more alpha power in the left hemisphere (so less attention for the right visual hemifield). Negative values indicate more alpha power in the right hemisphere (so less attention for the left visual hemifield). Trials with left incongruent distractors (\*\*AAA) elicit more alpha power in the right hemisphere (negative difference). Trials with right incongruent distractors (AAA\*\*) elicit more alpha power in the left hemisphere (positive values). This indicates that processing of incongruent flankers is inhibited by attenuating attention. This pattern of results is similar for SI (blue) and RI (orange) trials.



*Figure 6.* Alpha power (12 Hz) over time, measured at left and right hemisphere electrodes for left and right incongruent flankers. Trials with left incongruent distractors (\*\*AAA, panels A and B) elicit more alpha power (and hence more attentional inhibition) in the right (contralateral) hemisphere. Trials with right incongruent distractors (AAA\*\*, panels C and D) elicit more alpha power in the left (contralateral) hemisphere. Hence, both for AAA\*\* and \*\*AAA conditions, more alpha in the hemisphere contralateral to incongruent flankers is observed, indicating that attention for incongruent flankers is inhibited. This pattern of results is similar for SI (panels A and C in blue) and RI (panels B and D in orange) trials.

### Frontal theta power is modulated by stimulus incongruency

To examine frontal control mechanisms that might influence these sensory processes, the effect of congruency on frontal theta power was examined (see Figure 7). An LME model was fitted for theta power at the peak of the theta increase (160 ms) with congruency (CON vs. SI vs. RI) as a fixed factor, and a random intercept per subject. Results show a main effect of congruency,  $\chi^2(2, N = 20) = 10.9, p = 0.004$ . Follow-up contrasts revealed a significant difference between CON and RI trials,  $t(4533) = 3.23, p < 0.001$ , a marginally significant difference between CON and SI trials,  $t(4533) = 1.75, p = 0.08$  and no significant difference between SI and RI trials,  $t(4533) = 1.28, p = 0.20$ . To test if theta power predicts behavior, an LME model was fitted for RTs with theta power as a predictor and a random intercept per subject. Theta power was not significantly predictive of RTs,  $\chi^2(1, N = 20) = 0.33, p = 0.56$ .



*Figure 7.* Frontal theta power (6 Hz) in electrode Fz, time locked to stimulus presentation. Following stimulus presentation, theta power increases (peaks around 160 ms). Theta power is significantly influenced by congruency, with no significant difference in theta between RI and SI trials, significantly more theta power for RI trials compared CON trials and marginally significantly more power for SI trials compared to CON trials (peak amplitude).

### Theta power predicts alpha power on single trial level

To test our hypothesis of frontal theta leading control through alpha power modulations, we also fitted an LME model for alpha lateralization (alpha power contralateral minus alpha power ipsilateral to incongruent flanker presentation) with theta power as a predictor and a random intercept per subject. We found

evidence for a direct influence of theta power on alpha power modulations,  $\chi^2(1, N = 20) = 4.33$ ,  $p = 0.04$ , with higher theta power predicting more pronounced lateralized alpha modulations.

## DISCUSSION

We capitalized on the high temporal resolution of EEG to investigate within-trial modulations of cognitive control, specifically in sensory processing areas. To ensure sufficient spatial precision to localize activity in sensory areas, we applied a lateralized flanker paradigm. The LID showed early processing differences for congruent versus incongruent (both SI and RI) flankers. We used alpha power to determine whether this LID signifies increased or decreased attention for distracting information. We hypothesized that if visually distinct flankers capture attention, there should be less alpha power in areas processing incongruent flankers. These modulations should then be present in both SI and RI conditions, since the visual discrepancy appears in both. If on the other hand, incongruent flankers elicit cognitive control, there should be more alpha power in areas processing these incongruent flankers, reflecting active inhibition of attention. This effect should be present only in the RI condition, where a response conflict occurs, since response conflict is generally believed to drive cognitive control. We observed higher alpha power in areas processing incongruent flankers, which strongly supports the cognitive control hypothesis. However, this alpha modulation did not differ for SI and RI trials, suggesting that control was triggered by the stimulus incongruency rather than response conflict. Similarly, frontal theta power earlier in the trial, marking conflict detection, was also modulated by stimulus incongruency rather than response conflict. Moreover, theta power was predictive of alpha modulations, suggesting that stimulus incongruency was detected in

frontal regions and subsequently, control was implemented in specific sensory areas processing irrelevant information. Crucially, we show that these control mechanisms operate on a fast, within-trial timescale.

An important argument of the current study was that incongruent flankers might in principle decrease alpha power (indexing increased attention). Indeed, visual search literature shows that stimuli that differ from their surroundings ‘pop out’ and draw attention (Treisman, 1985). This phenomenon is known as attentional capture (Posner, 1980) and is strongly stimulus-driven (Jonides & Yantis, 1988; Yantis & Hillstrom, 1994). In a static array of visual stimuli a discontinuity involuntarily captures attention (Burnham & Neely, 2008; Burnham, Neely, Naginsky, & Thomas, 2010). Consistently, when stimuli are presented serially, neural responses gradually decrease for repeating visual stimuli, a phenomenon called repetition suppression (Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008). Similarly, alpha power decreases across repetitions (Engell & McCarthy, 2014). Taken together, studies with both simultaneous and serial stimulus presentation predict decreased attention for repeated stimuli but increased attention for discrepant stimuli. In the current study, we use a static array of visual stimuli where the target is repeated in one visual hemifield and a visual break between target and incongruent flankers is created in the other visual hemifield. Based on the attention literature above, we hypothesized that such a discontinuity might capture attention. However, we find exactly the opposite, namely less alpha power for repeating (congruent) flankers and more alpha power for discrepant (incongruent) flankers. This points to an active top-down control mechanism inhibiting the incongruent flankers rather than stimulus-driven attentional capture.

Our interpretation of increased alpha for incongruent flankers as a marker for increased cognitive control depends on the notion that alpha oscillations have an active inhibitory function. Initially alpha oscillations were thought to reflect cortical inactivity (Pfurtscheller, Stancák, & Neuper, 1996), but strong evidence currently supports the hypothesis that alpha oscillations mark active inhibition of irrelevant information, to promote the processing of relevant information (gating by inhibition, for a review see Jensen & Mazaheri, 2010). For instance, a number of studies show that alpha power decreases in brain regions that are actively involved in task performance, and that alpha modulations predict task performance (Kelly et al., 2006; Thut et al., 2006; Worden et al., 2000). Decreased alpha power has also been clearly linked to increased BOLD activity measured by fMRI (Laufs et al., 2003; Ritter et al., 2009). Finally, intracranial recordings in monkey during task performance demonstrate that neural firing is locked to the troughs of alpha oscillations in the local field potentials (Haegens et al., 2011). This strongly links alpha power modulations to the engagement and inhibition of certain brain areas and supports our interpretation of increased alpha as reflecting increased cognitive control.

Both classical (Botvinick et al., 2001) and more recent associative (Abrahamse et al., 2016; Egner, 2014; Verguts & Notebaert, 2008, 2009) accounts of cognitive control predict that control is guided by frontal regions that are activated when a challenging event, such as an incongruency or an error, occurs. This initial detection of conflict is reflected in a mid-frontal theta power increase for incongruent or error trials (Cavanagh et al., 2012; Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012). Earlier work observed an increased synchrony between frontal theta and occipital alpha on post-error trials, supporting the connection between error detection and control implementation (Cohen et al., 2009). Another study reported a correlation between frontal theta increases and



occipital alpha decreases following errors (Mazaheri, Nieuwenhuis, van Dijk, & Jensen, 2009). Consistently, we observed that theta power at 160 ms post-stimulus onset predicts alpha power modulations later in the trial, from 300 to 500 ms. Higher theta power was linked to a more pronounced inhibition of attention for irrelevant information. The timing of these events and their correlation strongly suggest that initial incongruency detection reflected in theta power leads control implementation in sensory areas later during the trial. Importantly, this happens on a very fast (within-trial) timescale, before the response is given. Such a fast timescale is predicted by associative models for control, but not by classical theories, that typically predict slower, trial-by-trial control modulations.

Theta and alpha power responded similarly to SI and RI conditions, suggesting that not response conflict but the visual stimulus incongruency initiates control implementation in this task. This aspect of the findings is in line with previous work (Nigbur et al., 2012) and can be interpreted from an associative control model perspective. Here, control is gradually learned while solving a task, depending on current task demands, and can occur at different levels. Subjects in an experiment search for and learn strategies that are useful for the particular task that is given to them, taking into account the stimuli and stimulus contingencies at hand (for a similar argument, see Brown, 2009; Pansky & Algom, 2002; Schmidt & De Houwer, 2012). In classical cognitive control tasks (where only CON and RI conditions are presented), ‘response conflict’ is the most relevant and obvious feature that predicts task performance and is picked up by participants. In the current context, we propose that subjects learn a different aspect of the task that predicts task performance. They learn that information in one or both hemifields can hinder performance. They consequently develop task-specific and location-specific (left and right hemifield) representations that detect whether target and flankers are different. When these representations are activated by an experimental

stimulus, they trigger control mechanisms and inhibit processing of incongruent flankers. These representations are formed based on visual discrepancy, so they are triggered by both SI and RI trials, inhibiting incongruent flankers in both SI and RI conditions. Although currently speculative, the account can lead to testable predictions. For example, future studies with more power to detect changes across trials can investigate the evolution of alpha during the experiment.

In conclusion, the current study shows that task-specific control (here triggered by stimulus incongruency) is implemented by inhibiting sensory processing of irrelevant stimuli, in sensory areas specific to these stimuli. This control process is guided by mid-frontal brain areas detecting the need for control, which is also task-specific. Crucially this occurs on a fast, within-trial timescale. The current study thus supports associative models for control that predict such fast and task-specific control mechanisms.

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**CHAPTER 4**  
**PREPARING FOR HARD TIMES:**  
**SCALP AND INTRACRANIAL PHYSIOLOGICAL**  
**SIGNATURES OF PROACTIVE ATTENTIONAL CONTROL<sup>1</sup>**

*Based on reward and/or difficulty information people can strategically adjust proactive attentional control. fMRI research shows that motivated proactive control is implemented through fronto-parietal attentional control networks that are triggered by both reward and difficulty cues. In the current study we investigated electrophysiological signatures of proactive control, triggered by task difficulty. Previously, the contingent negative variation (CNV) in the event-related potentials and oscillatory power in the alpha band (8-14 Hz) have been suggested as signatures of control implementation. However, experimental designs did not allow to separate control implementation from motor preparation. Critically, we used a mental calculation task and studied the stimulus-preceding negativity (SPN), carefully removing motor preparation, allowing us to interpret effects on the SPN and alpha power in a straightforward manner as proactive control implementation. We found a more negative SPN amplitude and decreased*

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<sup>1</sup>Janssens, C., Vassena, E., De Loof, E., De Taeye, L., Meurs, A., Van Roost, D., Boon, P., Raedt, R., & Verguts, T. (in preparation). Preparing for hard times: scalp and intracranial physiological signatures of proactive attentional control.

*alpha power for hard versus easy calculations in the period leading up to task onset, showing increased proactive control implementation when a difficult task was expected. In addition to scalp EEG recordings, we also collected intracranial local field potential recordings in an epilepsy patient. We observed a slow component in the posterior parietal cortex, that was more pronounced for hard trials, similar to the scalp SPN observed for healthy participants. This is in line with previously reported involvement of the fronto-parietal attentional network in motivated recruitment of proactive control for a difficult task. Also, we found a slow-drift activation pattern in the striatum (presumably putamen) and hippocampus, possibly reflecting task-specific preparation for difficult mental calculations. The current study thus shows that difficulty information triggers proactive control and demonstrates some of its neurophysiological signatures.*

## INTRODUCTION

When faced with a difficult or important task, humans can shift to a higher gear to perform the best they can. When warned about an upcoming task, top-down proactive cognitive control is used to regulate more basic cognitive processes (Braver, 2012). Control sharpens task performance, but also carries a cost (Kool, McGuire, Rosen, & Botvinick, 2010). This cost has to be weighed alongside possible benefits in the decision to enhance control (Shenhav, Botvinick, & Cohen, 2013; Westbrook & Braver, 2015). Whether or not cognitive control should be implemented is decided based on information about task difficulty and potential reward: control is expedient when a task is difficult and reward is likely. It has been shown in numerous studies that reward improves task performance (Aarts et al., 2014; Bijleveld, Custers, & Aarts, 2010; Botvinick & Braver, 2015; Janssens, De Loof, Pourtois, & Verguts, 2016; Padmala & Pessoa, 2010, 2011; Seitz, Kim, & Watanabe, 2009), and it is also well established that the experience (Gratton, Coles, & Donchin, 1992) or expectation (Aarts & Roelofs, 2011) of response conflict, a specific instance of task difficulty, enhances control. This influence of reward and difficulty information on control was also formalized in computational reinforcement learning models (Verguts, Vassena, & Silvetti, 2015).

This view on control is supported by fMRI studies showing that the anticipation of both reward and difficulty activate an overlapping brain network, consisting of several cortical and subcortical regions (Boehler et al., 2011; Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Padmala & Pessoa, 2011; Vassena et al., 2014). This network closely matches the fronto-parietal attentional control network, including also subcortical areas such as the dorsal

striatum (Corbetta & Shulman, 2002; Dosenbach et al., 2007; Gitelman et al., 1999; Hopfinger, Buonocore, & Mangun, 2000; Kastner & Ungerleider, 2000; Padmala & Pessoa, 2011). The subcortical areas involved in cognitive control are closely connected to cortical frontal and parietal control areas and make up some of the main targets of midbrain dopaminergic projections. Dopamine is a key component in motivational processes, activating and thus facilitating cognitive and behavioral processes (Wise, 2004). fMRI studies therefore concluded that both reward and difficulty information can act as motivational cues that influence strategic control through activation of dopaminergic pathways and the fronto-parietal control network.

