

Theta Neurofeedback Training and its Transfer to Cognitive and Memory Control Processes

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“ *In art, as in science, reductionism does not trivialize our perception – of color, light, and perspective – but allows us to see each of these components in a new way.* ”

— Eric R. Kandel, *The Age of Insight*, 2012

Abstract

Cognitive and memory enhancement is not only a desire of a gradually aging society, but also of a young, increasingly competitive, and achievement-oriented society. Cognitive and memory control processes are necessary to select appropriate behavior and memories out of interfering ones and seem to be reflected in frontal-midline (FM) theta activity. Neurofeedback training (NFT) is a neuro-scientific method that is increasingly used for the training of brain activity underlying cognitive processes. Previous studies showed mixed findings of FM theta NFT to cognitive control processes. Furthermore, transfer to memory control processes that especially support the accurate recollection of contextual details (source memory) has not been investigated. The present thesis provides novel insights in the neural mechanisms underlying cognitive control processes as well as FM theta NFT and its transfer to cognitive and memory control processes. *Study 1* revealed that although cognitive control processes occurring before and after cognitively demanding events (proactive and reactive control) are reflected in FM theta activity, their topographies differ depending on task requirements. While theta activity was focally activated at frontal sites in a proactive control task, it had a broader topographical distribution in a reactive control task. *Study 2* and *3* demonstrated greater FM theta increase over seven NFT sessions for a training group who trained individual FM theta activity compared to an active control group who trained session-wise randomly chosen frequency bands. Moreover, FM theta NFT showed transfer to proactive control and source memory performance not one but 13 days after the last training session that was additionally predicted by FM theta NFT increase. These findings suggest that cognitive control transfer might become manifest late after training and that enhancement of memory control processes possibly improves the protection of memories from proactive interference. Interestingly, training-induced behavioral transfer tended to be accompanied by decreased FM theta activity, suggesting a more efficient use of cognitive and memory control processes after training. Together, the present thesis constitutes an intervention technique for cognitive enhancement in young adults that might be potentially relevant for treatment of cognitive and memory decline in old age.

Zusammenfassung

Kognitions- und Gedächtnissteigerung ist nicht nur der Wunsch einer immer älter werdenden Gesellschaft, sondern auch einer jungen, zunehmend wettbewerbsorientierten und leistungsorientierten Gesellschaft. Kognitive Kontrollprozesse und Gedächtniskontrollprozesse sind notwendig, um angemessene Verhaltensoptionen und gewünschte Gedächtnisrepräsentationen aus vielen konkurrierenden Varianten auszuwählen. Diese Kontrollprozesse scheinen sich in der Theta-Aktivität, die über der frontalen Mittellinie (FM) gemessen wird, widerzuspiegeln. Neurofeedbacktraining (NFT) ist eine neurowissenschaftliche Methode, die zunehmend für das Training kognitiver Prozesse zugrunde liegender Gehirnaktivität eingesetzt wird. Bisherige Studien zeigten unterschiedliche Befunde zur Verbesserung von kognitiven Kontrollprozessen durch FM Theta NFT. Darüber hinaus wurde der Transfer eines solchen Trainings zu Gedächtniskontrollprozessen, die insbesondere die Erinnerung kontextueller Details (Quellengedächtnis) unterstützen, noch nicht untersucht. Die vorliegende Arbeit liefert neue Einblicke sowohl in die neuronalen Mechanismen, die kognitiven Kontrollprozessen zugrunde liegen, als auch in FM Theta NFT und dessen Transfer zu kognitiven Kontrollprozessen und Gedächtniskontrollprozessen. *Studie 1* offenbarte, dass kognitive Kontrollprozesse, die vor und nach kognitiv anspruchsvollen Ereignissen auftreten (proaktive und reaktive Kontrolle), beide in FM Theta-Aktivität reflektiert sind, sich jedoch je nach Aufgabenanforderung in ihrer Topographie unterscheiden. In einer Aufgabe, die hauptsächlich proaktive Kontrolle beanspruchte, war die gemessene Theta-Aktivität fokal an frontalen Elektroden präsent, während in einer Aufgabe, welche maßgeblich die reaktive Kontrolle involvierte, die Theta-Aktivität eine weitere topographische Verteilung hatte. In *Studie 2* und *3* zeigte eine Trainingsgruppe, die individuell bestimmte FM Theta-Aktivität trainierte, einen größeren FM Theta-Anstieg über sieben NFT Sitzungen im Vergleich zu einer aktiven Kontrollgruppe, die sitzungsweise zufällig ausgewählte Frequenzbänder trainierte. Darüber hinaus führte FM Theta NFT zu einer Verbesserung proaktiver Kontrolle und der Quellengedächtnisleistung

nicht einen Tag nach der letzten Trainingssitzung, sondern 13 Tage später. Das Ausmaß der Performanzverbesserung wurde zusätzlich durch den FM Theta NFT Anstieg vorhergesagt. Diese Ergebnisse deuten darauf hin, dass sich einerseits der Transfer zu kognitiven Kontrollprozessen möglicherweise spät nach dem Training manifestiert und andererseits die Verbesserung von Gedächtniskontrollprozessen vermutlich Erinnerungen vor proaktiver Interferenz schützt. Interessanterweise ging der trainingsinduzierte Transfer tendenziell mit einer verminderten FM Theta-Aktivität einher, was auf eine effizientere Nutzung von kognitiven und Gedächtniskontrollprozessen nach dem Training schließen lässt. Die vorliegende Arbeit stellt eine Interventionsmethode zur kognitiven Verbesserung bei jungen Erwachsenen mit potentieller Relevanz für die Behandlung von Kognitions- und Gedächtnisverlusten im Alter dar.

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List of Publications

This doctoral thesis is based on three studies that are already published, under review, or in preparation as articles in peer-reviewed journals. I am the first author of these articles and the authors who are listed below have contributed to the work. Apart from minor changes the articles are presented in their original form. Please note that both neurofeedback articles are based on one large neurofeedback training study that was split for the purpose of presenting transfer effects with a focus on cognitive and memory control, respectively. The first study served to validate previous findings concerning EEG characteristics in cognitive control tasks that were used for the investigation of transfer effects induced by neurofeedback training. All research conducted for the present thesis was funded by the German Research Foundation under grant GRK 1457.

Chapter 2 – Study 1: Topographical Differences of Theta Activity underlying Cognitive Control Processes

Eschmann, K. C. J., Bader, R., & Mecklinger, A. (2018). Topographical differences of frontal-midline theta activity reflect functional differences in cognitive control abilities. *Brain and Cognition*, *123*, 57–64. doi:10.1016/j.bandc.2018.02.002

Chapter 3 – Study 2: Theta Neurofeedback and Cognitive Control Processes

Eschmann, K. C. J. & Mecklinger, A. (in preparation). Improving cognitive control: Frontal-midline theta neurofeedback training enhances proactive rather than reactive control processes.

Chapter 4 – Study 3: Theta Neurofeedback and Memory Control Processes

Eschmann, K. C. J., Bader, R., & Mecklinger, A. (under review). Improving episodic memory: Frontal-midline theta neurofeedback training increases source memory performance.

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Abbreviations

| | |
|-----------------|---|
| α | rate of type I error alpha |
| η_p^2 | effect size partial eta squared |
| μV | microvolt |
| μV^2 | spectral power |
| χ^2 | test statistic from chi-squared distribution |
| ACC | anterior cingulate cortex |
| Ag/AgCl | silver/silver chloride |
| ADHD | attention-deficit/hyperactivity disorder |
| ANOVA | analysis of variance |
| b | regression coefficient |
| c | parameter of time-frequency resolution |
| cf. | <i>confer</i> – compare |
| cm | centimeter |
| d | effect size Cohen's d |
| dB/oct | decibel per octave |
| DMC | dual mechanisms of control |
| DMTS | delayed match to sample |
| EEG | electroencephalography |
| e.g. | <i>exempli gratia</i> – for example |
| EPSP | excitatory postsynaptic potential |
| ERP | event-related potential |
| ERS/ERD | event-related synchronization/desynchronization |
| F | test statistic from F -distribution |
| FFT | fast Fourier transform |
| FM | frontal-midline |
| fMRI | functional magnetic resonance imaging |
| Hz | hertz |
| i.e. | <i>id est</i> – that is |

| | |
|------------|--|
| ICA | independent component analysis |
| IIR | infinite impulse response |
| ITP | individual theta peak |
| k Ω | kilo-ohm |
| IPFC | lateral prefrontal cortex |
| <i>M</i> | mean |
| MCC | midcingulate cortex |
| MEG | magnetoencephalography |
| ms | milliseconds |
| <i>n</i> | number of cases |
| NFT | neurofeedback training |
| OSPAN | operation span |
| <i>p</i> | probability value |
| PFC | prefrontal cortex |
| <i>r</i> | Pearson's correlation coefficient |
| RMS | root mean square |
| RT | reaction time |
| SAM | questionnaire for the assessment of dispositional self-awareness |
| <i>SD</i> | standard deviation |
| <i>t</i> | test statistic from Student's <i>t</i> -distribution |
| WM | working memory |

Chapter 1

General Introduction

In order to act in the environment that we live in, our thoughts and actions need to be constantly coordinated and modified based on made experiences. These adaptive changes allow us to receive the best cognitive and behavioral outcome in the most efficient way. *Cognitive control processes* help us to select appropriate out of interfering information or behavior in a goal-directed manner. For instance, imagine searching for your car key. The information how it looks like and possible locations where it could be need to be maintained during the search. If the key is not at its usual place, this information needs to be updated and your search turned to other locations. The sight of your bunch of keys might elicit the response to grab it. That, however, needs to be inhibited because it is not the intended key of your car. Moreover, your search might be interfered by a door bell ring, leading you to switch from searching to opening the door. Altogether, cognitive control processes allow for the selection, maintenance, manipulation, and inhibition of as well as switching between behavioral responses or information (see Braver, 2012; Miyake et al., 2000, for reviews). Importantly, control processes are not restricted to the selection of behavior, but are applied to the selection of episodic memories, that is, the recollection of details of past events (Tulving, 2002), in a similar vein. If we want to retrieve a particular event, for example, where you parked your car, all the interfering memories about similar previous events, for instance, occasions in which you parked the car at the same parking lot, need to be inhibited. *Memory control processes* allow for the coordinated encoding and retrieval of such events by providing top-down control over episodic memories (see Klimesch, Freunberger, Sauseng, & Gruber, 2008; Nyhus & Curran, 2010; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010, for reviews). Notably, cognitive and memory control processes are not mutually exclusive since memory control processes reflect the type of cognitive control processes that are applied to memory representations.

Numerous cognitive training studies have tried to enhance cognitive and memory control processes by means of working memory (WM; e.g., Schneiders, Opitz, Krick, & Mecklinger, 2011), task-switching (e.g., Karbach & Kray, 2009), multi-tasking (e.g., Anguera et al., 2013), and even memory retrieval training (e.g., Jennings, Webster, Kleykamp, & Dagenbach, 2005). Transfer of successful training to the trained and other cognitive tasks demonstrated the remarkable capacity for plasticity of the adult brain (see Anguera & Gazzaley, 2015; Kelly & Garavan, 2004; Klingberg, 2010; Lövdén, Bäckman, Lindenberger, Schaefer, & Schmiedek, 2010, for reviews). According to the overlap hypothesis of training transfer, successful training leads to transfer if both tasks show functional and neural overlap, that is, the engagement of the same processing mechanisms and the activation of similar brain regions, respectively (Dahlin, Neely, Larsson, Backman, & Nyberg, 2008; see Buschkuhl, Jaeggi, & Jonides, 2012; Jonides, 2004; Lustig, Shah, Seidler, & Reuter-Lorenz, 2009, for reviews). Furthermore, these common brain substrates need to change as a function of training in order to result in training transfer (Lövdén et al., 2010). Assuming that both functional and neural overlap are reflected in shared electroencephalographical (EEG) dynamics, transfer should also occur if training alters the underlying oscillatory circuitry of trained and transfer tasks. Following this rationale, the question arises whether it is possible to enhance cognitive and memory control processes by directly modifying their underlying EEG dynamics.

A neuro-scientific method that enables training of oscillatory brain activity is the method of *neurofeedback training (NFT)*. It allows for the investigation of the causal relationship between trained oscillations and their superordinated cognitive processes. Originally stemming from a clinical background, neurofeedback was until recently mostly used for the treatment of disorders, especially attention-deficit/hyperactivity disorder (ADHD; see Arns, Heinrich, & Strehl, 2014; Strehl et al., 2017, for reviews). Nowadays, it is also increasingly applied for performance enhancement in healthy participants (see Gruzelier, 2014a, for review). During neurofeedback, oscillatory characteristics of the measured EEG signal are visualized online in order to inform the participant about its current state. Through active engagement, the participant learns to modify the visualized signal adaptively and the brain gets into the state of the trained oscillation more and more easily. *Frontal-midline (FM) theta* oscillations (4–8 Hz) that are measured over frontal scalp sites have been proposed to be the underlying neural mechanism of cognitive control processes (see Cavanagh & Frank, 2014; Helfrich & Knight, 2016; Sauseng et al., 2010, for reviews). Furthermore, several EEG studies revealed that FM theta oscillations seem to be the neural activity with the highest functional relevance for encoding and retrieval of episodic memories, especially for source

retrieval, that is, the accurate recollection of contextual details of prior episodes (e.g., Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011; T. Gruber, Tsivilis, Giabiconi, & Müller, 2008; Guderian & Düzel, 2005; Klimesch et al., 2001; Osipova et al., 2006). Thus far, only a few NFT studies could show transfer of FM theta NFT to a couple of cognitive control processes as well as motor and item memory performance (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Rozengurt, Barnea, Uchida, & Levy, 2016; Rozengurt, Shtoots, Sheriff, Sadka, & Levy, 2017; J.-R. Wang & Hsieh, 2013). Moreover, the temporal extension of these transfer effects has hardly been explored (Rozengurt et al., 2016; Rozengurt et al., 2017) and evidence for the modulation of FM theta activity underlying behavioral performance in the transfer tasks has been ambiguous (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014). Additionally, no study, thus far, has directly addressed whether memory control processes, which specifically support source retrieval, can be enhanced by modulating task-specific theta activity by means of neurofeedback.

Consequently, the main aim of the present thesis was to investigate whether cognitive and memory control processes can be enhanced by training FM theta oscillations with NFT. Moreover, the temporal extension of transfer effects and changes in underlying EEG dynamics were explored. By this, the present thesis aimed at extending the overlap hypothesis of training transfer from functional and neural overlap measured with brain imaging methods to overlap in EEG dynamics. In order to design an efficient NFT, three lines of research that provide valuable findings have to be considered: (1) cognitive training studies aiming at enhancing cognitive control processes or episodic memory performance, (2) studies investigating oscillations underlying cognitive and memory control processes, and (3) neurofeedback studies aiming at enhancing cognitive control processes or episodic memory performance. In the present Chapter 1, a theoretical framework of cognitive control will be given and thereupon the three mentioned research areas will be reviewed. Based on this overview, the research objectives of the present thesis will be derived. Thereafter, three studies investigating the topography of FM theta activity and its functional role for cognitive control processes (Chapter 2), transfer of FM theta NFT to cognitive control processes (Chapter 3), and NFT transfer to memory control processes (Chapter 4) will be reported. Finally, in Chapter 5 the presented findings will be summarized and discussed in the context of neuro-cognitive frameworks and the current state of research before limitations and an outlook for future research will be given.

1.1 Cognitive Control and Its Neural Basis

Over the last decades cognitive control processes have been investigated by different cognitive research areas. Due to their research foci, different concepts of cognitive control emerged and diverse subprocesses have been identified. For instance, cognitive control has been described as a supervisory attentional system in the model by D. A. Norman and Shallice (1986) or as a central executive in several WM models (e.g., Baddeley, 2003; Baddeley & Hitch, 1974; Cowan, 1999). In contrast, a finer differentiation between several cognitive control processes is made by executive function models that comprise processes such as inhibition, WM updating, and mental set shifting (e.g., Miyake et al., 2000). Despite their differing definitions, these theories commonly refer to cognitive control as one or several mechanisms that control behavioral and cognitive processing in a goal-directed manner (Miller & Cohen, 2001). An important aspect of cognitive control processes is their differentiation based on temporal dynamics that was postulated in the dual mechanisms of control (DMC) framework (Braver, Gray, & Burgess, 2007; Braver, 2012).

1.1.1 Dual Mechanisms of Control Framework

The DMC framework differentiates two cognitive control modes, namely proactive and reactive control, that occur before or after a cognitively demanding event, respectively (Braver et al., 2007; Braver, 2012). *Proactive control* is defined as an early selection process that facilitates processing of task-relevant information guided by task goals (Miller & Cohen, 2001). Therefore, task goal information is actively maintained in order to direct sensory processing of an expected cognitively demanding event in a top-down manner (Braver, 2012). As shown by brain imaging studies, the anticipatory task goal and context maintenance is reflected in sustained activation of the lateral prefrontal cortex (lPFC; Braver & Bongiolatti, 2002; Braver & Cohen, 2001; Miller & Cohen, 2001; Paxton, Barch, Racine, & Braver, 2007; Veltman, Rombouts, & Dolan, 2003). Contrarily, reactive control reflects a late correction process that is initiated if a highly interfering event is detected (Jacoby, Kelley, & McElree, 1999). *Reactive control* helps to resolve this interference by inhibiting prepotent information or responses in favor of selecting less prepotent ones (Braver et al., 2007). The DMC framework predicts that reactive control is reflected in transient lPFC activation but also recruits a larger fronto-parietal brain network compared to proactive control (Braver et al., 2007; Braver, 2012). The bottom-up reactivation of task goals reflected in lPFC activation is expected to occur upon sensory processing or episodic memory activation in posterior brain regions on the one hand and the detection of interference by conflict-monitoring areas, such

as the anterior cingulate cortex (ACC), on the other hand (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004; Braver et al., 2007; Braver, 2012). Brain imaging studies investigating tasks that mainly engaged reactive control processes could supportingly show activation of frontal areas, such as the IPFC, together with activation of posterior brain regions (e.g., Grandjean et al., 2012; Milham et al., 2002; Zysset, Müller, Lohmann, & von Cramon, 2001; see Niendam et al., 2012, for review).

According to the DMC framework, efficient cognition and adaptive behavior depend critically on both proactive and reactive control processes (Braver, 2012). Although both processes might occur simultaneously, characteristics of the situation, task, or individual influence whether one or the other cognitive control process is preferably utilized (Braver et al., 2007). It is assumed that reactive control might be the default mode given that it is more applicable in most situations and metabolically less costly (Braver et al., 2007). However, in tasks in which a highly interfering or cognitively demanding event can be expected, proactive instead of reactive control is recruited (Badre & Wagner, 2006; Braver, Reynolds, & Donaldson, 2003; Burgess & Braver, 2010; see Braver, 2012, for review). Moreover, cognitive differences between participants, such as WM capacity, intelligence, or motivation, influence whether proactive or reactive control is applied in tasks with high cognitive demands by determining how efficiently task goals can be maintained by the individual and whether proactive control recruitment is expected to result in beneficial consequences (e.g., Duncan, Emslie, Williams, Johnson, & Freer, 1996; Kane & Engle, 2002; Locke & Braver, 2008; see Braver, 2012, for review). Thus, situational and individual characteristics should be taken into account in order to define conditions under which successful training and transfer of cognitive and memory control processes occur.

1.2 Cognitive Training

The effectiveness of training interventions has been investigated in most cognitive training studies by applying a pre-post design that allows for the measurement of training-induced performance enhancement, namely, transfer effects. Therefore, behavioral performance in both the trained and other untrained tasks from before the training is compared with performance after its completion. Although a vast amount of studies were able to demonstrate performance enhancement in the trained and similar tasks, transfer to non-trained tasks that involve a broader range of cognitive control processes has been mixed, fostering a debate on the generalizability of cognitive training transfer (see Melby-Lervåg & Hulme, 2013; Morrison & Chein, 2010; Owen et al., 2010; Ran-

ganath, Flegal, & Kelly, 2011; Simons et al., 2016, for reviews). A possible reason for these inconsistent findings might be the heterogeneity of training designs and methodologies applied across studies, restricting their comparability (Karbach & Unger, 2014). In this regard, an important difference of training studies refers to whether cognitive strategies or processes are trained (see Morrison & Chein, 2010; Karbach & Unger, 2014; Lövdén et al., 2010; Ranganath et al., 2011, for reviews). Strategy-based training interventions provide certain approaches for how a task can be performed most effectively, resulting in acquisition of skills, which have limited applicability beyond the training task. Supportingly, strategy-acquisition studies that are mostly used to train memory encoding and retrieval strategies hardly found any transfer effects to untrained tasks (see Lustig et al., 2009; Ranganath et al., 2011; Rebok, Carlson, & Langbaum, 2007, for reviews). In contrast to strategy-based training, process-based training targets specific cognitive processes that are assumed to be involved in various cognitive functions, leading to improvement of abilities that induce gains in a wide range of tasks. Several of the process-based training studies aiming at specific cognitive processes, such as WM and task-switching (e.g., Buschkuhl et al., 2008; Dahlin et al., 2008; Jaeggi, Buschkuhl, Jonides, & Perrig, 2008; Jaeggi, Buschkuhl, Jonides, & Shah, 2011; Karbach & Kray, 2009; Li et al., 2008; Olesen, Westerberg, & Klingberg, 2003; Opitz, Schneiders, Krick, & Mecklinger, 2014; Salminen, Strobach, & Schubert, 2012; Schmiedek, Lövdén, & Lindenberger, 2010) or recollection of episodic memories (e.g., Jennings et al., 2005; Lustig & Flegal, 2008), demonstrated training-induced transfer to untrained tasks that differ from the trained task in needed strategies, response requirements, and perceptual expertise (Lövdén et al., 2010). Based on these process-training studies, the following theoretical frameworks were derived in order to provide assumptions about the conditions for successful training and its transfer.

1.2.1 Theoretical Framework of Adult Cognitive Plasticity

According to the framework of adult cognitive plasticity by Lövdén et al. (2010), plasticity defines the capacity of an individual's cognitive system to show a reactive change in response to a primary change in functional supply or environmental demands. Importantly, plastic changes only occur if a certain level of interference between the functional supply of the cognitive system and experienced environmental demands is present. In case of cognitive training, the primary change reflects an increase in environmental demands that leads to a negative mismatch, that is, a greater environmental demand than functional supply (Figure 1.1). Given the sluggish nature of plasticity, this negative mismatch has to be maintained for an extended period of time so that behavioral and structural changes of plastic alterations become manifest. The manifestation of plas-

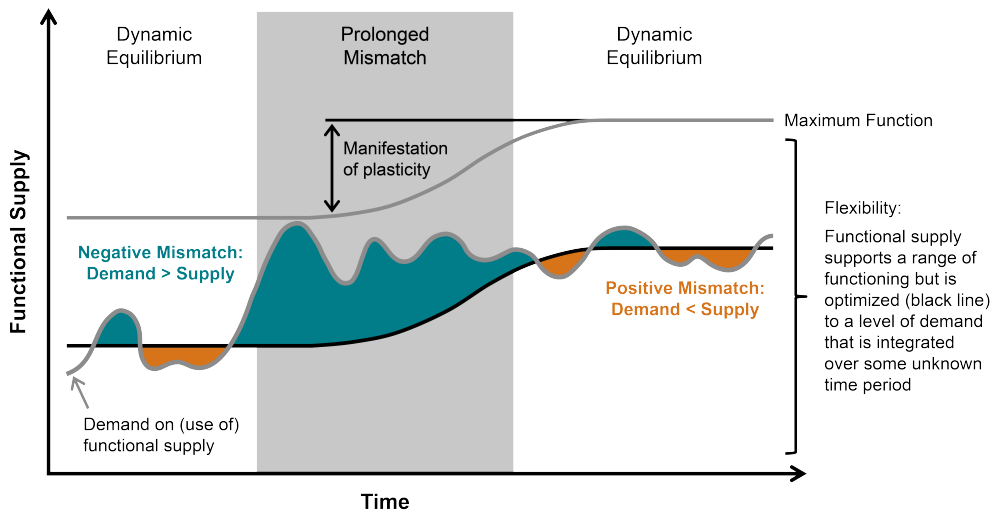


Figure 1.1. Schematic model of cognitive plasticity with a negative mismatch between functional supply and increased environmental demands as due to cognitive training (adapted from Lövdén et al., 2010, with permission from the American Psychological Association).

ticity results in a dynamic equilibrium with a greater level of functional supply than before training. An important restriction of plasticity is the individual’s present level of cognitive flexibility which is defined as the capacity to optimize performance within the limits of functional supply. Depending on this flexibility, the magnitude of experienced mismatch differs, determining the degree of plastic changes that are induced. Hence, in order to induce plasticity cognitive training demands must be near the individual’s limit of functional supply, but should not exceed or fall below it. To ensure a prolonged negative supply-demand mismatch throughout the course of training, many cognitive training studies individually adapted the difficulty of the training task to every participant’s current requirements. Studies using this adaptive training procedure were able to detect larger transfer effects than studies without adaptation of task difficulty (e.g., Jaeggi et al., 2008; Jennings et al., 2005; Karbach & Kray, 2009; Olesen et al., 2003).

Another important assumption of the framework of adult cognitive plasticity is that a manifestation of plastic modulations caused by cognitive training can only be assumed when both structural changes and their functional consequences are present (Lövdén et al., 2010). While structural changes can be measured with neuroimaging techniques, functional changes are visible in behavioral measurements. Thus, a successful training results in a manifest change of both the measured neural activity and behavioral performance in the trained and transfer task. Indeed, many cognitive training studies demonstrated training-induced neural changes that accompany behavioral transfer (see Jones et al., 2006; Kelly & Garavan, 2004; Klingberg, 2010, for reviews). To inspect the manifestation of plastic changes often a follow-up assessment after a certain time

interval is conducted (e.g., Anguera et al., 2013). The temporal extension of transfer effects suggests that the training intervention induced durable cognitive enhancement based on cognitive plasticity. The idea that both structural and functional changes have to be present for solid training transfer to occur was originally put forward by the overlap hypothesis of training transfer (Dahlin et al., 2008; see Buschkuehl et al., 2012; Jonides, 2004; Lustig et al., 2009, for reviews).

1.2.2 Overlap Hypothesis of Training Transfer

As stated in the overlap hypothesis of training transfer, training solely results in transfer effects when trained and transfer task (1) engage similar functional processes (functional overlap) and (2) activate similar underlying brain regions (neural overlap) that change over the course of training (Dahlin et al., 2008; see Buschkuehl et al., 2012; Lustig et al., 2009, for reviews). By this assumption, the overlap hypothesis offers an explanation for the positive transfer findings of process-based training compared to strategy-based training studies (Dahlin et al., 2008; Lustig et al., 2009). Process-based training enhances processes that are shared by both the trained and transfer task and are reflected in similar brain activity. In contrast, strategy-based training leads to the acquisition of skills that do not engage the same processes and underlying brain activity as needed for transfer task performance. Thus far, neural overlap between trained and transfer task has been investigated with functional magnetic resonance imaging (fMRI). Dahlin et al. (2008) reported transfer of a five-week WM updating training to an n -back task. Both the trained WM task and the n -back task showed increased striatum activation after training. Critically, training did not transfer to a Stroop task that did not engage the striatum for task performance, supporting the assumption that transfer is present when trained and transfer task share the same functional brain activity. However, neural activity is not only reflected in functional brain activity but can also be measured with EEG, which offers an especially precise temporal resolution (M. X. Cohen, 2011c). Therefore, it seems conceivable that cognitive training also induces transfer if trained and transfer task share the same EEG dynamics that underlie the engaged cognitive processes. By transferring the commonality logic to measured EEG characteristics, the present thesis aims at extending the overlap hypothesis of training transfer from neural overlap measured with fMRI to overlap of EEG dynamics. More precisely, in order to detect transfer effects with NFT, the frequency band that is trained has to be the same neural underpinning of the cognitive processes that are necessary for the accomplishment of the transfer tasks. In this regard, cognitive training studies that were able to induce training transfer that was accompanied by changes in underlying oscillatory brain activity are particularly informative.

1.2.3 Induced Neural Changes of Cognitive Training

Studies investigating changes of oscillatory EEG characteristics underlying training or transfer tasks are scarce and mainly focused on theta oscillations (Anguera et al., 2013; Jaušovec & Jaušovec, 2012; Mishra, de Villers-Sidani, Merzenich, & Gazzaley, 2014). Interestingly, Anguera et al. (2013) were able to improve older participants' behavioral performance in several cognitive control tasks by training participants in an adaptive version of a video game training for one month three times per week. Participants who practiced the multitasking condition, in which they had to drive a car while paying attention to street signs, reduced multitasking costs significantly compared to an active single task and a no-contact control group. The reduction of multitasking costs thereby attained levels beyond those achieved by untrained young participants and persisted up to six months. Essentially, these training gains were accompanied by a mediation of neural signatures reflected in enhanced FM theta activity and an increased fronto-parietal theta coherence during transfer task performance. Both measurements have previously been described as underlying neural activity of several cognitive control processes, such as WM maintenance (e.g., Jensen & Tesche, 2002; Mecklinger, Kramer, & Strayer, 1992; Onton, Delorme, & Makeig, 2005), sustained attention (e.g., Asada, Fukuda, Tsunoda, Yamaguchi, & Tonoike, 1999; Clayton, Yeung, & Kadosh, 2015; Sauseng, Hoppe, Klimesch, Gerloff, & Hummel, 2007), or interference resolution (e.g., M. X. Cohen, 2009; Hanslmayr et al., 2008; Nigbur, Ivanova, & Stürmer, 2011). In line with these findings, multitasking training also resulted in transfer effects to untrained tasks of WM and sustained attention, indicating that training in the interference-rich multitasking condition led to a change of cognitive control processes reflected in a fronto-parietal theta network (Sauseng, Klimesch, Schabus, & Doppelmayr, 2005; see Mizuhara & Yamaguchi, 2007; Sauseng et al., 2010, for reviews). Additionally, FM theta activity correlated with the training-induced enhancement in sustained attention and the manifestation of attention improvement in the six month follow-up assessment. This finding suggests that the cognitive control network (cf. Braver et al., 2007; Braver, 2012) is plastic even in late adulthood and can be enhanced by appropriate training involving a condition with long-lasting interference as proposed by the framework of adult cognitive plasticity (Lövdén et al., 2010).

Further supporting evidence comes from a cognitive training study with elderly conducted by Mishra et al. (2014), in which participants learned through reinforcement learning to select target tones out of gradually more challenging distractors. Twelve sessions of this adaptive distractor inhibition training resulted in increased FM theta activity for targets and attenuated fronto-occipital theta coherence for distractors, in-

dicating facilitated target and reduced distractor processing as a function of training. Furthermore, training induced an enhancement of participants' WM span and sustained attention for the training compared to an untrained control group, reflecting transfer beyond the trained task. Similarly, Jaušovec and Jaušovec (2012) demonstrated transfer of a WM training consisting of four WM tasks that were trained in twelve training sessions once per week to three different intelligence measurements. This transfer was accompanied by higher frontal, temporal, and parieto-occipital theta activity. Together, these findings show that transfer of cognitive training to different cognitive control processes is often accompanied by a modulation of theta oscillations, making them a likely candidate for a NFT of neural activity underlying cognitive control processes.

All in all, cognitive control processes can be trained even in late adulthood since the brain shows enormous capacity for plasticity (Lövdén et al., 2010). However, successful training with transfer to untrained tasks is only achieved if (1) a common neural substrate underlying shared functional processes of the trained and transfer task is changed as a function of training, (2) the training procedure involves prolonged mismatch or interference, and (3) structural as well as behavioral changes due to training are present (Dahlin et al., 2008; Lövdén et al., 2010). In order to decide on the EEG frequency and its characteristic which should be trained with neurofeedback for cognitive enhancement, EEG oscillations and their functional role for cognitive and memory control processes will be reviewed.

1.3 EEG Oscillations underlying Cognitive and Memory Control Processes

Generally, EEG oscillations comprise three main characteristics that are important for understanding the functional role of oscillatory brain activity for cognitive processes (e.g., see Klimesch et al., 2008, for review). The *amplitude* or power of an oscillation reflects the amount of synchronized underlying neural activity that is involved in a given process or task (e.g., Cavanagh & Frank, 2014; Klimesch et al., 2008). Consequently, the more cell assemblies are synchronously active forming a dynamic network for task-relevant processing (Singer, 2013), the larger is the measured amplitude (Figure 1.2.right). In contrast, oscillatory *phase* variations reflect the rhythmic fluctuations of the synchronized neurons' excitatory postsynaptic potentials (EPSP) that directly influence the timing of neural firing within a neural network (X.-J. Wang, 2010). In phases of increased excitability the participating neurons of a given oscillation are more likely to fire whereas in phases of decreased excitability neurons are less likely to fire (Figure 1.2.left). Importantly, the amplitude of the network's oscillation thereby affects

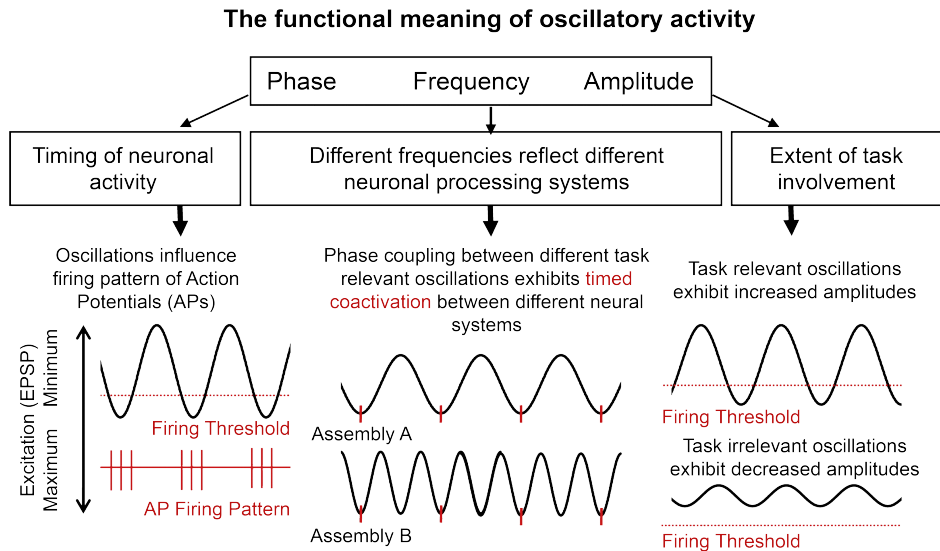


Figure 1.2. Functional meaning of phase, frequency, and amplitude of brain oscillations (adapted from Klimesch et al., 2008, with permission from Elsevier).

the extent of local neural spiking depending on how much it exceeds the neurons' firing thresholds (Klimesch et al., 2008). Finally, the number of the excitability fluctuations per second defines the *frequency* of an oscillation (Figure 1.2.middle). Neural assemblies that oscillate in different frequencies can couple in phase, indicating synchronous neural firing (Klimesch et al., 2008). This timed coactivation of different neural systems is thought to create temporal windows (Nadasdy, 2010) for information intake and transfer between these neural assemblies (Buzsáki, 2010; Canolty & Knight, 2010; Fries, 2005, 2015). It has been proposed that slower oscillations enable information transfer between more distant brain regions (Buzsáki & Draguhn, 2004; von Stein & Sarnthein, 2000) and hierarchically control faster oscillations (Lakatos et al., 2005). With regard to oscillations underlying cognitive and memory control processes, slow theta oscillations (4–8 Hz) and their interplay with faster gamma activity (> 30 Hz) have been investigated extensively and proposed to be a core neural mechanism for the implementation of those processes in the brain (see Axmacher, Mormann, Fernández, Elger, & Fell, 2006; Cavanagh & Frank, 2014; Düzel, Penny, & Burgess, 2010; Fell & Axmacher, 2011; Fries, 2015; Helfrich & Knight, 2016; L.-T. Hsieh & Ranganath, 2014; Kahana, Seelig, & Madsen, 2001; Klimesch, 1999; Klimesch et al., 2008; Klimesch, Freunberger, & Sauseng, 2010; Lisman & Jensen, 2013; Nyhus & Curran, 2010; Sauseng et al., 2010; Watrous & Ekstrom, 2014, for reviews).¹

¹ It is noteworthy that the synchronization as well as desynchronization of other frequency bands, such as delta (1–4 Hz), alpha (8–12 Hz), and beta (13–30 Hz), have also been related to cognitive and memory performance, suggesting that particular oscillations cannot be associated one-to-one with a precise functional role (e.g., see Hanslmayr & Staudigl, 2014; Hanslmayr, Staresina, & Bowman, 2016, for reviews). Nevertheless, the present thesis focuses on theta oscillations due to the compelling evidence for their role in cognitive and memory control processes.

