Drawn to the rhythm

This thesis experimentally investigated the role of oscillations during attention and learning across a variety of paradigms and combining different methodologies. In this framework, we conducted three tACS studies to test the functional role of parietal alpha oscillations during spatial orienting (part 1), an iEEG and DBS study to investigate the causal role of the anterior thalamus and its oscillatory dynamics during visual attention (part 2), and an EEG study to unravel the changes in oscillatory feedback mechanisms as a result of perceptual learning (part 3).

Overview of the findings

Chapter 2 (part 1) tested the causal or functional role of posterior alpha oscillations in visuospatial orienting and spatial attention control. To that aim, we verified whether unilateral alpha-tACS modulates visuospatial attention and if so, whether it leads to differential effects on conceptually different visuospatial attention processes. In separate sessions, we applied tACS at 10Hz or sham tACS to the left parietal cortex and measured visuospatial attention performance during stimulation with an endogenous attention, an exogenous attention, and a detection task. Our results revealed a task-specific tACS effect on visuospatial attention performance. More specifically, 10Hz tACS induced a visuospatial attentional leftward bias relative to sham only in the endogenous attention but not in the exogenous attention or detection task. This suggests that left parietal alpha oscillations are functionally relevant for endogenous visuospatial attention performance and that alpha-tACS at a fixed frequency of 10Hz can be used to modulate it. This study also indicates functional specificity for the role of alpha oscillations in visuospatial attention performance by revealing an effect of alpha-tACS on endogenous but not exogenous attention performance.

While the study of chapter 2 showcased the general feasibility of modulating visuospatial attention through alpha-tACS, it remains unclear whether this behavioral effect was indeed caused by a tACS-induced modulation of alpha power in the left parietal cortex. Furthermore, according to the synchronization theory, tACS effects are expected to be most pronounced when the stimulation frequency matches the individual alpha frequency, which can differ considerably from 10Hz. Stimulation at frequencies that deviate from the individual alpha frequency, on the other hand, is expected to induce weaker or no effects. This gave rise to the experiment reported in the following chapter. In chapter 3 (part 1) we individually tailored the tACS stimulation frequency to the dominant alpha frequency, the IAF, and assessed the effect of this intervention on visuospatial attention as well as offline alpha power. This stimulation condition was compared to tACS at flanking frequencies IAF+/-2Hz as well as sham stimulation. During tACS, we measured the visuospatial attention bias with an endogenous attention and a detection task. Before and after stimulation, we acquired three minutes of resting state EEG data to assess the relative change in alpha power. In line with our hypothesis, we found an electrophysiological and behavioral tACS effect only in the IAF but not IAF+/-2Hz stimulation condition relative to sham. tACS at IAF induced an increase in alpha power leftward lateralization from before to after tACS, which was significantly different from sham for the first minute of the post-EEG measurement. Across participants, the magnitude of this offline EEG effect correlated with the visuospatial attention bias, i.e., the greater the increase in alpha power leftward lateralization from before to after tACS, the greater the visuospatial attention leftward bias during tACS. According to a regression analysis, there was also a greater visuospatial attention leftward bias for IAF tACS relative to sham for a high value of the EEG effect. These results suggest frequency-specificity of the tACS effect on EEG and attention performance, thereby highlighting the relevance of individually tailored stimulation protocols.

In chapters 2 and 3, we found an effect of alpha-tACS on the endogenous attention but not the exogenous attention or detection tasks. These task-specific effects suggest functional specificity of parietal alpha oscillations. fMRI studies have previously demonstrated divergent roles of a dorsal fronto-parietal and a ventral fronto-temporoparietal network in endogenous and exogenous attention processes (Chica et al., 2013; Corbetta et al., 2008) and it therefore could be argued that the task-specific effects are associated with a functional distinction between these two attention networks. This gave rise to the experiment of chapter 4 (part 1). We applied IAF tACS to the dorsal parietal and ventral temporoparietal cortex of either hemisphere in four separate sessions and in a fifth session, we administered sham tACS to either of the four stimulation sites. During tACS, we measured visuospatial attention performance with an endogenous attention and an exogenous attention task. Before and after tACS, we acquired three minutes of resting state EEG data to measure the increase in alpha power. Our results revealed a four-way interaction between stimulated brain area, stimulated hemisphere, attention task and cue type, which was driven by a greater visuospatial attentional leftward bias in the left as compared to the right dorsal parietal stimulation condition (both sham-corrected) for the valid trials of the endogenous attention task. In contrast, ventral temporoparietal tACS did not modulate visuospatial attention performance in either attention task. There was no tACS effect in the EEG data. The behavioral findings support a functional role of dorsal parietal alpha oscillations in endogenous attention control. However, the absence of effects in the ventral temporoparietal condition speaks against a double dissociation with regard to the function of alpha oscillations in the two brain areas.