Many studies have looked for electrophysiological signatures of proactive control. One possible signature reported in the literature is the contingent negative variation (CNV), a slow negative deflection in the ERP, observed in the interval between a cue and an imperative stimulus requiring a speeded response (Brunia & van Boxtel, 2001; Walter, Cooper, Aldridge, McCallum, & Winter, 1964). Several studies show that reward information influences the CNV: the amplitude of the CNV is more pronounced when a rewarding task is expected (Schevernels, Krebs, Santens, Woldorff, & Boehler, 2014; van den Berg, Krebs, Lorist, & Woldorff, 2014). The influence of task difficulty on the CNV has also been investigated (Tecce, 1972). Just like a reward cue, a difficulty cue increases the CNV amplitude (Schevernels et al., 2014; Vanlessen, De Raedt, Mueller, Rossi, & Pourtois, 2015). Interestingly, the CNV amplitude correlates with activation in the fronto-parietal network (Grent-‘t-Jong & Woldorff, 2007). However, the CNV studies discussed above do not provide a clear electrophysiological signature of proactive attentional control implementation. Indeed, the CNV is believed to reflect not only cognitive control but also motor preparation for an

upcoming task (Brunia & van Boxtel, 2001) making it difficult to assign variations in CNV amplitude to changes specifically in activation of brain areas involved in proactive control. Some studies have separated motor and non-motor parts of the CNV, either by timing and topography or by applying experimental paradigms postponing the motor response. However, these were mostly simple discrimination studies that did not have the research focus on proactive cognitive control of the current study (Frost, Neill, & Fenelon, 1988; Rohrbaugh, Syndulko, & Lindsley, 1976; Ruchkin, Sutton, Mahaffey, & Glaser, 1986).

In the electrophysiological literature, attentional anticipation in absence of any motor component has been investigated extensively by studying the stimulus-preceding negativity (SPN; for reviews see Brunia & van Boxtel, 2001; van Boxtel & Böcker, 2004). The SPN is very closely related to the CNV. It is also a slow negative deflection in the ERP marking preparatory attentional processes. Critically, the SPN is not locked to a stimulus requiring a speeded response; it is typically defined as a preparatory component seen before a stimulus providing information on performance, such as a feedback or reward stimulus, and not before task onset. To make strong claims about cognitive proactive control (without the confound of motor preparation) in the current study, we studied the SPN; however, in contrast to most earlier studies, we did not study it locked to feedback, but instead to a cue relevant for active task preparation. In particular, we used a cognitive task that separates attentional from motor preparation. The task was taken from earlier fMRI research; here, difficulty information activated the anticipatory fronto-parietal network, in absence of motor preparation (Vassena et al., 2014). Like the CNV, the SPN has a more pronounced amplitude when a rewarding event is expected (Brunia, Hackley, van Boxtel, Kotani, & Ohgami, 2011; Fuentemilla

et al., 2013). The effect of difficulty information on the SPN has not been investigated often, since the SPN is usually studied before a feedback stimulus (i.e., after the task), rather than before a task onset cue. A few studies did investigate the effect of cued difficulty on the SPN in simple visual discrimination tasks and report little or no effect (Hillman, Apparies, & Hatfield, 2000; Kotani & Aihara, 1999). In contrast, based on computational models and fMRI research, we expected that similar to reward anticipation, also difficulty anticipation would influence the SPN.

The SPN (and the ERP approach in general) provides only one electrophysiological signature of control, namely phase-locked effects in the EEG (Kappenman & Luck, 2011). To provide a more complete picture of cognitive processes, including phase-locked and non-phase-locked events in the EEG signal, time-frequency decomposition of the signal can be used (Cohen, 2014). To study attentional control, power in the alpha band (8-14 Hz) is particularly interesting since a decrease in (occipital) alpha power has been observed when attention is increased in a visual attention paradigm (Kelly, Lalor, Reilly, & Foxe, 2006; Worden, Foxe, Wang, & Simpson, 2000). Also, increased parietal alpha power has been linked to suppression of external stimuli, whereas decreased parietal alpha power has been linked to increased attention for such external stimuli (Benedek, Schickel, Jauk, Fink, & Neubauer, 2014). In a cued speeded response task, the influence of reward expectation on control implementation is also reflected in alpha power, with less occipital and centro-parietal alpha power (so more attention) when a reward was expected (van den Berg et al., 2014). Unfortunately, just like in the CNV studies discussed above, alpha power measured in this study does not reflect pure cognitive preparation but is likely also influenced by motor preparation. Crucially, the effect of difficulty information on alpha power in

a cognitive task (unconfounded by motor preparation) has, to our knowledge, not been investigated thus far.

The first aim of the current study was to reveal a detailed electrophysiological signature of proactive control implementation in response to cued task difficulty. By studying both the SPN amplitude and alpha power changes we captured all aspects of attentional preparation in the EEG, both phase-locked and non-phase-locked. To provide an unambiguous and interpretable signal we carefully eliminated the motor response from the task. Participants performed a (purely cognitive) calculation task, that required no motor response until the calculation was finished, several seconds after SPN calculation. Hence any effects of difficulty information on pre-task activity can be assigned to changes in cognitive preparation. Based on theoretical models of proactive attentional control (Braver, 2012; Verguts et al., 2015) and previous fMRI research (Aarts & Roelofs, 2011; Krebs et al., 2012; Vassena et al., 2014) we hypothesized that difficulty information would influence control via activation of the fronto-parietal control network and subcortical areas, typically involved in top-down attentional control. We further hypothesized that this would be reflected in both decreased alpha power and increased SPN amplitude for hard trials compared to easy trials in the period leading up to the task.

The second aim of the current study was to directly link the observations at the scalp level to their putative source, the fronto-

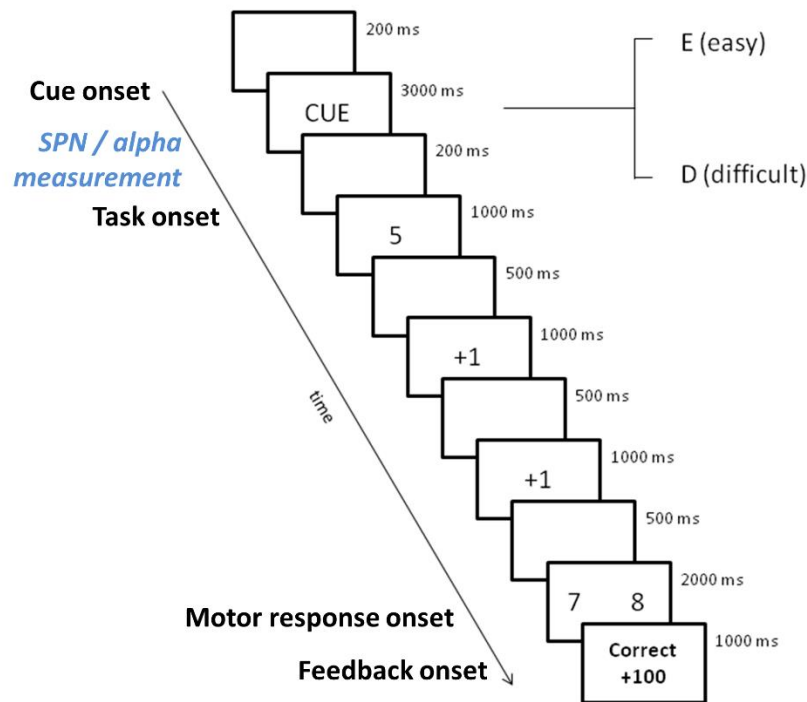
parietal control network. Through dipole fitting (Böcker, Brunia, & van den Berg-Lenssen, 1994) and PET (Brunia, de Jong, van den Berg-Lenssen, & Paans, 2000), several areas have been proposed as contributing sources to the SPN, including the lateral prefrontal cortex, insula and posterior parietal cortex. For the CNV, fMRI-seeded source modeling revealed again frontal and parietal areas contributing to the signal measured at the scalp, as well as visual-sensory occipital areas (Grent-‘t-Jong & Woldorff, 2007). These studies thus already suggest involvement of fronto-parietal network in generating these slow-wave attentional components. In the current study we used a more direct measure of electrical brain activity, namely intracranial local field potential recordings in a patient diagnosed with epilepsy. EEG source modeling techniques such as dipole fitting and sLORETA are not suited to investigate deep sources due to volume conduction, so intracranial recordings provide an excellent opportunity to investigate deep subcortical sources more reliably. In this study the resulting high spatial resolution measurements in the parietal cortex, dorsal striatum (putamen), insula and hippocampus were investigated and compared to the scalp measures of the control subjects, linking the scalp SPN to activity in these areas and the attentional control network in general.



## METHOD

### Experimental design

Nineteen paid subjects participated in this experiment. Participants performed 256 trials of a cued serial mental calculation task. Self-paced breaks occurred every 16 trials. Participants performed mental calculations that could be easy or difficult (both 50 % of trials). For an overview of trial events see Figure 1. On each trial, a cue was presented for 3000 ms, informing participants of the difficulty of the upcoming calculation ('E' for easy or 'D' for difficult). The cue was followed by a blank screen (200 ms) and an initial number (1000 ms), marking task onset. Two operations to perform on this initial number were presented serially (1000 ms each, interspersed by blank screens for 500 ms). Subjects were instructed to mentally perform each operation when presented, and they were finally asked to choose between two possible outcomes (presented for 2000 ms, which was also the response time limitation). The correct and an incorrect outcome were presented left and right on the screen (location of the correct outcome was random) and an outcome could be selected by pressing a left or right button, corresponding to the location on the screen. Following the response, feedback was presented (correct or incorrect, presented for 1000 ms). For correct responses participants received 100 points which was also shown in the feedback (+100 points, +0 points for incorrect responses). Trials were interspersed by a 200 ms blank screen.



*Figure 1.* Overview of a trial in the mental calculation task. At cue onset, a cue (letter E for easy or D for difficult) was presented, reliably predicting task difficulty. At task onset, a number was presented. This was followed by two operations to be performed on this number (presented sequentially). The SPN amplitude and power in the alpha frequency band were studied in the interval between the cue onset and task onset.

Before the start of the experiment participants completed the need for cognition questionnaire (Cacioppo, Petty, & Feng Kao, 1984). They also performed a training block of 16 trials. In this block they rated each calculation on how difficult and how enjoyable it was on a 7 point Likert scale. No EEG was recorded during this training block.

To assess effects of the difficulty manipulation on performance, a linear mixed effects model (LME) for reaction times (RTs) and an LME for binary responses for accuracy were fitted, with difficulty as a fixed factor and a random intercept per subject. Effects in the fitted models were tested by ANOVA type III. For RTs, F-statistics were calculated with Kenward-Roger adjustment of the degrees of freedom (Kenward & Roger, 1997). For accuracy no F-statistics could be calculated and therefore  $\chi^2$  statistics are reported.

### **EEG data acquisition, processing and analysis**

Continuous EEG activity was acquired at 512 Hz using a 64-channel (pin-type) Biosemi Active Two system (<http://www.biosemi.com>) referenced to the CMS-DRL ground and positioned according to the extended 10/20 international EEG system. Six additional electrodes were attached to the head: left and right mastoids, two electrodes for vertical and horizontal electro-oculogram. Data for two participants had to be removed due to excessive noise and technical difficulties.

EEG data were analyzed with EEGLAB (Delorme & Makeig, 2004) and ERPLAB (<http://erpinfo.org/erplab>) software, running on MATLAB. The data were re-referenced offline to linked mastoids. Independent component analysis (ICA) was applied to continuous data to identify and remove components associated with eye blinks. Epochs of -1000 to +3000 ms locked to cue onset were selected. Epochs were visually inspected and epochs containing artifacts were removed.

For ERP analysis the selected epochs were baseline corrected to the pre-cue period. Next, the epochs were averaged per condition per participant and

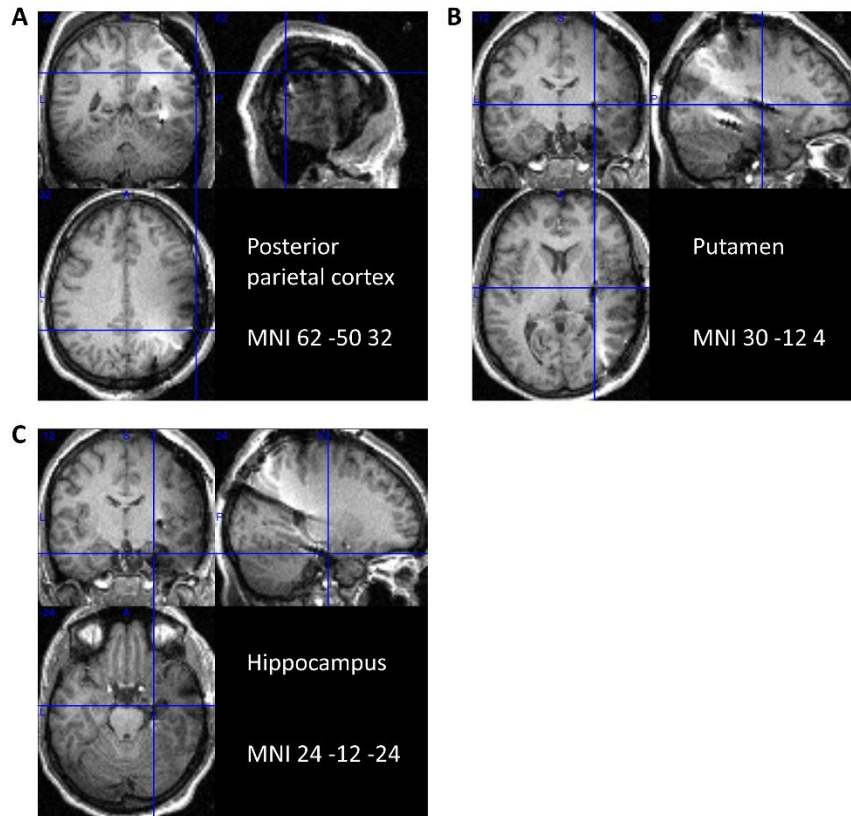
a grand average across participants was created resulting in one average ERP per condition. The SPN component was quantified in a centro-parietal ROI (electrodes CP1, CP2 and CPz) for further analysis. This ROI was selected because the SPN is maximal over centro-parietal sites (Brunia & van Boxtel, 2001). To determine differences in SPN for easy vs. hard conditions, a repeated measures 3x2 ANOVA was performed for average ERP amplitudes in the interval between 800 and 3000 ms post cue onset, with electrode site and difficulty as factors.