1.3.1 Frontal-midline Theta Oscillations

In particular, FM theta activity has been suggested to reflect a general cognitive control mechanism that supports both cognitive and memory performance (see Cavanagh & Frank, 2014; Düzel et al., 2010; L.-T. Hsieh & Ranganath, 2014; Klimesch et al., 2008; Nyhus & Curran, 2010; Sauseng et al., 2010, for reviews). FM theta oscillations, which are measured over mid-frontal scalp sites, are assumed to be generated in the midcingulate cortex (MCC) and parts of the prefrontal cortex (PFC) as revealed by source localization (Asada et al., 1999; Gevins, 1997; Hanslmayr et al., 2008; Onton et al., 2005; Sauseng et al., 2007), combined EEG-fMRI measurements (Debener, 2005; Meltzer, Negishi, Mayes, & Constable, 2007), and single cell recordings in humans and monkeys (Tsujimoto, Shimazu, Isomura, & Sasaki, 2010; C. Wang, Ulbert, Schomer, Marinkovic, & Halgren, 2005; Womelsdorf, Johnston, Vinck, & Everling, 2010). The MCC is the dorsal part of the ACC, a brain region important for the detection of interference and conflict (Botvinick et al., 2001; Botvinick et al., 2004). Additionally, the ACC has been proposed to be an essential component of the neural network subserving reactive control processes (Braver et al., 2007; Braver, 2012). Focusing on those reactive control processes, Cavanagh and Frank (2014) argued that a large variety of situations that share an increased need for cognitive control elicit enhanced

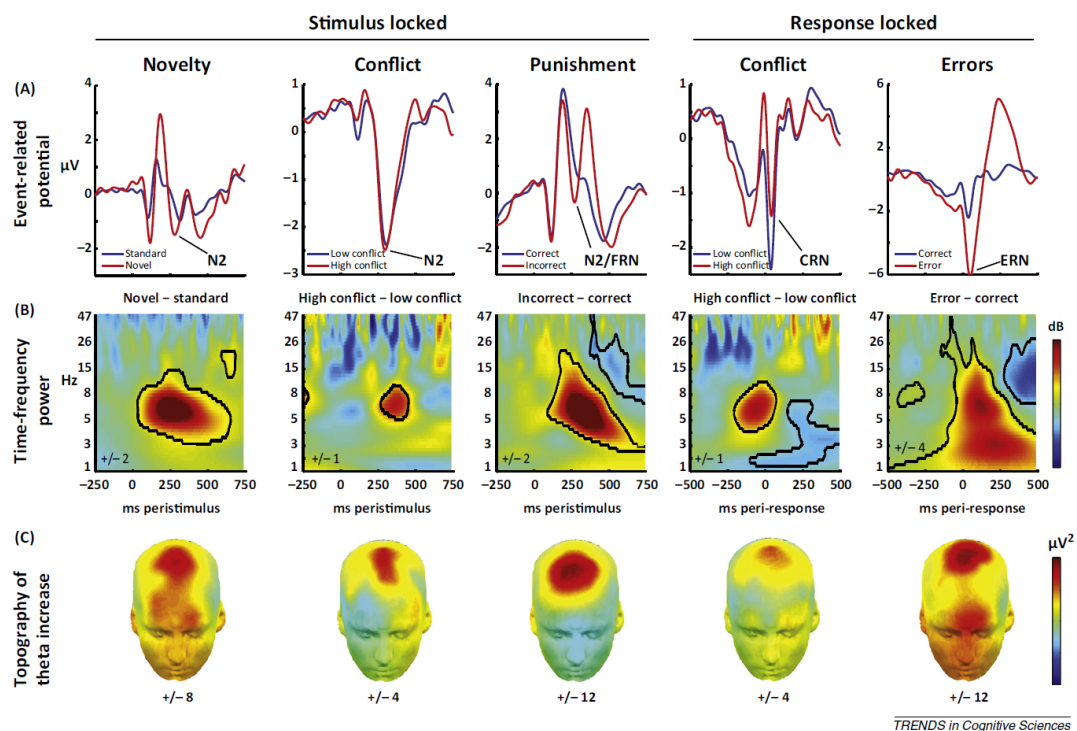


Figure 1.3. Events eliciting similar electrophysiological signatures on the scalp underlying cognitive control (reproduced from Cavanagh & Frank, 2014, with permission from Elsevier).

FM theta amplitudes with similar temporal (Figure 1.3.B) and topographical distributions (Figure 1.3.C). Previously, such situations have been associated with negative event-related potential (ERP) components that follow situations of novelty, conflict, negative feedback, and error (Figure 1.3.A; see Folstein & Petten, 2007; Walsh & Anderson, 2012, for reviews). Increased need for cognitive control and, thus, enhanced FM theta activity can be provoked by either externally presented stimuli reflecting novel information and negative feedback or internally generated responses that lead to conflict with other response mappings and errors (Cavanagh, Zambrano-Vazquez, & Allen, 2011; Cavanagh & Frank, 2014). For instance, task situations, in which the conflict between two contrary responses needs to be resolved, are accompanied by increased FM theta power (Hanslmayr et al., 2008; Nigbur et al., 2011). The increase of FM theta activity is thought to foster the temporal organization of neural processes that are enhanced due to interference situations (Cavanagh et al., 2011; Cavanagh & Frank, 2014). Therefore, theta phase synchronization of the conflict-detecting MCC and other task-relevant brain regions might form a dynamic neural network that supports interference resolution by allowing for top-down control through information transfer between the synchronized brain regions. Studies showing increased theta phase synchronization between mid-frontal and distal sites in interference situations support this interpretation (e.g., Cavanagh, Frank, Klein, & Allen, 2010; M. X. Cohen, 2009; M. X. Cohen & Cavanagh, 2011; Hanslmayr et al., 2008; Narayanan, Cavanagh, Frank, & Laubach, 2013; Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012).

Additionally to the investigation of reactive control processes, enhanced FM theta amplitudes have also been shown to underlie proactive control processes (see L.-T. Hsieh & Ranganath, 2014; Klimesch et al., 2008; Roux & Uhlhaas, 2014; Sauseng et al., 2010, for reviews). In many different WM studies, in which information had to be actively maintained for manipulation or later retrieval, FM theta activity was present (e.g., Gevins, 1997; L.-T. Hsieh, Ekstrom, & Ranganath, 2011; Meltzer et al., 2007; Meltzer et al., 2008; Raghavachari et al., 2006; Roberts, Hsieh, & Ranganath, 2013; Scheeringa et al., 2009). Interestingly, FM theta power was thereby shown to be load-dependent, that is, FM theta amplitudes were larger the more items had to be maintained (Jensen & Tesche, 2002). A theoretical model that explains the underlying oscillatory mechanism for holding several items in WM is the theta-gamma neural code (Jensen, 2006; Jensen & Lisman, 2005; Lisman & Idiart, 1995; Lisman & Jensen, 2013). According to this view, several items are maintained by cross-frequency coupling between theta and gamma oscillations. Therefore, the firing patterns of individual items are represented in single gamma amplitudes. These gamma amplitudes are nested onto a theta cycle in the order they are perceived and can be retrieved later in the

same order. Consequently, one theta cycle binds multiple items into a coherent WM representation with the theta phase coding the sequential order of the items. The maximum number of items that can be held in WM is determined by the number of gamma cycles that can be nested within a single theta cycle (Lisman & Idiart, 1995). The theta-gamma model receives support from an increasing number of studies showing enhanced theta-gamma phase-amplitude coupling measured either within or between frontal and parietal sites (e.g., Axmacher et al., 2010; Canolty et al., 2006; Griesmayr, Gruber, Klimesch, & Sauseng, 2010; Griesmayr et al., 2014; Sauseng et al., 2009; Voytek et al., 2015). Moreover, FM theta activity has been shown to be particularly relevant for maintenance of temporal sequence information (L.-T. Hsieh et al., 2011; Roberts et al., 2013; see L.-T. Hsieh & Ranganath, 2014, for review).

Based on the FM theta mechanisms underlying cognitive control processes, it has been proposed that theta oscillations as an indicator of cognitive control can act on two levels, namely on a representational level and a more general processing level (Sauseng et al., 2010; see also Fell & Axmacher, 2011; Nyhus & Curran, 2010). On the representational level several items are sequentially organized and bound together by theta-gamma cross-frequency coupling, whereas on the processing level theta phase synchronization allows for top-down control by providing the integration of task-relevant brain regions. Notably, the described proactive and reactive control processes that enable interference resolution or WM maintenance are both crucial for episodic memory performance (see Baddeley, 2003; Levy & Anderson, 2002, for reviews). Beside the finding that theta oscillations differentiate between good and bad memory performers (Doppelmayr, Klimesch, Schwaiger, Auinger, & Winkler, 1998), many episodic memory studies showed increased FM theta oscillations and theta phase synchronization between different brain regions during encoding, consolidation, and retrieval of episodic memories (see Axmacher et al., 2006; Düzel et al., 2010; Fell & Axmacher, 2011; Lisman & Jensen, 2013; Klimesch, 1999; Klimesch et al., 2010; Nyhus & Curran, 2010, for reviews). As the present thesis aims at enhancing not only cognitive but also memory control processes with NFT, the functional meanings of FM theta activity with respect to theta-gamma cross-frequency coupling as well as large-scale theta phase synchronization will be reviewed with a focus on episodic memory.

1.3.2 Functional Roles of Frontal-midline Theta Oscillations in Episodic Memory

Extending the rationale of the theta-gamma model from WM maintenance to episodic memory, it has been suggested that theta-gamma coupling represents a more general coding scheme for the temporal order of multiple items within the cortex (Axmacher

et al., 2010; Jensen & Colgin, 2007; Lisman, 2005; Lisman & Jensen, 2013). Therefore, WM maintenance by theta-gamma cross-frequency coupling acts as a buffer for episodic memory encoding (Jensen & Lisman, 2005) and for sorting of episodic memories during retrieval (Lisman, 1999). The underlying neural mechanism is supposed to be similar to space coding in the hippocampus (O'Keefe & Recce, 1993; Skaggs, McNaughton, Wilson, & Barnes, 1996; see Buzsáki & Moser, 2013, for review), a brain area that is assumed to be another locally distinct theta and gamma generator (Buzsáki, 2002). Information input induces a reset of the theta rhythm of the participating neurons so that input-specific hippocampal cells can fire during the theta phase with the highest excitability (see Axmacher et al., 2006, for review). In turn, this firing leads to synaptic strengthening so that afterwards less excitation is necessary to induce neural firing. In consequence, input-specific cells fire earlier in subsequent theta cycles, indicating that learning took place. As in WM tasks, enhanced theta-gamma cross-frequency coupling has not only been found within the hippocampus (Mormann et al., 2005), but also between frontal and parietal brain regions during episodic memory encoding (Friese et al., 2013) and retrieval (Kaplan et al., 2014; Köster, Friese, Schöne, Trujillo-Barreto, & Gruber, 2014). Consequently, the hippocampus as an individual theta and gamma generator is not necessarily contrary to a fronto-parietal theta network that connects more distant brain regions via phase synchronization (see Nyhus & Curran, 2010; Guderian & Düzel, 2005, for reviews). Nyhus and Curran (2010) proposed a unified model for episodic memory encoding and retrieval, in which they assume that theta and gamma oscillations allow for an efficient interaction between distributed cortical structures and the hippocampus both during encoding of unified memories and the reactivation of these memory representations during retrieval. Gamma oscillations within the hippocampus are suggested to reflect different memory features that are integrated by theta oscillations into a coherent episodic memory representation, presumably by ordering them temporally (see L.-T. Hsieh & Ranganath, 2014; Roux & Uhlhaas, 2014; Sauseng et al., 2010, for reviews). Indeed, it was shown that theta-gamma phase coupling in the hippocampus is especially supportive for the temporally ordered encoding of episodic sequences (Heusser, Poeppel, Ezzyat, & Davachi, 2016). During retrieval, theta and gamma feedback loops from the hippocampus to other cortical areas lead to the reactivation of memory representations while being top-down controlled from frontal theta activity (Guderian & Düzel, 2005; Helfrich & Knight, 2016). Thus, although theta and gamma oscillations can act independently within the hippocampus (Axmacher et al., 2006; Fell & Axmacher, 2011), their connection to distant cortical areas, especially the frontal cortex, seems to modify encoding and retrieval processes in episodic memory.

In line with the role of theta synchronization between different brain regions underlying cognitive control processes, it has been suggested that theta oscillations also provide top-down control for the coordinated encoding and retrieval of episodic memories (see Kahana et al., 2001; Klimesch, 1999; Klimesch et al., 2010; Klimesch et al., 2008; Nyhus & Curran, 2010; Sauseng et al., 2010, for reviews). This is assumed to be achieved by theta phase synchronization of frontal and parietal brain areas, such as the PFC and the hippocampus, whose connectivity has shown to be important for memory formation and retrieval (Backus, Schoffelen, Szabenyi, Hanslmayr, & Doeller, 2016; M. X. Cohen, 2011b; Herweg et al., 2016). With source localization of magnetoencephalography (MEG) data, Backus et al. (2016) demonstrated that successful encoding of memory associations was accompanied by increased theta phase coherence between the PFC and hippocampus, suggesting an integrative role of theta oscillations. Similarly, theta-alpha activity during successful recollection of contextual details was associated with increased connectivity of the hippocampus with the striatum and the PFC as demonstrated by combined EEG-fMRI measurements (Herweg et al., 2016). Moreover, several studies showed increased frontal or both frontal and parietal theta activity during encoding of later successfully retrieved memories (e.g., Fries et al., 2013; Osipova et al., 2006; Sederberg, Kahana, Howard, Donner, & Madsen, 2003; Summerfield & Mangels, 2005) and during recollection of contextual details of episodic memories (e.g., T. Gruber et al., 2008; Guderian & Duzel, 2005; Klimesch et al., 2001; Osipova et al., 2006). Interestingly, enhanced FM theta activity was also found preceding encoding and retrieval cues (e.g., Addante et al., 2011; M. J. Gruber, Watrous, Ekstrom, Ranganath, & Otten, 2013; Scholz, Schneider, & Rose, 2017), suggesting that FM theta oscillations can also guide upcoming memory encoding and retrieval processes (see N. Cohen et al., 2015; L.-T. Hsieh & Ranganath, 2014, for reviews). For instance, Addante et al. (2011) showed that prestimulus FM theta activity was higher for successful source memory retrieval, that is, the recollection of contextual details of a prior episode, relative to accurate item memory retrieval, that is, the recognition of previously learned items without contextual recollection. Moreover, this retrieval-preceding FM theta activity correlated with source memory performance as well as poststimulus theta activity at parietal sites which is assumed to reflect memory reinstatement (Nyhus & Curran, 2010). Together these findings suggest that FM theta oscillations reflect a top-down control mechanism that is exerted by theta phase coherence between frontal and posterior brain regions and supports the formation and retrieval of episodic memories (Klimesch et al., 2008; Nyhus & Curran, 2010). However, it remains an open question whether retrieval cue preceding FM theta oscillations reflect (1) a neuro-cognitive state that generally facilitates upcoming cue processing

or (2) the reinstatement of contextual details that were present during encoding and are suggested to be beneficial for later recognition of associated memories (see L.-T. Hsieh & Ranganath, 2014, for review). Such a neuro-cognitive state might be similar to an episodic retrieval mode, which prepares for retrieval by activating involved brain regions, such as the frontal and parietal cortex (Lepage, Ghaffar, Nyberg, & Tulving, 2000; Klimesch et al., 2001; see N. Cohen et al., 2015, for review). In contrast, reinstatement of context reflected in FM theta activity would be in line with the idea that the PFC provides temporal context information that modulates the activation of associated memories in a top-down manner (Polyn & Kahana, 2008).

Another role of theta oscillations in episodic memory might be the coordination of inhibition strength over memory representations that compete for retrieval (K. A. Norman, Newman, & Perotte, 2005; K. A. Norman, Newman, Detre, & Polyn, 2006). This idea is based on the finding that synaptic plasticity varies within a theta cycle with synaptic strengthening and suppression occurring at opposing theta phases (Huerta & Lisman, 1996; see Fell & Axmacher, 2011, for review). Due to the close relationship of theta oscillations with inhibitory interneurons (Buzsáki, 2002), K. A. Norman et al. (2005) suggested that theta oscillations reflect varying levels of inhibition strength that support the strengthening of target memories and the suppression of competitor representations (see L.-T. Hsieh & Ranganath, 2014, for review). Low levels of inhibition activate both weak target memories and strong distractor representations whereas high levels of inhibition activate only the strong competitor memories. Based on a learning algorithm, they could show that the activation difference between high and low levels of inhibition can help to identify target and distractor memories. While target memories can be identified and thereupon strengthened by raising inhibition levels, strong competitors can be determined and consequently weakened by lowering inhibition levels. The inhibition model has been used to explain findings of retrieval-induced forgetting, the phenomenon that retrieving a memory impairs the recall of related memories (K. A. Norman, Newman, & Detre, 2007). According to the model, theta oscillations strengthen the selectively retrieved memory and lead to the inhibition of related memories. Supportingly, it was shown that FM theta activity increases during selective retrieval and later decreases after competitor representations have been successfully inhibited (Ferreira, Marful, Staudigl, Bajo, & Hanslmayr, 2014). Furthermore, suppression of related memories was reflected in decreased theta activity over parietal sites (Spitzer, Hanslmayr, Opitz, Mecklinger, & Bäuml, 2009; Waldhauser, Bäuml, & Hanslmayr, 2014). Thus, interference due to competing retrieval seems to enhance control processes reflected in FM theta activity that support interference resolution through selective strengthening of target memories and inhibition of their competitors.

All in all, theta oscillations were shown to underly cognitive and memory control processes (L.-T. Hsieh & Ranganath, 2014; Klimesch et al., 2010; Nyhus & Curran, 2010). While theta-gamma coupling allows for the formation of memory representations, theta phase synchronization between different brain regions enables the maintenance, manipulation, and selection of both appropriate behavior as well as memory representations (Sauseng et al., 2010). Especially, FM theta oscillations that are measured over frontal scalp sites seem to mediate posterior brain regions in interference situations as part of a fronto-parietal theta network (Cavanagh & Frank, 2014; Helfrich & Knight, 2016). Although the exact functional mechanism of theta oscillations remains under debate, cognitive and memory control processes might be enhanced by increasing FM theta activity. In the following, the method of neurofeedback, with which oscillations can be modulated, and the implications for a FM theta NFT study will be reviewed.

1.4 Neurofeedback Training

1.4.1 Method of Neurofeedback

Neurofeedback training is a neuro-scientific method that enables its users to self-regulate their own brain activity by providing feedback in a closed-loop brain-computer interface (Birbaumer, Ruiz, & Sitaram, 2013; Huster, Mokom, Enriquez-Geppert, & Herrmann, 2014). Most neurofeedback interventions aim at regulating EEG signals but activity measured with other brain imaging methods, such as MEG or fMRI, can be modulated as well (see Sitaram et al., 2016; Thibault, Lifshitz, & Raz, 2016, for reviews). Over the last decades, NFT has been applied to improve symptoms of a large variety of disorders, such as ADHD (e.g., Arns et al., 2014), autism spectrum disorder (e.g., Thompson, Thompson, & Reid, 2009), epilepsy (e.g., Strehl, Birkle, Wörz, & Kotchoubey, 2014), posttraumatic stress disorder (e.g., Reiter, Andersen, & Carlsson, 2016), stroke (e.g., Kober et al., 2015), or tinnitus (e.g., Güntensperger, Thüring, Meyer, Neff, & Kleinjung, 2017). Additionally, an increasing number of studies investigated the enhancement of cognitive performance in healthy participants by applying NFT (see Gruzelier, 2014a, for review). In the case of EEG neurofeedback, the amplitude or power of a certain frequency band can be up- or downregulated, which is assumed to reflect a change in the de/synchronized firing of underlying neural assemblies (Buzsáki & Draguhn, 2004). Moreover, phase coherence between one or more frequencies at two different electrodes can be trained (e.g., Mottaz et al., 2015). In a closed-loop neurofeedback application, the EEG signal is recorded and an online frequency analysis is applied for feature extraction, for example, extraction of the theta amplitude (Figure 1.4). This feature is then transformed into visual, auditory, or even

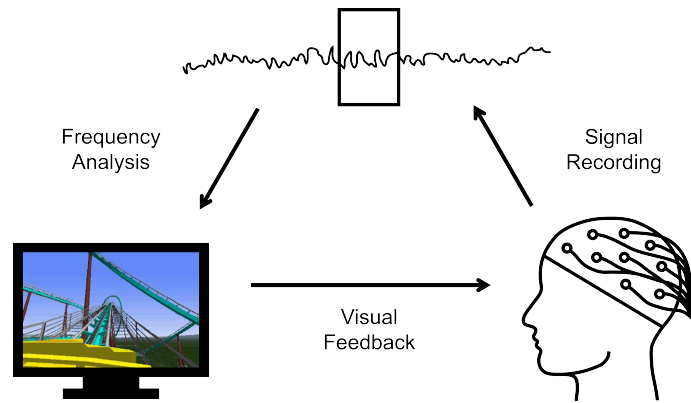


Figure 1.4. Example of a closed-loop brain-computer interface for neurofeedback training. The EEG signal is recorded and analyzed with an online frequency analysis that helps to extract the desired oscillatory feature for training. The perceived feedback informs the neurofeedback user about its current state and guides the self-regulated modulation of brain activity, leading to a change of the measured EEG signal and of the presented feedback in turn. (The image of a rollercoaster feedback was taken from BioGraph Infinity software by Thought Technology Ltd., Montreal, Canada.)

tactile feedback that serves the participant as an indicator of the current state of measured brain activity, supporting the user to gain control over this kind of brain activity and to modify it in the desired direction. The learning mechanism underlying NFT is considered to be operant conditioning, that is, the reinforcement of the desired brain state through immediately following positive feedback leads to a greater likelihood for it to occur in the future (see Sherlin et al., 2011, for review). However, it has been suggested that learning of self-regulation of brain activity can be seen as a type of skill learning and thus cannot be explained solely with operant conditioning (see Birbaumer et al., 2013; Strehl, 2014, for reviews). Several extensive reviews have tried to explain neurofeedback learning and its underlying neurophysiological mechanisms by taking psychological, neuro-cognitive, and engineering perspectives into account (see Davelaar, 2018; Gaume, Vialatte, Mora-Sánchez, Ramdani, & Vialatte, 2016; Gruzelier, 2014b; Ros, Baars, Lanius, & Vuilleumier, 2014; Sitaram et al., 2016; Strehl, 2014, for reviews). Despite the large variety of explanations, these reviews commonly suggest that neurofeedback learning involves the participation of cognitive control processes, which are also suggested to account for self-regulation supporting adaptive behavior (Hofmann, Schmeichel, & Baddeley, 2012). In line with this suggestion, Ninaus et al. (2013) could show that simply the attempt to modulate brain activity is accompanied by the activation of a fronto-parietal cognitive control network that involves brain regions, such as the PFC, ACC, and motor areas (see Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Niendam et al., 2012, for reviews). Since the MCC as part of the ACC is considered to be a source region of FM theta activity (see Cavanagh & Frank, 2014, for review), neurofeedback might be especially applicable to train this frequency.

Although there is accumulating evidence that NFT can be used to reduce clinical symptoms and enhance cognitive processes, the effectiveness of neurofeedback as an intervention technique is still under debate (see Dessy, Puyvelde, Mairesse, Neyt, & Pattyn, 2017; Thibault et al., 2016, for reviews). There are two factors that might contribute to this controversy. First, NFT studies have applied different training designs and methodologies, restricting the comparability of training and transfer effects. More specifically, NFT studies included the training of different frequency bands solely or while downregulating other frequency bands at various scalp locations for different time intervals and repetitions, leading to highly variable findings (see Gruzelier, 2014a, for review). Furthermore, several studies failed to successfully induce the enhancement of oscillatory brain activity or to show transfer to specific cognitive processes, indicating that not every NFT protocol induces reliable training and transfer effects (e.g., Staufenbiel, Brouwer, Keizer, & van Wouwe, 2014; Vernon et al., 2003). Second, many of these studies lack important experimental standards and thus cannot exclude the influence of non-specific factors that affect training and transfer outcomes (see Rogala et al., 2016; Vernon, 2005, for reviews). In consequence, a causal link between NFT and transfer effects cannot be drawn and results of these studies should be interpreted with caution (Rogala et al., 2016). However, even a well controlled double-blind study demonstrated that NFT was not better than placebo for the treatment of insomnia (Schabus et al., 2017), suggesting that specific NFT protocols are not applicable for certain types of treatment. Thus, in order to design an efficient NFT study with transfer to cognitive and memory control processes in young and healthy adults, experimental standards that allow coherent conclusions should be reviewed. Therefore, the focus should be on NFT studies enhancing cognitive processes in healthy participants in contrast to clinical NFT studies aiming at the regulation of abnormal brain activity. Unfortunately, NFT studies investigating the transfer to cognitive and memory performance in healthy individuals are very heterogeneous (e.g., Hanslmayr, Sauseng, Doppelmayr, Schabus, & Klimesch, 2005; Keizer, Verment, & Hommel, 2010; Reiner, Lev, & Rosen, 2018; Staufenbiel et al., 2014; J.-R. Wang & Hsieh, 2013). For instance, several studies revealed that NFT of the upper alpha band leads to improved WM performance (e.g., Hanslmayr et al., 2005; Nan et al., 2012; Zoefel, Huster, & Herrmann, 2011) while other studies showed increased feature binding after gamma NFT (Keizer, Verment, & Hommel, 2010; Keizer, Verschoor, Verment, & Hommel, 2010) and enhanced attention as well as cognitive control abilities after NFT of theta activity (e.g., Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; J.-R. Wang & Hsieh, 2013) or successive NFT of theta and alpha oscillations (Reis et al., 2016). Moreover, improved episodic memory performance was found after upregulation of the sensorimotor rhythm (Guez et al., 2014; Hoedlmoser

et al., 2008; Schabus et al., 2014), gamma activity (Keizer, Verment, & Hommel, 2010), and theta oscillations (Rozengurt et al., 2017). Additionally, motor memory was shown to be enhanced after theta NFT both at frontal (Rozengurt et al., 2016) and parietal sites (Reiner, Rozengurt, & Barnea, 2014; Reiner et al., 2018). Although these studies provide evidence that cognitive and memory performance can be trained with different types of NFT protocols, the importance of FM theta oscillations for top-down control as previously outlined (cf. Section 1.3) suggests that an enhancement of theta amplitudes measured at mid-frontal scalp sites by means of neurofeedback should increase cognitive and memory control processes in transfer tasks. In the following, guidelines for a FM theta NFT study will be reviewed on the basis of NFT studies that showed successful training of FM theta activity and transfer to cognitive and memory performance.

1.4.2 Guidelines for Frontal-midline Theta Neurofeedback Training

Neurofeedback Training Design

Similar to cognitive training studies, most NFT studies have investigated the transfer of training to cognitive tasks by applying a pre-post design (see Dessy et al., 2017; Gruzelier, 2014a; Vernon, 2005, for reviews). Between pre- and posttraining measurements neurofeedback is applied in one or several NFT sessions of a certain length. NFT studies differ greatly in the number and distribution of training sessions, making it difficult to define the optimal NFT protocol for neurofeedback learning (see Gruzelier, 2014b; Strehl, 2014, for reviews). With regard to the upregulation of FM theta amplitudes, one session (Rozengurt et al., 2016; Rozengurt et al., 2017) and eight or more sessions of about 15–30 minutes length applied over several days (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014; J.-R. Wang & Hsieh, 2013) have been proven to be effective. Importantly, in order to assess whether the regulation of the trained frequency was successful, it is not sufficient to solely measure the change in this specific brain activity since non-specific training effects, such as the attempt to regulate one's own brain activity, might induce brain activity changes (cf. Ninaus et al., 2013). Therefore, it is recommended to compare the training group to an active control group who either receives some pseudo-feedback, for example, a replay of the feedback of the training group (Enriquez-Geppert, Huster, & Herrmann, 2017), or trains other frequency bands than the training group. For instance, participants of a FM theta NFT study conducted eight 30-minute neurofeedback sessions over several days (Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014). Thereby, the training group successfully enhanced their FM theta activity compared to a control group who

saw a replay of the visual feedback from one of the participants of the training group during NFT. Additionally, both groups showed amplitude increases in the alpha and beta frequency bands, stressing the importance of a control group for determining the training specificity and validly interpreting training results (see Gruzelier, 2014b, for review). Interestingly, training and control group did not differ in their motivation and commitment during training, but the training group perceived the NFT as more difficult than the control group. Hence, the attempt to control pseudo-feedback might not require the same extent of active engagement as regulating one's own brain activity. In order to receive feedback based on oscillatory brain activity, an active control group might thus ideally train other frequency bands than the training group. Control groups of other FM theta NFT studies either trained to enhance amplitudes of frequency bands that were randomly chosen for each training session (J.-R. Wang & Hsieh, 2013) or the inverse ratio of two frequencies that the training group trained, for instance, beta/theta ratio relative to theta/beta ratio of the training group (Rozengurt et al., 2017). The control groups showed less FM theta increase compared to the respective training groups, indicating that the regulation of other frequency bands did not induce a similar increase in FM theta activity than its training. Another advantage of an active control group is that it allows for the control of repetition effects in the transfer tasks, that is, the increase in performance due to repeated conduction of a task. By comparing training groups with active control groups, NFT studies could reveal that the enhancement of FM theta amplitudes over several training sessions led to performance increases in cognitive control processes, such as task-switching, WM updating, and interference resolution (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; J.-R. Wang & Hsieh, 2013). Moreover, even one session of FM theta NFT showed transfer to motor and item memory for up to one week, suggesting that enhancement of FM theta activity supports the consolidation of memory representations learned before training (Rozengurt et al., 2016; Rozengurt et al., 2017).

Measurement and Feedback Characteristics

Beside FM theta NFT studies reporting training and transfer effects, some studies also describe no significant changes of theta activity or transfer effects to certain cognitive control processes (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Vernon et al., 2003; J.-R. Wang & Hsieh, 2013). For instance, in a study by J.-R. Wang and Hsieh (2013) enhancement of FM theta activity via NFT showed transfer to WM performance for older but not younger participants. On the one hand, NFT in young and healthy adults might not have caused a performance enhancement because these participants had a cognitive performance level which was already at ceiling prior to training and thus

could not be enhanced any further. On the other hand, training and thus transfer effects might not have been revealed because the trained theta frequency band was not individually estimated. It has been shown that frequency measurements demonstrate high inter-individual variability and intra-individual stability (Meltzer et al., 2007; Näpflin, Wildi, & Sarnthein, 2008). Consequently, the training effect of a NFT study might be diminished if a fixed frequency band is trained that includes not only the individual frequency peaks, that is, the most pronounced frequency within a given frequency range, but also neighboring frequency bands (cf. Doppelmayr, Klimesch, Pachinger, & Ripper, 1998; Klimesch, 1999). In studies in which individual theta activity was trained with neurofeedback, frequency ranges were determined in pre-training sessions by measuring EEG in transfer tasks requiring cognitive control processes for successful performance (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014). This approach additionally allows to measure individual task-specific phasic brain activity (cf. Gruzelier, 2014b; Vernon, 2005) and helps to define the number and location of electrodes that should be used for NFT in order assure the best possible transfer outcome. In FM theta NFT studies, usually electrode Fz is used solely (Reis et al., 2016; Rozengurt et al., 2016; Rozengurt et al., 2017; J.-R. Wang & Hsieh, 2013) or combined with other fronto-central electrodes (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014). FM theta increase has been shown to highly correlate with theta increases across other scalp locations, suggesting that training even with one electrode might modulate a larger theta network (Rozengurt et al., 2016; Rozengurt et al., 2017).

A central component of neurofeedback is the provision of feedback that informs the neurofeedback user comprehensively about the current state of the measured brain activity. The choice of feedback modality, graduation, and timing highly depends on the targeted frequency and the cognitive or motor processes that are aimed to be modulated (Enriquez-Geppert et al., 2017). Although clear guidelines do not exist, it has been suggested that (1) visual feedback is more efficient than auditory, (2) information-rich proportional feedback supports the self-regulation of brain activity more than binary feedback, and (3) feedback should be given as immediately as possible for neurofeedback learning to occur (see Sherlin et al., 2011; Strehl, 2014, for reviews). Furthermore, since neurofeedback involves the active engagement of participants to volitionally regulate their brain activity, it has been argued that feedback should be entertaining and motivating (Gaume et al., 2016; Strehl, 2014). Several studies used rather simple feedback, such as squares that change in color saturation (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014) or moving bars (Rozengurt et al., 2016; Rozengurt et al., 2017), whereas others applied more entertaining feedback, for example, a rollercoaster

animation that accelerated in speed with raising frequency amplitude (J.-R. Wang & Hsieh, 2013). Nevertheless, it should be considered that more complex feedback might induce other feedback processing and learning effects that are more difficult to control (Enriquez-Geppert et al., 2017). According to the theoretical framework of adult cognitive plasticity (Lövdén et al., 2010), a prolonged mismatch between functional supply and environmental demands must be present in order to induce plastic changes of brain function (cf. Section 1.2.1). With regard to designing an efficient training procedure with neurofeedback, mismatch between the current brain state and the perceived feedback might be assured by adaptively adjusting the feedback criterion of participant's oscillatory activity over the course of training, making it more difficult to receive positive feedback (e.g., Rozengurt et al., 2017). However, NFT differs to cognitive training in an important aspect, namely, that it critically depends on feedback validity (see Gaume et al., 2016, for review). Therefore, the displayed feedback must indeed reflect the measured EEG signal that can be regulated by the participant. If the provided feedback is not perceived as valid due to adaptive changes, this might lead to detrimental learning and motivational effects that hinder training success. For instance, adaptive changes of the feedback criterion that result in a fixed amount of positive feedback throughout the whole training reduce the informative value of the feedback (see Sherlin et al., 2011, for review). In these cases, the same percentage of positive feedback is displayed throughout a session irrespective of whether the measured brain activity changed in the desired or opposite direction, restricting the participant to gain control over the oscillatory brain activity. Thus, in contrast to cognitive training studies, in which an adaptive change of task difficulty is recommended in order to induce plastic changes (Lövdén et al., 2010), a constant feedback criterion that leaves enough room for improvement should be used for NFT.

In summary, neurofeedback is applied for the self-regulation of brain activity in a large variety of both clinical and cognitive interventions. Although NFT studies are heterogeneous and the underlying learning mechanisms and their neurophysiological underpinnings have to be better understood (Gaume et al., 2016; Sitaram et al., 2016), NFT studies have shown transfer to different cognitive processes (see Dessy et al., 2017; Gruzelier, 2014a, for reviews). Particularly, upregulation of FM theta activity that is associated with cognitive and memory control processes (Cavanagh & Frank, 2014; Nyhus & Curran, 2010) revealed transfer to cognitive and memory performance (e.g., Rozengurt et al., 2017; J.-R. Wang & Hsieh, 2013). For the interpretation of such findings, experimental standards, such as the inclusion of an active control group or the provision of valid feedback, must be obeyed. Despite the encouraging findings, open questions remain that will be addressed in the present thesis.

1.5 Research Objectives of the Present Thesis

Converging evidence of cognitive and neurofeedback training studies suggests that even the adult brain shows a notable capacity for cognitive and neural plasticity (Lövdén et al., 2010; Sitaram et al., 2016). Given that cognitive and memory control processes enable adaptive behavior and memory processing in a goal-directed manner, enhancement of these processes would ideally support functioning in everyday life. The present thesis aimed at enhancing cognitive and memory control processes by means of NFT, thereby extending the overlap hypothesis of training transfer from cognitive and neural overlap measured with fMRI to overlap in EEG dynamics (Dahlin et al., 2008). The most suitable oscillations for such a NFT seem to be FM theta oscillations that have been shown to underlie both proactive and reactive control processes (Cavanagh & Frank, 2014; Sauseng et al., 2010) as well as top-down memory control (Klimesch et al., 2008; Nyhus & Curran, 2010). Furthermore, behavioral transfer of cognitive training and partially also FM theta NFT was accompanied by changes in FM theta activity (e.g., Anguera et al., 2013; Enriquez-Geppert, Huster, Figge, & Herrmann, 2014). Despite extensive evidence, the precise functional role of FM theta oscillations, especially for episodic memory encoding and retrieval, remain elusive (L.-T. Hsieh & Ranganath, 2014). If applied appropriately, NFT enables the investigation of the causal relationship of cognitive processes and their neural underpinnings. Hence, a FM theta NFT that examines the transfer to cognitive and memory control processes would help to (1) gain knowledge about the trainability of these processes, (2) give insight into the neural changes underlying training and transfer effects, and (3) potentially shed more light on the functional role of the trained oscillation for the assessed cognitive processes.

In order to validate previous findings concerning FM theta activity in cognitive control tasks that were used as transfer tasks for NFT, *Study 1* investigated theta oscillations underlying cognitive control processes (Chapter 2). Based on the temporal differentiation of cognitive control processes by the DMC framework (Braver, 2012), both the temporal dynamics and topographic characteristics of FM theta oscillations were assessed in two tasks recruiting either proactive or reactive control processes. Both processes have been shown to be accompanied by increases in FM theta activity that is assumed to be part of a fronto-parietal theta network (see Cavanagh & Frank, 2014; Sauseng et al., 2010, for reviews). The DMC framework claims that the anticipatory maintenance of task goals and context information is reflected in IPFC activity whereas the reactive inhibition of prepotent information recruits a larger fronto-parietal network including the IPFC (Braver et al., 2007; Braver, 2012). Indeed, imaging and EEG evi-

dence suggests that proactive and reactive control processes engage different functional brain networks (e.g., Braver & Bongiolatti, 2002; Cooper et al., 2015; Grandjean et al., 2012). By contrasting theta activity measurements during proactive and reactive control within the same group of participants, this study gives insight as to whether cognitive control processes are reflected in differential theta topographies, indicating that FM theta activity acts functionally different depending on task requirements. Additionally, this study provides suggestions for scalp sites at which the EEG can be measured for an efficient NFT with transfer to cognitive control processes.

On the basis of the theoretical framework of adult cognitive plasticity (Lövdén et al., 2010) and the few FM theta NFT studies that examined transfer to cognitive and memory performance, a training design for the upregulation of individually determined FM theta amplitudes was derived. Participants of a training and an active control group took part in seven NFT sessions that were preceded by a pretraining and followed by two posttraining sessions. Behavioral transfer of FM theta NFT and the change of underlying EEG characteristics were assessed by *Study 2* and *3* with a focus on cognitive (Chapter 3) and memory control processes (Chapter 4), respectively. Previous research revealed that FM theta NFT does not result in transfer to all tasks that require cognitive control processes for task performance (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; J.-R. Wang & Hsieh, 2013). Disentangling the differences between tasks to which upregulation of FM theta activity shows transfer or not, would provide guidance for the targeted application of the FM theta NFT protocol for cognitive enhancement. Thus far, only one study investigated training-induced changes of task-specific oscillatory activity and revealed that changes in these EEG characteristics need not necessarily to go along with performance changes (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014). However, gaining deeper knowledge about changes in EEG dynamics that accompany training transfer would be helpful for the understanding of plasticity that is induced by NFT (cf. Lövdén et al., 2010). Moreover, the neurofeedback literature leaves open whether transfer to cognitive control and training-induced EEG changes are not limited to measurements one day after the last NFT session but temporally extend to later follow-up test. Hence, *Study 2* aimed at examining (1) whether FM theta NFT enhances both proactive and reactive control abilities and modulates the underlying EEG dynamics and (2) whether this transfer extends over two posttraining sessions.