For the time-frequency analysis, Fast-Fourier Transform (FFT) was applied to the selected epochs in a moving window (width: 250 time points/488 ms, with Hann tapering), resulting in power estimates ranging from -500 ms to 2750 ms (step 10 ms) locked to cue onset. Average and baseline-corrected event-related spectral perturbation (ERSP; i.e., power) estimates were acquired using the `newtimef` function from EEGLAB. Estimates were obtained for 15 uniformly distributed frequencies ranging from 2 to 30 Hz. We defined time-frequency ROIs (TF-ROIs) based on the grand-average time-frequency analysis (as in Cavanagh, Zambrano-Vazquez, & Allen, 2012), hence independent of the specific research question, thus avoiding double dipping (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009). TF-ROI 1 was defined as the initial power decrease in the alpha frequency band (14 Hz), 200 to 500 ms post cue-onset. This decrease was followed by TF-ROI 2, a more sustained alpha power decrease later in the trial, from 1000 to 2750 ms post cue onset (see Figure 4).

Power in these TF-ROIs was statistically analyzed. Alpha power in TF-ROI 1 was defined as mean power at 14 Hz in the interval 200-500 ms post cue onset, representing the observed alpha power decrease. Alpha power in

TF-ROI 2 was tested in 250 ms intervals, ranging from 1000 ms to 2750 ms post cue onset. In every interval alpha power was defined as mean power at 14 Hz. For each TF-ROI a 2 x 2 repeated measures ANOVA (per interval) was performed with difficulty (easy vs. difficult) and electrode (CP1 vs. CP2) as factors.

We also collected intracranial recordings from a patient suffering from epilepsy. Patient NB was a left-handed woman (age 29) with normal IQ. For these recordings the same experimental design was used as for the control EEG subjects, but with a cue – task interval of 4000 ms. Also, due to time constraints, only 128 trials were performed. Data were collected at 1024 Hz and downsampled offline to 256 Hz. Electrodes were implanted on several sites, including a right subdural temporo-parietal grid (5 x 8 contacts), depth electrodes in parahippocampal areas, hippocampus and fusiform cortex (10 contact points) and depth electrodes in insula, dorsal striatum (putative putamen) and pulvinar (10 contact points). The exact locations of these electrodes (MNI coordinates) were determined by two independent researchers based on a structural MRI scan taken after implantation (see Figure 2); the absolute mean deviation between their estimated coordinates was 0.4 mm.



*Figure 2.* MRI images displaying implantation of intracranial electrodes in patient NB. Three electrodes of interest are marked. Two independent researchers determined reliable MNI coordinates for these sites based on visual inspection of the MRI images. Locations and coordinates for sites in posterior parietal cortex (panel A), putamen (panel B) and hippocampus (panel C) are shown.

Epochs of -1000 to 4000 ms locked to cue onset were selected. Epochs were visually inspected and epochs containing epileptic activity or other artifacts were removed. The selected epochs were baseline corrected to the pre-cue period and were averaged per condition. To isolate locally specific patterns of activation, activation was inspected for every electrode referenced to the average of neighboring electrodes. Using Cartool software (<http://brainmapping.unige.ch/Cartool.php>), we tested for significant differences between easy and hard trials on every electrode. This was done by nonparametric analyses on the basis of randomization tests (for a similar approach see Pourtois, Spinelli, Seeck, & Vuilleumier, 2010). The observed data is compared to random shuffling of the same values over 1000 permutations to estimate the probability ( $p < .05$ ) that the data might be observed by chance.

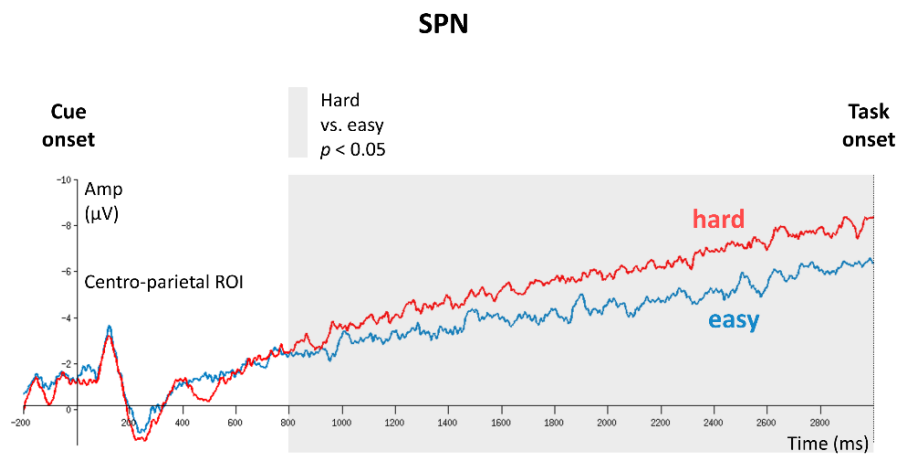
## RESULTS

### Behavioral results

As expected, LME analysis revealed a significant effect of difficulty on both error rates,  $\chi^2(1, N = 19) = 73.97, p < 0.01$  and reaction times  $F(1, 4678) = 140.89, p < 0.01$ , with more errors and slower responses for hard than for easy trials (error rate: 1%, RT: 425 ms for easy vs. error rate: 6%, RT: 492 ms for difficult). These results show that the difficulty manipulation was effective and performance was worse for hard trials.

**SPN**

The repeated measures ANOVA for SPN amplitude revealed a significant main effect of difficulty, with a more pronounced SPN component (more negative amplitude) leading up to task onset for hard trials than for easy trials, Wilks' Lambda = 0.78,  $F(1, 16) = 4.52$ ,  $p = 0.049$  (see Figure 3). This effect of difficulty did not interact with electrode, Wilks' Lambda = 0.82,  $F(2, 15) = 1.60$ ,  $p = 0.23$ .

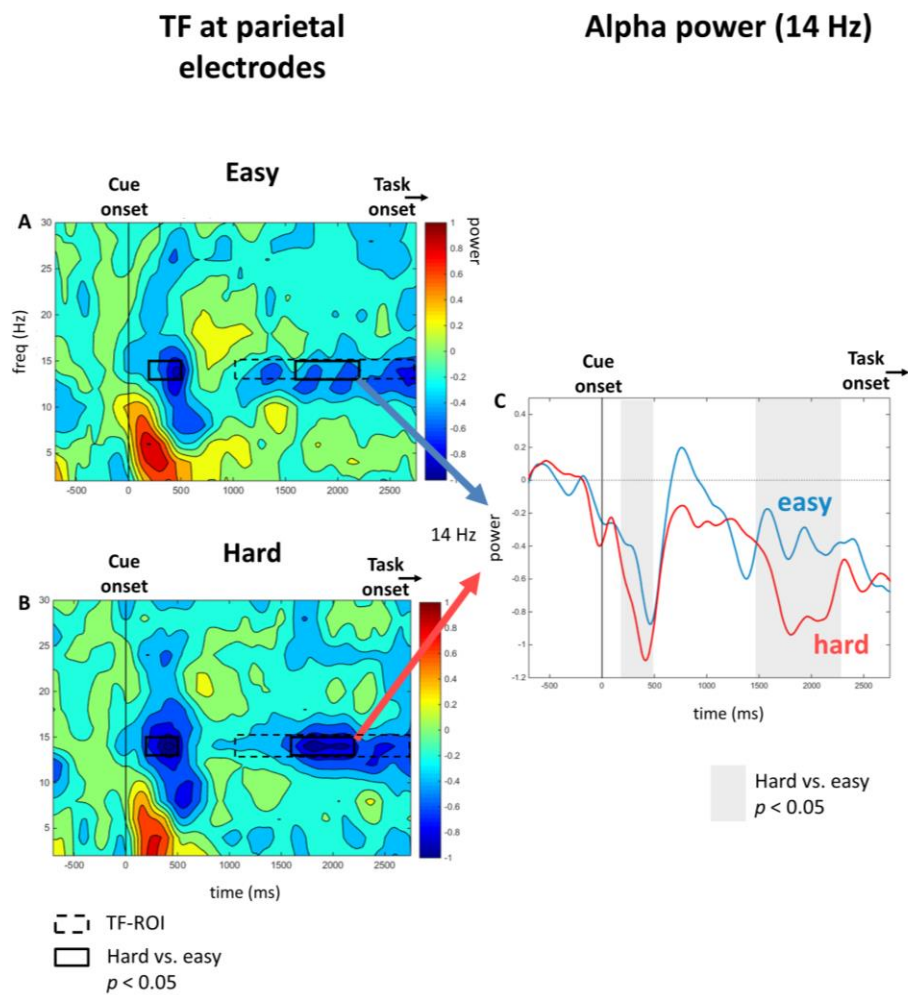


*Figure 3.* SPN for a centro-parietal ROI (electrodes CP1, CPz and CP2). The SPN component leading up to task onset is significantly more negative for hard trials compared to easy trials, from 800 to 3000 ms post cue-onset (indicated in gray). This reflects increased proactive control for hard trials.



**Time-frequency**

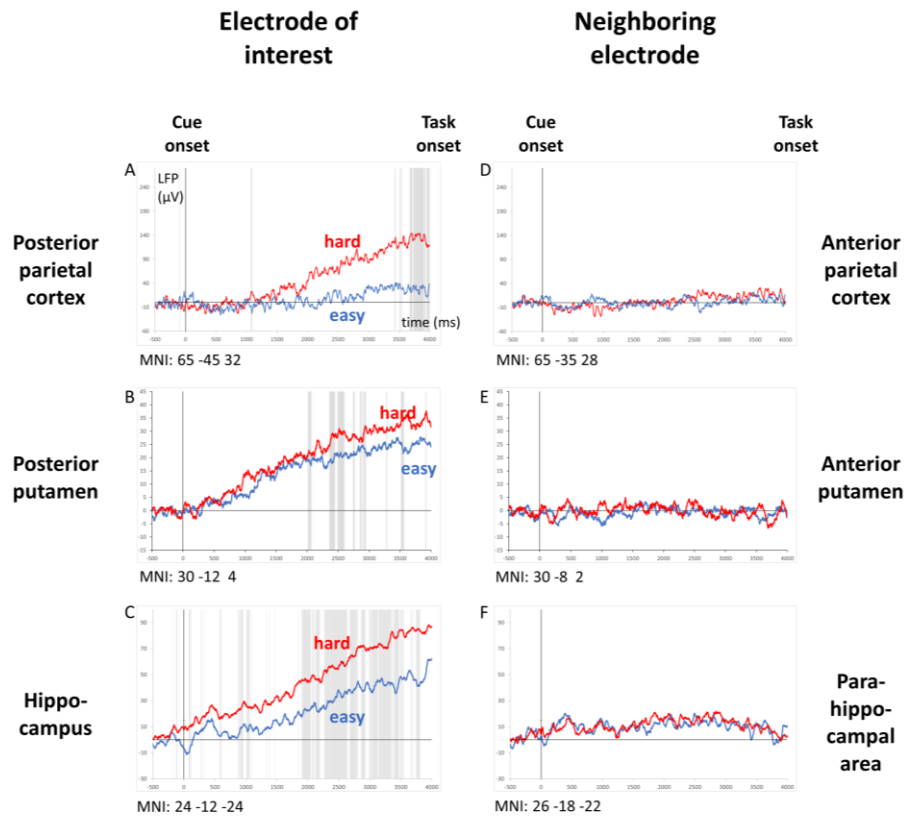
See Figure 4 for an overview of TF results. For TF-ROI 1, the initial alpha power decrease from 200 to 500 ms post cue onset, there was a significant difference between hard and easy trials, Wilks' Lambda = 0.71,  $F(1, 16) = 6.62$ ,  $p = 0.020$ , indicating a more pronounced alpha decrease for hard trials. For TF-ROI 2, the sustained alpha power decrease later in the cue period, we tested for differences between easy and hard trials in intervals of 200 ms. We observed significant differences in alpha power from 1600 to 2200 ms post cue onset ( $p < 0.05$ ), showing that the sustained alpha power decrease was more pronounced for hard than for easy trials. In all other 200 ms intervals tested, we observed no statistically significant differences ( $p > 0.05$ ).



*Figure 4.* Panels A and B show changes in power over time (relative to baseline, 0 marks cue onset) for different frequencies ranging from 2 to 30 Hz. Significant differences between easy (panel A) and hard (panel B) trials in alpha power are indicated with black boxes. Dotted line boxes represent TF-ROIs. Panel C shows the time course of alpha power (14 Hz) for hard (in red) and easy (in blue) trials in more detail. Significant differences between easy and hard trials are marked by grey areas. For TF-ROI 1 (200-500 ms), the initial alpha power decrease was more pronounced for hard than for easy trials. For TF-ROI 2 (1000-2750 ms), the sustained alpha power decrease was also larger for hard than for easy trials (significant difference from 1500 to 2250 ms).

### **Intracranial recordings**

Inspection of intracranial electrodes revealed a negative-going slow deflection of the field potential during the cue period, specific to three electrodes, one in the posterior parietal cortex (Figure 5A), one in the putative putamen (Figure 5B) and one in the hippocampus (Figure 5C). This pattern of activation was comparable to the SPN scalp ERP component observed in our healthy participants. Moreover, the slow SPN-like deflection observed in these areas was more pronounced for hard than for easy trials, again mirroring the effect in healthy participants. The difference was statistically assessed at every time point by non-parametric randomization tests (see Methods) and was significant on a number of time points throughout the cue period leading up to task onset (see Figure 5A-C, grey areas mark statistically significant time points,  $p < 0.05$ ). Notably, no such slow deflection was observed for the electrodes in the insular, pulvinar, parahippocampal or fusiform sites. To illustrate the local specificity of these findings, for each area a neighboring electrode is shown, showing that no slow-drift activation pattern or effect of the difficulty manipulation could be found there (see Figure 5D-F).



*Figure 5.* Cue-locked intracranial local field potential recordings at posterior parietal cortex (panel A), posterior putamen (panel B) and hippocampus (panel C). Following cue onset there was an SPN-like, slow drifting deflection in these areas, which was more pronounced for hard than for easy trials (statistically significant differences are colored in grey). Neighboring electrodes (panel D-F) show the local specificity of the observed signal in the electrodes of interest.