Single sessions of FM theta NFT have been demonstrated to be sufficient for improving motor and item memory performance of information that was learned before training, suggesting that FM theta enhancement supports the consolidation of these memory representations (Rozengurt et al., 2016; Rozengurt et al., 2017). However, it

remains unclear as to whether FM theta NFT is beneficial for more general memory control processes that support the encoding and retrieval of information newly learned after training. FM theta oscillations are interpreted to provide top-down control over episodic memory representations (Klimesch et al., 2008; Nyhus & Curran, 2010) and shown to correlate with accurate source retrieval (Addante et al., 2011). Consequently, *Study 3* is the first to assess (1) whether FM theta NFT improves source retrieval and modulates its EEG characteristics and (2) whether memory control enhancement is present both directly and late after training has finished. Thereby, this study extends the mentioned previous findings and gives novel insight into the enhancement of memory control processes by means of neurofeedback.

Study 1: Topographical Differences of Theta Activity underlying Cognitive Control Processes

2.1 Introduction

Cognitive control processes are needed to function in everyday life and are assumed to be reflected in theta activity (ca. 4–7 Hz)² that mainly occurs at mid-frontal electrode sites (see Cavanagh & Frank, 2014; Sauseng et al., 2010, for reviews). Although frontal-midline (FM) theta has been found in numerous studies investigating cognitive control abilities, its precise functional role is still under debate. In a recent comprehensive review, Cavanagh and Frank (2014) proposed that FM theta represents a general control mechanism that reflects the need for and the implementation of cognitive control. This assumption is based on observations of goal-directed or habituating behavior, in which cognitive control processes are needed in order to resolve a situation with the best possible outcome and to adaptively optimize performance for future encounters of similar situations. The assumption of a general control mechanism (Cavanagh & Frank, 2014) receives support by several electrophysiological studies investigating cognitive effort in a large variety of context situations, such as during working memory (WM) encoding and maintenance or episodic memory encoding and retrieval. For instance, both stimulus and response-locked event-related potential (ERP) components that are elicited by novelty, conflict, errors or negative feedback are accompanied by increased FM theta activity (Cavanagh et al., 2011). Moreover, in WM studies, FM theta power was shown to increase in conditions with high WM load and task difficulty (Gevins,

² Although theta oscillations generally refer to activity in the range of 4–8 Hz (e.g., L.-T. Hsieh & Ranganath, 2014), we analyzed a smaller range of 4–7 Hz in this study for better comparability with studies that investigated theta oscillations of the same range in highly similar cognitive control tasks (Berger et al., 2016; Griesmayr et al., 2014; Hanslmayr et al., 2008).

1997; Griesmayr et al., 2010; Jensen & Tesche, 2002; Onton et al., 2005; Roberts et al., 2013; Wilson, 1999; see Sauseng et al., 2010, for review). In some of these studies, the increase in theta activity during WM was also predictive of later long-term memory retrieval (T. Gruber et al., 2008; Khader, Jost, Ranganath, & Rösler, 2010; Osipova et al., 2006; Sederberg et al., 2003; see Nyhus & Curran, 2010, for review), suggesting that FM theta reflects cognitive control processes that serve both WM and episodic memory functions. In contrast to WM memory studies, difficulty of episodic memory retrieval can lead to both increases and decreases of FM theta, indicating that FM theta reflects different aspects of episodic memory, such as memory representation strength or memory evaluation processes (Klimesch et al., 2006). FM theta power was also shown to reflect the amount of cognitive control recruitment in interference situations in which two contrary responses are in conflict to each other, for example, in incongruent trials of a Stroop, Simon, and flanker task or No-Go trials in a Go/No-Go task (Hanslmayr et al., 2008; Nigbur et al., 2011). Additionally, FM theta activity declines with increasing interference resolution in competitive memory retrieval (Ferreira et al., 2014; Spitzer et al., 2009; Waldhauser et al., 2014). In these situations, memory representations, which either belong to the same category or are associated with each other, compete for retrieval. While interference induces FM theta activity, the successful suppression of competing associations leads to a decrease in FM theta activity.

FM theta oscillations are assumed to communicate and implement the need for cognitive control in different neural systems comprising both neighboring as well as distant brain regions (Cavanagh & Frank, 2014; Cavanagh et al., 2011; Helfrich & Knight, 2016). The synchronization of neurons that belong to assumed FM theta source regions, such as the anterior cingulate cortex (ACC) or the midcingulate cortex (MCC), is supposed to lead to FM theta amplitudes that provide temporal windows for segregating information intake via corresponding activity of other cortical populations (Cavanagh & Frank, 2014). The coincident activation between FM theta source regions and other task-relevant brain regions is reflected in theta phase synchronization and can be interpreted as information intake and transfer between these regions (Asada et al., 1999; M. X. Cohen, 2011a; Gevins, 1997; Onton et al., 2005). For instance, situations, in which an unexpected feedback or conflict occurs, are characterized by theta phase synchronization between areas that play an important role in conflict detection and the lateral prefrontal cortex (lPFC), an area critical for active task goal maintenance (Cavanagh et al., 2010). Accordingly, information about the detected conflict is communicated and leads to the adaptive modification of task goals. In contrast, after an erroneous response in a No-Go trial, mid-frontal brain areas synchronize with

occipital sensory regions in order to prevent response errors in the future (M. X. Cohen, 2009). This theta phase synchronization between mid-frontal and occipital areas after an error even persists into following trials. It is assumed that mid-frontal brain regions thereby exert top-down control over stimulus processing that happens in sensory areas. Consistent with this view, theta phase synchronization between mid-frontal brain regions and motor areas that was found in humans and in rats is interpreted to reflect the control over conflicting motor responses (Narayanan et al., 2013). All in all, although different brain regions synchronize in different tasks serving different control mechanisms due to different task demands, the neural activity reliably results in FM theta activity measured at mid-frontal sites (see Cavanagh & Frank, 2014, for review).

The aforementioned studies mainly focused on cognitive control processes that are recruited after events with enhanced need for control in order to adaptively modify behavior. The dual mechanisms of control (DMC) framework by Braver (2012) distinguishes these forms of reactive control from proactive control. Proactive control reflects an early selection process that supports the facilitated processing of task-relevant information in a top-down manner. This is achieved by the active maintenance of task goal information in order to bias sensory processing before the occurrence of a cognitively demanding event. The maintenance of task goals and task-contexts is assumed to be reflected in sustained IPFC activation. In line with this assumption, several brain imaging studies could show sustained IPFC activation during WM maintenance (Braver & Cohen, 2001; Braver & Bongiolatti, 2002; Paxton et al., 2007; Veltman et al., 2003). In contrast, reactive control is defined as a late correction process that is initiated when interference is detected and a prepotent response has to be inhibited in favor of a less prepotent one. According to the DMC framework, this reactive control is anchored in the IPFC and the ACC but also recruits a wider brain network compared to proactive control (Braver, 2012). Brain imaging studies investigating the reactive control mechanisms in color Stroop tasks could show simultaneous activation of prefrontal brain areas, such as the IPFC, and parietal regions (Grandjean et al., 2012; Milham et al., 2002; Zysset et al., 2001; see Niendam et al., 2012, for review). It is assumed that in the case of reactive control the processing of sensory or episodic memory information first leads to activation of posterior brain regions followed by conflict detection by the ACC before top-down control is exerted by PFC regions. In addition to imaging studies, studies investigating theta phase coherence between frontal and parietal sites could show the activation of different fronto-parietal theta networks in proactive and reactive control tasks (Cooper et al., 2015; Cooper, Wong, McKewen, Michie, & Karayanidis, 2017). However, for

the analysis of proactive control, these studies focused on transient changes in proactive control for trial-type preparation that might involve a different control network than sustained maintenance of task goals or stimuli (Cooper et al., 2015). In sum, previous research showed that proactive and reactive control processes are reflected in the activation of different networks, suggesting a smaller proactive control network including the IPFC and a wider reactive control network including frontal and parietal regions. Consequently, the question arises whether proactive and reactive control processes are also accompanied by scalp topographical differences of theta oscillations that become visible by directly comparing two tasks differing in the recruited cognitive control processes.

The present study aimed at investigating whether different forms of FM theta activity are recruited in two cognitive control tasks that are characterized by either proactive or reactive control demands. For this purpose, a delayed match to sample (DMTS) task and a color Stroop task, that were part of a larger study including also an episodic retrieval task, were analyzed. Although the study was not initially designed to compare proactive and reactive control processes, the DMTS and Stroop task were assumed to differentially recruit either proactive or reactive control mechanisms. In the DMTS task, participants have to maintain or manipulate a stimulus over a delay period in order to compare it to an expected probe afterwards. This task is assumed to mainly involve proactive control that supports the sustained and anticipatory maintenance of goal-relevant information. In contrast, in the color Stroop task, participants have to inhibit the prepotent response of reading the written color word that interferes with the task goal of naming the ink color. This is expected to primarily recruit reactive control that supports the suppression of the strongly activated task-irrelevant reading response and the strengthening of the weakly activated but task relevant color-naming response. In order to show that the degree of cognitive control recruitment has a behavioral and electrophysiological effect irrespective of the elicited cognitive control mode, both tasks contained a number of conditions differing in task difficulty and thus in the amount of cognitive control needed for performance of the respective condition. Based on previous findings, we expected slower reaction times (RTs) and lower accuracy in the conditions with high cognitive control compared to those with low cognitive control demands in both tasks. Additionally, stronger recruitment of cognitive control should be reflected in larger FM theta activation in the more difficult conditions of both tasks. Due to the fact that the cognitive control tasks differed in their proactive and reactive control demands, it was expected that the recruitment of differential cognitive control mechanisms would lead to scalp topographical differences of theta activity between both tasks.

2.2 Methods

2.2.1 Participants

Overall, 34 right-handed German volunteers who were recruited from Saarland University’s student community participated in the study. For analyses of the Stroop task, data of all 34 participants (11 male, $M_{\text{age}} = 23.15$ years, age range = 19–27 years) was used. For analyses of the DMTS task, seven participants had to be excluded due to chance performance (determined by individual χ^2 tests for each participant), resulting in a sample of 27 participants (9 male, $M_{\text{age}} = 22.81$ years, age range = 19–27 years). Consequently, as the comparison of theta activity between tasks was within-participants, we excluded the same seven participants also from task comparison analyses. According to self-report all participants were healthy, had normal or corrected-to-normal vision and no history of neurological or psychiatric problems. Participants provided written informed consent prior to the experiment and either received course credit or were paid 8€ per hour in return for their participation. The experimental procedure was approved by the local ethics committee in accordance with the declaration of Helsinki.

2.2.2 Experimental procedure

Participants were seated comfortably in a dimly lit and quiet experimental room in order to conduct a DMTS task adapted from Griesmayr et al. (2014) and a color Stroop task on a Dell Computer. Experimental stimuli were presented using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, USA) on a Dell 24-inch monitor placed at a viewing distance of approximately 70 cm. The order of DMTS and Stroop task was counterbalanced across participants. Both tasks were part of a larger study. Before performing the two tasks reported here, participants performed the learning phase of a source memory task, in which they learned 200 concrete nouns by judging the object denoted by the noun by different characteristics.

The DMTS task consisted of two conditions including 12 practice and 70 task trials each (Figure 2.1). Both conditions were presented in a blocked and counterbalanced design. Each task block consisted of 35 trials. Stimuli consisted of one or four colored squares integrated in a 6×6 matrix with a visual angle of $9.8^\circ \times 9.8^\circ$ and were presented for 500 ms. These encoded stimuli had to be maintained over a 2000 ms delay period in which the stimuli were masked by a matrix containing gradational grey colored squares. In the *retention condition* participants had to simply maintain the location of a green-colored square within the 6×6 matrix over the delay period whereas in the

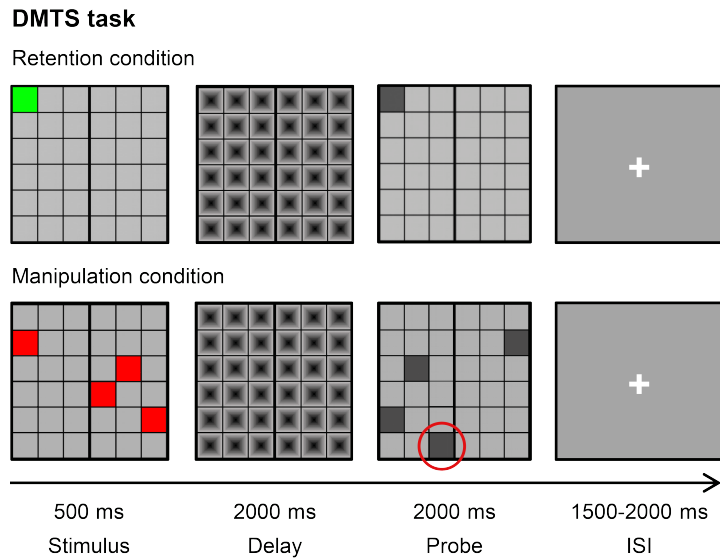


Figure 2.1. Trial procedure of the DMTS task. In the retention condition the stimulus had to be simply maintained whereas in the manipulation condition the colored squares of the stimulus had to be mirrored at the vertical midline. The red circle, which was not shown during the experiment, indicates the square of the probe that is in the wrong position, making the depicted trial a non-match.

manipulation condition participants had to mentally mirror four red squares on the vertical matrix midline and maintain their mirrored locations. After the delay period, a probe matrix with grey squares either matching or not matching the position of the colored squares of the encoded stimulus was presented for 2000 ms. Participants were instructed to indicate by a mouse button press with the left or right thumb whether the grey squares of the probe were identical (match) or different (non-match) from the colored squares' locations of the encoded stimulus. In the manipulation condition only one of the four squares did not match the correct mirrored position in the non-match trials. For half of the trials the correct response was match and for the other half non-match. Participants were asked to respond as fast and accurately as possible during the presentation of the probe. During a subsequent jittered intertrial interval of 1500–2000 ms a central fixation cross was presented. All instructions and stimuli were presented centrally against a grey background.

The color Stroop task contained a congruent, incongruent and neutral condition. Stimuli were presented in randomized order within eight blocks consisting of 24 stimuli each. Before the processing of the 192 task trials, participants could familiarize with the task in 24 practice trials. All words were presented with a visual angle of $4.1^\circ \times 1.2^\circ$ for 1000 ms against a black background and were preceded by a fixation cross which was presented for 1000 ms. In the *congruent condition* the German color words for green (“GRÜN”), red (“ROT”), blue (“BLAU”), and yellow (“GELB”) were presented in their respective ink color whereas in the *incongruent condition* the color words were shown in

a color different from their meaning. For the *neutral condition* the four neutral German words for leak (“LECK”), oath (“EID”), joke (“WITZ”), and misfortune (“PECH”) were used. These words were selected due to comparable length and because they did not share initial letters with the color words. Participants were instructed to indicate the ink color as fast and correctly as possible while ignoring the word meanings. Responses were given by pressing the colored keys “C” and “S” with the left and “M” and “L” with the right index and middle finger on a conventional keyboard. The color to key assignment was fixed across participants and experimental blocks.

2.2.3 Data acquisition and processing

Electroencephalographic (EEG) activity was recorded continuously with a sampling rate of 500 Hz from 32 Ag/AgCl electrodes using Brain Vision Recorder software and Brain Amp EEG amplifiers (Brain Products GmbH, Gilching, Germany). Scalp electrodes were mounted on a fitted cap according to the extended 10–20 system and four additional electrodes placed at the outer canthi of the eyes and above and below the right eye were used to record the electrooculogram for eye movement detection. During the continuous EEG recording, electrode impedances were kept below 5 k Ω and signals were filtered with an online low-pass filter of 100 Hz. All electrodes were referenced to the left mastoid electrode during data acquisition and re-referenced offline to averaged mastoids.

Offline analysis of EEG signals was performed using Brain Vision Analyzer 2.1 software (Brain Products GmbH, Gilching, Germany). Raw data was first inspected visually and nonstereotypic activity, such as muscle activity, was manually removed in order to improve artifact correction by ICA decomposition. Afterwards data was high-pass filtered at 0.5 Hz (12 dB/oct) and low-pass filtered at 40 Hz (24 dB/oct). An infomax ICA was run to identify and remove components representing eye movements, such as blinks and saccades. The continuous EEG of the DMTS task was segmented from –1500 ms prior to stimulus presentation until 4000 ms thereafter and in the color Stroop task from –1500 ms prior to word presentation until 2500 ms thereafter. Finally, segments with a maximal difference of 200 μ V were removed, resulting in comparable trial numbers between both tasks ($M_{\text{DMTS}} = 58.89$, $SD_{\text{DMTS}} = 3.75$; $M_{\text{Stroop}} = 60.84$, $SD_{\text{Stroop}} = 5.75$).

For calculation of frequency amplitude estimates, single trial activity from 1 Hz to 30 Hz was decomposed using a complex Morlet wavelet with 59 linear 0.5 Hz frequency steps and a time-frequency resolution indicated by a parameter c of 10. Subsequently, event-related synchronization/desynchronization (ERS/ERD) was calculated for every condition separately. ERS/ERD is defined as the percent power change relative to

a baseline, which was the time interval of -800 ms to -200 ms before stimulus onset for both tasks. In order to exclude distortions of lower frequency power changes by ERPs, ERS/ERD was calculated with the inter-trial variance approach that calculates the frequency power by referencing the power of each measurement point within a trial to the mean power of the according measurement point of all trials (Kalcher & Pfurtscheller, 1995). In this way, purely non-phase locked (induced) activity that is thought to reflect higher order processes is measured (David, Kilner, & Friston, 2006). ERS/ERD measures of theta activity in both tasks were taken from electrode Fz because condition effects of the DMTS and Stroop task were shown to be present at this electrode before (cf. Griesmayr et al., 2010; Griesmayr et al., 2014; Hanslmayr et al., 2008). Moreover, theta activity was largest at Fz for the more difficult condition of each task (manipulation condition of the DMTS task and incongruent condition of the Stroop task). Consistent with previous studies, five consecutive epochs with a length of 500 ms in the theta frequency range (4–7 Hz) at electrode Fz were extracted covering both the 500 ms encoding and 2000 ms maintenance phase of the DMTS task (Berger et al., 2016; Griesmayr et al., 2014). In contrast, theta effects in Stroop tasks of previous studies were shown to have a shorter temporal extension and to occur during the later stimulus presentation phase (Hanslmayr et al., 2008), where also corresponding ERP effects are present (Rebai, Bernard, & Lannou, 1997). Thus, two consecutive 400 ms epochs (0–400 ms and 400–800 ms) were chosen for the Stroop task, resulting in different but comparable time intervals for both tasks.

In order to compare the scalp topography of theta activity in the DMTS and the Stroop task and based on prior studies, we selected time intervals, in which the demand on cognitive control and the measured theta activity were largest for the more difficult conditions (see Berger et al., 2016; Griesmayr et al., 2014; Hanslmayr et al., 2008, for a similar approach). In both tasks this was the case in late time intervals during the maintenance phase (1500–2000 ms for DMTS) and stimulus presentation (400–800 ms for Stroop), respectively. The extracted activity from all scalp electrodes was rescaled using the vector scaling method (McCarthy & Wood, 1985; Picton et al., 2000; Wilding, 2006). This method was used to control for amplitude differences between conditions making the measured power values comparable across tasks, conditions, and electrodes. Therefore, difference scores of theta activity in both tasks (“manipulation – retention” at 1500–2000 ms for DMTS and “incongruent – congruent” at 400–800 ms for Stroop) were calculated and averaged across participants. The 25 electrodes used for the vector scaling method were Fp1, Fp2, F7, F3, Fz, F4, F8, FC5, FC3, FCz, FC4, FC6, T7, C3, Cz, C4, T8, CP3, CPz, CP4, P7, P3, Pz, P4, and P8.

2.2.4 Data analysis

Behavioral effects on reaction times (RTs) and accuracy were assessed by one-way repeated-measures analyses of variance (ANOVAs) including the within-subject factor Condition (retention vs. manipulation for the DMTS task and congruent vs. neutral vs. incongruent for the Stroop task). FM theta effects at electrode Fz were analyzed with repeated-measures ANOVAs. For the DMTS task the within-subject factors were Condition (retention vs. manipulation) and Time (0–500 ms vs. 500–1000 ms vs. 1000–1500 ms vs. 1500–2000 ms vs. 2000–2500 ms) whereas for the Stroop task the corresponding factors were Condition (congruent vs. incongruent) and Time (0–400 ms vs. 400–800 ms), respectively. The neutral condition of the Stroop task was discarded from EEG analyses since on the basis of a large amount of other studies largest effects were expected for the comparison of the two classical Stroop conditions, congruent and incongruent, respectively (e.g., Hanslmayr et al., 2008; see MacLeod, 1991, for review). Additionally, this made the Stroop task analyses better comparable to those of the DMTS task. Between-task differences in the scalp distribution of theta ERS/ERD were assessed by a repeated-measures ANOVA with the within-subject factors Task (DMTS vs. Stroop) and Electrode (25 electrodes) conducted for the rescaled condition differences (“manipulation – retention” for DMTS and “incongruent – congruent” for Stroop) in the 1500–2000 ms (DMTS task) and 400–800 ms (Stroop task) time intervals, respectively. For all analyses, only correct trials were included and the significance level was set to $\alpha = .05$. Whenever necessary, the Greenhouse-Geisser correction was applied and the adjusted p -values are reported. When post hoc comparisons were made, Bonferroni correction was applied in order to correct the α -level for multiple comparisons.

2.3 Results

2.3.1 Behavioral results

As expected and illustrated by Table 2.1, in the DMTS task reaction times were faster and performance accuracy higher in the retention than in the manipulation condition. Furthermore, in the Stroop task participants responded fastest and most accurate in the congruent condition whereas performance was slower and less accurate in the other two conditions with slowest reaction times and lowest accuracy in the incongruent condition. These observations were confirmed by the statistical analyses. The one-way repeated-measures ANOVAs of the DMTS task revealed a main effect of Condition for reaction times ($F(1, 26) = 381.38$, $p < .001$, $\eta_p^2 = .94$) and for accuracy ($F(1, 26) = 253.81$, $p < .001$, $\eta_p^2 = .91$). Analysis of the RTs in the Stroop task

Table 2.1. Behavioral results of the DMTS ($n = 27$) and Stroop task ($n = 34$).

| Task | Condition | Reaction times [ms] | Accuracy [%] | Difficulty |
|--------|--------------|---------------------|--------------|------------|
| DMTS | Retention | 684 (24) | 97.94 (0.43) | Low |
| | Manipulation | 1059 (32) | 73.97 (1.45) | High |
| Stroop | Congruent | 601 (9) | 92.14 (0.84) | Low |
| | Neutral | 619 (9) | 91.87 (0.83) | Medium |
| | Incongruent | 640 (10) | 88.05 (1.47) | High |

Note. Standard errors of the mean are depicted in parentheses. Each task contained conditions varying in difficulty and thus in the need for cognitive control.

with a one-way repeated-measures ANOVA revealed a significant main effect of Condition ($F(2, 66) = 55.34$, $p < .001$, $\eta_p^2 = .63$) and post hoc t -tests with a Bonferroni-corrected α -level of .017 showed that RTs in all three conditions differed significantly from each other with congruent < incongruent ($t(33) = 10.29$, $p < .001$, $d = 1.76$), neutral < incongruent ($t(33) = 6.00$, $p < .001$, $d = 1.03$), and congruent < neutral ($t(33) = 4.61$, $p < .001$, $d = 0.79$), reflecting increasing demands on interference resolution from congruent over neutral to incongruent trials. Differences in accuracy between Stroop conditions were revealed by a significant main effect of Condition ($F(2, 66) = 9.06$, $p = .001$, $\eta_p^2 = .22$). Further t -tests showed that with a Bonferroni-corrected α -level of .017 the congruent > incongruent ($t(33) = 3.25$, $p = .003$, $d = 0.56$) and neutral > incongruent ($t(33) = 3.43$, $p = .002$, $d = 0.59$) differences were significant whereas the difference between the congruent and neutral condition was not ($t(33) = 0.34$, $p = .733$, $d = 0.06$), indicating that an interference effect (incongruent < neutral) but not a facilitation effect (congruent > neutral) was present in the accuracy data (see MacLeod, 1991, for review). In sum, consistent with our hypotheses, performance was slower and less accurate in conditions that require increased cognitive control for the active maintenance and manipulation of information in visual WM (DMTS task) or the inhibition of a prepotent response in favor of a less preferred one (Stroop task), reflecting high demands on proactive and reactive cognitive control, respectively.

2.3.2 EEG results

For the DMTS task the repeated-measures ANOVA with the within-subject factors Condition (retention vs. manipulation) and Time (0–500 ms vs. 500–1000 ms vs. 1000–1500 ms vs. 1500–2000 ms vs. 2000–2500 ms) conducted for FM theta ERS/ERD showed a significant Condition by Time interaction ($F(2.14, 55.63) = 4.19$, $p = .018$, $\eta_p^2 =$

.14), indicating that theta activity changed differently over time for both conditions. Both main effects were not significant (p -values $> .056$). As apparent from Figure 2.2 and confirmed by further t -tests with a Bonferroni corrected α -level of .01, theta ERS was marginally higher in the manipulation condition than in the retention condition during the maintenance phase in the 1500–2000 ms time interval ($t(26) = 1.84$, $p = .039$, $d = 0.72$). Other comparisons between conditions were not significant (all p -values $> .069$). Further contrasts for the factor Time, that were calculated separately for both conditions, revealed that in the retention condition FM theta activity decreased linearly over the time intervals of the encoding and maintenance phase ($F(1, 26) = 10.67$, $p = .003$, $\eta_p^2 = .29$) whereas in the manipulation condition

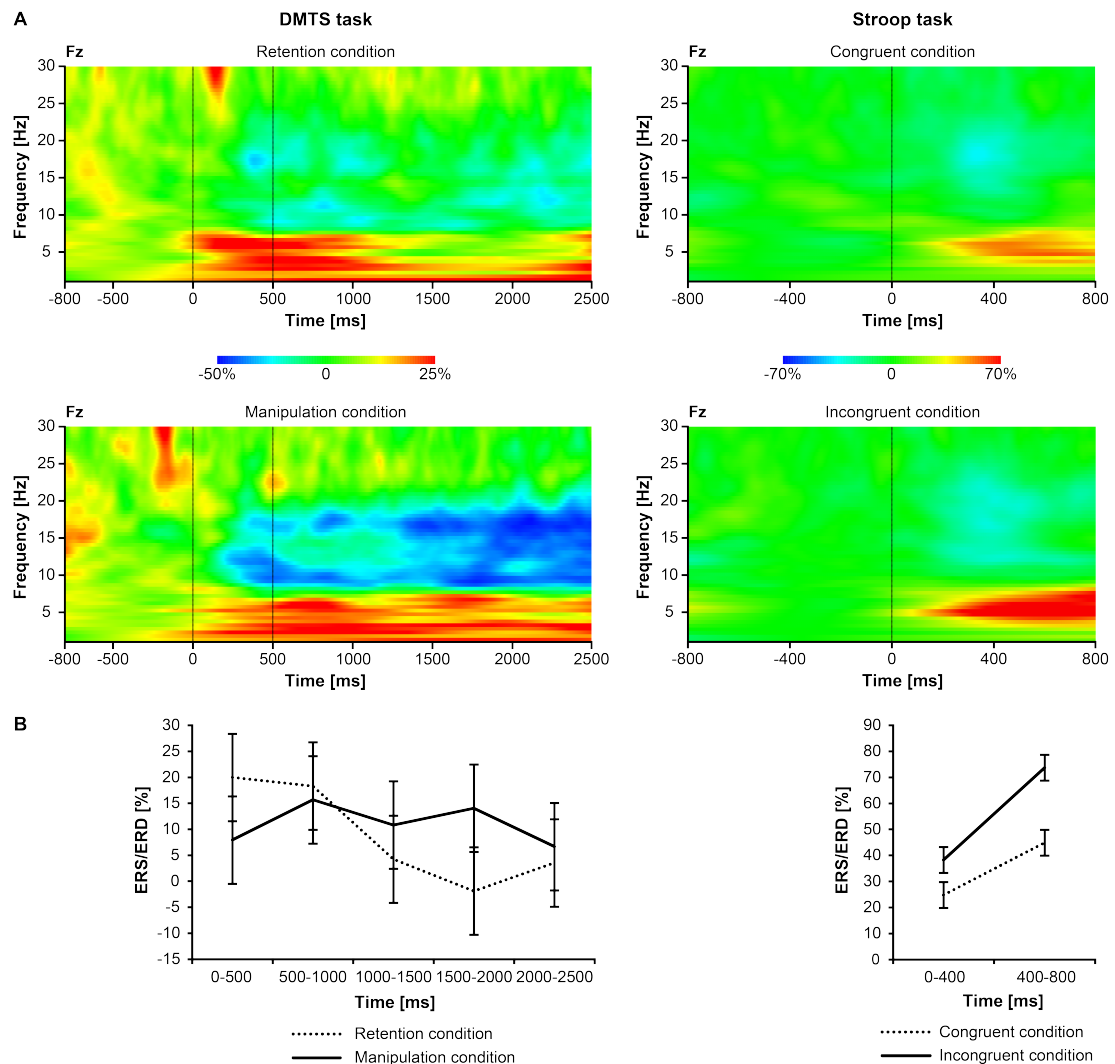


Figure 2.2. (A) Time-frequency plots of ERS/ERD activity for the retention and manipulation condition of the DMTS task ($n = 27$) and the congruent and incongruent condition of the Stroop task ($n = 34$) at electrode Fz. Vertical bars indicate stimulus and delay onset, respectively. For both tasks a 300 ms baseline was used. (B) Mean FM theta activity of the consecutive time intervals for the conditions of the DMTS and Stroop task at electrode Fz. Error bars indicate 95% confidence interval of the Condition by Time interaction for each task.

the linear trend was not significant ($F(1, 26) = 0.05$, $p = .817$, $\eta_p^2 = .002$). These findings suggest that in the retention condition cognitive control demands are high in the initial encoding phase and then decline during the maintenance phase whereas in the manipulation condition the demands on cognitive control are relatively stable across time.

Analysis of the FM theta ERS/ERD in the Stroop task with a repeated-measures ANOVA including the within-subject factors Condition (congruent vs. incongruent) and Time (0–400 ms vs. 400–800 ms) revealed both a significant main effect of Condition ($F(1, 33) = 52.48$, $p < .001$, $\eta_p^2 = .61$) and of Time ($F(1, 33) = 9.11$, $p = .005$, $\eta_p^2 = .22$). Furthermore, there was a significant Condition by Time interaction ($F(1, 33) = 6.97$, $p = .013$, $\eta_p^2 = .17$). As depicted in Figure 2.2, t -tests with a Bonferroni-corrected α -level of .025 revealed that the congruent < incongruent effect was more pronounced in the late time interval ($t(33) = 3.29$, $p = .001$, $d = 1.15$) than in the early time interval ($t(33) = 2.17$, $p = .019$, $d = 0.76$). This finding is in line with previous research showing that FM theta is especially pronounced in conditions with high need for cognitive control, such as the incongruent Stroop condition, and occurs in a late response-selection phase of the task, in which the prepotent word-reading response has to be inhibited.

The comparison of condition differences (manipulation – retention at 1500–2000 ms for the DMTS task and incongruent – congruent at 400–800 ms for the Stroop task) in the amplitude normalized theta scalp topography between both tasks with a repeated-measures ANOVA containing the within-subject factors Task (DMTS vs. Stroop) and Electrode (25 electrodes) revealed a significant Task by Electrode inter-

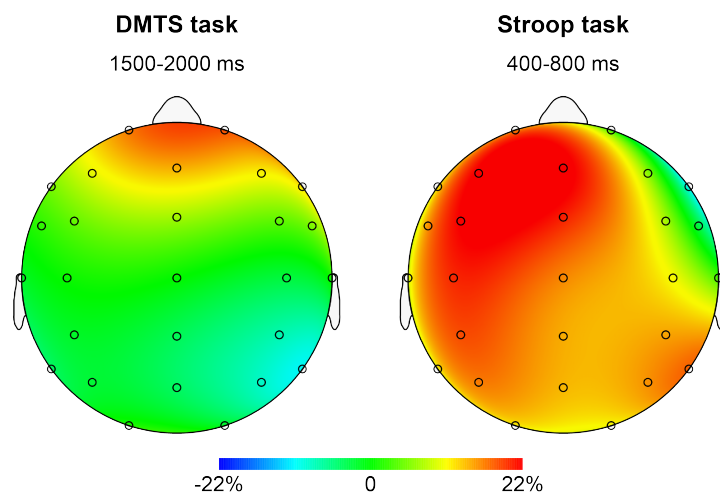


Figure 2.3. Topographic maps of FM theta activity difference of the DMTS task (manipulation – retention) at 1500–2000 ms ($n = 27$) and Stroop task (incongruent – congruent) at 400–800 ms ($n = 27$).

action ($F(4.05, 105.37) = 2.93$, $p = .024$, $\eta_p^2 = .10$). Figure 2.3 shows the topographical distribution of theta activity differences for both tasks across the 25 selected electrodes. The linear Task by Electrode interaction contrast was significant ($F(1, 26) = 5.85$, $p = .023$, $\eta_p^2 = .18$), indicating a focal FM theta activation at frontal recordings that linearly declined from anterior to posterior recordings in the DMTS task as compared to a broad activation in the Stroop task. All in all, these findings show that although the condition effects were pronounced at the same electrode Fz, the recruitment of proactive control in the DMTS task is reflected by a rather focal theta activation over frontal scalp sites whereas reactive control processes in the Stroop task are accompanied by a topographically more widespread theta activation.

2.4 Discussion

The present study aimed at investigating the functional role of FM theta activity in two tasks requiring cognitive control. Both tasks contained conditions that differed in their difficulty and consequently in their cognitive control demands. Behavioral results revealed the validity of the difficulty manipulation of the conditions in each task. Participants showed slower and less accurate performance in conditions with high need for control, namely the manipulation condition of the DMTS task and the incongruent condition of the Stroop task (Table 2.1). Moreover, we expected that the higher cognitive control demands in these conditions would be accompanied by higher FM theta compared to conditions with low control demands (cf. Cavanagh & Frank, 2014). Analyses of the electrophysiological activity at electrode Fz supported this assumption by revealing different temporal profiles of FM theta activity across the encoding and maintenance phase for the two conditions of the DMTS task and higher FM theta activity in the incongruent than in the congruent condition of the Stroop task (Figure 2.2). In the DMTS task, FM theta activity was high during the encoding phase in the retention condition and during the encoding and maintenance phase in the manipulation condition. This finding suggests different temporal trajectories of cognitive control in both conditions. While in the retention condition the internal representation of the stimulus can be build up immediately during encoding, in the manipulation condition a mirror transformation has to be performed first in order to construct an internal representation later in the maintenance period that can be matched with the upcoming probe. Consequently, FM theta might reflect cognitive control processes that serve both the construction (cf. T. Gruber et al., 2008; Khader et al., 2010; Osipova et al., 2006; Sederberg et al., 2003; see Nyhus & Curran, 2010, for review) and maintenance (Griesmayr et al., 2010; Roberts et al., 2013; see Sauseng et al., 2010, for review) of internal representations.

In the DMTS task the greatest difference in FM theta activity between the retention and manipulation condition was present in a later time window of the maintenance phase. Similarly, in the Stroop task FM theta was higher for the incongruent compared to the congruent condition in the later time interval where response-selection takes place and the prepotent word-reading response needs to be inhibited. Therefore, these time intervals were selected in order to investigate the specificity of theta activity as a neural correlate of cognitive control. It was expected that scalp topographical differences of theta oscillations might become apparent by directly comparing these two tasks which differ in the amount of proactive and reactive control, respectively. As expected, the distribution of theta activity over scalp electrodes differed significantly between both tasks (Figure 2.3). Theta activity in the DMTS task was strongest at frontal electrodes with decreasing theta activity from anterior to posterior sites whereas theta activity was topographically more broadly distributed in the Stroop task, as indicated by a linear interaction contrast in the amplitude normalized data. This result can be interpreted in the context of the DMC framework (Braver, 2012) that states that proactive control is reflected in sustained IPFC activation (Braver & Cohen, 2001; Braver & Bongiolatti, 2002; Paxton et al., 2007; Veltman et al., 2003) whereas reactive control recruits the IPFC and a wider network of brain areas (Grandjean et al., 2012; Milham et al., 2002; Zysset et al., 2001). The focal theta activation over prefrontal brain regions in the DMTS task probably reflects the proactive control mode that supports the sustained maintenance of stimulus representations and facilitates the processing of upcoming events, such as the probe. In contrast, the broad theta distribution in the Stroop task might reflect the reactive control mode that enables a late correction process that happens after situations characterized by high response conflict and thereby supports interference resolution. Consequently, the broader distributed theta scalp topography in the Stroop task as compared to the focal theta activity in the DMTS task might originate from the activation and synchronization of broadly distributed brain regions. Although this result shows only indirect evidence for large-scale theta synchronization, the present interpretation is partly supported by recent theta coherence studies that show the activation of different fronto-parietal theta networks during proactive compared to reactive control (Cooper et al., 2015; Cooper et al., 2017). However, Cooper et al. (2015) and Cooper et al. (2017) investigated transient changes in proactive control in the trial-preparation phase of a task-switching paradigm. By this, one cannot infer from their findings that the same network is involved in sustained proactive control (Cooper et al., 2015) that was investigated in the maintenance phase of the DMTS task in the present study.

Taken into account that FM theta activity was modulated in amplitude and topography by cognitive control demands in both tasks, the question arises which mechanisms are reflected in theta oscillations that serve both proactive and reactive control. In a recent review paper, L.-T. Hsieh and Ranganath (2014) proposed that FM theta oscillations might organize the sequential reactivation of individual items in WM that also supports long-term memory encoding and retrieval. Individual items are reflected by gamma activity that is superimposed onto one theta cycle by cross-frequency phase coupling and thus acquire a temporal order that can be sequentially reactivated (Jensen & Lisman, 2005; Lisman & Idiart, 1995; Lisman & Jensen, 2013). Consequently, the more individual items have to be maintained in WM the more FM theta activity is present. In support of the view that frontal theta activity is especially important for the maintenance of temporal order information, Roberts et al. (2013) showed that frontal theta activity was more pronounced when temporal order as compared to spatial information was maintained in WM. The results of the DMTS task can be interpreted in line with the sequential reactivation view. In the manipulation condition, the four squares of the stimulus are probably encoded, mirrored at the vertical stimulus midline and maintained sequentially and thus may be represented in WM by theta-gamma phase coupling. Consistently, theta activity was higher in the manipulation condition, in which participants had to manipulate and maintain four square positions of the stimulus, as compared to the retention condition, in which only one square position had to be maintained. Additionally, the difference between conditions in theta activity was especially pronounced at frontal sites. Thus, it is conceivable that especially the focally measured FM theta activity reflects temporal order information about the encoded stimuli.

Another related account for FM theta activity, which is also discussed by L.-T. Hsieh and Ranganath (2014), assumes that FM theta is involved in the systematic coordination of inhibition strength over strong and weak memory representations (K. A. Norman et al., 2005; K. A. Norman et al., 2006). It is assumed that inhibition levels vary with the theta cycle and thereby support the strengthening of weak target representations while suppressing strong competitors. In both tasks of the present study, inhibition plays a role for successful task performance. In the DMTS task, competing stimulus representations of previous trials and not yet mirrored stimulus representations of the present trial have to be inhibited during WM maintenance and the subsequent comparison with the probe. Thus, FM theta activity could proactively support the processing of the probe in a top-down manner by strengthening the task-relevant stimulus representation and inhibiting competing representations. However, inhibition strength probably is not as strong as in the Stroop task since there is no prepotent stimulus

or response representation that needs to be inhibited. In the color Stroop task, the response representation of naming the color word erroneously gets activated first and needs to be inhibited reactively in order to overcome interference and to name the word color. Therefore, the broad theta scalp distribution in the Stroop task probably reflects the inhibition of strong prepotent representations while supporting the weak task goal representation. Taken together, both accounts can explain the findings in the present study. Although the DMTS task involves aspects that can be explained by the account of inhibition strength coordination, the results of the DMTS task are best explained by the sequential reactivation account due to the sequential nature of the task. In contrast, the results of the Stroop task can be best interpreted in line with the account of theta activity as a coordination mechanism of inhibition strength due to larger interference in the Stroop compared to the DMTS task.

Although the findings of the present study can be interpreted in line with the DMC framework (Braver, 2012) and provide evidence for the view that theta can support different control functions depending on task requirements, some limitations of the present study have to be considered. Given that our analyses were exploratory in nature, these limitations might be addressed by future studies in order to substantiate the research on differential theta control networks. The tasks of the present study were not intentionally designed to specifically compare proactive and reactive processes reflected in theta amplitude and its topographical distribution. Both tasks were part of a larger study that additionally contained an episodic retrieval task and aimed at investigating the functional role of FM theta activity within these tasks. One might argue that theta differences between tasks are due to differences in task material and procedure. However, since the topographical comparison between the two tasks is based on differences between task conditions, the influence of different task materials between the tasks should be excluded or at least substantially attenuated. A study in which both forms of cognitive control are operationalized with the same verbal or visuo-spatial task material would directly address this latter issue and should shed further light on this topic. As in other studies the DMTS and Stroop task are not process-pure measures of proactive and reactive control processes, respectively, but recruit the one or the other processes to a greater extent. Moreover, in the DMTS task, task difficulty was defined by both task instruction and WM load whereas in the Stroop task only in/congruency of word and ink color determined task difficulty. Therefore, when discussing the functional role of theta activity, it has to be considered that the present results reflect a relative difference in cognitive control demands due to general task difficulty. However, both tasks are typically used in investigations of the DMC framework (cf. Braver, 2012).

All in all, to the best of our knowledge the present study is the first that shows scalp topographical differences of theta activity between tasks differing in their cognitive control demands, demonstrating the importance of taking scalp topographical differences into account in the functional interpretation of FM theta activity. In line with L.-T. Hsieh and Ranganath (2014), the present study supports the view that FM theta activity may reflect either the communication of temporal order information by sequential reactivation of items in WM or the coordination of inhibition strength, depending on task requirements. FM theta oscillations might inherit one or the other of these functional roles depending on either proactive or reactive cognitive control demands of the task.

Study 2: Theta Neurofeedback and Cognitive Control Processes

3.1 Introduction

In order to effectively coordinate and modify behavior based on made experiences, cognitive control processes are needed. Numerous cognitive training studies observed enhanced cognitive control processes after training of working memory (WM), task-switching, or multi-tasking (e.g., see Anguera & Gazzaley, 2015; Karbach & Kray, 2009; Klingberg, 2010; Morrison & Chein, 2010, for reviews). Notably, training transfer to both the trained and untrained tasks provided evidence for the remarkable capacity for plasticity of the adult brain (see Lövdén et al., 2010, for review). Despite these positive findings, not all training studies succeeded in showing transfer effects, provoking a debate about the effectiveness of cognitive trainings and the generalizability of training-induced changes (see Owen et al., 2010; Melby-Lervåg & Hulme, 2013; Simons et al., 2016, for reviews). Recently, Lindenberger, Wenger, and Lövdén (2017) suggested that the debated questions can only be answered if research not only focuses on changes occurring pre- to posttraining, but also investigates the underlying structural changes that arise during training, influencing performance outcome. According to the overlap hypothesis of training transfer (Dahlin et al., 2008; see Buschkuhl et al., 2012; Jonides, 2004; Lustig et al., 2009, for reviews), cognitive training leads to transfer if trained and transfer task engage similar functional processes (functional overlap) and activate similar brain regions (neural overlap). Furthermore, overlapping cognitive processes and shared brain activity need to change over the course of training for transfer to occur (Lövdén et al., 2010). Assuming that functional and neural overlap are both likewise reflected in overlap in EEG dynamics, it seems possible that transfer also oc-

curs if the same underlying oscillatory dynamics of trained and transfer tasks change as a function of training. Instead of applying cognitive training in order to investigate transfer to cognitive tasks, it might also be possible to directly modulate the EEG characteristics underlying the cognitive processes that are engaged in these tasks. A neuro-scientific method that allows to directly train particular oscillatory characteristics is the method of neurofeedback training (NFT). Thereby, participants learn to volitionally control their brain activity by receiving feedback, for example, about the amplitude of a particular frequency (see Gruzelier, 2014b, for review). Consequently, NFT might be used to directly induce plastic changes by training oscillations that underlie processes engaged in the transfer tasks. If participants are able to modulate oscillatory characteristics that underlie cognitive control processes, NFT should result in training transfer to tasks involving the same cognitive control processes reflected in the trained oscillatory brain activity.

A possible target frequency for NFT are frontal-midline (FM) theta oscillations (4–8 Hz) that have been suggested to reflect a general cognitive control mechanism in a large variety of cognitive tasks (see Cavanagh & Frank, 2014; Helfrich & Knight, 2016; L.-T. Hsieh & Ranganath, 2014; Sauseng et al., 2010; Klimesch et al., 2008, for reviews). For example, FM theta activity was shown to be enhanced in conditions with high WM load, in which many items had to be maintained in WM (e.g., Jensen & Tesche, 2002; Onton et al., 2005). Moreover, FM theta oscillations were pronounced in interference situations, in which the appropriate stimulus or response had to be selected out of two conflicting ones (e.g., M. X. Cohen & Cavanagh, 2011; Hanslmayr et al., 2008; Nigbur et al., 2011). In general, FM theta activity, which is assumed to be generated in the midcingulate cortex (MCC) and measured over mid-frontal scalp sites (Asada et al., 1999; Gevins, 1997; Sauseng et al., 2007), can act either on a representational level or on a more general processing level (see Sauseng et al., 2010, for review). On the representational level, cross-frequency coupling of theta phase with gamma amplitudes is assumed to provide a binding mechanism for holding several items in WM (see Jensen, 2006; Lisman & Idiart, 1995; Lisman & Jensen, 2013, for reviews) that also allows for the formation of episodic memory representations (see Fell & Axmacher, 2011; Lisman & Buzsaki, 2008; Nyhus & Curran, 2010, for reviews). Gamma amplitudes that represent the activation pattern of singular item representations are nested onto theta cycles, thereby acquiring a temporal order that is inherent to all episodic memories and can be reactivated if necessary (see L.-T. Hsieh & Ranganath, 2014, for review). Support comes from studies showing increased theta-gamma cross-frequency coupling associated with enhanced cognitive performance (e.g., Canolty et al., 2006; Griesmayr et al., 2010; Mormann et al., 2005; see Canolty & Knight, 2010; Jensen & Colgin, 2007,

for reviews). On a more general processing level, theta phase synchronization between different brain regions is assumed to allow for top-down control by integrating task-relevant brain regions (see Cavanagh & Frank, 2014; Sauseng et al., 2010, for reviews). Through phase synchronous activation of FM theta source regions, such as the MCC, and other task-relevant brain regions, temporal windows for information intake and transfer between those regions are provided (Asada et al., 1999; M. X. Cohen, 2011a; Gevins, 1997; Onton et al., 2005). Interestingly, the view that FM theta oscillations reflect cognitive control processes is supported by oscillation changes induced by multi-tasking training. Behavioral transfer of an interference-rich multi-tasking training with older participants was shown to be accompanied by an increase in FM theta activity as well as higher theta phase synchronization between frontal and parietal brain regions, suggesting increased engagement of cognitive control processes as a function of training (Anguera et al., 2013). Therefore, upregulation of FM theta activity with NFT might be an effective tool to increase cognitive control processes, leading to better behavioral performance in cognitive transfer tasks.

Over recent years, an increasing number of studies have tried to enhance cognitive performance with the help of neurofeedback (see Dessy et al., 2017; Gruzelier, 2014b; Vernon, 2005, for reviews). Training of FM theta activity was shown to result in transfer to several cognitive and memory tasks for both younger and older adults (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Reis et al., 2016; Rozengurt et al., 2016; Rozengurt et al., 2017; J.-R. Wang & Hsieh, 2013). Although most of these theta NFT studies used similar training protocols, transfer effects even solely for younger adults have been rather mixed. For instance, J.-R. Wang and Hsieh (2013) demonstrated that young adults who conducted eight theta NFT training sessions were less susceptible to interference in an attention task after training. In contrast, WM performance in a Sternberg task failed to increase as a function of NFT. In a similar vein, Enriquez-Geppert, Huster, Figge, and Herrmann (2014) found transfer of an eight-session theta NFT to a task-switching and an n -back task, but not to a Stroop and a stop-signal task. These results have been suggested to show that theta NFT improves proactive rather than reactive control processes (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014). According to the dual mechanisms of control (DMC) framework by Braver (2012), proactive control is a top-down selection process occurring before a cognitively demanding event that facilitates processing of task-relevant information by maintaining task goals and biasing sensory processing. Contrarily, reactive control is a correction process taking place after the detection of an erroneous or conflicting event that allows for the selection of adequate responses by inhibiting interfering ones. Although the DMC framework might explain some of the FM theta NFT findings, taking training-

induced changes in EEG characteristics into account makes them even more difficult to reconcile. Thus far, NFT-induced changes in theta activity during the transfer tasks have either not been investigated (Reis et al., 2016; Rozengurt et al., 2016; Rozengurt et al., 2017; J.-R. Wang & Hsieh, 2013) or resulted in mixed findings for proactive and reactive control (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014). Consequently, it remains an open question whether FM theta NFT transfers to proactive but not reactive control processes and whether behavioral transfer is accompanied by training-induced increases or decreases in underlying EEG dynamics. Moreover, the temporal extension of both behavioral transfer to cognitive control processes and their underlying EEG characteristics to later follow-up measurements has not been investigated (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Reis et al., 2016; J.-R. Wang & Hsieh, 2013), leading to the question whether NFT is an effective intervention technique for long-lasting cognitive enhancement.

Given that it has been proposed that more well-controlled studies are needed in order to evaluate the effectiveness of NFT (see Gruzelier, 2014b; Sherlin et al., 2011; Thibault et al., 2016, for reviews), the present study investigated transfer of FM theta NFT to cognitive control processes. More specifically, it was assessed (1) whether seven sessions of FM theta NFT improve performance in tasks requiring cognitive control processes, (2) whether behavioral transfer is accompanied by training-induced changes in EEG characteristics underlying cognitive control processes, and (3) whether training-induced behavioral and EEG changes are not only present one day after the last NFT session but persist to a second posttraining session. Therefore, a training group who trained to upregulate their individually estimated FM theta activity was compared to an active control group who received feedback to frequency ranges that were randomly chosen for each session. Transfer of NFT was investigated in a pre-post design with a posttest one day after the last NFT session and a second posttest 13 days after training. Behavioral transfer and changes in EEG characteristics were assessed in a delayed match to sample (DMTS) task recruiting proactive control and a Stroop task engaging reactive control. Both tasks contained conditions requiring different levels of cognitive control for task execution (cf. Eschmann, Bader, & Mecklinger, 2018). It was expected that successful FM theta NFT leads to better performance in both the DMTS and Stroop task for the training compared to the active control group, especially in conditions with more pronounced cognitive control recruitment. Besides, behavioral transfer to participants' WM capacity, processing speed, and self-awareness was measured in order to receive a broader picture of training-induced cognitive changes. If FM theta NFT improves cognitive control processes, this might be reflected in a greater WM operation span and faster processing speed, which both have been shown to influence a variety of cognitive

abilities (see Conway et al., 2005; Salthouse, 1996, for reviews). Furthermore, it is conceivable that NFT itself, irrespective of the trained frequency, increases participants' self-awareness since self-referential processes are needed in order to gain control over one's own brain activity (Ninaus et al., 2013). Overall, pre- to posttest measurements of all transfer tasks were expected to be predicted by the extent of FM theta upregulation during NFT. Training-induced changes in EEG dynamics in the DMTS and Stroop task were expected to either show increased or decreased FM theta activity, reflecting either increased recruitment or more efficient use of cognitive control processes (see Kelly & Garavan, 2004, for review). In line with behavioral analyses, FM theta NFT change should predict pre- to posttest EEG changes for the training but not the control group.

3.2 Methods

3.2.1 Participants

Altogether, 36 German students who were recruited from Saarland University's student community participated in the NFT study. Participants were assigned to a training group (TG; $n = 17$, five male, $M_{TG} = 22.65$ years, age range = 20–30 years) and an active control group (CG; $n = 18$, six male, $M_{CG} = 23.33$ years, age range = 19–27 years) that were matched in sex, age, and study subject. One participant of the training group had to be excluded from the analyses because of being a Tukey outlier in NFT theta increase and due to incorrect execution of the DMTS task. By means of an online questionnaire, participants indicated prior to the study that they enjoy rollercoaster driving with a score > 4 on a 7-point Likert scale and both groups did not differ in their preference for rollercoaster driving ($M_{TG} = 6.11$, $M_{CG} = 6.22$; $t(34) = 0.11$, $p = .710$, $d = 0.12$). According to self-report, participants were healthy, had normal or corrected-to-normal vision, and showed no history of neurological or psychiatric diseases. Furthermore, all participants were right-handed as indicated by the Edinburgh Handedness Inventory (Oldfield, 1971). Testing times were scheduled in accordance with each participant's chronotype based on the German version of the Morningness-Eveningness Questionnaire (D-MEQ; Griefahn, Kunemund, Brode, & Mehnert, 2001). Written informed consent was provided prior to the study and participants were paid 8€ per hour in return for their participation. If desired, the payment was partially replaced by course credit. The experimental procedure was approved by the local ethics committee in accordance with the declaration of Helsinki.

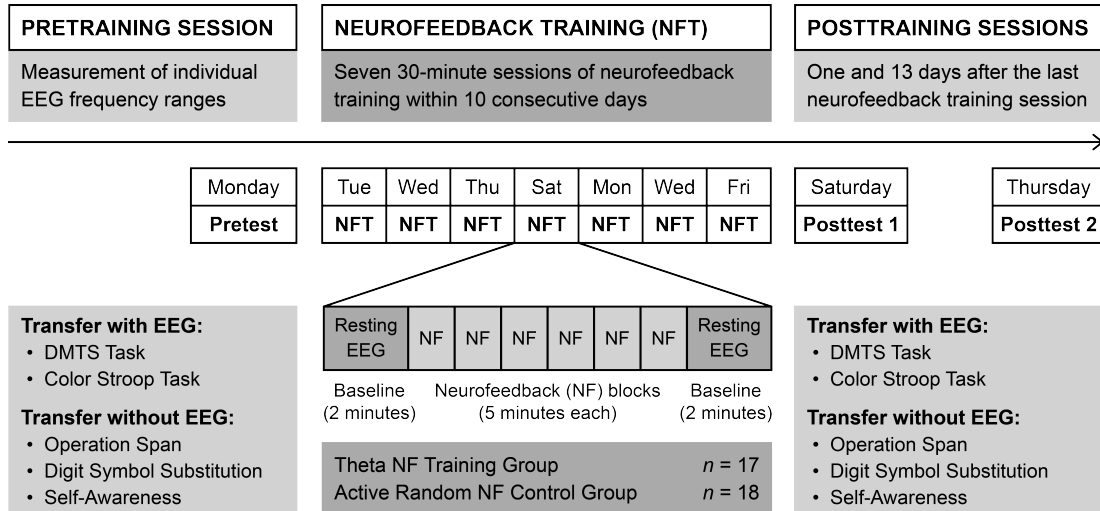


Figure 3.1. Training schedule with cognitive control transfer. Neurofeedback training consisted of seven neurofeedback sessions and transfer to cognitive control processes was investigated from one pretraining to two posttraining sessions. All sessions took place at the same fixed days for each participant.

3.2.2 Experimental design and data acquisition

Transfer effects from individual FM theta upregulation to performance in cognitive measurements were assessed in a pre-post design (Figure 3.1). In a pretraining and two posttraining sessions, all participants performed a delayed match to sample (DMTS) and a color Stroop task in which cognitive control processes have previously been shown to be accompanied by FM theta oscillations (Berger et al., 2016; Eschmann et al., 2018; Griesmayr et al., 2014; Hanslmayr et al., 2008). In every of the three transfer sessions, participants additionally conducted an operation span (OSPAN) task (Unsworth, Heitz, Schrock, & Engle, 2005), a paper-pencil version of the digit symbol substitution test (Wechsler, 1982), and a paper version of the German questionnaire for the assessment of dispositional self-awareness (SAM; Philipp & Freudenberg, 1989) in order to assess training-induced changes in participants’ operation span, processing speed, and self-awareness, respectively. NFT sessions took place on seven fixed days between the pre- and posttraining sessions for both the training and control group. For every testing and training session, participants were seated comfortably in a dimly lit and quiet experimental room. Computer-based tasks and NFT were presented on a Dell Computer with a Dell 24-inch monitor placed at a viewing distance of approximately 70 cm.

Task procedures

During pre- and posttraining sessions, participants first conducted a paper-pencil version of the *digit symbol substitution test*, in which nine symbols were assigned to the digits 1–9 (Wechsler, 1982). Within 90 seconds, participants had to draw as many

corresponding symbols under a list of 100 digits. They were asked to do so as fast and accurately as possible. The digit symbol test score was given by the total number of correctly added symbols.

Second, participants filled out a paper-pencil version of the *SAM* questionnaire for the assessment of dispositional self-awareness (Filipp & Freudenberg, 1989). This questionnaire measures *private* and *public* self-awareness with 14 and 13 statements, respectively, that are rated on a 5-point Likert scale ranging from 5 = *very often* to 1 = *very rarely*. Self-awareness scores are calculated as the sum of Likert ratings for the respective statements that focus either on aspects about the self that are only accessible for oneself (*private*) or on aspects that are publicly available (*public*). Afterwards, the encoding phase of a source memory task was conducted. Participants learned 200 concrete nouns by judging the object denoted by the noun by its pleasantness or animacy. Findings of NFT transfer to the source memory task are reported in Chapter 4.

Third, the *DMTS* and color *Stroop* task were assessed by presenting them with E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, USA). Task order was counterbalanced across participants but remained fixed across pre- and posttraining sessions. Stimuli and task procedures were the same as described in Section 2.2.2. In the *DMTS* task, participants had to either simply maintain the position of one green colored square (*retention condition*) or mirror the position of four red colored squares (*manipulation condition*) in a delay period (cf. Figure 2.1). During probe presentation, participants had to indicate via mouse button press whether the positions of one or four gray squares were matching or non-matching to the ones of the stimulus. Both conditions were presented in blocks and their order was counterbalanced across participants but stayed fixed across all pre- and posttraining sessions. The *Stroop* task consisted of a *congruent* (color word presented in the same ink color), *neutral* (neutral word depicted in one of four ink colors), and an *incongruent condition* (color word presented in a different ink color). In all pre- and posttraining sessions, *Stroop* conditions were presented intermixed and participants were asked to indicate the respective ink color of the stimulus via keyboard press. After the *DMTS* and *Stroop* task, the retrieval phase of the source memory task was conducted (Section 4.2.2).

Finally, participants performed an *OSPAN* task (Unsworth et al., 2005) that was presented with E-Prime 1.0 software (Psychology Software Tools, Pittsburgh, USA). All stimuli were presented in black against a white background. Participants were asked to remember 15 sets of letters with a set size ranging from three to seven. Three sets of every set size were conducted randomly. During presentation, letters were superimposed on a grey square and presented separately for 800 ms at the center of the screen. In order

to prevent rehearsal of previously learned letters of the same set, math problems needed to be solved before every letter presentation. Therefore, a math operation that had to be solved as fast as possible was presented. With a mouse button press participants could advance to the next screen, on which a possible answer consisting of one digit was presented. Participants clicked on either "true" or "false" depending on their calculated result. If it took participants longer than their mean math problem solving time plus $2.5 SD$, the correct solution was automatically given and the trial was counted as false. When all letters and math problems of a set were presented, a 4×3 recall matrix with the letters F, H, J, K, L, N, P, Q, R, S, T, and Y appeared. Participants were asked to click on the letters of the presented set in the order, in which they were presented, so that the respective position numbers appeared next to the chosen letters. The possibility to leave a blank position or to change already taken choices was given. After confirmation of their answer, participants received feedback about the number of correctly recalled letters and math errors of the respective set. In total, 75 letters and 75 math problems were presented. Before task execution, participants could familiarize with letter recall and math problem solving both separately and combined. The OSPAN score was calculated as the total number of letters of completely recalled sets.

Pre-/posttraining EEG recordings and processing

During the DMTS and Stroop task, electroencephalographic (EEG) activity was continuously recorded with a sampling rate of 500 Hz from 32 Ag/AgCl electrodes using a Brain Amp EEG amplifier and Brain Vision Recorder software (Brain Products GmbH, Gilching, Germany). Scalp electrodes were mounted on a fitted cap according to the extended 10–20 system. The electrooculogram was recorded for eye movement detection by four additional electrodes placed at the outer canthi of the eyes and above and below the right eye. During continuous EEG recordings, electrode impedances were kept below 5 k Ω and signals were filtered with an online low-pass filter of 100 Hz. All electrodes were referenced to the left mastoid electrode during data acquisition and re-referenced offline to averaged mastoids.

Offline analysis of EEG signals was performed using Brain Vision Analyzer 2.1 software (Brain Products GmbH, Gilching, Germany). First, raw data of both tasks was inspected visually and pronounced artifacts were removed manually in order to improve artifact correction by ICA decomposition. Second, data was band-pass filtered at 0.5 Hz and 40 Hz (48 dB/oct) before being re-referenced to linked mastoids. An infomax ICA was used to identify and remove components representing eye movements and other muscle artifacts. Afterwards, the continuous EEG of the DMTS task was segmented

from -1250 ms prior to stimulus presentation until 3500 ms thereafter, compromising both the 500 ms encoding and the 2000 ms maintenance interval. The EEG of the Stroop task was cut from -1250 ms prior to word presentation until 2000 ms thereafter. A baseline correction in the time domain from -200 ms to 0 ms prior to stimulus and word presentation and an automatic artifact rejection was applied. Segments exceeding a voltage step of $30 \mu\text{V}/\text{ms}$, a maximum-minimum difference of $100 \mu\text{V}$, and an amplitude of $\pm 60 \mu\text{V}$ were removed. Finally, any segments with remaining artifacts were removed by hand.

For calculation of frequency amplitude estimates, single trial activity from 1 Hz to 40 Hz was decomposed using a complex Morlet wavelet with 79 linear 0.5 Hz frequency steps and a time-frequency resolution indicated by a parameter c of 6 . Subsequently, event-related synchronization/desynchronization (ERS/ERD) was calculated for every condition separately. ERS/ERD is defined as the percent power change relative to a baseline, which was measured in the time interval of -800 ms to -200 ms before stimulus onset for both tasks. Segments of both tasks were separated into five equally sized time intervals, resulting in five 500 ms time intervals in the DMTS task (0 – 500 ms, 500 – 1000 ms, 1000 – 1500 ms, 1500 – 2000 ms, and 2000 – 2500 ms) and five 200 ms time intervals in the Stroop task (0 – 200 ms, 200 – 400 ms, 400 – 600 ms, 600 – 800 ms, 800 – 1000 ms). For analyses, ERS/ERD measures of theta activity (4 – 8 Hz) in these time intervals were taken from electrode Fz.

NFT protocol and processing

In order to train upregulation of theta activity by NFT, seven 30-minute neurofeedback sessions were conducted with a self-built feedback protocol using ProComp5 Infinity amplifier and BioGraph Infinity software (Thought Technology Ltd., Montreal, Canada). As in other FM theta NFT studies, individual FM theta ($\text{ITP} \pm 1$ Hz) determined from the DMTS task and the learning phase of the source memory task in the pretraining session was used for theta NFT of the training group (cf. Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014). As can be seen in Figure 1, each of the seven neurofeedback training sessions consisted of six 5-minute blocks between which participants were able to take self-paced breaks and were asked about the strategy they used in the preceding block. Before and after training blocks a 2-minute fixation cross was presented in order to conduct start and end baselines of resting EEG activity. During NFT, electrophysiological activity was recorded with a 256 Hz sampling rate from an electrode placed at the Fz position (Rozengurt et al., 2016; Rozengurt et al., 2017; J.-R. Wang & Hsieh, 2013) that was referenced and grounded by two

electrodes at the earlobes. Electrode impedances were kept below 5 k Ω . Frequency bands for feedback generation were extracted from raw EEG with an infinite impulse response (IIR) filter and amplitude changes were calculated as the root mean square (RMS) over a sliding window of 256 data points (equals one second) with a 300 ms butterworth buffer. Feedback was presented visually in form of a rollercoaster animation whose speed was controlled by the RMS of the to be trained frequency. Next to the rollercoaster animation, the speed of the rollercoaster was presented with a numerical speed indicator that depicted the percentage of the calculated RMS relative to the RMS value that was associated with the fixed maximum speed. Participants were asked to accelerate the rollercoaster speed for as fast and long as possible. While the training group trained their individual FM theta activity, the active control group received feedback to one of seven 2 Hz bands (10–12 Hz, 12–14 Hz, 14–16 Hz, 16–18 Hz, 18–20 Hz, 20–22 Hz, and 22–24 Hz) that was randomly chosen each session but was never used more than once (see J.-R. Wang & Hsieh, 2013, for a similar procedure). In order to ensure a similar feedback increase between both groups, the maximum speed of the rollercoaster in the control group was adjusted to the rollercoaster speed in the training group. Depending on the amplitude of the randomly chosen frequency band and how advanced the training was, maximal feedback in the control group could be obtained with even smaller amplitudes. Both groups received the same list of strategies on how to speed up the rollercoaster (e.g., mental imagery, arithmetic operations, motor imagery) and were encouraged to find their own strategies within the variable strategy phase (first three sessions) and to use their preferred strategy in the constant strategy phase (remaining four neurofeedback sessions). Two frequency bands (0.5–2 Hz and 43–59 Hz) were extracted in order to detect eye and muscle activity. Whenever an individually set threshold of those frequencies was exceeded, the rollercoaster stopped and an otherwise green light next to it lit up in red, indicating to the participant that there was an artifact. Participants did not know whether they belonged to the training or active control group, but were debriefed after the last posttraining session.

Offline analyses of the NFT data was conducted with Brain Vision Analyzer 2.1 software (Brain Products GmbH, Gilching, Germany). Raw data of training and baseline blocks were filtered with a 0.1–40 Hz bandpass filter (48 dB/oct) and segmented into 1-second intervals. Frequency analysis was performed with a fast Fourier transformation (FFT) with a 10% hamming window and normalization to overall power (1–24 Hz). Results were then averaged over all 1-second intervals for each block and each NFT session and amplitude values of individual theta (ITP \pm 1 Hz), alpha (ITP + 3–5 Hz), and beta (ITP + 7–9 Hz) frequencies were extracted.

3.2.3 Data analysis

NFT effects

Individual FM theta amplitude during NFT was calculated as the percentage increase from the start baseline measurement of the respective session to the mean of the session's training blocks. By using this procedure, inter-individual differences in theta amplitude and differences between sessions due to measurement variability were accounted for. Consequently, training effects were analyzed with a repeated-measures ANOVA with the between-subject factor Group (TG vs. CG) and the within-subject-factor Session (1–7). The same analysis was conducted with individual alpha and beta oscillations in order to investigate the specificity of FM theta NFT (see Gruzelier, 2014b, for review).

Behavioral transfer

Reaction times (RTs) and accuracy in the conditions of the DMTS and Stroop task were used to investigate NFT transfer to proactive and reactive control processes, respectively. First, performance differences between both groups in the post-training sessions were assessed by separate regression analyses with the predictor Group (TG vs. CG) while accounting for pre-training performance. For these analyses, regression coefficients b and t -tests solely for the predictor of interest, namely Group, are reported since pretraining performance was controlled for. Second, the influence of participants' NFT theta change on their pre- to posttraining performance gains were investigated with linear regression analyses. Therefore, participants' individual FM theta amplitude relative to the respective session's start baseline was used. NFT theta change was calculated as the increase from the variable strategy phase to the constant strategy phase of NFT. Participants' performance gain was calculated as the percentage increase from pretraining to the respective posttraining session.

NFT transfer to the OSPAN task, the digit symbol substitution test, and the SAM questionnaire were analyzed in the same manner as transfer to the two cognitive control tasks by computing separate regression analyses with the predictor Group (TG vs. CG) while accounting for pre-training performance. Additionally, the influence of NFT theta change on pre- to posttraining performance change was assessed with linear regression analyses.

EEG characteristics of transfer tasks

Comparable to the analyses of behavioral transfer, multiple regression analyses with the predictor Group (TG vs. CG) while accounting for pre-training activity were

conducted for FM activity during both the DMTS and Stroop task. For the DMTS task, FM theta ERS/ERD in the retention and manipulation condition was investigated for all 500 ms time intervals. For the Stroop task, FM theta ERS/ERD in the congruent, neutral, and incongruent condition was analyzed for all 200 ms time windows. If group differences were significant, the influence of participants' NFT theta change on their pre- to posttest theta change in the respective time window and condition was investigated with additional linear regression analyses. FM theta change was calculated as the percentage change from pre- to the respective posttest. For all analyses, the significance level was set to $\alpha = .05$ and, if not indicated differently, two-tailed results are reported. Whenever necessary, the Greenhouse-Geisser correction was applied and adjusted p -values are given. In order to correct for multiple comparisons of post-hoc tests, the Bonferroni correction method was applied and the adjusted α -level is reported. For all regression analyses, outliers were detected with the Tukey method using three interquartile ranges (Tukey, 1977) and bivariate outliers were calculated and excluded with the Mahalanobis distance method (Mahalanobis, 1936).

3.3 Results

3.3.1 NFT results

As can be seen in Figure 3.2.A, individual FM theta activity differed between training and control group over the seven NFT sessions. Repeated-measures ANOVA revealed a significant main effect of Group ($F(1, 33) = 6.31, p = .017, \eta_p^2 = .16$) and a significant Group by Session interaction ($F(6, 198) = 2.45, p = .026, \eta_p^2 = .07$) with a significant linear interaction contrast ($F(1, 33) = 9.17, p = .005, \eta_p^2 = .22$), indicating that the difference in theta activity between both groups increased linearly over the course of the seven NFT sessions. One-tailed t -tests with a Bonferroni adjusted α -level of .007 revealed that FM theta activity in the training group was higher than in the control group in the fourth ($t(33) = 2.60, p = .007, d = 0.87$) and sixth session ($t(33) = 3.16, p = .002, d = 1.06$) of NFT. FM theta activity of both groups did not differ in the first three sessions (all p -values $> .117$) as well as in the fifth ($t(33) = 2.33, p = .013, d = 0.79$) and seventh training session ($t(33) = 2.41, p = .011, d = 0.81$). Repeated-measures ANOVAs investigating participants' individual alpha and beta activity did not reveal any significant main effects or interactions (all p -values $> .063$), suggesting that NFT selectively enhanced FM theta oscillations in the training group (Figure 3.2.B).

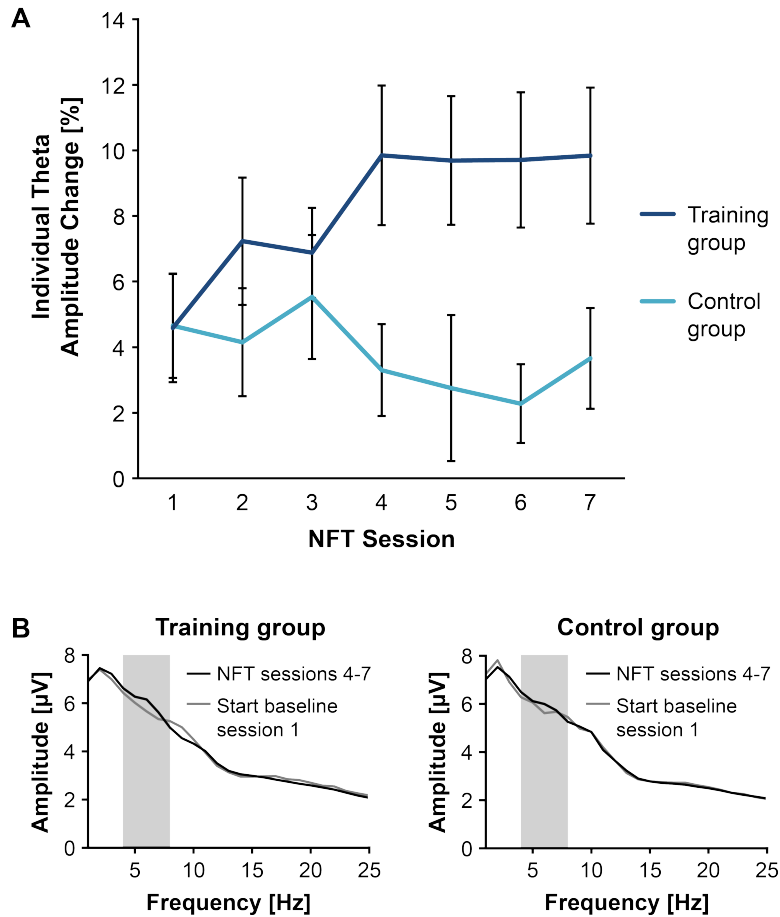


Figure 3.2. Neurofeedback training results for the training and control group. (A) Increase of normalized individual theta amplitude during NFT relative to the resting EEG start baseline of the respective session. Error bars indicate standard error of the group mean. (B) Power spectrum of the first session’s start baseline before any training took place relative to the power spectrum of the constant strategy phase (NFT sessions 4–7), in which participants used their preferred strategy to upregulate their brain activity. Theta activity (4–8 Hz) is marked by a gray bar.

3.3.2 Behavioral transfer

Behavioral transfer effects of NFT to RTs and accuracy in the first and second post-training session of the DMTS and Stroop task were analyzed separately and can be seen in Table 3.1. For the DMTS task, regression analyses of the retention condition revealed that the training group had faster RTs and higher accuracy compared to the control group in the second (RTs: $b = 56.62$, $t(32) = 2.37$, $p = .012$, one-tailed; accuracy: $b = 0.01$, $t(32) = 2.01$, $p = .026$, one-tailed) but not the first posttest (all p -values $> .072$, one-tailed). This indicates that FM theta NFT led to increased performance in the retention condition, in which participants had to simply maintain the position of one stimulus square and thus needed only a low level of cognitive control (Figure 3.3). Contrary to our hypotheses, RTs and accuracy in the manipulation condition did not differ between the training and control group in both the first and second posttraining

Table 3.1. Behavioral results of the DMTS and Stroop task.

| Task | Condition | Pretest | | Posttest 1 | | Posttest 2 | |
|----------------------------|--------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| | | TG | CG | TG | CG | TG | CG |
| <i>Reaction Times [ms]</i> | | | | | | | |
| DMTS | Retention | 674 (33) | 611 (25) | 597 (26) | 583 (24) | 547 (21) | 575 (20) |
| | Manipulation | 1089 (44) | 1032 (40) | 990 (44) | 975 (30) | 953 (46) | 946 (27) |
| Stroop | Congruent | 577 (13) | 587 (15) | 547 (14) | 565 (12) | 552 (12) | 560 (11) |
| | Neutral | 594 (13) | 594 (15) | 562 (15) | 577 (13) | 566 (14) | 573 (12) |
| | Incongruent | 619 (16) | 622 (15) | 586 (16) | 605 (15) | 585 (15) | 594 (13) |
| <i>Accuracy [%]</i> | | | | | | | |
| DMTS | Retention | 97.23 (0.75) | 97.38 (0.61) | 98.57 (0.46) | 97.62 (0.55) | 98.74 (0.40) | 97.70 (0.53) |
| | Manipulation | 70.17 (2.14) | 72.54 (1.75) | 76.72 (1.54) | 77.62 (1.69) | 78.40 (1.61) | 78.57 (1.08) |
| Stroop | Congruent | 94.12 (1.02) | 93.40 (1.14) | 95.50 (0.87) | 94.79 (0.84) | 94.76 (1.01) | 95.23 (1.04) |
| | Neutral | 92.19 (1.55) | 92.10 (1.40) | 93.11 (1.68) | 94.79 (1.21) | 93.01 (1.12) | 93.14 (0.97) |
| | Incongruent | 89.06 (1.94) | 87.93 (2.11) | 92.65 (1.40) | 91.23 (1.41) | 90.90 (1.70) | 91.84 (1.30) |

Note. Reaction times and accuracy of all transfer sessions are given separately for the conditions of each task and the training (TG) and control group (CG), respectively. Standard errors of the mean are depicted in parentheses.

session (all p -values $> .242$, one-tailed), indicating that theta NFT had no effect on the more difficult manipulation condition that required more cognitive control involvement in order to mirror and maintain the encoded stimulus.