## DISCUSSION

In this study we provide a detailed and reliable electrophysiological signature of proactive attentional control in a cognitive task. Following a difficulty cue, we showed a more pronounced SPN (see Figure 3) and more alpha power suppression (see Figure 4) for hard vs. easy trials, reflecting increased cognitive control. These electrophysiological markers show that pre-cued task difficulty motivates proactive control in a motor-free task. The SPN and alpha power modulations likely reflect stronger activation in the fronto-parietal attentional control network. This is further supported by intracranial recordings from the posterior parietal cortex. Here, a slow deflection in the local field potential, mirroring the scalp SPN in healthy subjects, was observed (see Figure 5). This slow component was also more pronounced for hard than for easy trials. Taken together, the scalp and intracranial recordings in the current study support the notion that difficulty information influences proactive control through activation of cortical fronto-parietal brain areas. This is in line with predictions by computational reinforcement learning models (Verguts et al., 2015) and fMRI research (Boehler et al., 2011; Krebs et al., 2012; Vassena et al., 2014).

To allow straightforward attribution of the ERP slow-wave amplitude and alpha power modulations solely to attentional preparation, we used a task that carefully excluded motor preparation from the period leading up to task performance. Our mental calculation task did not require a motor response until after the complete calculation was finished and two outcome options were presented (based on Vassena et al., 2014). It is therefore very unlikely that motor preparation occurred during the cue-task interval. We showed that task onsets in hard trials were preceded by a more pronounced SPN and

stronger alpha power suppression. Whereas previous studies failed to show an effect of difficulty on the SPN amplitude (Hillman et al., 2000; Kotani & Aihara, 1999), our study did provide evidence that difficulty information influences the CNV. This is in line with previous studies reporting effects of difficulty on the CNV (Schevernels et al., 2014; Vanlessen et al., 2015). In the current study, we show very clear effects of cued difficulty on the SPN and we thus confirm that difficulty information, in the absence of motor preparation, is an important cue motivating proactive attentional control.

The slow-drift component measured at the scalp is the result of summed postsynaptic potentials in pyramidal neurons from cortical areas involved in the upcoming task (Birbaumer, Roberts, Lutzenberger, Rockstroh, & Elbert, 1992; Elbert, 1993). The SPN and other negative slow components may derive from increased neural excitability of underlying source neurons. This may lower the threshold for firing in task-relevant areas, thus leading to fast engagement of these neurons at task onset (Elbert, 1993; McAdam, 1969). The SPN is therefore an excellent marker of cortical priming (Walter et al., 1964). Source localization studies have specified the origin of the SPN and report the fronto-parietal network as one of its main sources (Böcker et al., 1994; Brunia et al., 2000; Kotani et al., 2015; Tsukamoto et al., 2006). Also for the related CNV component, the fronto-parietal network together with motor areas have been proposed as the main sources (Gómez, Flores, & Ledesma, 2007; Grent-‘t-Jong & Woldorff, 2007).

As a second neural marker of control, we also observed decreased alpha power during the cue-target period. This decrease in alpha power was again larger for hard trials than for easy trials, between 1600 and 2200 ms following the difficulty cue (TF-ROI 2). This alpha power decrease very likely reflects

increased attention for upcoming stimuli, since alpha oscillations are a well-established mechanism for attentional suppression (Jensen, Bonnefond, & VanRullen, 2012; Jensen & Mazaheri, 2010). The gating by inhibition framework (for a review see Jensen & Mazaheri, 2010) states that alpha oscillations reflect inhibition of irrelevant input and can be strategically adjusted to admit relevant information into processing. Also, alpha power is negatively correlated with BOLD activity measured by fMRI (Laufs et al., 2003; Ritter, Moosmann, & Villringer, 2009) and neural firing in monkeys is locked to the troughs of alpha oscillations (Haegens, Nacher, Luna, Romo, & Jensen, 2011). Based on this, we hypothesized that alpha oscillations would play a role in proactive attentional control. In visual attention tasks, decreases in alpha power have been shown in occipital regions that are actively involved in task performance (Kelly et al., 2006; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden et al., 2000). Similar proactive alpha power modulations in somatosensory areas also show that alpha mechanisms are not limited to visual areas, but act in different areas depending on the task (Haegens, Händel, & Jensen, 2011). Alpha oscillations are also actively used to shield working memory from irrelevant distracting input (Bonnefond & Jensen, 2012, 2013). For cognitive tasks, alpha power before task onset predicts performance and can be strategically adjusted, e.g. following errors, to increase cognitive control (Mazaheri, Nieuwenhuis, Van Dijk, & Jensen, 2009). Our findings are in line with the findings above and show that alpha suppression can be triggered by a difficulty cue and marks proactive attentional control.

In addition to scalp measures we also recorded local field potentials from intracranial electrodes in an epilepsy patient. These recordings, especially those in posterior parietal cortex, provided an insight into the putative source of the SPN and supported the idea that proactive control relies

on the fronto-parietal attentional control network. In the posterior parietal cortex an SPN-like slow component was observed, which was more pronounced for hard than for easy trials, mirroring the scalp SPN for healthy subjects. This pattern of activation was locally specific, showing that it originates in the posterior parietal cortex and is not the reflection of a deeper or distant source. The posterior parietal cortex is an important part of the fronto-parietal attentional control network (Gitelman et al., 1999; Hopfinger et al., 2000) and many fMRI studies have shown activation of this area during proactive cognitive control (Engelmann, Damaraju, Padmala, & Pessoa, 2009; Knutson, Westdorp, Kaiser, & Hommer, 2000; Padmala & Pessoa, 2010; Rosell-Negre et al., 2014; Wu, Weissman, Roberts, & Woldorff, 2007). In the current study we observed more activation in this area following cue-onset for hard trials, supporting the idea that more proactive control is implemented for these cues through activation of the fronto-parietal control network. Note that the posterior parietal cortex is also involved in mental arithmetics (Rickard et al., 2000; Zago et al., 2001). Parietal intracranial activation measured in the current study might therefore also reflect task-specific parietal engagement.

The pattern of activation on posterior parietal intracranial sites was very similar to the scalp SPN recorded for control subjects, suggesting that this area might contribute to the SPN. This is in line with source localization studies naming the fronto-parietal network as one of the main sources for CNV (Gómez et al., 2007; Grent-‘t-Jong & Woldorff, 2007) and SPN (Böcker et al., 1994; Brunia et al., 2000; Kotani et al., 2015; Tsukamoto et al., 2006). Additionally, source modelling also revealed the (anterior) insula as an important source region contributing to the scalp SPN (Böcker et al., 1994). In the current study we did not find an SPN-like component or an effect of the difficulty manipulation in the insula. In the current study, the SPN was studied



before task onset rather than before reward feedback, as in the source modelling studies. The insula might be specifically involved in the expectation of an affective-motivational feedback stimulus, consistent with the role of the insula in saliency processing (Menon & Uddin, 2010). This may be why it was not activated in the current study.

We observed the SPN-like slow pattern of activation also in the dorsal striatum (likely posterior putamen, see Figure 2B and Figure 5B). This suggests the putamen as part of the subcortical network underlying motivated control. Subcortical areas, including the putamen, are often coactivated with the cortical fronto-parietal network (Gitelman et al., 1999; Hopfinger et al., 2000). Decision-making control models propose task difficulty, together with reward as a key motivator for control (Shenhav et al., 2013; Verguts et al., 2015). The putamen, and more generally the dorsal striatum, is activated alongside other subcortical areas and the fronto-parietal network in motivated control, during anticipation of an effortful task (Krebs et al., 2012; Kurniawan, Guitart-Masip, Dayan, & Dolan, 2013; Vassena et al., 2014) as well as during reward anticipation (Engelmann et al., 2009; Knutson, Adams, Fong, & Hommer, 2001; Padmala & Pessoa, 2011). Consistently, single unit recordings in monkeys show that caudate nucleus neurons fire during motivated proactive control, and this activation is correlated with improved task performance (Lauwereyns, Watanabe, Coe, & Hikosaka, 2002). The dorsal striatum and other dopaminergic subcortical areas might significantly influence the SPN. Activation in dopaminergic subcortical areas is indirectly linked to slow preparatory components as evidenced by genetic (Foti & Hajcak, 2012) and psychopharmacological (Tecce, 1991) dopamine effects on the CNV and SPN. Also, the CNV and SPN are reduced in dopamine-related clinical conditions, such as schizophrenia (Wynn, Horan, Kring, Simons, &

Green, 2010) and Parkinson's disease (Mattox, Valle-Inclán, & Hackley, 2006; Verleger et al., 1999).

Another possible explanation for putamen activation, is that the cue triggers the putamen because it is a task-specific area involved in mental calculations. The putamen, especially the posterior portion, is well known for its involvement in automatized processing (Ashby, Turner, & Horvitz, 2010; Lehericy et al., 2005). In this study the putamen was more involved in preparing for hard calculations. The hard calculations in this study rely more heavily on using well-learned arithmetic facts (e.g.,  $8+5=13$ ), whereas easy calculations can be solved simply by counting, since they consisted only of "+1" operations. It is possible to conceptualize the arithmetic mental operations used on difficult trials as covert actions, that are trained and automatized when children learn arithmetics (Rivera, Reiss, Eckert, & Menon, 2005). These automatic "actions" might involve the putamen, meaning that preparatory activation of the putamen reflects proactive control implementation in this task-specific area. This interpretation requires further research before it can be accepted.

The current study provides further evidence for proactive control being implemented in task-specific areas, namely in the hippocampus. Intracranial recordings in the hippocampus also showed a slow-drift component following cue-onset. Activation here was very specific to the hippocampus, since neighboring electrodes located in parahippocampal areas were not sensitive to the cue (see Figure 5, panel C and F). Activation in the hippocampus leading up to task onset likely reflects task-specific preparation rather than general attentional control. Mental calculation makes use of extensive brain networks, and some research has implicated the hippocampus in these networks. It has

been shown that the hippocampus is activated more strongly in addition operations with carrying, as in the hard condition in the current experiment, compared to additions without carrying, as in the easy condition in the current experiment (Kong et al., 2005). Also, the hippocampus is involved when a retrieval strategy is used but not when a counting strategy is used (Cho, Ryali, Geary, & Menon, 2011). In children, the hippocampus plays a role specifically in addition problems (compared to subtractions) and is activated for problems where a retrieval strategy is being used (De Smedt, Holloway, & Ansari, 2011). In the current study, easy mental calculations consisted solely of “+1” operations, strongly promoting a counting strategy, whereas hard calculations likely promoted different strategies, such as retrieval. These studies thus support the idea that the hippocampus plays a role specifically in the currently used mental calculation task, especially in the hard condition.

Taken together, effects of the cue on the SPN and alpha power recordings and on intracranial recordings in parietal cortex, putamen and hippocampus, show that preparation for a difficult task relies on general attentional networks as well as task-specific areas. This is in line with control models and fMRI research that predict control to be implemented by the fronto-parietal network in specific (sensory) areas involved in task execution (Egner & Hirsch, 2005; Grent-‘t-Jong & Woldorff, 2007; Hopfinger et al., 2000; Weissman, Warner, & Woldorff, 2004). It also corresponds to the idea that slow preparatory scalp components reflect activation in general attentional areas as well as task-specific areas (Birbaumer et al., 1992).

Computational models predict that both difficulty and reward information can motivate proactive control. In this study, cues indicating difficult trials were followed by an increased SPN and decreased alpha power.

Similarly, van den Berg et al. (2014) showed an increased CNV amplitude and decreased alpha power following reward cues. Although the paradigms used in the two studies differ substantially, these similar CNV/SPN and alpha modulations suggest comparable effects of reward and difficulty on motivating proactive control. Additionally, models predict that reward and difficulty could have interacting effects on control implementation: difficulty might influence task preparation only when reward is likely (Shenhav et al., 2013; Verguts et al., 2015). In a study by Schevernels et al. (2014), difficulty and reward information were combined in a cue leading up to a speeded response task. Here reward information influenced the early CNV. Later in the trial, also difficulty information influenced the CNV, but only for rewarded trials, showing an interaction of reward and difficulty information. This interaction in the context of non-motor, mental preparation remains to be studied in future research.

Computational models further predict that proactive control implementation will drop due to lack of motivation when the task becomes so difficult that reward becomes very unlikely, even when control is implemented (Verguts et al., 2015). The difficulty of calculations used in the current study was very low, with excellent performance also for hard trials (mean error rate 6% for hard trials, 1% for easy trials). Consequently, more control was implemented for hard trials, reflected in a larger SPN amplitude. Contrary to the current study, Silvetti, Nuñez Castellar, Roger, & Verguts (2014) showed a smaller CNV amplitude for hard compared to easy trials. In their study, a very difficult task was used, leading to a 60% error rate for hard trials and a 20% error rate for easy trials. This suggests that indeed control implementation fails when task difficulty becomes too high. Future research

should systematically manipulate task difficulty in order to investigate its hypothesized inverted-U relation with control implementation.

In conclusion, the current study provides a comprehensive electrophysiological signature of proactive control, unconfounded by motor preparation. We showed that proactive control is triggered by difficulty information, and this is reflected both in the SPN and alpha power. Also, we linked this scalp activity to underlying brain areas by intracranial recordings. Activity in the posterior parietal cortex showed an activation pattern similar to the SPN, suggesting the involvement of the fronto-parietal attentional network in proactive control. Also task-specific preparation in the dorsal striatum and hippocampus was observed. The neural signatures of control demonstrated in the current experiment provide an excellent tool for future research in cognitive control.

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## **CHAPTER 5**

### **GENERAL DISCUSSION**

The first aim of this PhD was to assess the role of difficulty and reward information in motivating proactive and reactive control. Theories on cognitive control have stated that control carries a cost, and is only implemented when properly motivated (Shenhav, Botvinick, & Cohen, 2013; Westbrook & Braver, 2015). Two motivational factors drive the decision to adapt cognitive control in a task, namely difficulty and reward information (Verguts, Vassena, & Silvetti, 2015). Control is implemented when it can improve task performance and when performing well is properly rewarded. Model simulations predict that these types of information are crucial for both proactive and reactive control implementation (Verguts et al., 2015), two important mechanisms for goal-directed behavior (Braver, 2012). The experiments presented in this dissertation, provide empirical support for this hypothesis. In Chapter 2, RT measures showed the rapid beneficial influence of reward on reactive cognitive control. In Chapter 3 and 4, the experience or expectancy of difficulty triggered reactive or proactive control processes. Moreover, we determined its electrophysiological signature using EEG.