In order to investigate the influence of NFT on performance enhancement from pre- to posttraining sessions, linear regressions with the predictor NFT theta change were conducted. Interestingly, NFT theta change predicted RT decrease in the retention condition of the second posttest for both the training ($b = 1.44$, $t(15) = 2.64$, $p = .019$) and control group ($b = 1.28$, $t(16) = 2.20$, $p = .043$), explaining 31.7% and 23.2% of the

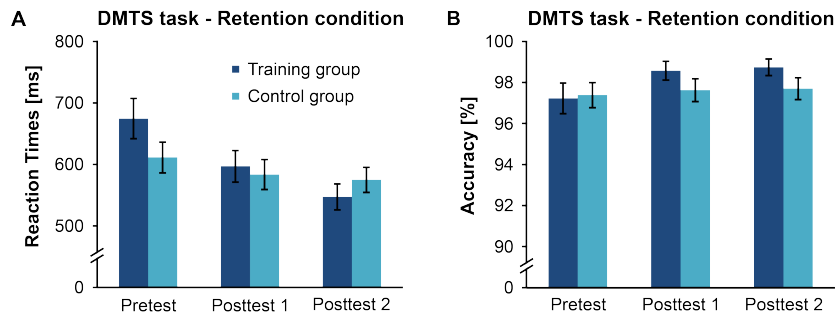


Figure 3.3. Behavioral results of the retention condition of the DMTS task. (A) Reaction times and (B) accuracy in the retention condition at pretest, first posttest, and second posttest are shown separately for training and control group. Error bars indicate standard error of the group mean. The training group showed faster reaction times and better accuracy than the control group in the second posttest, when pretest performance was controlled for.

variance, respectively (Figure 3.4.A). This finding suggests that although performance differences between the training and control group were found in the second posttest, RT decrease due to NFT was not specific for the training group. NFT theta change predicted neither RT changes to the first posttest nor accuracy changes from pretest to both posttests (all p -values $> .062$). Interestingly, linear regression analyses of the manipulation condition showed that performance enhancement from pretraining to the second posttraining session was predicted by NFT theta change for the training group (RTs: $b = 0.98$, $t(15) = 2.40$, $p = .030$; accuracy: $b = 1.60$, $t(15) = 2.34$, $p = .030$), explaining 27.8% and 27.7% of the variance, respectively (RTs: Figure 3.4.B; accuracy: Figure 3.4.C). Performance increase to the first posttraining session was not predicted by NFT theta change (all p -values $> .164$). Additionally, performance change to both posttraining sessions of the control group was also not predicted by NFT theta change (all p -values $> .684$). These results indicate that FM theta NFT predicts performance change of the training group in the more difficult manipulation condition, in which more cognitive control was needed for task performance than in the retention condition, but transfer effects might have been too small to become apparent in the group level analysis.

For the Stroop task, both RTs and accuracy in the congruent, neutral, and incongruent condition did not differ between training and control group in the first and second posttest, when pretraining performance was controlled for (all p -values $> .095$, one-tailed). Moreover, NFT theta change did not predict performance changes in any of the conditions from pretraining to both posttraining sessions for both groups (all p -values $> .164$). This result indicates that theta NFT did not induce any changes in Stroop task performance.

Behavioral transfer to operation span, processing speed, and self-awareness (Table 3.2) were also investigated with multiple regression analyses for investigation of group

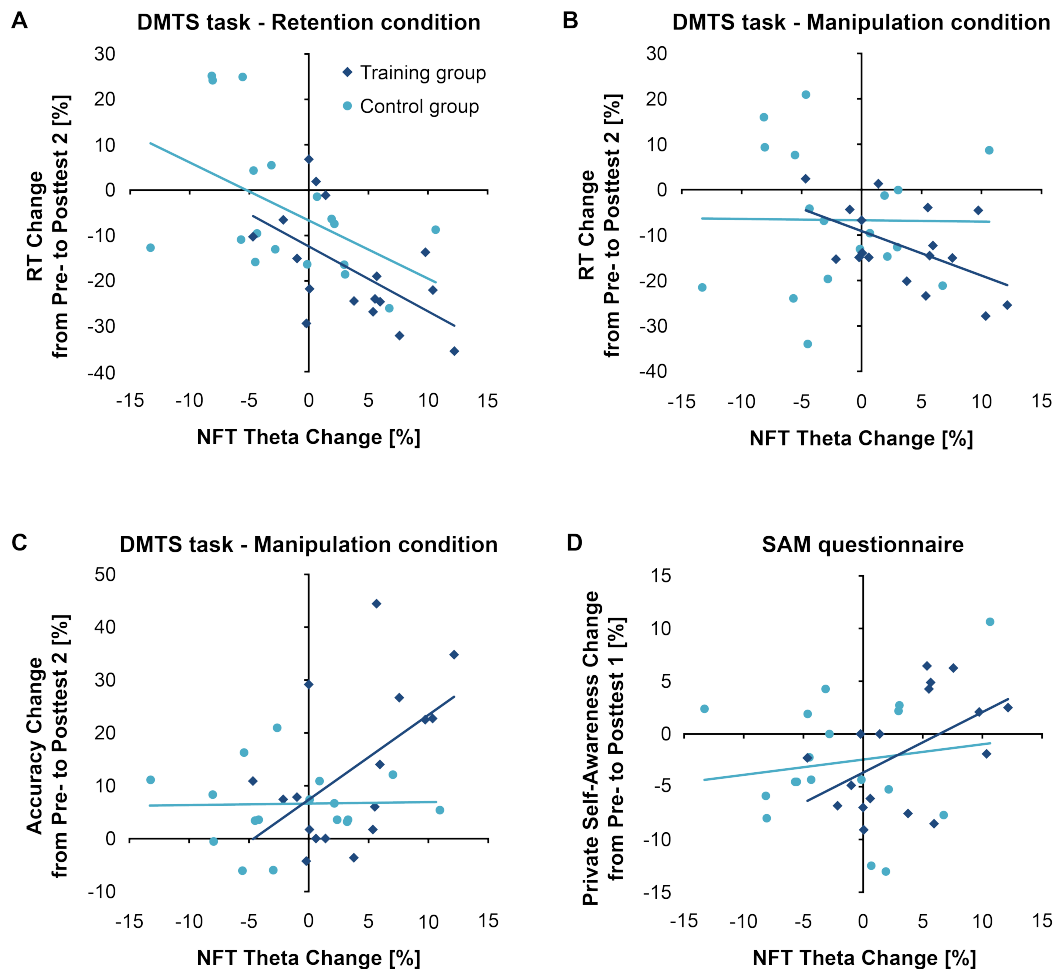


Figure 3.4. NFT effects on behavioral transfer for the training and control group. (A) NFT theta change significantly predicted the reaction time decrease in the retention condition from pre- to the second posttest for both the training and control group. (B) NFT theta change significantly predicted the reaction time decrease in the manipulation condition from pre- to the second posttest for the training but not for the control group. (C) NFT theta change significantly predicted the accuracy increase in the manipulation condition from pre- to the second posttest for the training but not for the control group. (D) NFT theta change significantly predicted the increase in private self-awareness from pre- to the first posttest for the training but not for the control group.

differences and with linear regression analyses for assessment of the influence of NFT theta change on pre- to posttest performance change. In the OSPAN task, group differences in the overall OSPAN score in both the first and second posttest were not significant (all p -values $> .115$). Furthermore, pretraining to posttraining changes were not predicted by NFT theta change (all p -values $> .257$).³ In the digit symbol substitution test, group differences in the test score, that is, the number of correctly added symbols, in both posttests were also not significant (all p -values $> .263$). NFT theta change did also not predict pre- to posttest changes for both groups (all p -values $>$

³ Please note that multiple and linear regressions with other measures from the OSPAN task, such as the total number of correctly recalled letters and the error rate of math calculations, were not significant either (all p -values $> .093$).

Table 3.2. Behavioral results of the OSPAN, digit symbol, and SAM.

| Assessment | Measure | Pretest | | Posttest 1 | | Posttest 2 | |
|--------------|---------|---------|--------|------------|--------|------------|--------|
| | | TG | CG | TG | CG | TG | CG |
| OSPAN | Score | 42.88 | 40.94 | 44.71 | 48.72 | 49.82 | 46.00 |
| | | (4.14) | (3.12) | (2.97) | (3.33) | (3.26) | (3.25) |
| Digit symbol | Score | 70.00 | 66.11 | 77.29 | 73.39 | 82.06 | 77.44 |
| | | (1.77) | (2.42) | (1.60) | (2.36) | (1.79) | (2.02) |
| SAM | Private | 44.29 | 47.39 | 43.47 | 46.00 | 42.88 | 44.56 |
| | | (1.36) | (1.18) | (1.29) | (1.07) | (1.46) | (1.47) |
| | Public | 44.47 | 48.94 | 44.94 | 46.67 | 43.82 | 45.94 |
| | | (1.16) | (1.35) | (1.49) | (1.33) | (1.44) | (1.22) |

Note. Absolute numbers of all performance measures are given separately for the training (TG) and control group (CG) for all transfer sessions. Standard errors of the mean are depicted in parentheses.

.315). These results suggest that FM theta NFT did not influence operation span and processing speed of the training compared to the control group. For the SAM questionnaire, group differences in private and public self-awareness in both posttraining sessions were not significant (all p -values $> .154$). Interestingly, NFT theta change significantly predicted increase in private self-awareness from pretest to the first posttest for the training group ($b = 0.57$, $t(15) = 2.28$, $p = .038$), but not for the control group ($b = 0.15$, $t(16) = 0.57$, $p = .578$), explaining 25.7% and only 2% of the variance, respectively. The more successful participants of the training group were in enhancing their theta amplitude with NFT, the more self-aware they were one day after the last training session (Figure 3.4.D). However, this effect seems to have a short duration since changes in private self-awareness from pre- to the second posttest were not predicted by NFT theta change for both groups (all p -values $> .115$). Pretraining to posttraining changes in public self-awareness were not predicted by NFT change for both groups (all p -values $> .103$), suggesting that FM theta NFT leads to changes in self-awareness of aspects that are only accessible by oneself.

3.3.3 EEG characteristics of the transfer tasks

FM theta ERS/ERD in the transfer tasks of the posttraining sessions was investigated for all poststimulus time intervals of the DMTS and Stroop task. For the DMTS task, regression analyses of retention condition revealed that the training group showed less FM theta ERS in the 1500–2000 ms time interval of the second posttest compared to

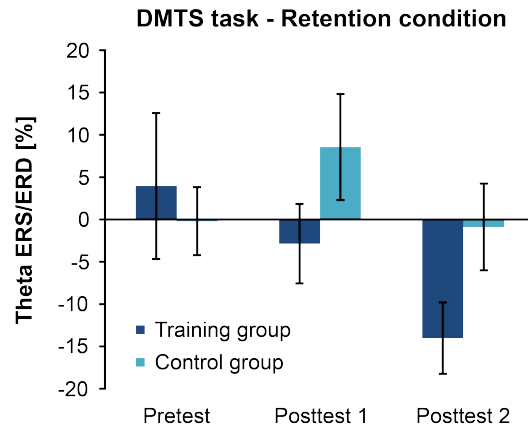


Figure 3.5. EEG characteristics in the retention condition of the DMTS task. FM theta ERS/ERD at electrode Fz in the 1500–2000 ms time interval during the maintenance phase of the retention condition of the DMTS task. EEG activity at pretest, first posttest, and second posttest is depicted separately for the training and control group. At the second posttest, the training group showed significantly less FM theta activity compared to the control group.

the control group ($b = 14.23$, $t(32) = 2.25$, $p = .031$). No such difference was found in any other time intervals of both posttraining sessions or in analyses of the manipulation condition (all p -values $> .100$). Consequently, better performance of the training group in the retention condition was accompanied by less FM theta activity in the late maintenance phase compared to the control group, suggesting that participants of the training group needed less cognitive control reflected in FM theta in order to maintain the stimulus. Interestingly, the largest difference in theta ERS between the retention and manipulation condition has been detected previously in the same 1500–2000 ms time interval (Eschmann et al., 2018). However, further simple linear regressions indicated that NFT theta change did not predict FM theta change from pretraining to the first or second posttraining session in the 1500–2000 ms time interval for both groups (all p -values $> .175$). This finding indicates that the change in FM theta ERS was not induced specifically for the training group by theta NFT.

In line with the behavioral findings of the Stroop task, FM theta ERS in all time intervals of the congruent, neutral, and incongruent condition did not differ between the training and the control group in both posttraining sessions (all p -values $> .160$), suggesting that no changes in theta activity of the Stroop task were present after NFT.

3.4 Discussion

Many studies have shown that cognitive control processes can be enhanced by cognitive training (e.g., see Anguera & Gazzaley, 2015; Karbach & Kray, 2009; Klingberg, 2010; Morrison & Chein, 2010, for reviews), providing evidence for cognitive plasticity of the adult brain (see Lövdén et al., 2010, for review). Based on the overlap hypothesis of

training transfer (Dahlin et al., 2008), it was assumed that direct also modulation of oscillatory characteristics, which were shown to accompany transfer of cognitive training (e.g., Anguera et al., 2013), should transfer to cognitive control processes. Given the prominent role of FM theta oscillations as a correlate of cognitive control processes in a variety of cognitive tasks (see Cavanagh & Frank, 2014; L.-T. Hsieh & Ranganath, 2014; Klimesch et al., 2008; Sauseng et al., 2010, for reviews), individually estimated FM theta amplitudes were trained to be enhanced over seven NFT sessions. Moreover, transfer to different cognitive control tasks, especially a primarily proactive control recruiting DMTS and a mainly reactive control engaging Stroop task, was investigated. In line with other FM theta NFT studies (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014; Reis et al., 2016; Rozengurt et al., 2016; Rozengurt et al., 2017; J.-R. Wang & Hsieh, 2013), the training group successfully enhanced their FM theta activity compared to the active control group, indicated by larger FM theta increases during NFT (Figure 3.2). Interestingly, behavioral transfer of FM theta NFT was observed in the DMTS but not in the Stroop task. Specifically, FM theta upregulation led to better performance in the retention condition of the DMTS task at the second but not the first posttest for the training compared to the control group (Figure 3.3). Furthermore, performance increases from pre- to the second posttest were predicted by FM theta increase for both the training and control group in the retention condition and only for the training group in the manipulation condition of the DMTS task (Figure 3.4). These findings indicate that the more successful participants enhanced their FM theta activity, the greater was the performance increase in the DMTS task from pretest to the second posttest. In contrast, group differences in all conditions of the Stroop task were not significant and pre- to posttest performance changes in the Stroop task were not predicted by FM theta increase during NFT (Table 3.1). These results favor the assumption that FM theta NFT especially supports proactive instead of reactive control processes (cf. Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; see Braver, 2012, for review).

Explanations for the transfer of FM theta NFT to proactive rather than reactive control processes might be derived from different neurofeedback characteristics that were applied in the present study. First, transfer to especially proactive control processes might have been present because FM theta amplitudes for NFT were measured solely at electrode Fz. According to the DMC framework, proactive control processes recruit the lateral prefrontal cortex (IPFC) whereas reactive control processes engage the IPFC and, additionally, a wider neural network (Braver, 2012). Brain imaging studies supported this assumption by providing evidence for sustained IPFC activity

during proactive control and a wider network recruitment during reactive control (e.g., Braver & Cohen, 2001; Veltman et al., 2003; Zysset et al., 2001; see Niendam et al., 2012, for review). In a previous study, we were able to show that enhanced FM theta activity as a function of cognitive control demands differed topographically, depending on whether proactive or reactive control processes were needed for task performance (Eschmann et al., 2018). While FM theta activity was focally activated at frontal sites in a proactive control engaging DMTS task, it had a broader topographical distribution in a reactive control recruiting Stroop task. Consequently, focally distinct upregulation of FM theta activity at frontal sites in the present study might only have transferred to the focal FM theta activation that accompanies proactive control processes. However, other studies demonstrated that FM theta upregulation at electrode Fz correlated with theta increase at distant scalp locations, suggesting that training even with one electrode modulates theta activity at across the scalp (Rozengurt et al., 2016; Rozengurt et al., 2017). Nevertheless, since both proactive and reactive control engage the IPFC, also reactive control might have profited from FM theta NFT but to a lesser extent. Second, FM theta NFT might have particularly supported transfer to proactive control processes because proactive control is needed for successful neurofeedback learning. In order to receive positive feedback during NFT, participants had to regulate their brain activity in the desired direction by exerting top-down control and if they achieved to do so, the altered brain state had to be actively maintained (see Gaume et al., 2016; Ros et al., 2014, for reviews). Moreover, the match and mismatch between inner state and external feedback had to be constantly monitored and probably led to the continuous adaptation of cognitive control over one's brain activity (Ninaus et al., 2013; see Birbaumer et al., 2013; Davelaar, 2018; Gaume et al., 2016; Gruzelier, 2014b; Ros et al., 2014, for reviews). Interestingly, it has been shown that the attempt to receive positive feedback during NFT, even if feedback is invalid, recruits regions of the fronto-parietal cognitive control network (Ninaus et al., 2013). In the present study, both the training and control group had to apply proactive control processes during NFT in order to upregulate their brain activity. Consistently, FM theta change during NFT predicted RT decreases from pretest to the second posttest for both the training and control group, who used the same strategies to upregulate the trained frequency bands. However, while proactive control processes might have been used by both groups, upregulation of FM theta oscillations in the training group might have even further facilitated the control processes that are reflected in FM theta activity, leading to the prediction of manipulation performance increase by NFT theta increase. For instance, sustained FM theta activity has been associated with constant action monitoring (e.g., Cavanagh et al., 2011), which needs to be applied during NFT (Gruzelier, 2014b). Additionally, it has

been proposed that self-regulation, as it might be used for the regulation of brain activity during neurofeedback, engages cognitive control processes (Hofmann et al., 2012). In line with this assumption, NFT theta increase predicted the increase in private self-awareness from pre- to the first posttest for the training but not the control group, indicating that successful theta NFT temporarily increased self-awareness of aspects that are only accessible by oneself, such as feelings, beliefs, or sensations. Hence, the engagement of cognitive control processes that support interoception in order to gain control over one's own brain activity during NFT (Gaume et al., 2016; Ninaus et al., 2013) might be especially pronounced by training of FM theta oscillations.

Based on previous studies demonstrating more pronounced FM theta activity in the manipulation compared to the retention condition in the DMTS task (Berger et al., 2016; Eschmann et al., 2018; Griesmayr et al., 2014), it was expected that theta NFT would especially enhance performance in the manipulation condition. However, performance differences between the training and control group were not significant for the more difficult manipulation condition of the DMTS task (Figure 3.3). In contrast to the retention condition, in which participants had to simply maintain the encoded stimulus, participants had to maintain and additionally mirror the encoded stimulus in the manipulation condition. Thus, successful performance in the manipulation condition probably involved additional WM subprocesses (see Sauseng et al., 2010, for review). Consequently, performance in the manipulation condition might not have been enhanced as much as in the retention condition due to FM theta NFT especially fostering stimulus maintenance. Although non-significant effects have to be interpreted with caution, the non-significant transfer effects for the OSPAN and digit symbol substitution task support this argumentation by suggesting that FM theta NFT did not induce any changes in other cognitive measurements, such as WM operation span or general processing speed (Table 3.2). Nevertheless, NFT theta change significantly predicted the pre- to second posttest performance increase in the manipulation condition for the training but not the control group (Figure 3.4). This finding indicates that participants who successfully enhanced their FM theta activity during training showed greater performance enhancement (i.e., faster RTs and higher accuracy), stressing the importance of taking individual differences in the ability to upregulate FM theta activity into account. Even if individually estimated theta band ranges are trained, about one third or more participants have shown to be non-responsive to NFT (see Alkoby, Abu-Rmileh, Shriki, & Todder, 2018, for review). Interestingly, MCC morphology was shown to predict the success of FM theta NFT (Enriquez-Geppert et al., 2013). It is conceivable that based on individual differences in FM theta upregulation, transfer in the manipulation condition was not present on the group but solely on the individual level.

Analyses of EEG characteristics in the transfer tasks substantiated the behavioral transfer to the retention condition in the DMTS task. At the second posttest, the training group showed less FM theta ERS in the 1500–2000 ms time interval of the retention condition compared to the control group (Figure 3.5). Contrarily, Enriquez-Geppert, Huster, Figge, and Herrmann (2014) found greater FM theta ERS in an *n*-back task for the training relative to the control group after FM theta NFT, which, however, was not accompanied by behavioral performance increases in the same condition. The simultaneous FM theta activity decrease and performance increase after NFT in the present study might be part of a training-induced redistribution of functional activity (see Kelly & Garavan, 2004, for review). Brain imaging studies have shown that performance increases after cognitive training are accompanied by activation decreases in brain regions that are important for attention and cognitive control (Debaere, Wenderoth, Sunaert, Hecke, & Swinnen, 2004; Schneiders et al., 2011; see Kelly & Garavan, 2004, for review). These activation decreases in brain regions such as the ACC were interpreted to reflect less demands on cognitive control processes needed for task performance. Thus, FM theta decrease during the late maintenance phase that was associated with enhanced retention performance in the training group might reflect less demands on cognitive control that is required for stimulus maintenance. Decreases in FM theta activity, hence, might be an indicator of increased task proficiency (see Lindenberger et al., 2017, for review). This interpretation is in line with the understanding of FM theta activity as a general cognitive control mechanism that reflects the need for and implementation of cognitive control in a large variety of tasks (see Cavanagh & Frank, 2014; Helfrich & Knight, 2016; Sauseng et al., 2010, for reviews). Thus, less FM theta activity presumably reflects less need for and recruiting of cognitive control.

In contrast to other FM theta NFT studies, behavioral transfer to proactive control processes and changes of its underlying EEG characteristics were present only 13 days after the last NFT session and not one day after training (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Rozengurt et al., 2016; Rozengurt et al., 2017; J.-R. Wang & Hsieh, 2013), suggesting that transfer effects became apparent late after training took place.⁴ This finding can be interpreted in light of brain plasticity characteristics which show that training-induced behavioral and neurophysiological changes do not neces-

⁴ It is conceivable that non-significant transfer effects were caused by chance performance of some participants during the posttests. In the initial analyses, chance performers were included because it was assumed that both training and control group had an equal chance of showing improved performance after NFT. However, only one participant of the control group showed chance performance in the manipulation condition at the first posttest. When this participant was removed from analyses, the pattern of behavioral results remained the same, that is, no group differences in RTs and accuracy of the manipulation condition at the first posttest (all *p*-values > .575) and no prediction of performance increases from pretest to the first posttest by NFT theta change for the control group were observed (all *p*-values > .762).

sarily increase linearly (see Lindenberger et al., 2017; Lövdén et al., 2010; Wenger, Brozzoli, Lindenberger, & Lövdén, 2017, for reviews). According to the expansion-renormalization model, training induces an initial regional increase of brain volume that is followed by a renormalization due to the selection of the functionally most efficient cortical pathways (Wenger et al., 2017). On the neural level, these changes are reflected in a period of synaptic overproduction that is pursued by a reduction of irrelevant connections, which is referred to as pruning, and a stabilization of functionally relevant synapses (see Hübener & Bonhoeffer, 2014; Lindenberger et al., 2017, for reviews). Expansion and renormalization periods have been shown during training of non-dominant hand writing and drawing by an initial gray matter volume increase of motor cortices during the first four weeks of training that was followed by a volume decrease during the last three weeks of training (Wenger et al., 2016). Since renormalization and, thus, pruning were shown to occur after weeks of training, it is conceivable that in the present study continuous FM theta upregulation led to synaptic overproduction that might still have been present at the first posttest whereas pruning and stabilization of functional activity essentially happened between the first and second posttest. Consequently, increased performance in proactive control and reduction in functional brain activity might have been present only after pruning occurred, that is, at the second posttraining measurement. Based on the expansion-renormalization model, it also seems reasonable that FM theta NFT led to theta increases one day after NFT (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014) whereas FM theta decreases occurred late after training as it was the case in the present study. Future studies might examine the exact mechanisms underlying the functional and structural changes occurring during and especially after NFT that allow for long-lasting cognitive enhancement. Although brain plasticity characteristics might explain why behavioral transfer and changes of underlying EEG dynamics occurred only in the second posttest, it should be noted that a greater statistical power might have revealed transfer effects also in the first posttraining session.

Altogether, the present study is the first to demonstrate transfer effects to a DMTS but not to a Stroop task that were observed 13 days after the last FM theta NFT session. Although these tasks do not allow process-pure measurements, the present findings suggest that FM theta NFT improves proactive rather than reactive control processes and that these training-induced changes become manifest late after training is completed. Behavioral improvements were partially accompanied by decreases in FM theta activity, suggesting less demands on proactive control processes as a function of training. Thus, FM theta NFT may constitute an efficient tool to enhance cognitive control processes in adult participants by inducing plastic changes.

Study 3: Theta Neurofeedback and Memory Control Processes

4.1 Introduction

The adult brain shows remarkable capacity for plasticity evidenced by transfer from working memory (WM) or multi-tasking training to other cognitive control processes (see Anguera & Gazzaley, 2015; Kelly & Garavan, 2004; Lövdén et al., 2010, for reviews). For instance, training gains of multi-tasking training in elderly were shown to be accompanied by an increase of frontal-midline (FM) theta activity (4–8 Hz) that predicted transfer to performance in untrained attention and WM tasks (Anguera et al., 2013). Interestingly, enhancement of FM theta oscillations over several sessions of neurofeedback training (NFT), a form of operant conditioning that allows for training of oscillatory characteristics, resulted in transfer to cognitive control processes, such as task-switching, WM updating, and interference resolution (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; J.-R. Wang & Hsieh, 2013). Although cognitive and neurofeedback training show transfer to cognitive control processes, it remains unclear whether training-induced upregulation of FM theta oscillations also transfers to memory control processes that are required for the coordination of encoding and retrieval in episodic memory.

Theta oscillations have been suggested to play a key role in episodic memory encoding and retrieval on both a representational and a processing level (see Nyhus & Curran, 2010; Sauseng et al., 2010, for reviews). While on the representational level, theta-gamma coupling allows for the formation of memory representations by item-context binding, on the processing level theta phase coherence between frontal and posterior brain regions provides top-down control over memory representations. Support for FM

theta as a top-down control mechanism comes from studies demonstrating enhanced theta activity at both frontal and posterior sites for successful recollection of contextual details (T. Gruber et al., 2008; Guderian & Düzel, 2005; Klimesch et al., 2001). In a similar vein, combined EEG-fMRI measurements could show that recollection-related theta-alpha oscillations are associated with increased connectivity of the hippocampus with the striatum and prefrontal cortex, two areas that have been related to top-down control (Herweg et al., 2016). Interestingly, Addante et al. (2011) showed that FM theta activity preceding a retrieval cue correlated with correct source retrieval, that is, the accurate recollection of contextual details of a prior episode, but not item memory retrieval. Moreover, this frontal prestimulus theta activity correlated with parietal poststimulus theta activity indicative of correct source retrieval, further supporting the view that FM theta oscillations exert top-down control for retrieval of episodic memories (see Klimesch et al., 2008, for review).

Direct modulation of FM theta activity underlying memory control processes offers a tool for investigating their causal relationship. One session of FM theta NFT applied directly after learning was shown to transfer to motor and item memory for up to one week as revealed by better recall of motor sequences and words that were learned before training (Rozengurt et al., 2016; Rozengurt et al., 2017). Even though these studies are interesting in that they suggest that NFT can improve consolidation of memory representations, it is still unclear whether FM theta NFT leads to enhancement of memory control processes that especially support source memory. In order to draw such conclusions about transfer to more general memory control processes, it is necessary to let participants learn and retrieve new information after NFT. Consequently, the present study investigates (1) whether source retrieval for items learned newly after NFT can be improved by enhancing FM theta oscillations via NFT and (2) whether this transfer is not only present one day after NFT, but persists to later learning and retrieval situations. Therefore, participants took part in seven NFT sessions in either an individual FM theta feedback training group or an active control group who trained session-wise randomly chosen frequency bands. Behavioral transfer to source retrieval and its underlying EEG characteristics, measured in an interval preceding the retrieval cue, were investigated in a pre-post design with a posttest one day after the last NFT session and a follow-up measurement 13 days later. As many other training studies we expected a performance increase after training. FM theta enhancement during NFT should lead to better source memory performance at posttests for the training compared to the control group. Furthermore, FM theta increase during NFT should predict source memory performance enhancement from pretest to both posttests. Regarding the EEG characteristics underlying

source retrieval, we expected either increased or decreased prestimulus FM theta activity, implying either increased recruitment or a more efficient use of these processes after NFT.

4.2 Methods

4.2.1 Participants

The sample consisted of the same 36 German volunteers who were recruited from Saarland University's student community and participated in Study 2 that is reported in Chapter 3. Participants were assigned to a training group (TG; $n = 17$, five male, $M_{TG} = 22.65$ years, age range = 20–30 years) and an active control group (CG; $n = 18$, six male, $M_{CG} = 23.33$ years, age range = 19–27 years) that were matched in sex, age, and study subject. One participant of the training group had to be excluded from analyses because of being an outlier in NFT theta increase. Prior to testing, participants conducted an online questionnaire inquiring the following characteristics considered important for recruitment. All recruited participants indicated to enjoy rollercoaster driving with a score > 4 on a 7-point Likert scale and both groups did not differ in their preference for rollercoaster driving ($M_{TG} = 6.11$, $M_{CG} = 6.22$; $t(34) = 0.11$, $p = .710$, $d = 0.12$). According to self-report, participants were healthy, had normal or corrected-to-normal vision, and showed no history of neurological or psychiatric diseases. Moreover, all participants were right-handed as indicated by the Edinburgh Handedness Inventory (Oldfield, 1971). Testing times were scheduled in accordance with each participant's chronotype based on the German version of the Morningness-Eveningness Questionnaire (D-MEQ; Griefahn et al., 2001). Written informed consent was provided prior to the study and participants were paid 8€ per hour in return for their participation. If desired, the payment was partially replaced by course credit. The experimental procedure was approved by the local ethics committee in accordance with the declaration of Helsinki.

4.2.2 Experimental design and data acquisition

Transfer effects from individual FM theta upregulation during NFT to episodic memory performance were assessed in a pre-post design (Figure 4.1). Participants performed an intentional source memory task adapted from Addante et al. (2011) in a pretraining and two posttraining sessions. NFT for both groups took place on seven fixed days between the pre- and posttraining sessions. For all sessions, participants were seated

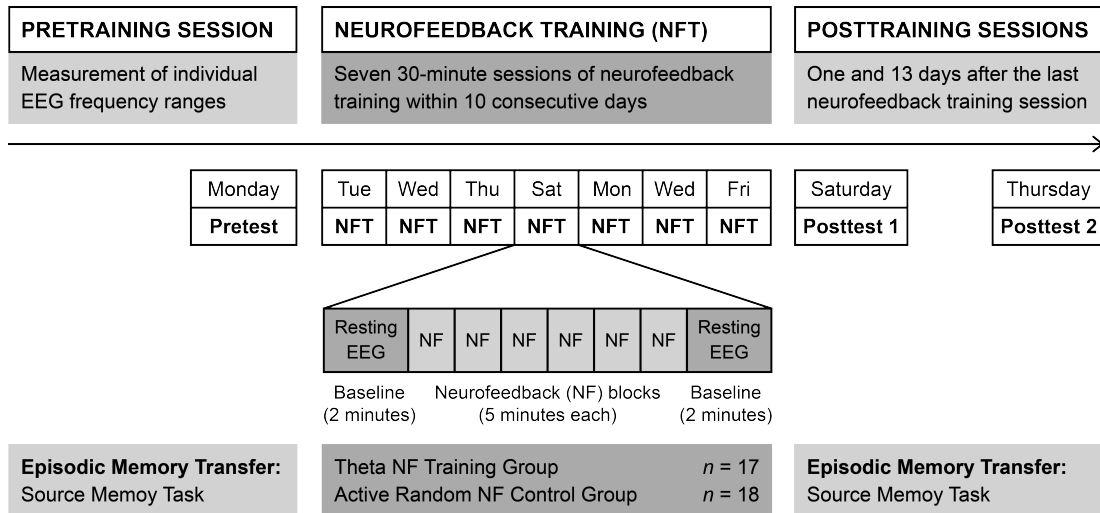


Figure 4.1. Training schedule with source memory transfer. Neurofeedback training consisted of seven neurofeedback sessions and transfer to source memory was investigated from one pre-training to two posttraining sessions. All sessions took place at the same fixed days for each participant.

comfortably in a dimly lit and quiet experimental room and experimental stimuli and NFT were presented on a Dell Computer with a Dell 24-inch monitor placed at a viewing distance of approximately 70 cm.

Source memory task

During encoding, 200 concrete German nouns were presented in four 50-item blocks that were counterbalanced for word length and frequency, using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, USA). Participants were asked to rate the animacy or pleasantness of the stimuli blockwise in an ABBA design. Therefore, the question “lebendig?” (German for “alive?”) or “angenehm?” (German for “pleasant?”) followed a 1000 ms fixation cross and a 1500 ms word presentation. The question remained until participants indicated their yes/no response with their left and right index fingers on the keys “C” and “M” on a conventional keyboard. During the approximately 30-minute retention phase, participants performed a delayed match to sample and a color Stroop task. In the following retrieval phase, the 200 previously learned words were presented intermixed with 100 new words in six blocks with 50 words each. After a 1000 ms fixation cross and a 1500 ms word presentation, participants were asked to indicate their item memory (old or new) on a 5-point Likert scale. If participants indicated the word as being old or rather old, they were subsequently asked to indicate their source memory (animacy or pleasantness) on a 5-point Likert scale. Left and right index and middle fingers were positioned on the number keys “1”, “2”, “4” and “5”. The “don’t know” response on number key “3” was given with the right index finger.

Response to key assignments were counterbalanced across participants but stayed fixed for each participant across all pre- and posttraining sessions.

Pre-/posttraining EEG recordings and processing

During the source memory task of the pre- and posttraining sessions, electroencephalographic (EEG) activity was recorded continuously with a sampling rate of 500 Hz from 32 Ag/AgCl electrodes using a Brain Amp EEG amplifier and Brain Vision Recorder software (Brain Products GmbH, Gilching, Germany). Scalp electrodes were mounted on a fitted cap according to the extended 10–20 system. Four additional electrodes placed at the outer canthi of the eyes and above and below the right eye were used to record the electrooculogram for eye movement detection. During the continuous EEG recording, electrode impedances were kept below 5 k Ω and signals were filtered with an online low-pass filter of 100 Hz. All electrodes were referenced to the left mastoid electrode during data acquisition and re-referenced offline to averaged mastoids.

Offline analysis of EEG signals was performed using Brain Vision Analyzer 2.1 software (Brain Products GmbH, Gilching, Germany). Raw data of both the encoding and retrieval phase was first inspected visually and artifact containing activity was removed manually in order to improve artifact correction by ICA decomposition. Data was then high-pass filtered at 0.5 Hz (48 dB/oct) and low-pass filtered at 40 Hz (48 dB/oct) before being re-referenced to linked mastoids. An infomax ICA was run to identify and remove components representing eye movements, such as blinks and saccades. Afterwards, the continuous EEG from encoding and retrieval was segmented from –1250 ms to 2400 ms around stimulus presentation. A baseline correction in the time domain from –200 ms to 0 ms prior to word presentation was applied as it was done in other time-frequency studies investigating prestimulus activity (e.g., M. J. Gruber et al., 2013). Finally, an automatic artifact rejection was applied with a maximal allowed voltage step of 30 μ V/ms, a maximum-minimum difference of 100 μ V, and an allowed amplitude of \pm 60 μ V. Segments with remaining artifacts were removed by hand. Trials were then divided into (1) correct item and source memory and (2) only correct item memory conditions.

For calculation of frequency power estimates, single trial activity from 1 Hz to 40 Hz was decomposed using a complex Morlet wavelet with 79 linear 0.5 Hz frequency steps and a time-frequency resolution indicated by a parameter c of 6. Prestimulus activity of the retrieval phase was separated in three epochs each, resulting in three 200 ms intervals (–600 to –400 ms, –400 to –200 ms, and –200 to 0 ms). To account for between-subject variability in the dominant theta frequency peak and to align FM theta activity measures during NFT and the transfer task, individual theta activity

was used for analyses. Based on previous findings of FM theta in episodic memory, especially its role for source retrieval (L.-T. Hsieh & Ranganath, 2014), electrode Fz was selected for the analyses of EEG characteristics in the transfer task and also for NFT. The individual FM theta range, which was also used for NFT, was defined as the individual FM theta peak (ITP) \pm 1 Hz and determined between 4 and 8 Hz from EEG activity of the (1) item and source memory correct and (2) only item memory correct condition in the encoding phase and the delayed match to sample task of the pretraining session, conditions which are known to be reliably associated with enhanced theta activity (Friese et al., 2013; Osipova et al., 2006; Sederberg et al., 2003; Summerfield & Mangels, 2005).

NFT protocol and processing

In order to train upregulation of theta activity by NFT, seven 30-minute neurofeedback sessions were conducted with a self-built feedback protocol using ProComp5 Infinity amplifier and BioGraph Infinity software (Thought Technology Ltd., Montreal, Canada). As in other FM theta NFT studies, individual FM theta (ITP \pm 1 Hz) determined from the learning phase of the pretraining session was used for theta NFT of the training group. As can be seen in Figure 4.1, each of the seven neurofeedback training sessions consisted of six 5-minute blocks between which participants were able to take self-paced breaks and were asked about the strategy they used in the preceding block. Before and after training blocks a 2-minute fixation cross was presented in order to conduct start and end baselines of resting EEG activity. During NFT, electrophysiological activity was recorded with a 256 Hz sampling rate from an electrode placed at the Fz position (Rozengurt et al., 2016; Rozengurt et al., 2017; J.-R. Wang & Hsieh, 2013) that was referenced and grounded by two electrodes at the earlobes. Electrode impedances were kept below 5 k Ω . Frequency bands for feedback generation were extracted from raw EEG with an infinite impulse response (IIR) filter and amplitude changes were calculated as the root mean square (RMS) over a sliding window of 256 data points (equals one second) with a 300 ms butterworth buffer. Feedback was presented visually in form of a rollercoaster animation whose speed was controlled by the RMS of the to be trained frequency. Next to the rollercoaster animation, the speed of the rollercoaster was presented with a numerical speed indicator that depicted the percentage of the calculated RMS relative to the RMS value that was associated with the fixed maximum speed. Participants were asked to accelerate the rollercoaster speed for as fast and long as possible. While the training group trained their individual FM theta activity, the active control group received feedback to one of seven 2 Hz bands (10–12 Hz, 12–14 Hz, 14–16 Hz, 16–18 Hz, 18–20 Hz, 20–22 Hz, and 22–24 Hz) that

was randomly chosen each session but was never used more than once (see J.-R. Wang & Hsieh, 2013, for a similar procedure). In order to ensure a similar feedback increase between both groups, the maximum speed of the rollercoaster in the control group was adjusted to the rollercoaster speed in the training group. Depending on the amplitude of the randomly chosen frequency band and how advanced the training was, maximal feedback in the control group could be obtained with even smaller amplitudes. Both groups received the same list of strategies on how to speed up the rollercoaster (e.g., mental imagery, arithmetic operations, motor imagery) and were encouraged to find their own strategies within the variable strategy phase (first three sessions) and to use their preferred strategy in the constant strategy phase (remaining four neurofeedback sessions). Two frequency bands (0.5–2 Hz and 43–59 Hz) were extracted in order to detect eye and muscle activity. Whenever an individually set threshold of those frequencies was exceeded, the rollercoaster stopped and an otherwise green light next to it lit up in red, indicating to the participant that there was an artifact. Participants did not know whether they belonged to the training or active control group, but were debriefed after the last posttraining session.

Offline analyses of the NFT data was conducted with Brain Vision Analyzer 2.1 software (Brain Products GmbH, Gilching, Germany). Raw data of training and baseline blocks were filtered with a 0.1–40 Hz bandpass filter (48 dB/oct) and segmented into 1-second intervals. Frequency analysis was performed with a fast Fourier transformation (FFT) with a 10% hamming window and normalization to overall power (1–24 Hz). Results were then averaged over all 1-second intervals for each block and each NFT session and amplitude values of individual theta (ITP \pm 1 Hz), alpha (ITP + 3–5 Hz), and beta (ITP + 7–9 Hz) frequencies were extracted.

4.2.3 Data analysis

NFT effects

Individual FM theta amplitude during NFT was calculated as the percentage increase from the start baseline measurement of the respective session to the mean of the session's training blocks. By using this procedure, inter-individual differences in theta amplitude and differences between sessions due to measurement variability were accounted for. Consequently, training effects were analyzed with a repeated-measures ANOVA with the between-subject factor Group (TG vs. CG) and the within-subject factor Session (1–7). The same analyses were conducted with individual alpha and beta oscillations in order to investigate the specificity of FM theta NFT.

Behavioral transfer

NFT transfer effects to episodic memory were assessed with item and source memory performance as indicated by Pr scores (hits – false alarms) and the number of correct source judgments in the source memory task. Source memory is commonly calculated as the number of correct source judgments relative to all hits. However, a problem with this relative source memory measure is that it does not control for response bias in the item memory judgments that may differ across participants. Therefore, we also computed an absolute source memory score, that is, the number of correct source judgments relative to all old items, to control for influences of response bias. For reasons of greater transparency both source memory scores will be reported. Behavioral transfer was investigated by two different sets of regression analyses. First, separate multiple regression analyses for both posttests with the predictor Group (TG vs. CG) assessed group differences in posttraining accuracy of the first and second posttest, respectively. To control for possible differences in pretraining performance the predictor of pre-training accuracy was also included. For these analyses, regression coefficients b and t -tests solely for the predictor of interest, namely Group, are reported since pre-training performance was controlled for. Second, the influence of participants' NFT theta change on their pre- to posttraining memory performance gain was investigated with linear regression analyses. Participants' individual FM theta amplitude relative to the respective session's start baseline was used in this analysis. NFT theta change was calculated as the increase from the variable to the constant strategy phase and participants' performance gain was calculated as the percentage increase from pretraining to the respective posttraining session.

EEG characteristics of the transfer tasks

For analyses of the EEG characteristics in the transfer task individual theta activity from electrode Fz was used. First, it was determined whether source memory specific FM theta activity at pretest was present irrespective of group. Therefore, individual FM theta activity in three prestimulus time intervals of the retrieval phase (–600 to –400 ms, –400 to –200 ms, and –200 to 0 ms) was tested with independent sample t -tests. Source memory specific FM theta activity was determined by subtracting the activity of the only item memory correct condition from the item and source memory correct condition (item and source – item only). Second, consistent with the analyses of behavioral transfer, multiple regression analyses with the predictor Group (TG vs. CG) while accounting for pretraining activity were conducted separately for source memory specific FM theta activity in all three prestimulus time intervals of both posttests.

Third, the influence of participants' NFT theta change on their pre- to posttest theta change was investigated with additional linear regression analyses similarly to the analyses of the behavioral transfer data. Therefore, FM theta change was calculated as the percentage change from pre- to the respective posttest. For all analyses, the significance level was set to $\alpha = .05$ and, if not indicated differently, we used two-tailed tests. Whenever necessary, the Greenhouse-Geisser correction was applied and adjusted p -values are provided. In order to correct for multiple comparisons of post-hoc tests, the Bonferroni correction method was applied and adjusted α -levels are given. For all regression analyses, univariate outliers were detected with the Tukey method using three interquartile ranges (Tukey, 1977) and bivariate outliers were calculated and excluded with the Mahalanobis distance method (Mahalanobis, 1936).

4.3 Results

4.3.1 NFT results

As depicted in Figure 3.2.A, individual FM theta activity differed between training and control group over the seven NFT sessions (cf. Section 3.3.1). Repeated-measures ANOVA revealed a significant main effect of Group ($F(1, 33) = 6.31, p = .017, \eta_p^2 = .16$) and a significant Group by Session interaction ($F(6, 198) = 2.45, p = .026, \eta_p^2 = .07$) with a significant linear interaction contrast ($F(1, 33) = 9.17, p = .005, \eta_p^2 = .22$), indicating that the difference in theta activity between both groups increased linearly over the course of the seven NFT sessions. One-tailed t -tests with a Bonferroni adjusted α -level of .007 revealed that FM theta activity in the training group was higher than in the control group in the fourth ($t(33) = 2.60, p = .007, d = 0.87$) and sixth session ($t(33) = 3.16, p = .002, d = 1.06$) of NFT. FM theta activity of both groups did not differ in the first three sessions (all p -values $> .117$) as well as in the fifth ($t(33) = 2.33, p = .013, d = 0.79$) and seventh training session ($t(33) = 2.41, p = .011, d = 0.81$). Repeated-measures ANOVAs investigating participants' individual alpha and beta activity did not reveal any significant main effects or interactions (all p -values $> .063$), suggesting that NFT selectively enhanced FM theta oscillations in the training group (Figure 3.2.B).

4.3.2 Behavioral transfer

Behavioral transfer effects from NFT training were investigated for the first and second posttraining session separately while controlling for pretraining performance (Table 4.1 and Figure 4.2). Item memory was not significantly better for the training compared

Table 4.1. Behavioral results of the source memory task.

| Memory | Measure | Pretest | | Posttest 1 | | Posttest 2 | |
|-----------------|--------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| | | TG | CG | TG | CG | TG | CG |
| Item | Pr score | .69 (.03) | .69 (.03) | .72 (.03) | .68 (.03) | .71 (.04) | .66 (.03) |
| Relative source | Accuracy [%] | 68.29 (3.67) | 71.54 (2.69) | 74.85 (3.56) | 74.42 (2.53) | 77.35 (3.48) | 74.37 (2.21) |
| Absolute source | Accuracy [%] | 56.24 (3.88) | 58.36 (2.68) | 62.56 (4.16) | 58.67 (2.99) | 64.79 (4.29) | 58.33 (3.17) |

Note. Pr score (hits – false alarms) for item memory and accuracy for relative and absolute source memory are given separately for the training (TG) and control group (CG). Standard errors of the group means are depicted in parentheses

to the control group in the first ($b = 0.02$, $t(32) = 1.42$, $p = .082$, one-tailed) and second posttest ($b = 0.03$, $t(32) = 1.65$, $p = .055$, one-tailed), indicating that theta NFT did not induce a significantly greater increase in item memory performance in the training compared to the control group. In contrast, although absolute source memory performance did not differ between groups in the first posttest ($b = 0.03$, $t(32) = 1.46$, $p = .077$, one-tailed), performance of the training group was significantly better in the second posttest ($b = 0.04$, $t(32) = 1.81$, $p = .040$, one-tailed) conducted 13 days after the last NFT session. This finding demonstrates that the training group gave 4% more correct source memory responses in the second posttest compared to the control group, when pretest performance was controlled for. Results for relative source memory were not significant (all p -values $> .093$, one-tailed). These results indicate that theta NFT specifically enhanced source memory performance for the training compared to the active control group.⁵

Further linear regressions supported this claim by showing that NFT theta change predicted the gain in relative source memory performance from pretraining to the first ($b = 2.22$, $t(15) = 2.21$, $p = .043$) and second posttraining session for the training

⁵ Participants with chance performance at posttests were included in the initial analyses because we assumed that participants in both groups had an equal chance to show improved source memory performance after NFT. When these chance performers (three in the training and one in the control group) were removed, relative and absolute source memory performance was better for the training ($n = 14$) compared to the control group ($n = 17$) at both posttests. For relative source memory, the training group had better performance than the control group in the first ($b = 0.04$, $t(28) = 1.75$, $p = .045$, one-tailed) and second posttest ($b = 0.07$, $t(28) = 2.83$, $p = .004$, one-tailed). Similarly, the training group showed better absolute source memory performance in the first ($b = 0.06$, $t(28) = 1.94$, $p = .031$, one-tailed) and second posttest ($b = 0.11$, $t(28) = 2.89$, $p = .004$, one-tailed). This suggests that differential findings for relative and absolute source memory in the initial analyses are not due to a qualitative difference of those measures but are rather caused by the inclusion of chance performance.

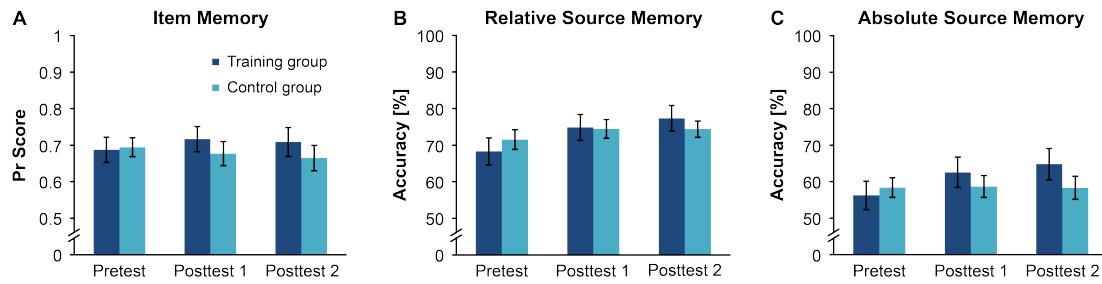


Figure 4.2. Behavioral results of (A) item memory, (B) relative source memory, and (C) absolute source memory for pretest and the two posttests split for training and control group. Error bars indicate standard error of the group means. The training group showed better absolute source memory performance than the control group in the second posttest.

group ($b = 2.88$, $t(15) = 2.57$, $p = .021$) with NFT theta change explaining 24.5% of the variance in performance gain to the first posttest and 30.6% to the second posttest, respectively (Figure 4.3). As expected, the control group did not show a significant relationship of NFT theta change and memory accuracy gain from pre- to both posttraining sessions (all p -values $> .216$). Absolute source memory performance gains for both groups from pretraining to both posttraining sessions were not predicted by NFT theta change (all p -values $> .054$) as were item memory performance gains (all p -values $> .104$).⁶

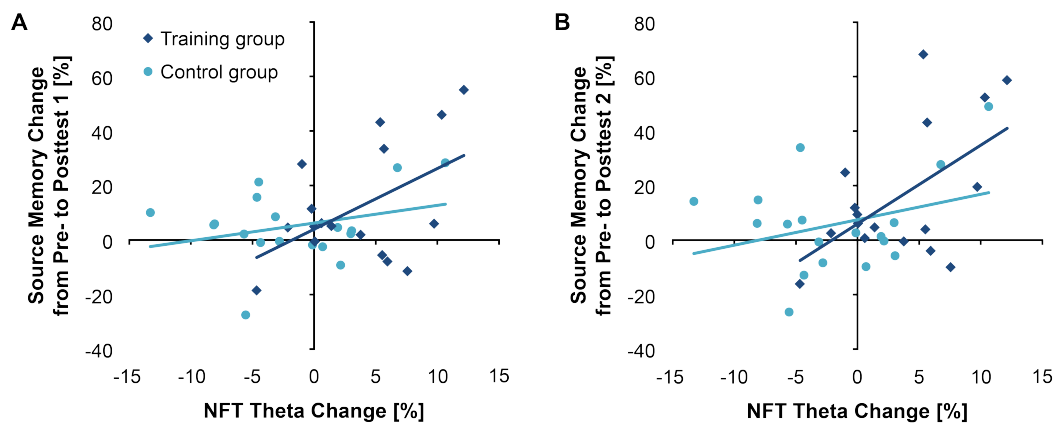


Figure 4.3. NFT effects on source memory transfer for the training and control group. NFT theta change significantly predicted the change of relative source memory from pretest to (A) the first and (B) the second posttest for the training but not for the control group.

⁶ Even though between group differences in item memory at both posttests and linear regressions with NFT theta gain as predictor were not significant when performance was measured by Pr scores, it could still be the case that analyses with either hit or false alarm rates may have revealed significant results. However, the same pattern of results was found when hits and false alarms were analyzed separately with no significant group differences at both posttests (all p -values $> .058$, one-tailed) and no significant prediction of pre- to posttest changes by NFT theta change for both groups (all p -values $> .177$).

4.3.3 EEG characteristics of the transfer task

Using a priori t -tests we explored whether prestimulus FM theta activity was present irrespective of group during pretest. These t -tests revealed that source memory specific FM theta activity was significantly larger than zero in the -400 to -200 ms ($t(34) = 1.73$, $p = .046$, $d = 0.29$, one-tailed) and -200 to 0 ms prestimulus interval ($t(34) = 1.74$, $p = .046$, $d = 0.29$, one-tailed), but not during the -600 to -400 ms prestimulus interval ($t(34) = 1.28$, $p = .104$, $d = 0.22$, one-tailed; Figure 4.4).⁷ In a next step, group differences in source memory specific FM theta activity in all three prestimulus time intervals of the retrieval phase at both posttests (-600 to -400 ms, -400 to -200 ms, and -200 to 0 ms) were analyzed with multiple regression analyses that controlled for pretest activity (Figure 4.5.A). These analyses revealed a non-significant trend of prestimulus theta reduction for the training compared to the control group in the -400 ms to -200 ms time interval of the second posttest ($b = 1.69$, $t(32) = 1.73$, $p = .093$). Group differences in FM theta activity for the other time intervals and all time intervals of the first posttest were not significant (all p -values $> .286$). To minimize the possibility for false positive findings, the influence of NFT theta change on EEG characteristics in the source memory task was investigated in the -400 to -200 ms time interval, in which theta activity has previously been associated with source memory performance (Addante et al., 2011). Therefore, linear regression analyses with the percentage change

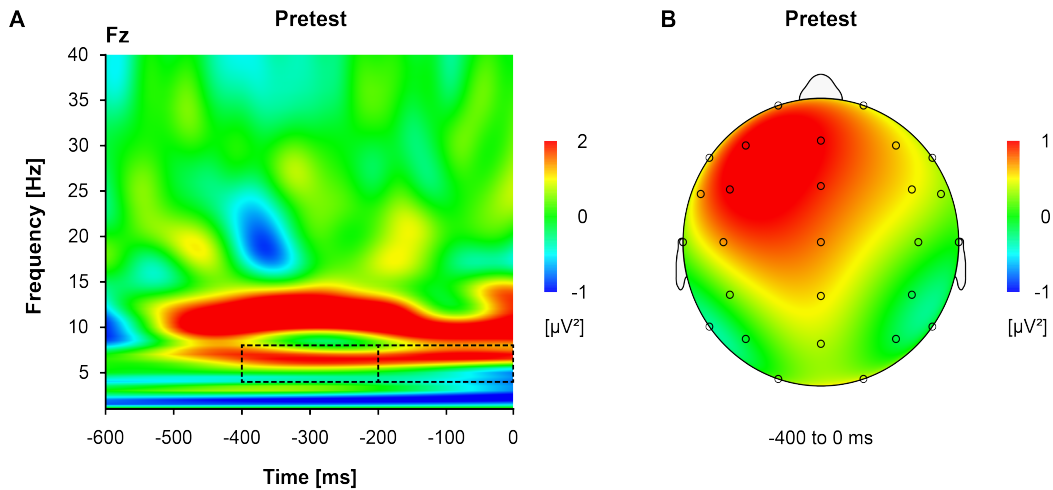


Figure 4.4. EEG characteristics of the source memory task at pretest. (A) Time-frequency plot of source memory specific prestimulus activity during retrieval at electrode Fz averaged over participants of both groups. Time intervals of significant individual theta activity are marked by black dashed squares. (B) Topographical map of source memory specific individual theta power from -400 to 0 ms during retrieval averaged over all participants of both groups.

⁷ Prestimulus FM theta activity has previously been shown to correlate with source retrieval (Addante et al., 2011). This correlation was replicated for both relative and absolute source memory performance with EEG and behavioral data of the present study (Appendix B).

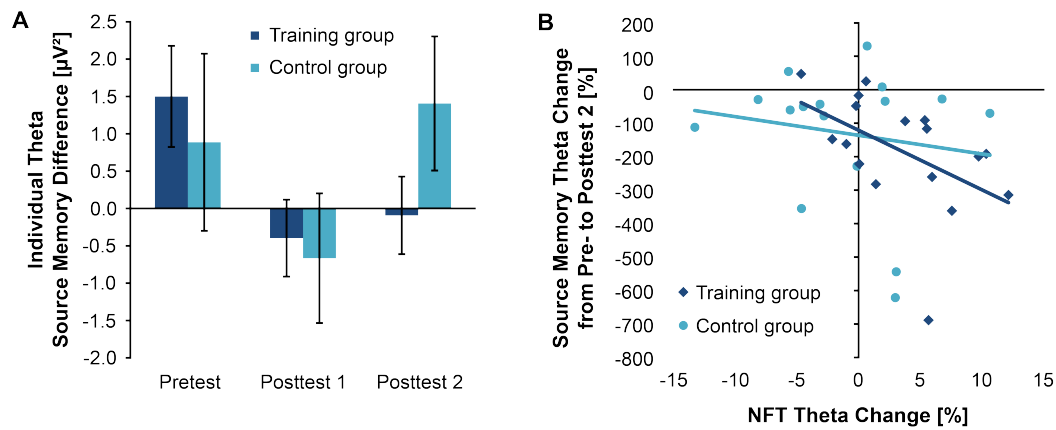


Figure 4.5. NFT effects on EEG characteristics of the source memory task for the training and control group. (A) Source memory specific prestimulus theta power from -400 to -200 ms during retrieval at pretest, first posttest, and second posttest at electrode Fz shown separately for training and control group. Error bars indicate standard error of the group means. The training group tended to show less theta activity than the control group in the second posttest. (B) NFT theta change significantly predicted the change of source memory specific FM theta from -400 to -200 ms during retrieval from pretest to the second posttest for the training but not for the control group.

of theta activity from pre- to the first and second posttest as dependent variables were conducted separately for both groups. As shown in Figure 4.5.B, NFT theta change significantly predicted FM theta change in the -400 to -200 ms time interval from pre- to the second posttest for the training group ($b = 17.80$, $t(15) = 2.16$, $p = .047$), explaining 23.7% of the variance of theta decrease, but not for the control group ($b = 5.57$, $t(14) = 0.60$, $p = .557$). NFT theta change did not predict FM theta change from pre- to the first posttest for both groups (p -values $> .450$). These findings indicate that FM theta NFT induced a decrease in source memory specific FM theta activity during the prestimulus interval of the retrieval phase in the second posttest. Together with the better source retrieval of the training group in the second posttest these results may suggest a more efficient use of memory control processes after training.

4.4 Discussion

Cognitive and neurofeedback training studies have shown transfer to cognitive control processes that are associated with FM theta oscillations (Anguera et al., 2013; Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; J.-R. Wang & Hsieh, 2013). Given that FM theta activity also provides top-down control for episodic memory retrieval (see Klimesch et al., 2008; Nyhus & Curran, 2010; Sauseng et al., 2010, for reviews), especially for source retrieval (Addante et al., 2011), the present study investigated whether FM theta upregulation also transfers to memory control processes. More specifically, we assessed whether FM theta NFT transfers to source memory performance for infor-

mation newly learned after training and its underlying EEG characteristics. Additionally, we explored the time course of this training transfer (Figure 4.1). As expected, seven NFT sessions of individually defined theta band ranges led to FM theta increase compared to an active control group who was matched on all relevant aspects but received feedback for frequency bands that were randomly chosen for each session, adding to a growing body of studies showing that FM theta oscillations can be trained with neurofeedback (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014; Reis et al., 2016; Rozenfurt et al., 2016; Rozenfurt et al., 2017; J.-R. Wang & Hsieh, 2013). Of note, NFT theta changes were not accompanied by changes in neighboring frequency bands, such as individual alpha and beta activity, indicating that oscillatory changes were specific to the trained activity (see Gruzelier, 2014b, for review). Interestingly, theta NFT improved source memory performance at the second posttest as revealed by higher absolute source memory performance of the training compared to the control group (Figure 4.2). Linear regression analyses revealed that the gain in source memory performance from pretest to both posttests was predicted by NFT theta changes for the training but not the control group (Figure 4.3). These results indicate that source memory performance can be improved by enhancing FM theta oscillations with neurofeedback and that the amount of FM theta NFT success predicts the performance benefit. By assessing source memory, the present study extends previous findings of NFT transfer to motor and item memory (Rozenfurt et al., 2016; Rozenfurt et al., 2017). Moreover, as these FM theta NFT studies tested memory for movements and words that were learned before NFT, they solely allow conclusions about the consolidation of already learned information. In contrast, the present study is the first to demonstrate that FM theta upregulation transfers to source retrieval of newly learned information and thereby provides unique evidence that NFT can enhance memory control processes needed for the encoding and retrieval of episodic memories.

Contrary to our expectations, theta NFT showed transfer to source memory performance in the second but not the first posttest, indicating that performance differences between groups were detectable not one but only 13 days after the last NFT session. An explanation for these temporally specific transfer effects can be derived from the characteristics of the applied source memory task. Since participants learned new words and their respective source in every of the pre- and posttraining sessions, the amount of already learned information increased with each of these transfer sessions, leading to greater proactive interference in the second posttest than in preceding sessions. Consequently, NFT transfer effects might only be present when demands on memory control processes are particularly high as in interference situations, suggesting that NFT of FM

theta oscillations help to prevent this interference. An objection against this interpretation would be that memory performance should decrease with increasing interference, which was not the case in the present study. However, repeating task performance may have compensated the deteriorating effects of proactive interference on memory performance. Theta upregulation may have altered three mechanisms that support the protection from proactive interference. First, theta upregulation might have enhanced the adaptation of a neuro-cognitive state that supports retrieval of all memories irrespective of their context, similar to the idea of retrieval mode (Klimesch et al., 2001; Lepage et al., 2000). However, if this would have been the case, item memory performance should have profited from theta NFT to a similar extent. Second, in the present study, binding of items with their source context (animacy or pleasantness) and during later sessions also temporal context (session in which item-source association was learned), was important to achieve good source memory performance. Reinstating aspects of the encoding context, that is, what items were associated with which source in which encoding session, may have been beneficial for correct source retrieval upon presentation of the test cue. In particular in situations, in which the risk for confusing words from different encoding and retrieval phases, that is, different temporal contexts, was high, upregulation of FM theta amplitudes during training might have enabled more precise – especially temporal – context reinstatement which in turn led to a better recollection of the learned item-source associations (see L.-T. Hsieh & Ranganath, 2014; Nyhus & Curran, 2010, for reviews). Third, FM theta upregulation could have supported protection from proactive interference by coordinating inhibition over competing memory representations (K. A. Norman et al., 2005; K. A. Norman et al., 2006). The inhibition account proposes that theta oscillations reflect varying levels of inhibition strength that influence retrieval competition in a way that target representations are strengthened and distractors get suppressed. In the present study, proactive interference occurred mainly due to competition of source and temporal contexts associated with the learned items and, consequently, theta NFT might have protected participants of the training group from this interference by providing greater inhibition of interfering context representations of current and previous sessions. Altogether, behavioral transfer to source memory performance suggests that theta NFT supports protection from proactive interference which might be accomplished by providing more precise context representations.

Analyses of EEG characteristics during pretest revealed the presence of source memory specific prestimulus FM theta activity (Figure 4.4) that has previously been shown to correlate with source memory performance (Addante et al., 2011). The group difference in prestimulus theta activity in the second posttest showed only a trend of

less theta activity for the training group and, thus, has to be interpreted carefully (Figure 4.5.A). Nevertheless, NFT theta change significantly predicted FM theta decrease from pre- to the second posttest for the training but not the control group (Figure 4.5.B). This finding might be surprising since other cognitive training studies examining transfer to cognitive control showed increases in FM theta activity associated with behavioral transfer (Anguera et al., 2013). However, decreased neural activation associated with performance increases after cognitive training are reported frequently in brain imaging studies (Debaere et al., 2004; Schneiders et al., 2011) and are interpreted to be part of a redistribution of functional activity after training (see Kelly & Garavan, 2004, for review). By this view, activation decreases in areas important for attention and cognitive control, such as the anterior cingulate cortex (ACC), reflect less demands on control processes needed for successful task performance. Given that the dorsal ACC, also referred to as midcingulate cortex (MCC), is a source region of FM theta activity (Cavanagh & Frank, 2014), it is conceivable that the simultaneous decrease in theta activity and performance increase in the training group at the second posttest might reflect less demands on memory control processes as a function of NFT.

In the present study, individual NFT theta change predicted both performance and theta change from pre- to posttraining, demonstrating the importance of taking individual differences for the efficiency of NFT into account. Even if individually estimated frequency bands are trained, some participants have shown to be non-responsive to NFT (Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014; Hanslmayr et al., 2005; Weber, Köberl, Frank, & Doppelmayr, 2011), which in the case of FM theta training might be influenced by MCC morphology (Enriquez-Geppert et al., 2013). However, FM theta NFT might be a helpful tool for older participants who show small FM theta amplitudes that are not related to small MCC volume but are associated with cognitive decline (Kardos, Tóth, Boha, File, & Molnár, 2014). Cognitive and NFT studies with older participants have shown that FM theta can be changed with training and is associated with cognitive control transfer (Anguera et al., 2013; Reis et al., 2016; J.-R. Wang & Hsieh, 2013). Given that older participants show a specific associative memory deficit (Naveh-Benjamin, Hussain, Guez, & Bar-On, 2003) and the present study showed transfer to memory control processes important for source memory performance, FM theta NFT might be potentially helpful in improving older adults' associative memory deficit.

In conclusion, the present study is the first that shows transfer from FM theta NFT to source retrieval for information newly learned after training, demonstrating that neurofeedback can be used to improve memory control processes. The present findings suggest that training of individually estimated FM theta oscillations leads to protection

from proactive interference especially in situations with a high risk of memory confusions. Even though the exact mechanisms by which this protection from interference is achieved have to be unveiled, it is not unlikely that training-induced source memory improvements are accomplished by greater precision of context representations. Consequently, individual FM theta NFT constitutes an intervention technique for memory enhancement in young adults with potential relevance for treatment of decline in memory control in old age.

General Discussion

The aim of the present thesis was to investigate whether cognitive and memory control processes can be enhanced by modulating frontal-midline (FM) theta oscillations with the help of neurofeedback training (NFT). By extending the overlap hypothesis of training transfer from neural overlap measured with brain imaging methods to overlap in EEG dynamics (Dahlin et al., 2008), it was assumed that the upregulation of FM theta activity transfers to cognitive and memory control processes. Additionally, the temporal extension of behavioral transfer effects and the changes in EEG dynamics underlying the measured cognitive and memory control processes were of particular interest. In *Study 1*, previous findings of FM theta activity in cognitive control tasks, which were used as transfer tasks for NFT, were validated (cf. Griesmayr et al., 2014; Hanslmayr et al., 2008). Both cognitive control processes occurring before and after cognitively demanding events, namely, proactive and reactive control (Braver, 2012), were accompanied by increased FM theta activity. However, topographies of theta activity differed depending on task requirements. While theta activity was focally activated at frontal sites in a task recruiting proactive control, it had a broader topographical distribution in a task engaging reactive control. These findings indicate that FM theta activity acts functionally different depending on task requirements. In *Study 2* and *3*, seven sessions of NFT resulted in a greater FM theta increase for a training group who trained individual FM theta activity compared to an active control group who trained session-wise randomly chosen frequency bands (cf. J.-R. Wang & Hsieh, 2013). This FM theta NFT showed transfer to proactive control (*Study 2*) and source memory performance (*Study 3*) not one but 13 days after the last training session. Performance enhancement was additionally predicted by the increase of FM theta activity during NFT. These findings suggest that cognitive control transfer might become manifest late after training and that enhancement of memory control processes

possibly improves the protection of memories from proactive interference. Interestingly, training-induced behavioral transfer tended to be accompanied by decreased FM theta activity, suggesting a more efficient use of cognitive and memory control processes after training. The described results of the present thesis extend findings of previous FM theta NFT studies that did not explore transfer to memory control processes as well as the temporal extension of transfer effects, and, moreover, did not find consistent changes of underlying EEG dynamics (e.g., Enriquez-Geppert, Huster, Figge, & Herrmann, 2014).

In the following, the findings of the present thesis will be integrated and discussed with a focus on (1) topographical differences of theta activity underlying cognitive control processes, (2) the trainability of FM theta oscillations by means of NFT, and (3) the training-induced changes of cognitive and memory control processes, that is, behavioral transfer effects, and their underlying EEG characteristics. Therefore, the obtained results will be interpreted comprehensively in the context of theoretical neuro-cognitive frameworks and the current state of research. Subsequently, the limitations of these interpretations and implications for future research will be reconsidered, closing with an overall conclusion.

5.1 Topographical Differences of Theta Oscillations

According to the dual mechanisms of control (DMC) framework by Braver (2012), cognitive control processes can be divided into two modes, namely, proactive and reactive control. In *Study 1*, FM theta oscillations in a delayed match to sample (DMTS) task requiring proactive control and a color Stroop task recruiting reactive control were conducted within the same group of participants. Both tasks contained conditions with low and high cognitive control demands. In line with numerous previous findings (e.g., Jensen & Tesche, 2002; Onton et al., 2005; Roberts et al., 2013), pronounced FM theta activity was found in conditions with high cognitive control demands. These findings support the proposal that FM theta oscillations reflect a general cognitive control mechanism that is engaged in a large variety of tasks (see Cavanagh & Frank, 2014; Sauseng et al., 2010, for review), suggesting that the DMTS and Stroop task are applicable for the use as transfer tasks in an FM theta NFT intervention. Besides, different temporal trajectories for the retention and manipulation condition of the DMTS task were observed. FM theta activity was highest during encoding in the retention condition whereas it was most pronounced during encoding and the maintenance phase in the manipulation condition. Given that in the manipulation condition the presented stimulus had to be encoded and additionally mirrored, cognitive control

demands might have been engaged longer than in the retention condition, in which the stimulus simply had to be encoded. Consequently, FM theta activity might not only reflect cognitive control processes but also the construction of internal memory representations (e.g., Khader et al., 2010; Osipova et al., 2006; Sederberg et al., 2003; see Nyhus & Curran, 2010, for review). Importantly, the DMC framework assumes that proactive control involves the activation of the IPFC whereas reactive control recruits the IPFC and a wider brain network (Braver, 2012). By transferring this assumption to theta activity, it was assumed that although cognitive control recruitment should be reflected in the amplitude of FM theta oscillations, theta topography should differ depending on whether proactive or reactive control is required for task performance. In support of this hypothesis, theta activity, which was derived for each task by taking the difference between conditions with low and high cognitive control demands, was indeed focally activated at frontal sites in the DMTS task whereas it had a broader topographical distribution in the Stroop task. Thus, both proactive and reactive control seem to be reflected in FM theta activity but reactive control is additionally characterized by a broader theta activation. Based on these findings, it was concluded that FM theta oscillations act functionally different depending on task requirements.

Although the results of *Study 1* can be interpreted in line with the DMC framework and related fMRI findings (cf. Section 2.4), it should be noted that the conducted topographical analysis was exploratory in nature. Thus, further research is necessary to draw a direct link between the measured theta topography and the underlying neural networks that are activated during proactive and reactive control, respectively. The distributed theta topography in the Stroop task provides indirect evidence for theta phase coherence between distant brain regions underlying reactive control processes (see Cavanagh & Frank, 2014, for review). In order to substantiate this matter, the identification of a theta network by means of connectivity measures offers a more straightforward methodology. By using connectivity measures of theta activity, it has been shown that different fronto-parietal theta networks are active during proactive and reactive control (Cooper et al., 2015). Moreover, theta activity of the ACC, which is important for conflict detection, and the IPFC, which is involved in providing top-down control, was more synchronous in incongruent compared to congruent Stroop trials (Hanslmayr et al., 2008), indicating increased information transfer between these areas in the condition with high reactive control demand. Although reactive control processes recruit a broader neural network, source localization methods have revealed the dorsal ACC, which is also named the MCC, as the main source region of FM theta activity (e.g., Hanslmayr et al., 2008; Sauseng et al., 2007; see Cavanagh & Frank,

2014, for review). Interestingly, Töllner et al. (2017) revealed two independent but simultaneously measured FM theta activity clusters in a Simon-like task, in which reactive control is recruited in order to inhibit an interfering prepotent response in favor of selecting a correct less prepotent one. The clusters were measured at prefrontal and frontal electrode sites, respectively, and their sources were localized in and near the dorsal ACC. Importantly, only the frontal cluster reflected response conflict and trial-by-trial conflict adaptation. Together with the findings of *Study 1*, this suggests that in order to define a functional role for FM theta oscillations, not only differences between proactive and reactive control should be made but also a distinction between conflict-related and conflict-unrelated processes even within a cognitive control recruiting tasks. With regard to proactive control, the focal theta activity at frontal sites that was detected in the DMTS task might seem contradicting to studies finding topographically more distributed theta activation (Cooper et al., 2015; Cooper et al., 2017). This discrepancy might be explained by differences in the measurement of proactive control. The mentioned studies focused on transient changes of proactive control that was needed for stimulus preparation. This measurement presumably captures a different aspect of proactive control than the sustained proactive control during stimulus maintenance, which was investigated in the DMTS task (cf. Cooper et al., 2015). Nevertheless, these studies and the findings of *Study 1* are in line with the assumption of a fronto-parietal cognitive control network that comprises different sub-networks that are differentially engaged by different types of cognitive control (see Niendam et al., 2012, for review). However, the exact neural networks for different aspects of cognitive control, for example, sustained proactive control, remain to be further elaborated.

Based on the topographical differences of theta activity underlying proactive and reactive control processes, implications for the enhancement of cognitive control processes by means of NFT might be derived. If reactive control is reflected in a broader topographical theta distribution compared to proactive control, NFT of theta activity measured at locally distributed scalp sites should lead to an enhancement of reactive control. In contrast, enhancement of FM theta activity measured focally at frontal sites should support proactive control recruitment. FM theta NFT studies that investigated transfer to cognitive control processes measured theta activity either solely at electrode Fz (e.g., J.-R. Wang & Hsieh, 2013) or at several electrodes located closely to each other over frontal sites (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014). Interestingly, these studies and the findings of *Study 2*, in which feedback was derived from electrode Fz, suggest that both single and several electrode measurements for FM theta NFT support rather proactive than reactive control processes. Thus, in order to

result in transfer to reactive control, more distributed EEG measurement sites during NFT might be necessary (cf. Rogala et al., 2016). A finding speaking against this interpretation is the strong correlation between theta activity at electrode Fz, at which theta activity was measured for NFT, and more distal scalp sites during NFT (Rozenfurt et al., 2016; Rozenfurt et al., 2017). If FM theta NFT modulates theta activity measured at distant scalp sites, there might be no need for topographically distributed EEG measurements during NFT. Another possibility to promote transfer to reactive control would be the usage of theta phase coherence measures as feedback for training. However, coherence measures are used rarely for NFT (e.g., Mottaz et al., 2015) and have the disadvantage that both increases in the desired brain activity as well as in measurement noise can lead to an increase in coherence measures between recording sites, possibly leading to detrimental learning effects. All in all, the differences in theta topography underlying proactive and reactive control that were found in *Study 1* give insight into the neural dynamics that accompany cognitive control processes and might be helpful for the choice of measurement characteristics in order to enhance these processes with the help of neurofeedback.