The second aim of this PhD was to specify the time course of cognitive control processes. Classical control models conceptualize control as rather slow, typically operating between trials of a psychological experiment (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Posner & Presti, 1987;

Shiffrin & Schneider, 1977). In contrast, more recent associative models predict that control can also be implemented on a fast timescale, within the trial (Abrahamse, Braem, Notebaert, & Verguts, 2016; Egner, 2014; Verguts & Notebaert, 2008, 2009). In this view, stimulus and/or motor representations become associated with control representations and over time will trigger these control representations automatically, making fast control not only possible but likely. In this dissertation it was revealed that indeed, fast, within-trial control can occur, both in response to reward and difficulty information. This provides support for associative models of control. In Chapter 2, motivational effects of reward on control were observed when reward information was presented 200 ms before or even simultaneous to the task onset, indicating that reward affects reactive control very rapidly, within the trial. In Chapter 3, EEG measures revealed that the experience of stimulus and response conflict rapidly led to increased reactive control, as soon as 400 ms after stimulus onset.

Finally, not just the theoretical construct of cognitive control, but also the neural mechanisms that underlie cognitive control were a principal focus of this PhD. Previous fMRI research has shown the importance of the mid-frontal cortex in conflict detection and of a fronto-parietal control network in controlled attention (Corbetta & Shulman, 2002; Dosenbach et al., 2007; MacDonald, Cohen, Stenger, & Carter, 2000; Nobre et al., 1997). Additionally, control is believed to be implemented in task-specific sensory areas (Egner & Hirsch, 2005a; Polk, Drake, Jonides, Smith, & Smith, 2008; Weissman, Warner, & Woldorff, 2004). Finally, neural oscillations in these areas, such as theta and alpha oscillations, have proven to be important in control implementation (Cavanagh & Frank, 2014; Cavanagh, Zambrano-Vazquez, & Allen, 2012; Cohen & Cavanagh, 2011). Synchronization of these

oscillations is a likely mechanism for long range communication between distinct control regions (Cohen & Van Gaal, 2013; Cohen, van Gaal, Ridderinkhof, & Lamme, 2009; Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012; Womelsdorf, Ardid, Everling, & Valiante, 2014). This dissertation shows how various control brain regions and neural mechanisms are implicated specifically in reactive and proactive control, and describes how they are activated by reward and difficulty information. In Chapter 3, a theta power increase was observed for incongruent trials, reflecting the detection of conflict. This theta increase was predictive of ensuing alpha power modulations in specific visual areas processing incongruent flankers. Here, alpha power was increased for incongruent flankers during the trial, reflecting control implementation. In Chapter 4 the stimulus preceding negativity (SPN) and parietal alpha power were shown to reflect increased proactive control following a difficulty cue. Also, intracranial local field potential differences between easy and hard trials in parietal regions, as well as in the dorsal striatum (putamen) and the hippocampus, show the involvement of the fronto-parietal network and of task-specific areas.

In the three empirical chapters of this dissertation, I used behavioral, scalp EEG and intracranial EEG measures to study the time course of both reactive and proactive cognitive control, triggered by reward or difficulty information. In what follows, I will review the results of these studies in more detail and I will discuss their implications for cognitive control theories. I will also discuss how future research might further advance our knowledge of cognitive control and its neural mechanisms. There were three main aims in this PhD. In the three sections of this discussion I will explain how the results of the empirical chapters serve these three main aims and how they answer the research questions I laid out in the introduction. I will first discuss what my

research has taught us about the influence of reward and difficulty information on cognitive control. I will then explain how my results support the hypothesized fast timescale of control. Finally, I will discuss the neural networks underlying control and their time course.

### **REWARD AND DIFFICULTY INFORMATION MOTIVATE CONTROL**

The first aim of this PhD was to investigate if and how reward and difficulty information each influence control adaptation. Their influence on control is predicted by computational reinforcement learning models and neuro-economic decision making control theories (Botvinick & Braver, 2015; Shenhav et al., 2013; Verguts et al., 2015; Westbrook & Braver, 2015). From this neuro-economic perspective, control is conceptualized as the decision to invest cognitive effort and upregulate control, taking into account both the benefits and costs of control. The EVC model defines how these costs and benefits are taken into account (Shenhav et al., 2013). Similarly, the adaptive effort investment model describes how control (or in their terminology: mental effort) can be adaptively learned taking into account benefits and costs (Verguts et al., 2015). According to reinforcement learning principles applied in these models, actions are selected to maximize a value function (Sutton & Barto, 1998). Although cognitive control is not an overt action, it has consequences in the outside world, and can therefore be subject to reinforcement learning principles. Control is thus adapted to maximize the value function. What the optimal level of control is to obtain maximal value, depends on task difficulty and expected reward. Due to the reinforcement learning basis of these models, it is additionally expected that control can be adaptively learned for a specific task, during task execution. This learning of

control results over time in automatic activation of the optimal control representation when certain task stimuli are presented (Verguts et al., 2015). In this dissertation, to test predictions put forward by these models and to assess the influence of reward and difficulty information on proactive and reactive control, four research questions in a two by two structure were postulated in Chapter 1. The effect of reward on proactive control is well-studied in the literature (Aarts, Roelofs, & van Turenout, 2008; Bijleveld, Custers, & Aarts, 2010; Brian Knutson, 2005; Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Padmala & Pessoa, 2011), and therefore not recapitulated in this dissertation. Chapter 2 describes the influence of reward on reactive control. Chapter 3 tackles difficulty influences on reactive control. Finally, Chapter 4 shows the effect of difficulty on proactive control.

### **Reward motivates cognitive control**

The motivational role of reward prospect on cognitive control has been assessed numerous times in psychology. When performance-contingent rewards are introduced in a task, these improve task performance, which can be attributed to enhanced control (for a review see Botvinick & Braver, 2015). Research has mostly focused on slow adjustments of proactive control. In blocks where rewards are provided, performance improves (Leotti & Wager, 2010; Padmala & Pessoa, 2010). Also a cue informing participants about reward has been shown to improve proactive control in various tasks, ranging from Stroop-like tasks (Aarts et al., 2014; Padmala & Pessoa, 2011), to visual discrimination tasks (Krebs et al., 2012; Schevernels, Krebs, Santens, Woldorff, & Boehler, 2014), and simple detection tasks (Brian Knutson, 2005) but also to more complicated mental arithmetic tasks (Bijleveld et al., 2010; Vassena et al., 2014) or working memory tasks (Taylor et al., 2004).

Since the effects of reward on proactive control have been extensively studied in the past, this research question was not addressed further in this dissertation.

Studies describing the impact of reward on reactive control on the other hand, are relatively scarce. There is some prior evidence that reward intensifies trial-by-trial control adaptations following conflict or errors (Braem, Verguts, Roggeman, & Notebaert, 2012; Stürmer, Nigbur, Schacht, & Sommer, 2011). Also some studies suggested previously that reward might trigger fast reactive control processes. In a Stroop task, Krebs, Boehler, & Woldorff (2010) systematically rewarded stimuli with certain colors and show improved performance for these rewarded stimuli. Similarly, improved performance for rewarded stimuli was observed in a stop-signal task (Boehler, Hopf, Stoppel, & Krebs, 2012). However, in these studies rewarded stimulus-response (S-R) associations rather than increased control could account for the beneficial effects of reward. In Chapter 2 we used a visual discrimination task, and crucially we made the reward manipulation orthogonal to the S-R mapping. This allows reward effects to be attributed indisputably to increased control. This study provides new and robust evidence that reward indeed boosts reactive cognitive control on a fast within-trial timescale.

### **Task difficulty calls for cognitive control investment**

In Chapter 3, EEG revealed within-trial control adaptations following both stimulus and response incongruency. According to the conflict monitoring theory (CMT) response conflict is a necessary prerequisite to trigger control (Botvinick et al., 2001). However, in our study theta and alpha power reflecting control processes responded similarly to SI and RI conditions. This points to visual stimulus incongruency as the main driver for control implementation in this task. The finding that response conflict is not

necessary to evoke control, but that also stimulus incongruency can act as a control signal is not new (see e.g. Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012) and can easily be explained from an associative decision-making perspective such as the EVC or adaptive effort model (Shenhav et al., 2013; Verguts et al., 2015). Stimulus incongruency impedes performance in the task, and is therefore a marker for task difficulty. Since control adaptation following such a difficulty cue results in the optimization of the value function (successful task performance), this type of “control behavior” is learned gradually during the task. Implementing control following stimulus incongruency proves to be a useful strategy for this particular task, and is therefore adopted. Which strategies are useful depends on the stimuli and stimulus contingencies at hand (for a similar argument, see Brown, 2009; Pansky & Algom, 2002; Schmidt & De Houwer, 2012). In classical congruency tasks, response conflict is often the most relevant and obvious marker for task difficulty, predicting task performance. Response conflict is consequently the usual, but as it turns out, not the necessary driver of control. In conclusion, in Chapter 3 stimulus incongruency serving as a difficulty cue was shown to boost reactive cognitive control.

Chapter 4 describes how difficulty expectation motivates proactive control. We manipulated the difficulty of operations in a mental calculation task, warning participants about upcoming task difficulty a few seconds before task onset. Here, any motor preparation was carefully removed from the cue-task interval, by evoking only a mental response to the task. In the CMT motor processes play a special role in control, since conflict between competing motor responses is believed to trigger activation in the conflict monitoring unit and ensuing control. However, in decision making models task difficulty motivating control is not necessarily related to response conflict and motor

processes. Previous research has often confounded motor and attentional preparation, by investigating the contingent negative variation (CNV) to study task preparation (Schevernels et al., 2014; Walter, Cooper, Aldridge, McCallum, & Winter, 1964). Alternatively, pure attentional expectation has been studied via the stimulus preceding negativity (SPN). However, the SPN has been used almost exclusively to study expectation of feedback or other stimuli not requiring any (mental) task performance (Brunia & van Boxtel, 2001; van Boxtel & Böcker, 2004). So SPN studies normally do not investigate proactive cognitive control. In Chapter 4 we used the SPN to capture the ERP signature of proactive control, free of any motor signal. Additionally, also parietal alpha oscillations were studied. Both the amplitude of the SPN and alpha power modulations were larger for hard compared to easy trials. The neurophysiological signatures in this study thus clearly show that control is boosted when a difficult task is expected.

### **The interaction of reward and difficulty**

Decision-making control models based on reinforcement learning principles predict that reward and difficulty information will interact, with control only being implemented when both are sufficiently high (Shenhav et al., 2013; Verguts et al., 2015). Control will be invested only when this could be beneficial for performance (for a difficult task) and when reward is likely. In this dissertation, we focused on the separate effects of reward and difficulty rather than on their interaction. Nevertheless, Chapter 2 does allow some evaluation of the interaction. In the experiments of Chapter 2 not only reward but also task difficulty was manipulated. We expected an interaction of reward and difficulty, however we found no evidence for this. We speculate that the timing of the difficulty information, by definition at task onset, occurred too



late in time to interact with reward information. Reward information presented simultaneous to task onset only had an effect in very simple task conditions, when only two possible reward cues were used, but not in more complicated task conditions, when three possible cues were used. When reward information was presented later, after task onset, it no longer had an effect. These results show that any effects we do find, are on the timing limits of control possibilities. Processing and integrating both the reward and difficulty information to make a decision about control possibly took too much time to influence behavior. For proactive control, Schevernels et al., (2014) used EEG to show that reward influences control earlier in time than difficulty information. Consistently, they show an interaction of reward and difficulty only after considerable time (1100 ms post cue onset). To test whether reward and difficulty information also interactively influence reactive control, the paradigm of Chapter 2 could be used but with an added difficulty cue presented a short interval before task onset. Manipulating the timing of difficulty information could reveal just how much time is vital for the two types of information to be integrated and influence reactive control.

### **When reward is just not worth it anymore**

Decision-making control models predict that control will not be implemented if a task becomes too difficult (Shenhav et al., 2013; Verguts et al., 2015). In this case, upregulating control does not optimize the value function since it does not improve task performance and hence does not increase the likelihood of obtaining a reward. Indeed, decision-making studies have shown that incentives do not motivate cognitive effort when task requirements exceed a person's skill set (Awasthi & Pratt, 1990) or processing capacity (Bonner & Sprinkle, 2002). Also, task difficulty is directly linked to

the cost of cognitive control i.e. the mental effort required to succeed in the task (Kool, McGuire, Rosen, & Botvinick, 2010). When task difficulty increases significantly, the cost of control might outweigh the benefits. In decision making literature, the phenomenon *effort discounting* describes how a positive outcome or reward is discounted by physical or mental effort (Botvinick, Huffstetler, & McGuire, 2009; Croxson, Walton, O'Reilly, Behrens, & Rushworth, 2009; Salamone & Correa, 2012). In the present dissertation, task performance was very good, even for difficult trials. In all three chapters, error rates never exceeded 10%, indicating that the task requirements were well within subject's processing capacity. The experimental setup of the experiments in this dissertation therefore does not allow us to study (the absence) of control implementation in very challenging conditions. Using a very difficult task, Silvetti, Nuñez Castellar, Roger, & Verguts (2014) showed a lower CNV amplitude for hard compared to easy trials, reflecting less control for hard than for easy trials. In this study the error rate for hard trials was 60% (vs. 20% error rate for easy trials). This suggests that indeed control implementation fails when task difficulty becomes too high. Future research should explore the boundaries for control, searching for the tipping point where increased difficulty does no longer promote control but discourages it. This tipping point might be individually different, depending on dopaminergic limbic loop functioning. Dopamine depletion in rats results in a refusal to invest effort to obtain rewards (Salamone, Cousins, & Bucher, 1994), and in humans, patients suffering from depression are often effort averse and refrain from investing effort to obtain rewards (Cohen, 1982; Treadway & Zald, 2011). Detailed insight into the complex equilibrium of reward and task difficulty in the investment of cognitive control is necessary

for our understanding of goal-directed behavior and is crucial to understand and treat related disorders.

### **CONTROL CAN ACT ON A FAST, WITHIN-TRIAL TIMESCALE**

The second aim of this PhD was the specification of the time course of cognitive control. In contrast to classical control models, associative models predict that reactive control can be rapidly recruited on a within-trial timescale (Abrahamse et al., 2016; Egner, 2014; Verguts & Notebaert, 2008, 2009). This hypothesis was tested in Chapter 2 and 3.

#### **Reactive control can be recruited within 400 ms**

In Chapter 2 we specified the time course of control by assessing the influence of reward timing on RTs and error rates in a visual discrimination task. When a reward-predictive cue was presented 200 ms before target onset, it improved processing efficiency. This reward effect was smaller for simultaneous cue and target presentation, and was absent when cues were presented after target onset. Average response times were around 450 ms, in reference to the task onset. In the cue-pre-target condition, reward based control processes thus had approximately 650 ms to unfold and influence the response. In the simultaneous conditions this dropped to 450 ms, and in the cue-post-target condition this was further reduced to 250 ms. Since the reward cue had no effect when it was presented after task onset, we can infer that control implementation had not progressed enough to influence the response after 250 ms. It had however sufficiently advanced to influence behavior after 450 ms (as evident from the reward effect in the simultaneous cue-target

condition). This reveals that the time needed for influential control processes is between 250 ms and 450 ms for this task.

In Chapter 3, we exploited the high temporal resolution of EEG to show that control was modulated within-trial, as soon as 400 ms after stimulus onset. A lateralized flanker task was used, where incongruent flankers were presented in only one hemifield. Incongruent stimuli led to a power increase in the theta frequency band, peaking around 160 ms. This increase likely reflects the early detection of incongruency (Cavanagh et al., 2012). Further, we captured activity specific to the processing of incongruent flankers by computing the lateralized incongruency difference (LID). The signal for trials with incongruent flankers in the right visual hemifield was subtracted from the signal for trials with incongruent flankers in the left visual hemifield. Consistent with previous research using this paradigm (Appelbaum, Smith, Boehler, Chen, & Woldorff, 2011), the LID revealed that processing differs for congruent versus incongruent flankers, and this difference first occurs around 250 ms post stimulus onset. To determine whether this processing difference reflected distraction (decreased attention) or control (increased attention) we investigated alpha power. We hypothesized that incongruent flankers would elicit cognitive control, and this would be reflected in more alpha power in areas processing these incongruent flankers marking active inhibition of attention (Jensen & Mazaheri, 2010; Worden, Foxe, Wang, & Simpson, 2000). Indeed, we observed more alpha power for incongruent flankers, and this active inhibition process peaked around 400 ms.

It is important to note that this time-frequency result does not have the same millisecond precision as ERP results. Power was calculated by performing a Fast Fourier Transform on data in a 488 ms (moving) time

window. Consequently, power estimations cannot capture power precisely on one moment, but reflect average power during a larger time interval. This loss in timing precision is inevitable when performing time-frequency analysis, since power estimation of a certain frequency requires data containing at least one cycle (and preferably more) of this frequency (Cohen, 2014). Our estimation of control timing is therefore not millisecond precise. Nevertheless, we can reliably claim that control processes occurred rapidly, within the trial.

The timing of control in Chapter 2 and Chapter 3 was comparable. In Chapter 2 control could influence task performance somewhere between 250 to 450 ms post task onset. In Chapter 3, the LID onset occurred at 250 ms and alpha modulations reflecting control peaked around 400 ms after stimulus onset. Taken together these findings suggest that reactive control (at least in these tasks) can be recruited within 400 ms. This is in line with previous findings reporting fast within-trial control. In an EEG experiment using frequency tagging, Scherbaum, Fischer, Dshemuchadse, & Goschke (2011) showed that attention was modulated continuously throughout an incongruent trial, with attention being directed towards relevant information and away from irrelevant information. Also following errors, fast control processes have been shown (Cohen et al., 2009). The experiments presented in Chapter 2 and 3 add to these findings by further specifying the rapid time course of control, both triggered by reward and difficulty information.

### **Fast control supports associative models of control**

The findings presented in Chapter 2 and 3 support associative models of control (Egner, 2014; Verguts & Notebaert, 2008, 2009) over more classical control models, that conceptualize cognitive control as a slow process typically operating between trials (Botvinick et al., 2001, 2004; Braver, 2012;

Posner & Presti, 1987; Shiffrin & Schneider, 1977). Associative models implicitly predict fast control is possible and even likely, but they do not explicitly define control timing. The current findings add to these models by explicitly specifying the timing constraints of cognitive control. They thus provide an empirical basis for future and more advanced models, that can explicitly model and predict fast control processes. In the current studies, control processes seem to take 400 ms to influence behavior. The timing of these effects is similar to that of other associative processes, e.g. associative priming (Perea & Gotor, 1997; Perea & Rosa, 2002; Sailor, Brooks, Bruening, Seiger-Gardner, & Guterman, 2009).

Another prediction of associative models is that subjects may learn associations between perceptual and control representations during the task. Consequently, these models predict that cued control might require training. This implicates that the timing of control processes might change after extensive training. To test this, future research is needed that monitors control processes throughout the course of training for a task.

### **THE NEURAL TIME COURSE OF COGNITIVE CONTROL**

The third aim of this PhD was to gain insight into the neural mechanisms of cognitive control and their timing. fMRI research has previously shown the involvement of the medial frontal cortex, the fronto-parietal control network and task-specific sensory processing areas (Corbetta & Shulman, 2002; Egnér & Hirsch, 2005a; MacDonald et al., 2000; Polk et al., 2008; Weissman et al., 2004). However, since these studies rely mostly on fMRI, they are unable to reveal the time course of control processes.

### **Alpha oscillations reveal fast attentional modulations**

In Chapter 3 we used EEG to capture the time course of control. We specifically wanted to assess how fast control is implemented in specific sensory processing areas. To allow us to isolate processing of incongruent irrelevant stimuli, we applied a lateralized flanker task. In this task, a central target stimulus is flanked by incongruent flankers in only one visual hemifield (congruent flankers are presented in the opposite hemifield), confining sensory processing of these flankers to the occipital cortex of the contralateral hemisphere. By comparing the EEG for left vs. right hemisphere electrodes we revealed processing specific to incongruent flankers. This approach was used previously by Appelbaum et al. (2011), who calculated the lateralized incongruency difference (LID) and observed that incongruent flankers are processed differently from congruent ones. However, they could not attribute this processing difference to either increased attention (i.e. control implementation) or increased distraction by incongruent flankers drawing attention. Indeed, previous research supports the idea that visually distinct stimuli in a stream of static stimuli capture attention (Burnham & Neely, 2008; Burnham, Neely, Naginsky, & Thomas, 2010). This attentional capture process might explain the LID. To determine whether the LID reflects control processes, we investigated alpha oscillations.

In the current study, alpha oscillations revealed that the LID indeed reflects increased control by suppressing processing of incongruent flankers, and that it does not reflect increased distraction. We observed more alpha power on occipital sites over the hemisphere processing incongruent flankers than on occipital sites over the opposite hemisphere, processing congruent flankers. Alpha oscillations are a well-known mechanism for neural

suppression and can be actively used to suppress processing of irrelevant information (Jensen, Bonnefond, & VanRullen, 2012; Jensen & Mazaheri, 2010). They have often been reported in the context of proactive control or cued spatial attention, where they mark attention for relevant stimuli and where they significantly predict task performance (Kelly, Lalor, Reilly, & Foxe, 2006; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden et al., 2000). In the current study, we observed alpha modulations within the trial (peaking around 400 ms post-stimulus onset), following stimulus or response conflict. We thus show that alpha oscillations in visual areas also underlie control on a fast timescale, providing insight into the neural processes supporting reactive control.

In Chapter 4, we again investigated alpha oscillations. In this study we observed a sustained decreased alpha power in the period between a difficulty cue and task onset. This alpha power decrease was maximal at parietal electrodes and reflects increased attention for the upcoming task stimuli. Parietal alpha power has been linked to increased attention for external stimuli (Benedek, Schickel, Jauk, Fink, & Neubauer, 2014). We further hypothesize that this parietal alpha power modulation reflects increased activation in the fronto-parietal attentional control network, since alpha power has been shown to correlate negatively with BOLD activity (Laufs et al., 2003; Ritter, Moosmann, & Villringer, 2009). In our study, alpha power was decreased more strongly for hard than for easy trials, indicating increased control. A sustained suppression of alpha oscillations similar to that in the current study was observed previously by van den Berg, Krebs, Lorist, & Woldorff, (2014). In their study, alpha power in the cue-target interval was modulated by reward information, with less alpha (and thus more attention) for rewarded vs. non-rewarded trials. The similarity of these alpha characteristics, in terms of



topographical maximum, timing and modulation, suggest that reward and difficulty influence attentional control through similar mechanisms, relying on oscillations in the alpha frequency band.

### **Control is implemented through the fronto-parietal network and in task-specific areas**

Based on control models and previous fMRI research, we hypothesized that control would be implemented through a fronto-parietal attentional control network (Corbetta & Shulman, 2002; Dosenbach et al., 2007; Gitelman et al., 1999; Nobre et al., 1997) but would also be implemented locally, in brain areas specific to the task at hand (Egner & Hirsch, 2005a; Polk et al., 2008; Verguts & Notebaert, 2009; Weissman et al., 2004). The results from Chapter 3 and 4 confirm this hypothesis. Crucially, our findings add to previous fMRI research by also revealing the time course of these control processes.

In Chapter 4 we made use of scalp and intracranial recordings to show the involvement of the fronto-parietal attentional network and task-specific areas in proactive control. We observed a larger SPN in the period between a difficulty cue and task onset. The SPN is believed to reflect postsynaptic potentials of pyramidal neurons in cortical areas involved in the upcoming task (Birbaumer, Roberts, Lutzenberger, Rockstroh, & Elbert, 1992; Elbert, 1993). The SPN and other slow negative components likely reflect increased neural excitability of underlying source neurons. In these neurons, the threshold for generating an action potential is lowered, to prime these neurons to fire at task onset (Elbert, 1993; McAdam, 1969). Source localization studies have revealed the cortical areas that drive the SPN. The main sources of the SPN are believed to be the fronto-parietal network, and the anterior insula

(Böcker et al., 1994; Brunia et al., 2000; Kotani et al., 2015; Tsukamoto et al., 2006). The fronto-parietal network is believed to underlie attentional processes, whereas the anterior insula likely responds to the emotional valence of the expected stimulus (Menon & Uddin, 2010). For the related negative slow CVN component, the fronto-parietal network has also been proposed as the main source, together with motor areas involved in motor preparation (Gómez, Flores, & Ledesma, 2007; Grent-‘t-Jong & Woldorff, 2007). The slow component measured in the current study thus very likely reflects the involvement of the fronto-parietal network in proactive control. Moreover, the high temporal resolution of EEG shows that this involvement continuously increases throughout the cue period, peaking before task onset.

Intracranial recordings in the posterior parietal cortex further supported the hypothesized involvement of the fronto-parietal network in proactive control. Intracranial local field potential recordings provided us with an excellent opportunity to study the brain areas involved in control. In contrast to scalp EEG measures, these recordings do not only provide excellent temporal resolution, but are also very locally precise. The posterior parietal cortex is an important part of the fronto-parietal network (Gitelman et al., 1999; Hopfinger, Buonocore, & Mangun, 2000) and many fMRI studies have supported its role in proactive cognitive control (Engelmann, Damaraju, Padmala, & Pessoa, 2009; Brian Knutson, Westdorp, Kaiser, & Hommer, 2000; Padmala & Pessoa, 2010; Rosell-Negre et al., 2014; Wu, Weissman, Roberts, & Woldorff, 2007). In Chapter 4, a slow negative deflection, similar to the scalp SPN in our healthy subjects, was observed in the posterior parietal cortex. This slow wave was much more pronounced for hard than for easy trials. This difference increased throughout the trial until task onset, showing

again how attention is continuously increased during the cue period through activation of the fronto-parietal control network.

The intracranial recordings in Chapter 4 also revealed control related activation in the dorsal striatum (likely putamen). Scalp EEG measures mostly capture superficial brain activation and deep sources typically do not show up in the EEG (Elbert, 1993; Kappenman & Luck, 2011). Intracranial recordings thus present a great opportunity to study also the neurophysiology of deeper, subcortical areas. Using fMRI, these areas have been shown to play an important role in (motivated) control (Boehler et al., 2011; Krebs et al., 2012; Vassena et al., 2014). Subcortical areas are often co-activated with the cortical fronto-parietal network (Gitelman et al., 1999; Hopfinger et al., 2000). Also, the dorsal striatum is reliably activated during motivated control, both during anticipation of an effortful task (Krebs et al., 2012; Kurniawan, Guitart-Masip, Dayan, & Dolan, 2013; Vassena et al., 2014) and during reward anticipation (Engelmann et al., 2009; Knutson, Adams, Fong, & Hommer, 2001; Padmala & Pessoa, 2011). On a more physiological level, caudate nucleus neurons have been shown to fire during motivated proactive control, and this activation is correlated with improved task performance (Lauwereyns, Watanabe, Coe, & Hikosaka, 2002). Many subcortical areas play an important role in dopaminergic processes, which are vital for motivated control (Salamone & Correa, 2012; Wise, 2004). Dopamine depletion in animals is related with reduced willingness to invest effort, whereas dopaminergic stimulation increases effort (Bardgett, Depenbrock, Downs, Points, & Green, 2009). Also in humans, dopamine has been shown crucial for cognitive effort (Westbrook & Braver, 2016). In sum, these findings indicate an important role for subcortical areas in control. Based on this, activation of these areas during proactive control, as part of the extended general attentional control network,

can be expected. In line with this, we indeed observed increased dorsal striatum (likely posterior putamen) involvement during anticipation of hard trials (compared to easy).

Control is not only implemented through the fronto-parietal network, but also acts locally, in task-specific brain areas. In Chapter 3, we showed control implementation in areas specific to processing task-irrelevant flankers. Attention for these incongruent flankers was suppressed during the trial, as evidenced by increased alpha power in areas processing these flankers. By using a lateralized flanker paradigm, we could spatially separate relevant from irrelevant stimulus processing. This allowed us to study control in task-specific areas. In this study, we showed that control is indeed implemented in these areas. This is in line with fMRI studies showing that control can be implemented by suppressing processing for irrelevant stimuli (Polk et al., 2008). Since relevant stimuli were presented centrally in this study, we cannot assess how processing of these stimuli was adapted during the trial. Based on previous fMRI research, we could hypothesize that processing in these relevant areas would be increased (Egner & Hirsch, 2005a; Weissman et al., 2004). Crucially, we revealed the time course of control in task-specific areas. We showed that attention for irrelevant information was rapidly suppressed, within the trial. To our knowledge, no prior research has revealed the timing of such fast control processes in task-specific areas, since previous studies relied on fMRI.