5.2 Trainability of Frontal-midline Theta Oscillations

In the present thesis the method of neurofeedback was used for the training of EEG dynamics underlying cognitive and memory control processes. Therefore, a NFT intervention consisting of seven 30-minute NFT sessions was applied within ten consecutive days to a training and an active control group (see *Study 2* and *3* for details). During NFT, the training group received feedback to their FM theta amplitudes whereas the active control group trained different frequency bands that were randomly chosen for each session (see J.-R. Wang & Hsieh, 2013, for a similar procedure). Since it has been shown that frequency measurements demonstrate high inter-individual variability but intra-individual stability (Meltzer et al., 2007; Näpflin et al., 2008), FM theta frequency bands for NFT of the training group were estimated individually based on the EEG signal recorded in the DMTS and source memory tasks of the pretest (see Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014, for a similar procedure). As expected, the training group showed a larger FM theta increase over the course of training compared to the active control group, suggesting that participants of the training group were able to successfully enhance their FM theta activity. Importantly, no other frequency bands, such as individual alpha and beta activity, were modulated by NFT, assuring the specificity of the neurofeedback intervention (Gruzelier, 2014b).

The FM theta NFT effect can be interpreted in context of the theoretical framework of adult cognitive plasticity (Lövdén et al., 2010). According to this model, training-induced plastic changes only occur if a prolonged supply-demand mismatch is present throughout the training. Thereby, an increased environmental demand that exceeds the functional supply of the cognitive system leads to the manifestation of plasticity. During NFT, this supply-demand mismatch might consist of the mismatch between externally provided information, that is, the feedback conveying information about the current state of the measured brain activity, and the perceived internal state (Ninaus et al., 2013). It has been shown that even the attempt to control pseudo-feedback during neurofeedback activates brain areas of the fronto-parietal cognitive control network (Dosenbach et al., 2008; Ninaus et al., 2013). Accordingly, cognitive control is thought to be applied continuously in order to regulate brain activity in a way that the mismatch is reduced (cf. Hofmann et al., 2012). If valid feedback is provided, progressively less cognitive control should be necessary over the course of NFT since the desired oscillatory brain state should be achieved more and more easily due to learned self-regulation. In contrast, cognitive control is probably applied throughout the whole training to a similar degree if feedback is not genuine and, thus, the mismatch cannot be resolved (Ninaus et al., 2013). Considering that FM theta activity is thought to be a general neural mechanism for cognitive control (see Cavanagh & Frank, 2014, for review), it is conceivable that the enhancement of FM theta activity measured during NFT reflects not only the volitionally controlled change of FM theta activity but also the recruitment of control processes that are needed for dissolving the mismatch between external feedback and perceived internal state. In the present NFT, FM theta activity, which reflected cognitive control recruitment, might have become smaller with progressively resolved mismatch the further the training proceeded, making it more difficult for participants of the training group to further increase their FM theta amplitudes purposely during later NFT sessions. This may explain why, despite a linearly increasing difference between training and control group in FM theta activity over NFT sessions (interaction contrast), NFT theta increase of the training group remained relatively stable over the last four sessions (cf. Section 3.3.1). Similarly to the training group, the active control group needed to apply cognitive control processes for NFT, which probably also modulated their non-normalized FM theta activity during training (cf. Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014). According to Gruzelier (2014b), increase of theta activity during FM theta NFT reflects learning, self-regulation, attention, and particularly action monitoring. Since these factors should be similar for both training and control group, comparing their increase in FM theta activity should disentangle to what extent participants of the

training group were able to actively upregulate their FM theta activity.⁸ Important for this inference is that the active control group was provided with the same strategies for brain activity modulation as the training group (e.g., mental imagery, arithmetic operations, motor imagery). In other FM theta NFT studies, participants of the training and control group received different strategy instructions, making it impossible to infer training and transfer effects exclusively to differences in brain activity changes (Rozenfurt et al., 2016; Rozenfurt et al., 2017). Thus, the active control group in *Study 2* and *3* can be considered a quite conservative comparison since the provided strategies aimed at enhancing FM theta oscillations. In order to further explore the influence that cognitive control processes during NFT have on FM theta activity measured during training and also on transfer effects, the comparison to a passive control group would be desirable in future studies (see Rozenfurt et al., 2017, for the application of a movie viewing control group). Altogether, FM theta increase of the training group most likely reflected not only cognitive control recruitment but volitionally changes of brain activity. Moreover, several factors of the NFT design and individual characteristics might have influenced NFT success of the present neurofeedback intervention.

5.2.1 Neurofeedback Training Characteristics

Beside the already mentioned NFT characteristics, such as the choice of measurement sites and feedback feature (e.g., amplitude or coherence), other training aspects influence training success and, thus, transfer outcome. For instance, the number, length, and distribution of training sessions affect the magnitude of brain activity modulation. However, optimal neurofeedback protocols, especially for FM theta NFT, have not been determined yet (Gruzelier, 2014b) and clinical research suggests that they crucially depend on the learning abilities of the individual (see Strehl, 2014, for review). Consequently, FM theta NFT in the present thesis was designed on the basis of the few FM theta NFT studies that showed transfer to different cognitive control processes, such as task-switching, WM updating, and interference resolution (Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014; J.-R. Wang & Hsieh, 2013). According to the observed NFT effect in the present thesis, a training of seven NFT sessions with one or two days between training sessions can be assumed to be effective for theta upregulation.

Another design-related issue regarding training with neurofeedback methods concerns whether the modulated brain activity is task-specific. Neurofeedback, which is

⁸ Please note that for analysis of the NFT effect, FM theta activity normalized to the overall power was used. This probably reduced the measured FM theta increase of the control group as participants upregulated frequency bands that were part of the overall power. Nevertheless, the proposed rationale remains the same.

used for cognitive enhancement in healthy participants, aims at inducing transfer to cognitive control abilities that are accompanied by the trained brain activity. Importantly, major differences between resting-state and task-related EEG activity exist. For example, cognitive and memory performance are associated with theta increases and alpha decreases during task-related EEG measurements whereas efficient cognitive processing is assumed to be reflected by theta decreases and alpha increases during resting-state EEG measurements (Doppelmayr, Klimesch, Schwaiger, et al., 1998; Klimesch, 1999). Interestingly, these differences are only detectable if fixed frequency bands are abandoned and individually frequency bands are measured (Klimesch, 1999). Thus, neurofeedback, which involves the upregulation of FM theta activity, is required to feed back task-specific EEG activity, which is ideally estimated individually, in order to induce transfer effects. Previously, Vernon (2005) suggested that task-specific EEG activity can only be trained if neurofeedback is applied during task performance, which, however, is difficult to operationalize practically. A different approach uses EEG activity derived from the transfer tasks for NFT (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014; see Gruzelier, 2014b, for review). This method has the advantage that it allows not only for the definition of task-specific EEG activity, but also for the extraction of individually estimated frequency bands. By applying this approach, the participants of the present thesis presumably regulated task-specific FM theta activity during NFT. Furthermore, it might be argued that the strategies that were provided for theta upregulation contained aspects of cognitive control, making it more likely that EEG activity, which was similar to the transfer tasks, was learned to be regulated by the participants during NFT. In *Study 1*, it was shown that significant differences in FM theta activity due to enhanced cognitive demands were present at electrode Fz for both the DMTS and Stroop task – although with different topographies. On the basis of this finding, individually estimated theta frequency bands at electrode Fz were trained in *Study 2* and *3* in order to enhance cognitive and memory control processes. Interestingly, although training was successful, transfer to the DMTS and source memory task, but not to the Stroop task was observed, indicating transfer to proactive but not reactive control processes. In line with the assumption that FM theta activity during NFT reflects particularly action monitoring (Gruzelier, 2014b), this finding might suggest that especially proactive control processes are needed during NFT and are even further enhanced by FM theta NFT. Alternatively, FM theta NFT training at electrode Fz might not have fully represented the broad theta topography of reactive control in the Stroop task. Given that differences in theta topography might account for this finding, future studies should consider this aspect for determining task-specific EEG activity for NFT.

5.2.2 Individual Differences in Neurofeedback Training

Previous neurofeedback literature has emphasized the role of individual differences in neurofeedback learning (see Gruzelier, 2014b; Strehl, 2014, for reviews). Interestingly, it has been shown that about one third or even more participants in NFT studies are not able to learn the self-regulation of their brain activity, fostering a debate about the causes of this inability (e.g., Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Hanslmayr et al., 2005; Zoefel et al., 2011; see Alkoby et al., 2018; Weber et al., 2011, for reviews). Unfortunately, these so-called responders and non-responders were identified on the basis of heterogeneous NFT learning indices, making it difficult to compare the characteristics of non-responders across studies (see Alkoby et al., 2018; Gruzelier, 2014a, for reviews). Nevertheless, several psychological and neurophysiological characteristics have been suggested to influence training success. For instance, entertaining and individualized feedback was suggested to positively influence participants' motivation and ability to learn the self-regulation of their brain activity (Alkoby et al., 2018; Strehl, 2014). In *Study 2* and *3*, susceptible factors that influence the motivation of participants were tried to be controlled by including solely participants who liked rollercoaster driving and fitting feedback of the control group to the power of the randomly chosen frequency band in order to make feedback between the groups more comparable. Moreover, participants were supported to find their preferable strategy for NFT and were tested at approximately the same time of day. Most importantly, the training group trained individually estimated frequency bands. Although all these factors should increase the likelihood of successful neurofeedback learning, it cannot be excluded that non-responders were also participating in the present neurofeedback intervention. Nevertheless, a NFT effect was still detected. Neurophysiological characteristics that are assumed to predict NFT success include the resting-state EEG amplitude of the trained frequency (e.g., Wan, Nan, Vai, & Rosa, 2014), the initial training success (e.g., Neumann, 2003), and the volume of brain regions that are activated during NFT (e.g., Halder et al., 2013). For example, Enriquez-Geppert et al. (2013) could show that the MCC morphology of participants predicted their training success in a FM theta NFT. Furthermore, other studies demonstrated that the volume of brain areas needed for cognitive control is associated with NFT success of different frequency bands (Halder et al., 2013; Ninaus et al., 2015), indicating that these brain regions influence the general ability of participants to learn the self-regulation of brain activity. Future studies might investigate whether this influence is completely deterministic or whether NFT, even if less successful, can lead to plastic changes in these regions.

In summary, the significant NFT effect reported in *Study 2* and *3* adds to previous research by demonstrating that FM theta activity can be upregulated by means of neurofeedback. NFT theta increase of a training group was compared with the NFT theta increase of an active control group who showed comparable individual characteristics (e.g., preference for rollercoaster driving) and executed the same training design except for the trained frequency band (e.g., provided strategies). By this, it was concluded that the increase of FM theta activity during NFT reflected the learned FM theta modulation and not solely cognitive control processes needed for self-regulation (cf. Ninaus et al., 2013). Moreover, this finding suggests that the training of individualized task-specific EEG activity proves to be applicable for NFT. However, further individual predictors of NFT success might be derived in order to make neurofeedback interventions even more effective.

5.3 Training-induced Changes of Cognitive and Memory Control Processes and Their EEG Characteristics

According to the overlap hypothesis of training transfer, training solely results in transfer effects when trained and transfer task show functional and neural overlap, which both need to change over the course of training (Dahlin et al., 2008; see Buschkuhl et al., 2012; Lustig et al., 2009, for reviews). Based on the overlap hypothesis, it was assumed that transfer to cognitive and memory control processes should be observed if FM theta activity, which is associated with these processes (see Cavanagh & Frank, 2014; Sauseng et al., 2010, for review), is modulated directly by means of neurofeedback. Indeed, successful upregulation of FM theta activity transferred to specific cognitive and memory control processes. In *Study 2*, behavioral transfer was observed mainly in a DMTS task engaging proactive control processes, but not in a Stroop task requiring reactive control processes. Specifically, the training group showed better performance compared to the control group in the retention condition of the DMTS task at the second but not the first posttest. Moreover, performance increases from pre- to the second posttest were predicted by NFT theta change for both groups in the retention condition and for the training but not the control group in the manipulation condition. In contrast, none of the group differences in the Stroop task were significant and pre- to posttest performance changes were not predicted by FM theta increase. These findings are in line with findings of a previous FM theta NFT study, suggesting that FM theta NFT particularly enhances proactive instead of reactive control processes (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014). Interestingly, behavioral transfer in the retention condition of the DMTS task was accompanied by less FM theta

activity for the training compared to the control group in the second posttest, indicating less cognitive control demands after training. An explanation for the transfer to rather proactive control processes might be derived from the characteristics of the applied FM theta NFT (cf. Section 3.4). In line with the DMC framework (Braver, 2012), *Study 1* revealed that proactive control was associated with a focal FM theta activation at frontal scalp sites whereas reactive control seemed to be accompanied by a broader topographical distribution of FM theta topography (Eschmann et al., 2018). Thus, NFT of FM theta activity at electrode Fz might have primarily modulated theta activity underlying proactive control processes. Moreover, as outlined before, successful self-regulation of brain activity in neurofeedback interventions might especially require proactive control processes, such as action-monitoring and maintenance of the desired brain state (Hofmann et al., 2012; Gruzelier, 2014b). Consequently, these processes might have been especially supported by NFT, leading to transfer to the DMTS task.

In *Study 3*, NFT transfer to a source memory task was investigated. In contrast to other NFT studies showing that one session of FM theta NFT transfers to item memory of material that was learned before NFT (Rozengurt et al., 2017), participants of the present study learned new words in every transfer session. This procedure assured that conclusions about the trainability of memory control processes, which especially support source retrieval (Addante et al., 2011), could be drawn. After training, the training group showed better source retrieval relative to the control group in the second but not the first posttest. This finding was interpreted to show that enhancement of memory control processes through NFT seems to improve protection of newly formed memories from proactive interference of information learned at previous sessions. Similar to the findings of *Study 2*, training-induced improvements in source retrieval tended to be accompanied by less source memory specific theta activity. Furthermore, FM theta decrease from pre- to the second posttest was also predicted by NFT theta change for the training but not the control group, suggesting a more efficient use of memory control processes after training. *Study 3* is the first to demonstrate that FM theta NFT can enhance memory control processes that are needed for the retrieval of episodic memories.

Taken together, both studies provide evidence for the transfer of FM theta NFT to proactive rather than reactive control (*Study 2*) as well as memory control processes that especially support source retrieval (*Study 3*). Notably, behavioral transfer effects and their underlying EEG dynamics showed the same temporal characteristics, that is, transfer to the second but not the first posttest, and similar FM theta decreases as a function of training. These findings can be interpreted in the context of different brain

plasticity models and might provide suggestions for the functional role of FM theta oscillations underlying cognitive and memory control processes.

5.3.1 Temporal Characteristics of Transfer and Implications for the Functional Role of Frontal-midline Theta Oscillations

Both behavioral transfer of FM theta NFT and the training-induced changes of underlying FM theta activity were mainly observed in the second posttest, which took place 13 days after the last NFT session, but not as originally expected in the first posttest one day after training. In contrast, other FM theta NFT studies found transfer to different cognitive control processes already one day after the last training session (Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014; Reis et al., 2016; J.-R. Wang & Hsieh, 2013) and transfer to motor and item memory even directly after one NFT session (Rozenfurt et al., 2016; Rozenfurt et al., 2017). The temporally specific transfer findings of *Study 2* and *3* might be explained in line with the expansion-renormalization model (Wenger et al., 2017). It has been shown that training-induced behavioral and underlying neurophysiological changes do not necessarily increase linearly (see Lindenberger et al., 2017; Lövdén et al., 2010; Wenger et al., 2017, for review). According to the expansion-renormalization model, training induces two phases of plastic brain changes. The first initial phase of regional brain volume expansion is followed by a phase of brain volume renormalization. These phases are assumed to be accompanied by underlying neurogenesis, synaptic overproduction and pruning, and changes in number and morphology of glial cells (Zatorre, Fields, & Johansen-Berg, 2012). The latter phase of brain volume renormalization was shown to occur after a few weeks of a motor task training (Wenger et al., 2016). Since the second posttest in the present studies was conducted about three weeks after NFT had started, it is conceivable that FM theta NFT led to brain volume expansion that might still have been present at the first posttest whereas renormalization and stabilization of functional activity essentially happened between the first and second posttest. Thus, behavioral transfer and underlying neural changes became measurable after renormalization occurred. In line with this assumption, it seems reasonable that FM theta NFT led to theta increases one day after NFT (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014) whereas FM theta decreases occurred late after training as it was the case in *Study 2* and *3*. Moreover, other NFT studies might not have been able to find transfer effects because they missed the critical stabilization period by examining only one posttest. Notably, self-regulation of brain activity by means of neurofeedback has been proposed to be akin to skill learning that crucially depends on the subcortical motor system and especially the basal ganglia (see Birbaumer et al., 2013, for review).

Accordingly, the learning of brain activity regulation in any neurofeedback intervention might result in brain volume changes in motor areas similar to motor training studies (see Wenger et al., 2017, for review). In line with this assumption, brain volume of the supplementary motor area, besides other brain regions such as the ACC, was shown to predict NFT success of different frequency bands (e.g., Halder et al., 2013; Ninaus et al., 2015). Future studies might examine the underlying functional and structural changes occurring during and especially after NFT that allow for neurofeedback learning and long-lasting cognitive enhancement, for instance, by acquiring structural brain images over the course of NFT. Importantly, these studies need to differentiate plastic changes, which are caused by neurofeedback learning itself, and training-induced changes, which are based on the active modulation of brain activity.

While the expansion-renormalization model might explain the temporal characteristics of transfer to both cognitive and memory control processes, an alternative explanation for the transfer to source memory performance and its underlying EEG dynamics in the second posttest of *Study 3* can be derived from the characteristics of the source memory task. Learning of new item-source associations in every transfer session might have increased proactive interference progressively with each transfer session, leading to the greatest interference in the second posttest. Thus, transfer of FM theta NFT might only have been present when demands on memory control processes were especially high as in the case of interference situations. Upregulation of FM theta oscillations during NFT might have helped to prevent this interference. Based on the present transfer findings, two functional roles of FM theta oscillations that might have enabled protection from interference seem suitable.

FM theta activity has been assumed to allow for top-down control over episodic memory representations (see Klimesch et al., 2008; Nyhus & Curran, 2010; Sauseng et al., 2010, for review). The specific training-induced enhancement of source but not item memory performance suggests that this top-down control might be realized by reinstatement of contextual details that support upcoming episodic memory retrieval. Additionally to the experimentally required binding of items with their respective source context (animacy or pleasantness), the association with temporal context (session in which item-source association was learned) was important for successful source memory performance in later transfer sessions. FM theta upregulation might have led to a more precise reinstatement of the encoding context particularly in situations in which the risk for confusing items from different temporal contexts was high. This was especially the case in the second posttest, in which encoding and retrieval phases of the two previous sessions could be confused. Supporting this assumption, it has been proposed that the PFC provides temporal context information that guides the upcoming retrieval

of item-context associations (see Polyn & Kahana, 2008, for review). Furthermore, a large body of research has demonstrated the importance of FM theta oscillations for the temporal ordering of items held in WM (e.g., L.-T. Hsieh et al., 2011; Roberts et al., 2013; see Lisman & Jensen, 2013, for review), which can act as an episodic buffer (Jensen & Lisman, 2005) for the encoding and retrieval of episodic memories (e.g., Heusser et al., 2016; see L.-T. Hsieh & Ranganath, 2014, for review). In line with these findings, behavioral transfer to the DMTS task in *Study 2* suggests that the present FM theta NFT also modulated theta oscillations that support temporal ordering of memory representations during WM maintenance. Although performance in the manipulation condition of the DMTS task did not differ between training and control group, NFT theta change predicted performance increase in the manipulation condition, in which several squares had to be mentally mirrored and maintained, for the training but not the control group. FM theta upregulation might have specifically supported the temporal order maintenance of both the encoded square positions and the already mirrored square locations. Consequently, the transfer effects found in *Study 2* and *3* can both be interpreted in line with a functional role of FM theta activity in temporally ordering memory representations in both WM and episodic memory that helps to provide context information for upcoming retrieval in a proactive manner.

Another suggestion for a FM theta mechanism that might have helped to protect episodic memory representations from proactive interference is provided by the inhibition account (K. A. Norman et al., 2005; K. A. Norman et al., 2006). According to this view, theta oscillations reflect varying levels of inhibition strength that influence retrieval competition in a way that target representations are strengthened and competing representations are suppressed. Proactive interference in the source memory task was mainly induced by competition of different source and temporal contexts associated with the encoded items. A more precise coordination of inhibition strength through FM theta upregulation might have led to less interference by weakening competing context representations but probably also by strengthening target item-context associations. In contrast, transfer effects to performance in the DMTS task from *Study 2* are more difficult to reconcile with the inhibition account. It is conceivable that during WM maintenance and comparison with the probe, competing stimulus representations of previous trials needed to be inhibited for successful task performance. FM theta upregulation might have led to a more precise differentiation of task-relevant and competing stimulus representations. However, the DMTS task is rather proactive in nature and NFT transfer was not found in the Stroop task, where interference between competing stimulus-response mappings is much higher than in the DMTS task. Thus, FM theta activity in the DMTS task might better be explained by sequential reactiva-

tion (cf. *Study 1*), suggesting that FM theta NFT rather supported temporal ordering and not the differentiation of competing memory representations.

Altogether, the temporally specific transfer effects of the NFT intervention in the present thesis can be explained on the basis of the expansion-renormalization model (Wenger et al., 2017), suggesting that transfer became manifest after renormalization of structural changes and functional brain activity occurred. An alternative interpretation for transfer to memory control processes proposes that FM theta modulation helps to protect episodic memory representations from progressively higher proactive interference during posttraining sessions. In line with previous research, transfer to both proactive control and memory control suggests that FM theta oscillations that were modulated by NFT enable enhanced task performance either by providing temporal and encoding context information or by coordinating inhibition strength over competing memory representations. Notably, both functional roles of FM theta oscillations are not necessarily contrary to each other. Although FM theta oscillations have been assumed to reflect a general neural mechanism for cognitive control (Cavanagh & Frank, 2014), it has been proposed that it might be oversimplifying to assume one functional role for FM theta activity (L.-T. Hsieh & Ranganath, 2014).

5.3.2 Decreases of Frontal-midline Theta Oscillations Underlying Behavioral Transfer

At first glance, the decreases in FM theta activity, which accompanied performance increases in the retention condition of the DMTS task and predicted performance increase in the source memory task, seem to contradict increases of FM theta activity that were associated with behavioral transfer in cognitive training studies (Anguera et al., 2013; Jaušovec & Jaušovec, 2012; Mishra et al., 2014). However, these cognitive training studies differ to the present neurofeedback intervention in an important aspect. While in these studies older adults participated in a multi-tasking (Anguera et al., 2013) and an inhibition training (Mishra et al., 2014), younger adults conducted the FM theta NFT in *Study 2* and *3*. Considering that older adults demonstrate decreased FM theta activity compared to younger adults, which has been associated with cognitive decline (Anguera et al., 2013; Kardos et al., 2014; see Klimesch, 1999, for review), the same EEG changes induced by cognitive training should not inevitably be found after cognitive training with younger adults. Similarly, NFT might not induce FM theta decreases in older participants who already show low theta activity. Nevertheless, both younger and older adults have shown successful FM theta upregulation that transferred to similar cognitive control processes, such as interference resolution (J.-R. Wang & Hsieh, 2013).

An interpretation of activity decreases after training is provided by imaging studies that found decreased neural activity and associated performance increases after cognitive training (e.g., Debaere et al., 2004; Schneiders et al., 2011). According to Kelly and Garavan (2004), training-induced changes in activation of brain areas important for attention and cognitive control, such as the ACC, can be interpreted as part of a redistribution of functional activity after training. Redistribution comprises a combination of activity increases and decreases in task-relevant brain regions that are associated with performance enhancement and a reduction of cognitive control demands as a function of task proficiency. In line with this view, FM theta decreases in *Study 2* and *3* that were accompanied by simultaneously measured increases in retention and source memory performance might reflect less demands on proactive control and memory control processes, respectively. In accordance with the framework of adult cognitive plasticity, this would resemble enhanced functional supply of the cognitive system and, thus, a more efficient use of cognitive and memory control processes as a function of training (Lövdén et al., 2010).

5.4 Limitations and Outlook for Future Research

Despite the encouraging findings about the trainability of FM theta activity and its transfer to cognitive and memory control processes that were brought forward by the studies of the present thesis, some restricting limitations have to be considered. By comparing the DMTS and Stroop task, *Study 1* and *2* revealed differing scalp topographies of theta activity underlying proactive and reactive control processes as well as transfer of FM theta NFT to rather proactive than reactive processes, respectively. However, both tasks do not allow for process-pure measurements of these processes. The DMTS and Stroop task contain both proactive and reactive aspects but require the engagement of one or the other process to a greater extent. According to the DMC framework (Braver, 2012), proactive and reactive control processes might occur simultaneously but situational and, more importantly, individual characteristics influence whether proactive or reactive control is preferentially utilized (Braver et al., 2007). Interestingly, differences in WM capacity or motivation between participants have been shown to influence whether the more demanding proactive control is applied in highly demanding cognitive tasks (Kane & Engle, 2002; Locke & Braver, 2008; see Braver, 2012, for review). Thus, in order to substantiate the findings of the present thesis, future studies should aim at differentiating proactive and reactive control more clearly and take individual differences in the preferential application of proactive and reactive control into account. In particular, since the retention and manipulation condition of

the DMTS task differed not only in WM load but also in task instruction, the investigation of conditions that do not differ in more than one aspect would be desirable.

Contrary to other FM theta NFT studies that observed cognitive transfer immediately or one day after training (e.g., Enriquez-Geppert, Huster, Scharfenort, Mokom, Zimmermann, & Herrmann, 2014; Rozengurt et al., 2017; J.-R. Wang & Hsieh, 2013), transfer effects and training-induced changes of their underlying neural characteristics occurred specifically in the second but not the first posttest. Although brain plasticity characteristics as described by the expansion-renormalization model (Wenger et al., 2017) might explain these temporally specific transfer effects of *Study 2* and *3*, it seems possible that a greater statistical power might have revealed transfer effects also in the first posttraining session. Interestingly, removal of participants whose performance was at chance level in the source memory task at one or both posttests revealed significant transfer to source memory performance in both the first and second posttest.

As in other cognitive and neurofeedback training studies, the choice of training design and applied methodology ties the generalizability of training and transfer effects to the made observations. For instance, although NFT involves proactive control aspects, it cannot be strictly excluded that a longer and more distributed NFT or the choice of a different reactive control task would have revealed transfer effects also to reactive control processes. Furthermore, it can be argued that participants in the neurofeedback intervention were a selective group of students who were invited for participation based on their matching with the exclusion criteria (e.g., enjoying rollercoaster driving). Hence, it is difficult to generalize the present findings to people of, for instance, another age or with a different educational background. In order to reveal the effectiveness of neurofeedback as a clinical intervention usually double-blinded studies are conducted (e.g., Schabus et al., 2017). In contrast, the present NFT was solely single-blinded since the experimenter had to set both the individually estimated theta and randomly chosen frequency bands for the training and control group, respectively, prior to each training session. Consequently, although participants were comparably encouraged during NFT, motivational influences by the experimenter that might have influenced training success and transfer outcome cannot be fully excluded. Regarding the applied methodology, the EEG analyses of *Study 3* were based on the finding that prestimulus FM theta activity correlated with source memory retrieval (Addante et al., 2011), which could be replicated in the present thesis (Appendix B). A vast amount of studies have shown that FM theta oscillations support not only upcoming episodic memory retrieval, but also the initial encoding and reinstatement of these memories (see L.-T. Hsieh & Ranganath, 2014; Nyhus & Curran, 2010, for review). FM theta NFT might have also enhanced memory control processes during encoding and poststimulus retrieval, leading

to better source memory performance for the training compared to the control group. Moreover, although modulations of FM theta amplitude and power were found during NFT and in the transfer tasks, this does not mean that other related measurements, such as theta-gamma phase coupling or theta phase coherence, have not been altered. Theta-gamma phase coupling is assumed to allow for item-context binding whereas theta phase coherence is thought to enable process binding and, thus, top-down control (see Sauseng et al., 2010, for review). Future studies might investigate both theta measures in order to gain a deeper understanding of the underlying neural mechanisms that can be trained by means of neurofeedback. This might additionally inform on why NFT of other frequency bands, such as posterior gamma activity, found similar transfer effects as FM theta NFT (Keizer, Verment, & Hommel, 2010).

Considering that cognitive decline with increasing age is associated with a decrease in FM theta activity (e.g., Anguera et al., 2013; Kardos et al., 2014), future research might take the findings of the present thesis as a basis for investigating whether FM theta NFT can be used to prevent cognitive and especially memory decline. Some NFT studies already showed that also older adults are able to enhance their FM theta activity with the help of neurofeedback and show improved cognitive performance after training (Reis et al., 2016; J.-R. Wang & Hsieh, 2013). With regard to memory performance, older participants demonstrate a specific deficit in associative memory (Naveh-Benjamin et al., 2003) and FM theta NFT in the present thesis showed transfer to memory control processes that are especially important for source memory performance, a type of associative memory. Thus, FM theta NFT might be potentially helpful in improving older adults' associative memory deficit. Importantly, future studies should control for brain pathology, such as mild cognitive impairment and dementia, since these are characterized by abnormally increased theta activity that are related to cognitive deficits (e.g., Klimesch, 1999).

5.5 Conclusion

In summary, the findings of the present thesis provide encouraging insights in the role of FM theta oscillations for cognitive and memory control processes and their trainability by means of neurofeedback. In three consecutive studies, previous findings about FM theta activity underlying cognitive control processes were verified and the transfer of a FM theta NFT intervention to cognitive and memory performance was assessed. Crucially, the temporal extension of NFT transfer and the alteration of FM theta characteristics underlying behavioral transfer were explored. Together these studies revealed (1) differing theta topographies underlying proactive and reactive control pro-

cesses, suggesting that FM theta activity acts functionally different depending on task requirements, (2) transfer of successful FM theta upregulation during NFT to proactive rather than reactive control processes, and (3) NFT transfer to source memory performance, indicating that cognitive and memory control processes can be modulated by FM theta NFT. Interestingly, training-induced behavioral transfer tended to be accompanied by a decrease in FM theta activity, suggesting less demands on cognitive and memory control processes after training and, thus, a more efficient use of these processes. Both behavioral transfer effects and changes in their underlying EEG dynamics were observed in the second but not first posttest. The temporally specific characteristics of transfer effects might suggest a late manifestation of transfer after expansion and renormalization of brain substrates (Wenger et al., 2017) or an increased protection of episodic memories from proactive interference, which gets progressively larger with every transfer session. Interpreted in the context of previous research, the present findings equally suggest that FM theta oscillations support cognitive and memory control either by providing temporal context information (see L.-T. Hsieh & Ranganath, 2014; Nyhus & Curran, 2010, for review) or by coordinating inhibition strength over competing memory representations (K. A. Norman et al., 2006; K. A. Norman et al., 2007). Future research might further explore the functional role of FM theta oscillations and whether FM theta NFT might be used for the treatment of cognitive and memory decline in old age.

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Stimulus material of the source memory task

In study 3, transfer effects of neurofeedback training were assessed to a source memory task. Therefore, 900 concrete German nouns were derived from the data base dlexDB (Heister et al., 2011). The following three lists of 300 words were used for the pre-training and two posttraining sessions, respectively. List to session assignments were counterbalanced across participants. All lists were divided into three 100-word sets (A, B, and C) that were used as item sets for the two source judgments (animacy and pleasantness) and as a new item set during retrieval. Sets were further divided into blocks of 50 words in order to present them in an ABBA design. All blocks and sets were balanced for word length and frequency and were used in a counterbalanced manner.

A.1 Word list 1 of the source memory task (p. 134)

A.2 Word list 2 of the source memory task (p. 137)

A.3 Word list 3 of the source memory task (p. 140)

Table A.1. Word list 1 of the source memory task.

| Set | Block 1 | | | Block 2 | | |
|-----|-------------------|--------|-----------|-------------------|--------|-----------|
| | Word | Length | Frequency | Word | Length | Frequency |
| A | Anemone | 7 | 0.07 | Alge | 4 | 0.16 |
| A | Arbeitszimmer | 13 | 4.25 | Artischocke | 11 | 0.47 |
| A | Asteroid | 8 | 0.02 | Backofen | 8 | 1.27 |
| A | Ballspieler | 11 | 0.12 | Barren | 6 | 1.64 |
| A | Bauchnabel | 10 | 0.25 | Besucher | 8 | 19.04 |
| A | Bibel | 5 | 14.19 | Blumenkübel | 11 | 0.05 |
| A | Bildschirmschoner | 17 | 0.07 | Dachs | 5 | 2.14 |
| A | Campingplatz | 12 | 0.23 | Daumen | 6 | 9.04 |
| A | Chamäleon | 9 | 0.47 | Diaprojektor | 12 | 0.05 |
| A | Darm | 4 | 5.98 | Drahtseil | 9 | 0.66 |
| A | Dübel | 5 | 0.29 | Fackel | 6 | 4.26 |
| A | Einhorn | 7 | 0.76 | Friseur | 7 | 3.73 |
| A | Falltür | 7 | 0.60 | Gastronom | 9 | 0.10 |
| A | Flugplatz | 9 | 4.93 | Goldfischglas | 13 | 0.07 |
| A | Fußabdruck | 10 | 0.05 | Granatapfel | 11 | 0.12 |
| A | Gesangbuch | 10 | 0.92 | Hai | 3 | 0.67 |
| A | Kakerlake | 9 | 0.04 | Hammer | 6 | 6.03 |
| A | Kies | 4 | 3.23 | Journalist | 10 | 7.20 |
| A | Kinderwagen | 11 | 2.12 | Kehlkopf | 8 | 1.63 |
| A | Kissen | 6 | 11.70 | Kommentator | 11 | 0.83 |
| A | Kopfbedeckung | 13 | 1.84 | Kreditkarte | 11 | 0.38 |
| A | Kosmetikerin | 12 | 0.09 | Laser | 5 | 1.01 |
| A | Künstler | 8 | 51.08 | Messerblock | 11 | 0.01 |
| A | Liegestuhl | 10 | 1.26 | Mixer | 5 | 0.43 |
| A | Mähne | 5 | 1.45 | Naht | 4 | 2.43 |
| A | Matte | 5 | 1.84 | Narbe | 5 | 3.25 |
| A | Medaille | 8 | 3.76 | Pilz | 4 | 2.12 |
| A | Metzger | 7 | 1.44 | Pistazie | 8 | 0.03 |
| A | Mieter | 6 | 7.28 | Pizzeria | 8 | 0.07 |
| A | Milchbrötchen | 13 | 0.05 | Planetarium | 11 | 0.14 |
| A | Panda | 5 | 0.11 | Priester | 8 | 28.76 |
| A | Pauke | 5 | 1.15 | Rennstrecke | 11 | 0.34 |
| A | Pool | 4 | 0.60 | Rotwein | 7 | 4.92 |
| A | Pumpnickel | 12 | 0.34 | Rückenwirbel | 12 | 0.20 |
| A | Rabbiner | 8 | 2.72 | Salamander | 10 | 0.54 |
| A | Radio | 5 | 28.02 | Schaufensterpuppe | 17 | 0.11 |
| A | Rock | 4 | 19.33 | Schulhof | 8 | 1.28 |
| A | Rücksitz | 8 | 0.92 | Senf | 4 | 1.85 |
| A | Sägewerk | 8 | 0.32 | Skistock | 8 | 0.02 |
| A | Saugglocke | 10 | 0.02 | Sonnenschirm | 12 | 1.00 |
| A | Schärpe | 7 | 0.76 | Spielfeld | 9 | 0.34 |
| A | Schuppe | 7 | 0.43 | Sternschnuppe | 13 | 0.17 |
| A | Spachtel | 8 | 0.38 | Straßenlaterne | 14 | 0.28 |
| A | Trauerweide | 11 | 0.16 | Suppe | 5 | 11.47 |
| A | Vogelfutter | 11 | 0.20 | Tempel | 6 | 14.45 |
| A | Walze | 5 | 2.13 | Thermostat | 10 | 0.25 |
| A | Wasserspeier | 12 | 0.14 | Türsteher | 9 | 0.23 |
| A | Widder | 6 | 0.01 | Verkehr | 7 | 49.73 |
| A | Zebra | 5 | 0.18 | Wels | 4 | 0.84 |
| A | Zeigefinger | 11 | 8.96 | Zierfisch | 9 | 0.02 |

Table A.1. Word list 1 of the source memory task.