The idea that control can be implemented in task-specific areas is also supported by intracranial recordings in Chapter 4. In the cue-target interval we found increased activation in the hippocampus for hard vs. easy trials. The task used in Chapter 4 was a mental calculation task. The hippocampus has

been implicated in neural networks underlying mental calculations. More specifically, the hippocampus is activated when a retrieval strategy is used to solve a calculation (Cho, Ryali, Geary, & Menon, 2011; De Smedt, Holloway, & Ansari, 2011). Also, the hippocampus is more involved for difficult calculations requiring carrying, than for easy calculations not requiring carrying (Kong et al., 2005). These studies support the idea that the hippocampus is a task-specific area involved in mental calculations. Activity in the hippocampus during the cue period in our task, can thus be interpreted as a marker for increased control implementation in a task-specific area.

The activation in the posterior parietal cortex and putamen interpreted above as activation of the (extended) fronto-parietal control network, could also be explained in terms of task-specific control. The posterior parietal cortex is not only involved in the fronto-parietal network, but also plays an important part in mental arithmetic processes (Rickard et al., 2000). The putamen is typically involved in automatized processing (Ashby, Turner, & Horvitz, 2010; Lehericy et al., 2005). It might be activated in anticipation of hard calculations in our mental calculation task, because these hard calculations rely on using well-learned arithmetic facts (e.g.,  $7+4=11$ ). In contrast, counting can be used to solve easy calculations, since they consisted only of “+1” operations. Arithmetic mental operations used to solve hard trials can be conceptualized as covert actions, that have previously been learned and automatized (Rivera, Reiss, Eckert, & Menon, 2005). Activation of these automatic “actions” might involve the putamen. In this view, preparatory activation in the posterior parietal cortex and in the putamen reflect proactive control implementation in task-specific areas. Further research, applying various tasks, is needed to clearly separate the roles of the fronto-parietal attentional network and specific areas in control.

Based on the research of Chapter 3 and 4, we can conclude that both the fronto-parietal control network and task-specific areas are critical in control implementation. This is in line with associative control models. These models predict that general control networks are used to implement control in sensory areas. When a cue for control is perceived, perceptual and/or motor input activates associated control representations. These representations in turn generate an arousal boost leading to increased binding between cortical areas that are active at that moment, i.e. task-relevant cortical areas (Verguts & Notebaert, 2009). It is also consistent with fMRI studies showing interacting roles for the fronto-parietal network and task-specific areas for control (Egner & Hirsch, 2005b; Slagter et al., 2007; Weissman et al., 2004).

### **Detection of difficulty in the MFC can drive reactive control implementation**

Chapter 3 provides evidence for the idea that a detection signal in the medial frontal cortex (MFC) triggers reactive control processes. In this experiment we observed a frontal theta power increase, which was correlated with control implementation later in the trial. The theta increase peaked around 160 ms post stimulus onset and very likely reflects the detection of stimulus and response conflict by the MFC (Cavanagh & Frank, 2014; Cavanagh et al., 2012). This theta detection signal was correlated with the alpha modulations reflecting control implementation later in the trial: more theta power was related to more attentional suppression for irrelevant information. Since these alpha power modulations occurred later in the trial, peaking around 400 ms post-stimulus onset, we hypothesize that theta might drive alpha modulations. This is consistent with the idea that the MFC triggers control implementation in sensory specific areas. Previous oscillation studies

have already shown how the MFC and occipital areas interact during control implementation. Synchrony between frontal theta and occipital alpha is increased on post-error trials (Cohen et al., 2009) and frontal theta increases have been correlated with occipital alpha decreases following errors (Mazaheri, Nieuwenhuis, Van Dijk, & Jensen, 2009). Here we show that similar mechanisms operate to implement control within the trial, following stimulus presentation.

This proposed dynamic between MFC and sensory areas is compatible with the CMT, proposing a conflict detection unit located in the MFC (Botvinick et al., 2001). It also supports associative control models that claim control is implemented locally, in sensory areas involved in the task (Verguts & Notebaert, 2009). fMRI studies show that activation in the ACC triggers the involvement of the DLPFC (MacDonald et al., 2000), which in turn influences activity in sensory specific areas (Egner & Hirsch, 2005a; Polk et al., 2008; Weissman et al., 2004). However, because of the slow nature of the BOLD response, these studies could not reveal the time course of the MFC – sensory areas dynamic. In Chapter 3 we show that the MFC can rapidly recruit sensory areas to adapt control.

## CONCLUSION

The experiments presented in this dissertation, provide empirical support for the hypothesis that both reward and difficulty information drive motivated cognitive control, as predicted by decision-making control theories and computational models of control (Shenhav et al., 2013; Verguts et al., 2015; Westbrook & Braver, 2015). I systematically tested and confirmed this

hypothesis for both reactive and proactive control, two important mechanisms of control (Braver, 2012). One of the cardinal aims of this PhD was to gain insight into the time course of control. By using stimulus timing manipulations or by exploiting the excellent temporal resolution of EEG, I showed that control can occur rapidly, within a trial. In our tasks, control was implemented as fast as within 400 ms post stimulus onset. This provides support for associative control models, that imply that stimulus representations can rapidly activate associated control representations (Abrahamse et al., 2016; Egner, 2014; Verguts & Notebaert, 2008, 2009). Moreover, my results provide an important empirical basis for the advancement of future models, that can explicitly model fast control processes. Finally, in this dissertation I also provide further evidence for the fronto-parietal network and task-specific areas as important neural substrates for control. Moreover, I also demonstrated the fast nature of the neural processes underlying control, adding crucial new information to observations from fMRI research (e.g. Corbetta & Shulman, 2002; Egner & Hirsch, 2005; Gitelman et al., 1999; Polk et al., 2008). The medial frontal cortex was shown to trigger reactive control, that was implemented later in the trial in sensory areas processing task-specific information. By demonstrating alpha power increases in areas processing incongruent stimuli I revealed that control is implemented there through attentional suppression reliant on alpha oscillations. This is in line with the gating by inhibition view, assuming an active inhibitory role for alpha oscillations (Jensen & Mazaheri, 2010) and shows that these oscillations can be rapidly adapted to serve goal-directed action. Also for proactive control, scalp and intracranial measures revealed the involvement of task-specific areas, as well as the fronto-parietal network and subcortical areas. My findings



suggest that in all these areas, control is gradually increased during task preparation.

The current findings provide crucial empirical validation of hypotheses put forward by various cognitive control models. Importantly, they reveal the time course of control implementation and of neural processes underlying it. Timing is an aspect that is often overlooked, because fMRI is used or because paradigms are not well adapted to look for fast control implementation. The timing of these processes is however crucial information, if we want to truly understand and define cognitive control. Control is often needed on short notice, so more insight into its timing is necessary to specify control processes in detail. The research performed during my PhD provides a step in that direction, and might inspire future control models and theories to take fast control processes into account. However, many open questions for future research remain. How do reward and difficulty interact in motivating fast control processes? What network dynamics link various brain areas involved in control? How do task requirements influence control timing? How can training change control associations and thus possibly the time course of control? These and many other questions will require further systematic empirical research in years to come.

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## **CHAPTER 6**

### **NEDERLANDSTALIGE SAMENVATTING**

Mensen zijn in staat om hun gedrag te sturen op basis van de doelen die ze willen bereiken. Ze kunnen aandacht focussen op taakrelevante stimuli en de verwerking van irrelevante stimuli onderdrukken. Om taakgericht te handelen vertrouwen mensen op cognitieve controle, een set van top-down processen die meer eenvoudige processen coördineren. Controle is meestal bevorderend voor de prestaties in een cognitieve taak. Anderzijds houdt controle ook een kost in, aangezien het een mentale inspanning vraagt (Kool, McGuire, Rosen, & Botvinick, 2010). De voor- en nadelen van het inzetten van controle worden door ons cognitief systeem tegen elkaar afgewogen (Shenhav, Botvinick, & Cohen, 2013; Verguts, Vassena, & Silvetti, 2015; Westbrook & Braver, 2015). De eerste onderzoeksvraag in dit doctoraatsproefschrift was welke factoren mensen kunnen motiveren om controle uit te oefenen, ondanks de kost. Een tweede belangrijke onderzoeksvraag was op welke tijdsschaal cognitieve controleprocessen kunnen verlopen. Ten derde had dit proefschrift ook als bedoeling de neurale processen onderliggend aan controle te onderzoeken. Meer specifiek werd onderzocht op welke tijdsschaal verschillende hersengebieden en mechanismen actief zijn tijdens het uitoefenen van controle en hoe deze processen samenhangen.

### **INFORMATIE OVER BELONING EN TAAKMOEILIKHEID MOTIVEERT COGNITIEVE CONTROLE**

Cognitieve controle helpt ons om efficiënt en taakgericht te functioneren. Maar controle vraagt ook een mentale inspanning, en houdt dus eent in (Kool et al., 2010). Neuro-economische beslissingsmodellen hebben de factoren omschreven die een rol spelen bij het al dan niet verhogen van controle (Shenhav et al., 2013; Westbrook & Braver, 2015). De voor- en nadelen van controle worden tegen elkaar afgewogen. Er zijn twee factoren die bepalen of het verhogen van controle waardevol is, gegeven de situatie (Verguts et al., 2015). Het eerste aspect is taakmoeilijkheid. Controle kan de prestaties enkel verhogen als de taak moeilijk genoeg is en dus het cognitief systeem uitdaagt. Het tweede aspect is beloning. Verhoogde controle is enkel waardevol als goede prestaties ook beloond worden. Deze modellen voorspellen dus dat zowel informatie over taakmoeilijkheid als over beloning cognitieve controle kan motiveren. De empirische hoofdstukken in dit proefschrift onderzoeken het effect van moeilijkheid en beloning op controle. Daarbovenop wordt in controle het onderscheid gemaakt tussen reactieve en proactieve controle (Braver, 2012). Reactieve controle treedt op wanneer zich een conflict of andere moeilijkheid voordoet. Proactieve controle daarentegen wordt ingezet tijdens de voorbereiding van een taak, bijvoorbeeld na een cue die de taak aankondigt. Wanneer we het effect van beloning en taakmoeilijkheid, op zowel reactieve als proactieve controle willen beschrijven bekomen we vier onderzoeksvragen. Drie van deze vragen vormen de centrale onderzoeksvragen in de drie empirische hoofdstukken van dit proefschrift. In Hoofdstuk 2 en 3 werd onderzocht hoe reactieve controle wordt beïnvloed door beloning en moeilijkheid. In Hoofdstuk 4 werd



onderzocht hoe het vooruitzicht op een moeilijke taak proactieve control beïnvloedt. De overblijvende vraag, namelijk hoe beloning verhoogde proactieve controle uitlokt, is al uitvoerig onderzocht in het verleden (Aarts et al., 2014; Bijleveld, Custers, & Aarts, 2010; Brian Knutson, 2005; Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Padmala & Pessoa, 2011; Schevernels, Krebs, Santens, Woldorff, & Boehler, 2014) en wordt dus niet verder behandeld in dit doctoraatsproefschrift.

In Hoofdstuk 2 werd op elke trial een cue gepresenteerd die aanduidde of de trial beloond kon worden of niet. De effecten van deze cue op reactieve cognitieve controle werden onderzocht. Beloningscues leidden tot snellere en accuratere responsen, en hadden dus een positieve invloed op taakprestaties. Enkele eerdere studies hadden al effecten van beloningscues op reactieve prestaties gerapporteerd (Boehler, Hopf, Stoppel, & Krebs, 2012; Krebs, Boehler, & Woldorff, 2010), maar in die studies was de beloningsinformatie direct gelinkt aan taakrelevante stimuli. In dat geval kunnen sterkere stimulus-responsassociaties voor steeds opnieuw beloonde stimuli het effect van beloning verklaren. In de huidige studie werd beloning volledig onafhankelijk van de stimulus-responsassociaties in de taak gemanipuleerd, waardoor het effect in onze studie met zekerheid toe te schrijven valt aan verhoogde reactieve controle door de beloningscue.

In Hoofdstuk 3 gebruikten we EEG in een flankertaak om reactieve cognitieve controle te bekijken. Controle werd gedurende de trial aangepast door de verwerking van irrelevante flankers te onderdrukken. Deze vorm van controle gebeurde voor stimulusincongruente en responsincongruente trials. De conflict monitoring theorie conceptualiseert conflict dat controle uitlokt specifiek als responsconflict (Botvinick, Braver, Barch, Carter, & Cohen,

2001). In deze studie tonen we aan dat responsconflict niet noodzakelijk is om controle uit te lokken, maar dat taakmoeilijkheid controle in gang zet.

In Hoofdstuk 4 tenslotte gebruikten we opnieuw EEG maar ditmaal om proactieve controle te bekijken. Er werd een cue getoond die taakmoeilijkheid aanduidde, waarna een mentale rekentaak moest worden uitgevoerd. Om enkel cognitieve processen te vatten gebruikten we een taak zonder directe motorrespons. In het interval tussen de cue en de taak zagen we een grotere amplitude voor de “stimulus preceding negativity” (SPN) voor moeilijke trials. Deze ERP component weerspiegelt zeer waarschijnlijk aandachtsprocessen (Brunia & van Boxtel, 2001). Onze bevindingen wijzen er dus op dat er meer controle werd uitgeoefend ten gevolge van de cue, en dat informatie over taakmoeilijkheid dus proactieve controle kan sturen.

### **CONTROLE KAN SNEL, BINNEN DE TRIAL, VERHOOGD WORDEN**

Klassieke cognitieve controlemodellen omschrijven controle als een typisch traag proces, dat tussen trials optreedt (Botvinick et al., 2001; Shiffrin & Schneider, 1977). Veel voorgaand empirisch onderzoek ging dan ook op zoek naar trage effecten, tussen trials in een psychologisch experiment (Gratton, Coles, & Donchin, 1992). Daartegenover conceptualiseren associatieve controlemodellen controle als een associatief proces tussen stimulus- of motorrepresentaties en controlerepresentaties (Abrahamse, Braem, Notebaert, & Verguts, 2016; Egner, 2014; Verguts & Notebaert, 2008, 2009). Wanneer een stimulus getoond wordt, geraakt deze geassocieerd met een bepaalde mate van controle. Later zal de stimulus dan automatisch dezelfde controlerepresentatie opnieuw oproepen. Deze associatieve modellen

voorspellen dus dat controle ook snel, binnen een trial, kan optreden. Deze predictie werd getest in Hoofdstuk 2 en in Hoofdstuk 3.