| Set | Block 1 | | | Block 2 | | |
|-----|-----------------|--------|-----------|------------------|--------|-----------|
| | Word | Length | Frequency | Word | Length | Frequency |
| B | Ameisenhaufen | 13 | 0.65 | Armreif | 7 | 0.20 |
| B | Angestellter | 12 | 3.07 | Augenklappe | 11 | 0.09 |
| B | Bandwurm | 8 | 0.49 | Autobahn | 8 | 4.77 |
| B | Banktresor | 10 | 0.02 | Badeanzug | 9 | 0.74 |
| B | Bierdose | 8 | 0.14 | Bänker | 6 | 0.02 |
| B | Boot | 4 | 20.08 | Blutkörperchen | 14 | 2.49 |
| B | Bulldogge | 9 | 0.20 | Chemiker | 8 | 7.08 |
| B | Chef | 4 | 59.12 | Dachdecker | 10 | 0.47 |
| B | Dekan | 5 | 2.35 | Erwachsener | 11 | 1.86 |
| B | Drehbuch | 8 | 1.28 | Feuersalamander | 15 | 0.25 |
| B | Espresso | 8 | 0.26 | Geländer | 8 | 4.33 |
| B | Fliegenklatsche | 15 | 0.02 | Gepäckträger | 12 | 0.91 |
| B | Gallenstein | 11 | 0.07 | Gewürz | 6 | 1.05 |
| B | Gebäck | 6 | 2.18 | Hacke | 5 | 2.06 |
| B | Globus | 6 | 2.69 | Handtasche | 10 | 3.29 |
| B | Haarspray | 9 | 0.08 | Iris | 4 | 0.24 |
| B | Hausmädchen | 11 | 0.61 | Klammer | 7 | 1.59 |
| B | Henne | 5 | 1.67 | Kleid | 5 | 18.49 |
| B | Hexe | 4 | 5.15 | Kloster | 7 | 15.11 |
| B | Hörmuschel | 10 | 0.17 | Kochtopf | 8 | 0.86 |
| B | Inliner | 7 | 0.01 | Kompass | 7 | 0.04 |
| B | Kehrblech | 9 | 0.05 | Kreuzfahrtschiff | 16 | 0.06 |
| B | Knödel | 6 | 0.74 | Krümel | 6 | 0.69 |
| B | Küken | 5 | 0.99 | Mandarine | 9 | 0.35 |
| B | Laternenpfahl | 13 | 0.32 | Molke | 5 | 0.44 |
| B | Leggings | 8 | 0.02 | Murmel | 6 | 0.15 |
| B | Lenkstange | 10 | 0.39 | Nadel | 5 | 6.24 |
| B | Makler | 6 | 1.81 | Nase | 4 | 44.59 |
| B | Melone | 6 | 0.53 | Pastinake | 9 | 0.16 |
| B | Möwe | 4 | 0.94 | Pförtner | 8 | 2.46 |
| B | Ofen | 4 | 12.03 | Posaune | 7 | 1.12 |
| B | Orthopäde | 9 | 0.10 | Pyramide | 8 | 3.62 |
| B | Parfait | 7 | 0.06 | Rechenbrett | 11 | 0.04 |
| B | Plakat | 6 | 5.80 | Sack | 4 | 11.21 |
| B | Porträt | 7 | 7.72 | Schnabeltier | 12 | 0.31 |
| B | Pump | 4 | 0.34 | Sessellift | 10 | 0.02 |
| B | Redner | 6 | 25.39 | Spinnennetz | 11 | 0.38 |
| B | Rettungsring | 12 | 0.22 | Stecker | 7 | 0.60 |
| B | Rüstung | 7 | 8.69 | Stehleiter | 10 | 0.09 |
| B | Schiffbauer | 11 | 0.18 | Strohhut | 8 | 1.40 |
| B | Schrotflinte | 12 | 0.11 | Stufe | 5 | 31.14 |
| B | Stoppel | 7 | 1.16 | Tambourin | 9 | 0.12 |
| B | Tropfen | 7 | 13.57 | Taschenrechner | 14 | 0.29 |
| B | Untertasse | 10 | 0.81 | Trinkglas | 9 | 0.11 |
| B | Vene | 4 | 0.43 | Videospiel | 10 | 0.01 |
| B | Wurm | 4 | 4.10 | Wäscheständer | 13 | 0.01 |
| B | Zahnspange | 10 | 0.03 | Waschsalon | 10 | 0.07 |
| B | Zauberer | 8 | 3.81 | Wolke | 5 | 9.59 |
| B | Zeder | 5 | 0.13 | Yacht | 5 | 0.56 |
| B | Zündkerze | 9 | 0.28 | Zeitungsjunge | 13 | 0.19 |

Table A.1. Word list 1 of the source memory task.

| Set | Block 1 | | | Block 2 | | |
|-----|----------------|--------|-----------|-----------------|--------|-----------|
| | Word | Length | Frequency | Word | Length | Frequency |
| C | Ast | 3 | 3.90 | Agent | 5 | 4.00 |
| C | Autor | 5 | 21.80 | Bergsteiger | 11 | 0.89 |
| C | Babysitter | 10 | 0.11 | Bettwäsche | 10 | 1.48 |
| C | Bauklotz | 8 | 0.06 | Bumerang | 8 | 0.28 |
| C | Bisamratte | 10 | 0.11 | Chiropraktiker | 14 | 0.01 |
| C | Brecheisen | 10 | 0.29 | Dorn | 4 | 1.91 |
| C | Brille | 6 | 10.86 | Dosenöffner | 11 | 0.02 |
| C | Brotkrume | 9 | 0.07 | Duschhaube | 10 | 0.01 |
| C | Chips | 5 | 1.21 | Eierlikör | 9 | 0.50 |
| C | Diener | 6 | 23.17 | Einwohner | 9 | 16.06 |
| C | Eisbahn | 7 | 0.56 | Essigflasche | 12 | 0.04 |
| C | Erdbeere | 8 | 0.24 | Fahrzeug | 8 | 8.44 |
| C | Farn | 4 | 0.19 | Forelle | 7 | 1.17 |
| C | Fasan | 5 | 0.65 | Gabelstapler | 12 | 0.20 |
| C | Fechter | 7 | 0.42 | Gartenzwerg | 11 | 0.10 |
| C | Fischschwanz | 12 | 0.13 | Halskette | 9 | 0.33 |
| C | Fleischkäse | 11 | 0.02 | Kamin | 5 | 4.49 |
| C | Funkgerät | 9 | 0.36 | Klavierhocker | 13 | 0.03 |
| C | Gameboy | 7 | 0.02 | Ladeninhaber | 12 | 0.26 |
| C | Geige | 5 | 4.71 | Lenkrad | 7 | 2.53 |
| C | Golfball | 8 | 0.01 | Leselampe | 9 | 0.21 |
| C | Grube | 5 | 7.89 | Lötkolben | 9 | 0.13 |
| C | Handabdruck | 11 | 0.03 | Luftpumpe | 9 | 0.34 |
| C | Italiener | 9 | 12.38 | Margarine | 9 | 5.64 |
| C | Kaffeemaschine | 14 | 0.45 | Mausefalle | 10 | 0.46 |
| C | Kappe | 5 | 2.62 | Milbe | 5 | 0.16 |
| C | Karussell | 9 | 1.31 | Papier | 6 | 41.59 |
| C | Kürbis | 6 | 0.97 | Parmesan | 8 | 0.17 |
| C | Lappen | 6 | 5.36 | Pfannkuchen | 11 | 0.94 |
| C | Laufsteg | 8 | 0.31 | Pflaster | 8 | 6.45 |
| C | Leinwand | 8 | 6.92 | Podest | 6 | 1.07 |
| C | Mandel | 6 | 0.52 | Poster | 6 | 0.38 |
| C | Monogramm | 9 | 0.80 | Presslufthammer | 15 | 0.11 |
| C | Ölzweig | 7 | 0.15 | Ratte | 5 | 2.31 |
| C | Papagei | 7 | 1.99 | Restaurant | 10 | 9.97 |
| C | Person | 6 | 75.28 | Schere | 6 | 3.38 |
| C | Robe | 4 | 0.88 | Schulter | 8 | 33.72 |
| C | Rüschenbluse | 12 | 0.02 | Sombrero | 8 | 0.09 |
| C | Saxophon | 8 | 0.69 | Strafzettel | 11 | 0.06 |
| C | Schneeball | 10 | 0.37 | Strampelanzug | 13 | 0.02 |
| C | Schöpfkelle | 11 | 0.19 | Strandkorb | 10 | 0.40 |
| C | Schornstein | 11 | 2.86 | Tanker | 6 | 1.77 |
| C | Seekuh | 6 | 0.05 | Trophäe | 7 | 0.58 |
| C | Sternwarte | 10 | 1.71 | Turbine | 7 | 0.73 |
| C | Tarantel | 8 | 0.25 | Turnhalle | 9 | 1.55 |
| C | Teelöffel | 9 | 3.54 | Villa | 5 | 13.04 |
| C | Trittleiter | 11 | 0.08 | Webstuhl | 8 | 0.78 |
| C | Türke | 5 | 1.59 | Wespe | 5 | 0.63 |
| C | Verwandter | 10 | 2.22 | Zielfernrohr | 12 | 0.07 |
| C | Wimper | 6 | 1.07 | Zitrone | 7 | 3.00 |

Table A.2. Word list 2 of the source memory task.

| Set | Block 1 | | | Block 2 | | |
|-----|-----------------|--------|-----------|------------------|--------|-----------|
| | Word | Length | Frequency | Word | Length | Frequency |
| A | Adventskranz | 12 | 0.09 | Alm | 3 | 0.60 |
| A | Ahorn | 5 | 0.29 | Baseballschläger | 16 | 0.11 |
| A | Antenne | 7 | 1.01 | Binnenschiff | 12 | 0.05 |
| A | Armbinde | 8 | 0.47 | Bowle | 5 | 1.45 |
| A | Bär | 3 | 4.24 | Brechstange | 11 | 0.25 |
| A | Bauch | 5 | 19.42 | Delfin | 6 | 1.14 |
| A | Bierflasche | 11 | 0.47 | Drachenbaum | 11 | 0.05 |
| A | Blumenkohl | 10 | 2.40 | Feuerlöscher | 12 | 0.20 |
| A | Boxring | 7 | 0.07 | Funke | 5 | 2.43 |
| A | Cafeteria | 9 | 0.25 | Garnele | 7 | 0.03 |
| A | Dingo | 5 | 0.11 | Gaspedal | 8 | 0.76 |
| A | Doktor | 6 | 52.03 | Halbinsel | 9 | 7.19 |
| A | Elektriker | 10 | 0.83 | Hecht | 5 | 1.15 |
| A | Esszimmer | 9 | 0.06 | Hefeteig | 8 | 0.23 |
| A | Gummibärchen | 12 | 0.16 | Hütte | 5 | 9.08 |
| A | Jäger | 5 | 14.18 | Kaffeetasse | 11 | 0.92 |
| A | Kaminsims | 9 | 0.23 | Kanone | 6 | 2.72 |
| A | Korridor | 8 | 8.94 | Karpfen | 7 | 2.11 |
| A | Kotflügel | 9 | 0.66 | Keks | 4 | 0.48 |
| A | Kuh | 3 | 7.38 | Klebestreifen | 13 | 0.07 |
| A | Mannschaft | 10 | 11.75 | Kran | 4 | 1.44 |
| A | Mäppchen | 8 | 0.03 | Lamm | 4 | 3.71 |
| A | Mast | 4 | 2.75 | Lampenschirm | 12 | 0.28 |
| A | Medizinball | 11 | 0.12 | Lastwagen | 9 | 6.04 |
| A | Meerrettich | 11 | 1.00 | Laufband | 8 | 0.07 |
| A | Milcheis | 8 | 0.32 | Maske | 5 | 11.42 |
| A | Monokel | 7 | 1.63 | Maulkorb | 8 | 0.60 |
| A | Mundharmonika | 13 | 1.27 | Meise | 5 | 0.16 |
| A | Nudel | 5 | 0.18 | Pferd | 5 | 29.20 |
| A | Nummernschild | 13 | 0.34 | Reinigungsmittel | 16 | 0.38 |
| A | Offizier | 8 | 27.70 | Salat | 5 | 4.91 |
| A | Rasenmäher | 10 | 0.20 | Schließfach | 11 | 0.14 |
| A | Raucher | 7 | 1.64 | Schneemobil | 11 | 0.01 |
| A | Riemen | 6 | 3.77 | Schokoriegel | 12 | 0.09 |
| A | Ringordner | 10 | 0.02 | Schwimmweste | 12 | 0.12 |
| A | Schaffner | 9 | 3.22 | Seifenblase | 11 | 0.34 |
| A | Schaufel | 8 | 2.40 | Sklave | 6 | 3.25 |
| A | Scheibenwischer | 15 | 0.54 | Spule | 5 | 1.84 |
| A | Schranke | 8 | 4.95 | Stecknadel | 10 | 0.54 |
| A | Sonnenhut | 9 | 0.04 | Stirnband | 9 | 0.32 |
| A | Spardose | 8 | 0.02 | Stube | 5 | 18.94 |
| A | Staffelei | 9 | 1.26 | Sumpf | 5 | 4.28 |
| A | Stelze | 6 | 0.01 | Tragetuch | 9 | 0.02 |
| A | Tiefkühlfach | 12 | 0.14 | Umhängetasche | 13 | 0.17 |
| A | Trikot | 6 | 0.84 | Universität | 11 | 48.65 |
| A | Türschwelle | 11 | 0.54 | Wal | 3 | 0.76 |
| A | Waran | 5 | 0.08 | Wimpel | 6 | 0.92 |
| A | Waschlappen | 11 | 0.67 | Xylophon | 8 | 0.43 |
| A | Wurst | 5 | 5.97 | Zahnseide | 9 | 0.02 |
| A | Zäpfchen | 8 | 0.38 | Zuschauer | 9 | 14.61 |

Table A.2. Word list 2 of the source memory task.

| Set | Block 1 | | | Block 2 | | |
|-----|-----------------|--------|-----------|----------------|--------|-----------|
| | Word | Length | Frequency | Word | Length | Frequency |
| B | Baggerloch | 10 | 0.02 | Allee | 5 | 4.07 |
| B | Banner | 6 | 2.80 | Ampel | 5 | 1.40 |
| B | Barthaar | 8 | 0.14 | Bass | 4 | 3.31 |
| B | Blitzer | 7 | 0.01 | Baugerüst | 9 | 0.20 |
| B | Brücke | 6 | 25.38 | Bein | 4 | 18.21 |
| B | Dutt | 4 | 0.24 | Benzinkanister | 14 | 0.32 |
| B | Eiche | 5 | 3.07 | Bohrer | 6 | 1.12 |
| B | Eidechse | 8 | 0.81 | Buchseite | 9 | 0.16 |
| B | Fahrstuhl | 9 | 2.05 | Büroklammer | 11 | 0.07 |
| B | Fusel | 5 | 0.60 | Busch | 5 | 9.65 |
| B | Fußeiste | 9 | 0.12 | Comicheft | 9 | 0.01 |
| B | Grashalm | 8 | 0.86 | Eisvogel | 8 | 0.26 |
| B | Hauptmann | 9 | 20.12 | Fliegenfänger | 13 | 0.19 |
| B | Hosenanzug | 10 | 0.09 | Gürtel | 6 | 6.29 |
| B | Hyäne | 5 | 0.56 | Haar | 4 | 44.00 |
| B | Jutesack | 8 | 0.02 | Handfeger | 9 | 0.16 |
| B | Keramik | 7 | 3.82 | Heftklammer | 11 | 0.04 |
| B | Klimaanlage | 11 | 0.38 | Herdplatte | 10 | 0.39 |
| B | Kolosseum | 9 | 0.35 | Horizont | 8 | 15.28 |
| B | Kommissar | 9 | 8.68 | Klippe | 6 | 1.47 |
| B | Laubblatt | 9 | 0.08 | Knete | 5 | 0.13 |
| B | Laus | 4 | 0.99 | Koala | 5 | 0.02 |
| B | Lawine | 6 | 1.67 | Krawattennadel | 14 | 0.25 |
| B | Leguan | 6 | 0.15 | Kuchenform | 10 | 0.07 |
| B | Leopard | 7 | 0.69 | Kühltruhe | 9 | 0.12 |
| B | Maultier | 8 | 1.05 | Kutsche | 7 | 2.67 |
| B | Pflanze | 7 | 13.54 | Luftmatratze | 12 | 0.11 |
| B | Psychiater | 10 | 4.79 | Metalldetektor | 14 | 0.02 |
| B | Reitstiefel | 11 | 0.18 | Murmeltier | 10 | 0.49 |
| B | Rohrkolben | 10 | 0.03 | Nadelbaum | 9 | 0.10 |
| B | Rosenkranz | 10 | 1.59 | Nagel | 5 | 1.87 |
| B | Rücken | 6 | 62.02 | Ohr | 3 | 31.15 |
| B | Schraubenmutter | 15 | 0.06 | Pfeil | 5 | 4.35 |
| B | Schuhsohle | 10 | 0.18 | Puppenspieler | 13 | 0.42 |
| B | Skizzenbuch | 11 | 0.47 | Receiver | 8 | 0.05 |
| B | Socke | 5 | 0.29 | Rentier | 7 | 0.78 |
| B | Spielzeug | 9 | 5.15 | Rochen | 6 | 0.53 |
| B | Stethoskop | 10 | 0.31 | Sandkasten | 10 | 0.61 |
| B | Strauß | 6 | 0.04 | Schäferhund | 11 | 0.91 |
| B | Strumpfhose | 11 | 0.11 | Schnürsenkel | 12 | 0.61 |
| B | Terrier | 7 | 0.44 | Seide | 5 | 7.08 |
| B | Tesafilm | 8 | 0.06 | Ski | 3 | 0.74 |
| B | Theke | 5 | 3.81 | Strandmuschel | 13 | 0.01 |
| B | Therapeut | 9 | 1.28 | Taschenuhr | 10 | 1.16 |
| B | Umschlag | 8 | 7.72 | Tasse | 5 | 11.19 |
| B | Wacholder | 9 | 0.65 | U-Boot | 6 | 3.61 |
| B | Werkstatt | 9 | 12.05 | Untertitel | 10 | 1.80 |
| B | Zeitgenosse | 11 | 2.18 | Wangenknochen | 13 | 0.34 |
| B | Zimmerdecke | 11 | 1.23 | Weber | 5 | 0.94 |
| B | Zipfelmütze | 11 | 0.22 | Zange | 5 | 2.35 |

Table A.2. Word list 2 of the source memory task.

| Set | Block 1 | | | Block 2 | | |
|-----|----------------|--------|-----------|-----------------|--------|-----------|
| | Word | Length | Frequency | Word | Length | Frequency |
| C | Arena | 5 | 2.87 | Anwalt | 6 | 10.05 |
| C | Atemloch | 8 | 0.06 | Apotheke | 8 | 3.38 |
| C | Auge | 4 | 77.95 | Aquarium | 8 | 1.36 |
| C | Badehose | 8 | 0.56 | Arbeitsblatt | 12 | 0.07 |
| C | Bibliothek | 10 | 17.69 | Batterie | 8 | 6.54 |
| C | Brettchen | 9 | 0.69 | Biber | 5 | 1.11 |
| C | Brotkorb | 8 | 0.25 | Biskuitrolle | 12 | 0.04 |
| C | Chardonnay | 10 | 0.01 | Bratwurst | 9 | 0.33 |
| C | Deich | 5 | 1.55 | Brennofen | 9 | 0.07 |
| C | Efeu | 4 | 1.32 | Briefpapier | 11 | 1.17 |
| C | Entertainer | 11 | 0.11 | Chinese | 7 | 1.49 |
| C | Faust | 5 | 22.01 | Deck | 4 | 5.62 |
| C | Feile | 5 | 0.52 | Dinosaurier | 11 | 0.89 |
| C | Fischgräte | 10 | 0.09 | Drossel | 7 | 0.28 |
| C | Flugbegleiter | 13 | 0.03 | Fingerhut | 9 | 0.50 |
| C | Fön | 3 | 0.16 | Floß | 4 | 1.77 |
| C | Frachtgut | 9 | 0.24 | Frisbee | 7 | 0.02 |
| C | Geweih | 6 | 0.97 | Gans | 4 | 4.50 |
| C | Girlande | 8 | 0.34 | Gehweg | 8 | 0.34 |
| C | Handschelle | 11 | 0.03 | Grille | 6 | 0.63 |
| C | Hausmeister | 11 | 2.22 | Heuhaufen | 9 | 0.21 |
| C | Insekt | 6 | 1.99 | Hof | 3 | 41.55 |
| C | Karamel | 7 | 0.15 | Johannisbeere | 13 | 0.10 |
| C | Kleiderschrank | 14 | 1.70 | Kinn | 4 | 13.03 |
| C | Krug | 4 | 3.53 | Knöchel | 7 | 1.91 |
| C | Kurbel | 6 | 0.88 | Kralle | 6 | 0.38 |
| C | Locke | 5 | 4.70 | Leser | 5 | 33.85 |
| C | Manager | 7 | 5.38 | Magnolie | 8 | 0.17 |
| C | Millimeter | 10 | 3.90 | Panzer | 6 | 16.08 |
| C | Mobile | 6 | 0.19 | Pfandhaus | 9 | 0.13 |
| C | Oboe | 4 | 0.65 | Pillenschachtel | 15 | 0.01 |
| C | Orchester | 9 | 12.47 | Pirat | 5 | 0.21 |
| C | Passagier | 9 | 1.20 | Rasierwasser | 12 | 0.26 |
| C | Pony | 4 | 1.11 | Rathaus | 7 | 8.44 |
| C | Regisseur | 9 | 6.91 | Rezeptionist | 12 | 0.02 |
| C | Salon | 5 | 10.82 | Rose | 4 | 0.05 |
| C | Salzstreuer | 11 | 0.19 | Rotkohl | 7 | 0.58 |
| C | Samurai | 7 | 0.31 | Schalthebel | 11 | 0.72 |
| C | Schneeschuh | 11 | 0.06 | Schiedsrichter | 14 | 2.53 |
| C | Schrittzähler | 13 | 0.02 | Schlittschuh | 12 | 0.39 |
| C | Schubkarre | 10 | 0.29 | Schwertfisch | 12 | 0.16 |
| C | Schulbus | 8 | 0.09 | Spitzer | 7 | 0.95 |
| C | Schwein | 7 | 7.97 | Sprühdose | 9 | 0.11 |
| C | Seemann | 7 | 2.61 | Steinmetz | 9 | 0.46 |
| C | Stricknadel | 11 | 0.40 | Straßensperre | 13 | 0.13 |
| C | Telefonkabel | 12 | 0.11 | Taille | 6 | 3.00 |
| C | Viehzüchter | 11 | 0.44 | Taube | 5 | 3.98 |
| C | Vogeltränke | 11 | 0.02 | Vase | 4 | 2.31 |
| C | Wasserhahn | 10 | 0.80 | Wasserpistole | 13 | 0.02 |
| C | Zugbrücke | 9 | 0.36 | Windmühle | 9 | 0.78 |

Table A.3. Word list 3 of the source memory task.

| Set | Block 1 | | | Block 2 | | |
|-----|-----------------|--------|-----------|-----------------|--------|-----------|
| | Word | Length | Frequency | Word | Length | Frequency |
| A | Arملهنه | 8 | 0.29 | Artist | 6 | 0.83 |
| A | Aufzug | 6 | 3.79 | Assistent | 9 | 4.30 |
| A | Birne | 5 | 1.83 | Ball | 4 | 11.35 |
| A | Bügeleisen | 10 | 0.92 | Banjo | 5 | 0.26 |
| A | Bürger | 6 | 52.70 | Billardkugel | 12 | 0.14 |
| A | Büro | 4 | 19.50 | Blüte | 5 | 14.73 |
| A | Cowboy | 6 | 0.38 | Brotdose | 8 | 0.04 |
| A | Druckknopf | 10 | 0.23 | Bulldozer | 9 | 0.16 |
| A | Gärtner | 7 | 5.85 | Busfahrer | 9 | 0.32 |
| A | Gasthof | 7 | 2.75 | Ehering | 7 | 0.66 |
| A | Gefängniswärter | 15 | 0.31 | Feuerwerk | 9 | 2.09 |
| A | Haken | 5 | 7.54 | Geier | 5 | 1.65 |
| A | Haselnuss | 9 | 0.02 | Gewand | 6 | 6.10 |
| A | Hörsaal | 7 | 1.86 | Glatze | 6 | 2.15 |
| A | Hubschrauber | 12 | 2.38 | Goldfisch | 9 | 0.34 |
| A | Kaffeekanne | 11 | 0.74 | Kabine | 6 | 3.27 |
| A | Kassierer | 9 | 1.14 | Kaktus | 6 | 0.23 |
| A | Kater | 5 | 3.16 | Kaninchen | 9 | 3.68 |
| A | Kerzendocht | 11 | 0.01 | Kneipe | 6 | 5.92 |
| A | Kugelfisch | 10 | 0.02 | Krankenakte | 11 | 0.01 |
| A | Labor | 5 | 2.44 | Martini | 7 | 0.03 |
| A | Mandoline | 9 | 0.60 | Meißel | 6 | 0.93 |
| A | Mauer | 5 | 27.26 | Mikrofon | 8 | 1.00 |
| A | Milz | 4 | 1.46 | Milchmann | 9 | 0.43 |
| A | Mohn | 4 | 0.85 | Nachtclub | 9 | 0.02 |
| A | Mozzarella | 10 | 0.04 | Nagetier | 8 | 0.20 |
| A | Nacken | 6 | 14.01 | Patrone | 7 | 1.25 |
| A | Nagellack | 9 | 0.18 | Pipette | 7 | 0.16 |
| A | Nichte | 6 | 4.21 | Pollunder | 9 | 0.60 |
| A | Plantage | 8 | 0.43 | Postkarte | 9 | 2.50 |
| A | Python | 6 | 0.08 | Rasensprenger | 13 | 0.07 |
| A | Reinigung | 9 | 8.86 | Reiseführer | 11 | 0.48 |
| A | Salbei | 6 | 0.47 | Rückspiegel | 11 | 1.15 |
| A | Sänger | 6 | 11.83 | Schultafel | 10 | 0.14 |
| A | Schlüsselloch | 13 | 1.41 | Seepferdchen | 12 | 0.28 |
| A | Schreibfeder | 12 | 0.17 | Sportreporter | 13 | 0.10 |
| A | Sonnenbrand | 11 | 0.55 | Sturm | 5 | 30.08 |
| A | Spaniel | 7 | 0.07 | Süßkartoffel | 12 | 0.01 |
| A | Spielkarte | 10 | 0.16 | Thermometer | 11 | 2.74 |
| A | Steak | 5 | 0.35 | Türriegel | 9 | 0.07 |
| A | Stempelkarte | 12 | 0.03 | Ulme | 4 | 0.39 |
| A | Straßenfeger | 12 | 0.09 | Unternehmer | 11 | 18.73 |
| A | Tennisball | 10 | 0.12 | Visier | 6 | 1.63 |
| A | Turban | 6 | 0.68 | Vorschlaghammer | 15 | 0.11 |
| A | Turnschuh | 9 | 0.03 | Wand | 4 | 46.51 |
| A | Wasserpumpe | 11 | 0.16 | Waschbär | 8 | 0.04 |
| A | Wendeltreppe | 12 | 1.01 | Weste | 5 | 4.89 |
| A | Wiege | 5 | 5.01 | Wiesel | 6 | 0.75 |
| A | Windrad | 7 | 0.11 | Wohnzimmer | 10 | 9.31 |
| A | Zaunpfahl | 9 | 0.25 | Zahnrad | 7 | 0.54 |

Table A.3. Word list 3 of the source memory task.

| Set | Block 1 | | | Block 2 | | |
|-----|-----------------|--------|-----------|-----------------|--------|-----------|
| | Word | Length | Frequency | Word | Length | Frequency |
| B | Astronaut | 9 | 0.11 | Augentropfen | 12 | 0.09 |
| B | Baguette | 8 | 0.05 | Bienenstock | 11 | 0.52 |
| B | Bahnhof | 7 | 24.93 | Bilderrahmen | 12 | 0.39 |
| B | Bahre | 5 | 2.82 | Couch | 5 | 2.50 |
| B | Bauleiter | 9 | 0.56 | Fernrohr | 8 | 1.88 |
| B | Beißring | 8 | 0.02 | Flaschenöffner | 14 | 0.06 |
| B | Beuteltier | 10 | 0.09 | Gabel | 5 | 11.07 |
| B | Bremspedal | 10 | 0.31 | Gardist | 7 | 0.14 |
| B | Burg | 4 | 7.03 | Geschäft | 8 | 43.41 |
| B | Distel | 6 | 0.15 | Grübchen | 8 | 0.62 |
| B | Drehscheibe | 11 | 0.69 | Hackbraten | 10 | 0.16 |
| B | Eiscreme | 8 | 0.12 | Halle | 5 | 15.48 |
| B | Fahrzeuggestür | 11 | 0.02 | Handy | 5 | 0.50 |
| B | Fondue | 6 | 0.29 | Hummer | 6 | 1.39 |
| B | Grill | 5 | 0.81 | Kindergarten | 12 | 3.05 |
| B | Hülse | 5 | 0.87 | Klemme | 6 | 0.94 |
| B | Kabel | 5 | 3.85 | Koffer | 6 | 18.09 |
| B | Kinnriemen | 10 | 0.07 | Kompresse | 9 | 0.28 |
| B | Kranker | 7 | 1.68 | Kopfstütze | 10 | 0.02 |
| B | Landtag | 7 | 12.17 | Kreide | 6 | 4.05 |
| B | Liberaler | 9 | 0.98 | Lord | 4 | 31.93 |
| B | Makrele | 7 | 0.24 | Mango | 5 | 0.04 |
| B | Mayonnaise | 10 | 2.04 | Marionette | 10 | 0.78 |
| B | Mops | 4 | 0.36 | Obstkuchen | 10 | 0.20 |
| B | Niete | 5 | 0.47 | Ohrkneifer | 10 | 0.01 |
| B | Paar | 4 | 20.54 | Palme | 5 | 0.33 |
| B | Page | 4 | 1.30 | Perücke | 7 | 2.33 |
| B | Pilot | 5 | 2.20 | Pfeiler | 7 | 4.42 |
| B | Ranzen | 6 | 0.59 | Physiotherapeut | 15 | 0.02 |
| B | Rasierer | 8 | 0.06 | Pianist | 7 | 3.33 |
| B | Rauch | 5 | 13.24 | Puppe | 5 | 5.74 |
| B | Rosmarin | 8 | 0.16 | Rotfeuerfisch | 13 | 0.01 |
| B | Satteltasche | 12 | 0.19 | Schachfigur | 11 | 0.11 |
| B | Schaukel | 8 | 1.22 | Scheckbuch | 10 | 0.26 |
| B | Schnorchel | 10 | 0.25 | Schlafsack | 10 | 0.33 |
| B | Schreibmaschine | 15 | 5.22 | Segelschiff | 11 | 0.90 |
| B | Schwebebalken | 13 | 0.38 | Singvogel | 9 | 0.17 |
| B | Servierwagen | 12 | 0.18 | Sofa | 4 | 9.78 |
| B | Skateboard | 10 | 0.03 | Steißbein | 9 | 0.22 |
| B | Statue | 6 | 4.77 | T-Shirt | 7 | 0.65 |
| B | Stoppuhr | 8 | 0.44 | Uhrmacher | 9 | 1.11 |
| B | Strandkleid | 11 | 0.02 | Waffeisen | 11 | 0.07 |
| B | Studio | 6 | 2.67 | Waisenhaus | 10 | 1.79 |
| B | Tannenbaum | 10 | 0.69 | Wange | 5 | 6.34 |
| B | Teddy | 5 | 1.05 | Weinberg | 8 | 1.48 |
| B | Tiramisu | 8 | 0.01 | Whirlpool | 9 | 0.13 |
| B | Tochter | 7 | 63.95 | Wintergarten | 12 | 1.16 |
| B | Urne | 4 | 1.58 | Zauberstab | 10 | 0.42 |
| B | Zeiger | 6 | 3.60 | Zuckerstange | 12 | 0.04 |
| B | Zentimeter | 10 | 8.57 | Zwilling | 8 | 0.74 |

Table A.3. Word list 3 of the source memory task.

| Set | Block 1 | | | Block 2 | | |
|-----|-----------------|--------|-----------|------------------|--------|-----------|
| | Word | Length | Frequency | Word | Length | Frequency |
| C | Abstellgleis | 12 | 0.15 | Atlas | 5 | 1.50 |
| C | Altenheim | 9 | 0.11 | Auto | 4 | 36.30 |
| C | Architekt | 9 | 6.83 | Badekappe | 9 | 0.11 |
| C | Bett | 4 | 81.37 | Baumwolltuch | 12 | 0.03 |
| C | Bizeps | 6 | 0.27 | Bergwerksschacht | 16 | 0.01 |
| C | Brezel | 6 | 0.21 | Bunker | 6 | 5.55 |
| C | Briefkopf | 9 | 0.56 | Dartscheibe | 11 | 0.02 |
| C | Brombeere | 9 | 0.21 | Eigentumswohnung | 16 | 0.30 |
| C | Computer | 8 | 12.61 | Floh | 4 | 0.79 |
| C | Dachboden | 9 | 1.95 | Gänseblümchen | 13 | 0.37 |
| C | Dünger | 6 | 3.96 | Gondel | 6 | 0.96 |
| C | Einrad | 6 | 0.02 | Gouda | 5 | 0.11 |
| C | Erdmännchen | 11 | 0.02 | Haarbürste | 10 | 0.19 |
| C | Fernbedienung | 13 | 0.27 | Handrührgerät | 13 | 0.02 |
| C | Fernsehsessel | 13 | 0.04 | Hebel | 5 | 4.54 |
| C | Formular | 8 | 1.73 | Jagdhorn | 8 | 0.09 |
| C | Fußgängerbrücke | 15 | 0.04 | Kimono | 6 | 0.37 |
| C | Gästebuch | 9 | 0.63 | Kiosk | 5 | 1.18 |
| C | Glaser | 6 | 0.02 | Koppel | 6 | 0.25 |
| C | Grammophon | 10 | 2.23 | Kreisel | 7 | 0.72 |
| C | Haifischhaut | 12 | 0.02 | Küche | 5 | 39.81 |
| C | Handschuh | 9 | 2.58 | Lokal | 5 | 10.08 |
| C | Holzkohle | 9 | 0.96 | Lungenfisch | 11 | 0.14 |
| C | Hose | 4 | 10.75 | Motor | 5 | 16.30 |
| C | Kameramann | 10 | 1.07 | Pelz | 4 | 5.43 |
| C | Kokosnuss | 9 | 0.01 | Pinzette | 8 | 0.63 |
| C | Krater | 6 | 1.32 | Politur | 7 | 0.46 |
| C | Loch | 4 | 17.44 | Pullover | 8 | 3.51 |
| C | Mappe | 5 | 4.59 | Radieschen | 10 | 1.10 |
| C | Nabelschnur | 11 | 0.88 | Radiologe | 9 | 0.01 |
| C | Oma | 3 | 4.66 | Rollschuh | 9 | 0.07 |
| C | Opernhaus | 9 | 2.99 | Sägebock | 8 | 0.15 |
| C | Pflaumenbaum | 12 | 0.13 | Sandale | 7 | 0.19 |
| C | Porzellanfigur | 14 | 0.08 | Schienbein | 10 | 0.89 |
| C | Rabe | 4 | 1.54 | Schlepper | 9 | 1.76 |
| C | Roman | 5 | 22.38 | Schmuck | 7 | 12.94 |
| C | Salatschüssel | 13 | 0.16 | Schneesturm | 11 | 1.35 |
| C | Saphir | 6 | 0.34 | Schraube | 8 | 1.92 |
| C | Sardelle | 8 | 0.07 | Speiche | 7 | 0.45 |
| C | Schlagloch | 10 | 0.11 | Spekulatius | 11 | 0.11 |
| C | Schokolade | 10 | 6.61 | Stiefbruder | 11 | 0.29 |
| C | Sehne | 5 | 0.80 | Tänzer | 6 | 3.97 |
| C | Speisekammer | 12 | 1.19 | Taschentuch | 11 | 8.27 |
| C | Stier | 5 | 3.92 | Teich | 5 | 3.40 |
| C | Stimmgabel | 10 | 0.33 | Tischleuchte | 12 | 0.03 |
| C | Terminkalender | 14 | 0.51 | Vogelkäfig | 10 | 0.24 |
| C | Toga | 4 | 0.41 | Warzenschwein | 13 | 0.07 |
| C | Wäschekorb | 10 | 0.41 | Wasserzeichen | 13 | 0.57 |
| C | Wimperntusche | 13 | 0.11 | Zopf | 4 | 2.29 |
| C | Zwirn | 5 | 0.70 | Zwerg | 5 | 2.54 |

Appendix B

Correlation of FM theta activity with source memory performance

In study 3, transfer effects of neurofeedback training to a source memory task that was adapted from Addante et al. (2011) were investigated. Addante et al. (2011) were able to show that prestimulus FM theta activity during retrieval correlated with source memory performance. This finding could be replicated by using source memory specific prestimulus EEG activity (item and source – item only) of all participants, both from the training and control group, at the pretest of Study 3. Therefore, univariate outliers defined by the Tukey method using 1.5 interquartile ranges were removed (Tukey, 1977). Individual FM theta power at –400 to 0 ms preceding the retrieval cue correlated significantly with relative ($r = .46, p = .007$; Figure B.1.A) and absolute source memory

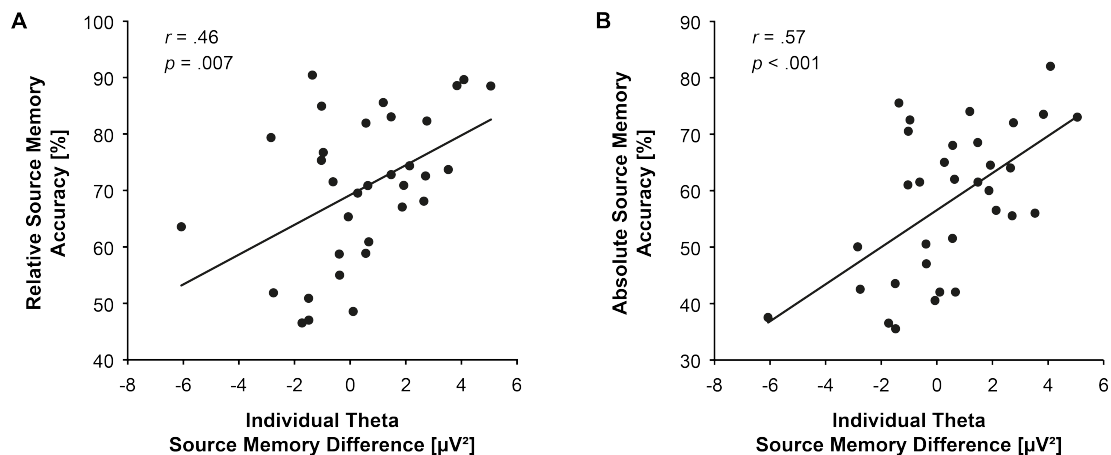


Figure B.1. Correlation of FM theta activity with source memory performance. Source memory specific individual FM theta activity (item and source – item only) measured at electrode Fz at –400 to 0 ms during retrieval correlated significantly with (A) relative and (B) absolute source memory performance.

performance ($r = .57, p < .001$; Figure B.1.B). These results support the functional role of FM theta activity in source retrieval.