In Hoofdstuk 2 werd een visuele discriminatietaak gebruikt. Er werd ook een cue aangeboden die proefpersonen informatie gaf over een mogelijke beloning. Deze cue werd 200 ms voor, tegelijk met, of 200 ms na de start van de taak getoond. Door deze tijdsmanipulatie konden we nagaan hoe snel controle kon worden verhoogd, en konden we zo het tijdsverloop van controleprocessen bepalen. De voorspelling van beloning leidde tot verhoogde cognitieve controle. We toonden bovendien aan dat controle zeer snel geïmplementeerd kon worden, wanneer de beloningscue slechts 200 ms voor of zelfs gelijktijdig met de taak werd getoond. Aangezien de gemiddelde responstijd ongeveer 450 ms was, en beloning die simultaan met de taak getoond werd een effect had, kunnen we besluiten dat controle in deze taak binnen  $\pm 400$  ms voldoende kon worden aangepast om gedrag te beïnvloeden. Deze resultaten bieden dus evidentie voor associatieve modellen die snelle controle voorspellen.

In Hoofdstuk 3 werd een flankertaak gebruikt in combinatie met EEG. Incongruente stimuli leidden tot verhoogde power in de theta frequentie, met een piek rond 160 ms na het presenteren van de stimulus. Dit soort verhogingen in theta power in congruentietaken wordt in de literatuur vaak omschreven (Cavanagh, Zambrano-Vazquez, & Allen, 2012) en deze thetaverhoging reflecteert waarschijnlijk de detectie van conflict in de frontale cortex (Cavanagh & Frank, 2014). Na deze detectie volgden er later in de trial controleprocessen, tussen 300 en 500 ms na stimulusaanbieding. We observeerden verhoogde power in de alfafrequentie in sensorische gebieden die instonden voor de verwerking van irrelevante flankers. Alpha oscillaties

zijn gelinkt aan verlaagde neurale activiteit (Laufs et al., 2003) en zelfs aan actieve neurale inhibitie (Jensen & Mazaheri, 2010). Dat deze oscillaties sterker aanwezig waren in gebieden die irrelevante flankers verwerkten wijst er dus op dat de verwerking van deze flankers onderdrukt werd. Er werd dus cognitieve controle toegepast op een zeer snelle tijdsschaal, namelijk binnen  $\pm 400$  ms. Dit bevestigt opnieuw het idee van associatieve controlemodellen, dat controle snel en binnen een trial kan aangepast worden aan de taakvereisten.

### **HET NEURALE TIJDSVERLOOP VAN COGNITIEVE CONTROLE**

In dit proefschrift wilde ik ook zicht krijgen op het tijdsverloop van de neurale processen onderliggend aan cognitieve controle. Stuedies die gebruik maken van fMRI hebben aangetoond dat een netwerk van frontale en pariëtale gebieden een grote rol speelt in controle (Corbetta & Shulman, 2002; Gitelman et al., 1999; Krebs et al., 2012; Vassena et al., 2014). Dit algemene fronto-pariëtale netwerk stuurt controleprocessen die worden geïmplementeerd in hersengebieden die specifiek bij de taak betrokken zijn, zoals sensorische verwerkingsgebieden (Egner & Hirsch, 2005; Polk, Drake, Jonides, Smith, & Smith, 2008; Weissman, Warner, & Woldorff, 2004). Deze bevindingen ondersteunen associatieve controlemodellen, die stellen dat controle inderdaad lokaal geïmplementeerd wordt, in gebieden specifiek voor de taak (Verguts & Notebaert, 2009). Verder hebben fMRI-studies ook gesuggereerd dat reactieve controleprocessen in gang worden gezet door de detectie van (respons)conflict (MacDonald, Cohen, Stenger, & Carter, 2000), dat in de mediale frontale cortex plaatsvindt (Carter & van Veen, 2007). De grootste beperking van deze fMRI-studies is dat zij niet in staat zijn om een

precieze schatting te maken van de timing van deze processen. In dit proefschrift gebruikten we EEG precies om wel de tijdsschaal van deze processen te kunnen vatten en om neurale mechanismes te kunnen identificeren.

In Hoofdstuk 3 maakten we gebruik van een gelateraliseerde flankertaak om activatie in specifieke sensorische hersengebieden te kunnen isoleren. Incongruente stimuli werden in slechts één visueel hemiveld gepresenteerd, waardoor ze enkel verwerkt werden in de contralaterale hemisfeer. Door activatie in deze contralaterale hemisfeer te vergelijken met deze in de ipsilaterale hemisfeer (waar congruente stimuli werden verwerkt) konden we activatie specifiek voor incongruente stimuli vatten. Deze methode werd eerder toegepast door Appelbaum, Smith, Boehler, Chen, & Woldorff (2011), maar zij konden niet bepalen of de specifieke effecten die ze observeerden te interpreteren waren als verhoogde controle (dus minder aandacht) voor incongruente stimuli, of juist verhoogde afleiding (dus meer aandacht) voor incongruente stimuli. In Hoofdstuk 3 bekeken we alpha oscillaties specifiek in de gebieden die incongruente stimuli verwerken. Hier zagen we een verhoging van alfa-power, wat wijst op verlaagde aandacht, dus versterkte cognitieve controle (Jensen & Mazaheri, 2010). Deze studie toonde dus aan dat controle geïmplementeerd wordt in specifieke sensorische gebieden, zoals voorspeld door associatieve controlemodellen. Bovendien observeerden we ook een verhoging in thetapower op frontale elektroden. Dit reflecteert wellicht een conflictdetectiesignaal in de mediale frontale cortex (Cavanagh & Frank, 2014). Deze thetaverhoging was ook gecorreleerd aan latere alfa-modulaties: hogere theta was gelinkt aan meer onderdrukking van incongruente stimuli. Dit biedt evidentie voor het idee dat de mediale frontale

cortex controle in gang zet, die dan geïmplementeerd wordt in sensorische gebieden.

In Hoofdstuk 4 toonden we een grotere SPN-amplitude en verlaagde alfa-power in het interval tussen een moeilijkheidsniveau en de taak. De bron van de SPN werd in voorgaand onderzoek geschat in het fronto-pariëtaal netwerk (Böcker, Brunia, & van den Berg-Lenssen, 1994). De modulatie van de SPN wijst er dus op dat dit netwerk actief werd ingezet om proactieve controle te bewerkstelligen. Dit idee werd ook bevestigd door intracraniale EEG-metingen in de posterieure pariëtaal cortex van een epilepsiepatiënt. In de posterieure pariëtaal cortex, een belangrijk onderdeel van het fronto-pariëtaal netwerk (Corbetta & Shulman, 2002), zagen we ook een verhoogde activatie voor moeilijke trials. Via intracraniale metingen konden we ook observeren dat er verhoogde activatie was tijdens de voorbereiding van een moeilijke taak in het dorsale striatum (meer specifiek posterieur putamen). Dit subcorticale gebied wordt samen met andere subcorticale gebieden vaak geactiveerd samen met het fronto-pariëtaal netwerk (Gitelman et al., 1999; Hopfinger, Buonocore, & Mangun, 2000). Het dorsaal striatum speelt een belangrijke rol in (gemotiveerde) cognitieve controle, tijdens de anticipatie van een beloning (Engelmann et al., 2009; Knutson, Adams, Fong, & Hommer, 2001; Padmala & Pessoa, 2011) of van een moeilijke taak (Krebs et al., 2012; Kurniawan, Guitart-Masip, Dayan, & Dolan, 2013; Vassena et al., 2014). Tenslotte vonden we ook verhoogde activatie voor een moeilijke taak in de hippocampus. Activatie hier reflecteert waarschijnlijk proactieve controle in een taakspecifiek gebied. De hippocampus is betrokken in rekenen, meer specifiek wanneer mensen opgeslagen rekenfeiten ophalen uit het geheugen (Cho, Ryali, Geary, & Menon, 2011; De Smedt, Holloway, &

Ansari, 2011) of voor moeilijke optellingen met overdraging (Kong et al., 2005).

Samengevat bieden de studies in dit doctoraatsproefschrift dus evidentie voor de betrokkenheid van het fronto-pariëtale netwerk en taakspecifieke gebieden in zowel reactieve als proactieve controle. Bovendien werpen de huidige bevindingen licht op de tijdsschaal waarop deze processen opereren. Controleprocessen in taakspecifieke gebieden kunnen op zeer korte termijn, binnen een trial, geïmplementeerd worden. Tijdens proactieve controle zagen we dat activatie in het fronto-pariëtale netwerk en in specifieke gebieden stelselmatig toenam naarmate de start van de taak naderde.

## CONCLUSIE

Ten eerste bieden de empirische hoofdstukken van dit proefschrift evidentie voor de hypothese dat belonings- en moeilijkheidsinformatie cognitieve controle kunnen motiveren. Dit bevestigt verschillende controletheorieën en modellen (Shenhav et al., 2013; Verguts et al., 2015; Westbrook & Braver, 2015). Ten tweede demonstren de huidige resultaten de snelle tijdsschaal waarop controle werkzaam kan zijn. Door het gebruik van tijdsmanipulaties en EEG toonden we dat controle snel, binnen een trial kan optreden. Dit biedt evidentie voor associatieve controlemodellen (Abrahamse et al., 2016; Egner, 2014; Verguts & Notebaert, 2008, 2009). Bovendien kunnen deze resultaten een empirische basis vormen voor toekomstige modellen, die expliciet en preciezer de tijdsschaal van controle modelleren. Tenslotte werd verdere evidentie aangebracht dat het fronto-pariëtale netwerk en taakspecifieke hersengebieden een belangrijke rol spelen

in controle. Daarenboven werd aangetoond dat deze neurale processen zeer snel, binnen een trial, kunnen aangepast worden. Deze bevindingen vormen een cruciale aanvulling op vroeger fMRI-onderzoek (bv. Corbetta & Shulman, 2002; Egner & Hirsch, 2005; Gitelman et al., 1999; Polk et al., 2008).



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In compliance with the UGent standard for research accountability, transparency and reproducibility, the location of the datasets used in this dissertation are added below. For each of the empirical chapters (i.e., chapters 2 to 4) a separate Data Storage Fact Sheet is completed, detailing which data and analysis files are stored, where they are stored, who has access to the files and who can be contacted in order to request access to the files. In addition, the Data Storage Fact Sheets have been added to my public UGent Biblio account.

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\* Who has direct access to the raw data (i.e., without intervention of another person)?

- ☒ main researcher
- ☐ responsible ZAP
- ☐ all members of the research group
- ☐ all members of UGent
- ☐ other (specify): ...

### 3b. Other files

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\* Which other files have been stored?

- ☒ file(s) describing the transition from raw data to reported results. Specify: Word document describing the analyses performed
- ☐ file(s) containing processed data. Specify: ...
- ☒ file(s) containing analyses. Specify: R scripts (containing all processing steps and their justification)
- ☒ files(s) containing information about informed consent (printed informed consents stored in folder)
- ☐ a file specifying legal and ethical provisions
- ☐ file(s) that describe the content of the stored files and how this content should be interpreted. Specify: ...
- ☐ other files. Specify: ...

\* On which platform are these other files stored?

- ☒ individual PC
- ☐ research group file server
- ☐ other: ...

\* Who has direct access to these other files (i.e., without intervention of another person)?

- ☒ main researcher
- ☐ responsible ZAP
- ☐ all members of the research group
- ☐ all members of UGent
- ☐ other (specify): ...

## 4. Reproduction

=====

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\* Have the results been reproduced independently?: [ ]  
 YES / [x] NO

\* If yes, by whom (add if multiple):  
 - name:  
 - address:  
 - affiliation:  
 - e-mail:

v0.2

**DATA STORAGE FACT SHEET FOR CHAPTER 4**

% Data Storage Fact Sheet

% Name/identifier study

% Author: Clio Janssens

% Date: 04-11-2016

## 1. Contact details

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## 1a. Main researcher

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- name: Clio Janssens  
 - address: Henri Dunantlaan 2 9000 Gent  
 - e-mail: janssensclio@gmail.com or  
 clio.janssens@ugent.be

## 1b. Responsible Staff Member (ZAP)

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- name: Tom Verguts
- address: Henri Dunantlaan 2 9000 Gent
- e-mail: Tom.Verguts@ugent.be

If a response is not received when using the above contact details, please send an email to data.pp@ugent.be or contact Data Management, Faculty of Psychology and Educational Sciences, Henri Dunantlaan 2, 9000 Ghent, Belgium.

## 2. Information about the datasets to which this sheet applies

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\* Reference of the publication in which the datasets are reported:

Chapter 4 of PhD dissertation (third empirical chapter):  
Preparing for hard times: scalp and intracranial  
physiological signatures of proactive attentional  
control

\* Which datasets in that publication does this sheet  
apply to?:

All data from the reported experiments.

## 3. Information about the files that have been stored

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### 3a. Raw data

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\* Have the raw data been stored by the main researcher?  
[x] YES / [ ] NO  
If NO, please justify:

\* On which platform are the raw data stored?

- [x] researcher PC
- [ ] research group file server

- ☐ other (specify): ...

\* Who has direct access to the raw data (i.e., without intervention of another person)?

- ☒ main researcher
- ☐ responsible ZAP
- ☐ all members of the research group
- ☐ all members of UGent
- ☐ other (specify): ...

### 3b. Other files

-----  
---

\* Which other files have been stored?

- ☒ file(s) describing the transition from raw data to reported results. Specify: Word document describing the analyses performed
- ☐ file(s) containing processed data. Specify: ...
- ☒ file(s) containing analyses. Specify: R scripts (containing all processing steps and their justification)
- ☒ files(s) containing information about informed consent (printed informed consents stored in folder)
- ☐ a file specifying legal and ethical provisions
- ☐ file(s) that describe the content of the stored files and how this content should be interpreted. Specify: ...
- ☐ other files. Specify: ...

\* On which platform are these other files stored?

- ☒ individual PC
- ☐ research group file server
- ☐ other: ...

\* Who has direct access to these other files (i.e., without intervention of another person)?

- ☒ main researcher
- ☐ responsible ZAP
- ☐ all members of the research group
- ☐ all members of UGent
- ☐ other (specify): ...

#### 4. Reproduction

=====

===

\* Have the results been reproduced independently?: [ ]

YES / [x] NO

\* If yes, by whom (add if multiple):

- name:
- address:
- affiliation:
- e-mail:

v0.2