In chapter 5 (part 2), we investigated the causal or functional role of the anterior thalamus in attention performance. Previous neuropsychological reports suggest that unilateral isolated damage of the anterior and surrounding thalamic nuclei leads to hemineglect symptoms (Ghika-Schmid & Bogousslavsky, 2000; Watson, 1981). Yet, it is still unknown whether anterior thalamic DBS, as used for the treatment of epilepsy, impairs attention performance. Furthermore, the oscillatory dynamics in these nuclei during attention performance are still unclear. We tested these research questions in four patients who recently underwent anterior thalamic DBS implantation surgery for the treatment of refractory epilepsy. We recorded local field potentials at different sites in the anterior thalamus while patients performed the endogenous attention task. Furthermore, we investigated the effects of right thalamic high-frequency (140Hz), low-frequency (individual alpha/theta frequency) and sham DBS on attention performance. We found various theta, alpha and gamma power changes in anticipation and response to the visual target during the endogenous attention task, especially in the ventral anterior thalamic nucleus. Most notable were gamma and theta power decreases before target onset followed by a power increase after target presentation. The post-target theta and gamma power negatively correlated with RTs on a trial-by-trial basis, which underlines the link between the oscillatory responses and the behavioral outcomes. Measurements of visual attention performance during stimulation of the anterior thalamus revealed a slowing of RTs during low- and high-frequency DBS relative to sham. These results support a causal or functional role of the anterior thalamus in visual attention performance and shed light on the oscillatory mechanism that underlie this process.

In all previous chapters, we focused on the role of low-frequency oscillations as a gating mechanism in the context of visual attention tasks. In chapter 6, we investigated whether these oscillations could play a role in a form of skill learning, namely, visual perceptual learning. This question was motivated by the tight link between attention and visual perceptual learning demonstrated in previous behavioral studies (for extensive review see Byers & Serences (2012)). This led us to the question whether the learning-induced enhancements in perception performance would be reflected in corresponding power modulations in alpha and beta range oscillations. Various perceptual learning theories support a role of feedback in perceptual learning (Crist et al., 2001; Fahle & Edelman, 1993; Roelfsema et al., 2010; Seitz et al., 2006, 2009), yet it remained unclear whether modified feedback input can account for stimulus-specific perceptual performance enhancements after extensive perceptual training. The EEG study of chapter 6 (part 3) addressed this research question by testing the effect of extensive perceptual training on alpha and beta power, two oscillatory mechanisms that have previously been linked to feedback processes (Arnal et al., 2011; Bastos et al., 2015; Bosman et al., 2012; Buffalo et al., 2011; Händel et al., 2011;

Lee et al., 2013; Michalareas et al., 2016; Popov et al., 2017; Richter et al., 2017; Sauseng et al., 2005a; G. Thut, 2006; von Stein et al., 2000; Worden et al., 2000). We trained twenty-one participants for eight sessions to detect slight differences in orientation of a sinusoidal grating and acquired EEG data before and after learning to assess the learning-induced alpha/beta-power changes. The stimulus-specificity of learning was measured after training with a rotated control stimulus. The behavioral results revealed that orientation discrimination performance improved with training. This effect was stimulus orientation-specific as shown by better performance for the trained stimulus as compared to the rotated control stimulus. The EEG data revealed changes in anticipatory alpha and beta power and late-post stimulus beta power specifically for the trained sinusoidal grating features but not for the rotated control stimulus. This suggests that feedback processes can account for at least part of the stimulus-specific performance enhancements as proposed by the read-out (Dosher et al., 2013; Dosher & Lu, 1998), reverse hierarchy (Ahissar & Hochstein, 2004) and related theories (Eckstein et al., 2004; Goldstone, 1998). By comparing the oscillatory responses while attention was directed towards the relevant stimulus and while attention was directed away from it due to a demanding task at fixation, this experiment also shed light on the link between perceptual learning and attention. We found the learning-induced alpha and beta power changes in the pre- and early post-stimulus interval in both attention conditions, which might be indicative of an enhancement in the efficiency of read-out mechanisms independent of attention deployment. However, it is important to note at this point that the observed changes in feedback input do not contradict previous findings that indicate attention-independent neural correlates of learning corresponding to lower-level visual areas modifications (Bao et al., 2010; Furmanski et al., 2004; Raiguel et al., 2006; Schoups et al., 2001; Vogels, 2010; Zivari Adab & Vogels, 2011). In fact, these two mechanisms might co-exist to enhance perceptual performance. Besides the effects of learning on oscillatory power, we also found an association between sinusoidal grating contrast and pre-stimulus, early post-stimulus and late post-stimulus alpha and beta power. These effects did not interact with learning stage, which indicates that in our experimental design, unlike attention (McAdams & Maunsell, 1999; Reynolds et al., 2000), perceptual learning does not alter performance for various contrast levels differentially. This experiment showcased the role of alpha and beta oscillations in stimulus-specific perceptual learning and shed light on the interactions and potential parallels between attention and perceptual learning.

The functional role of alpha oscillations in attention

Various experiments have demonstrated that the distribution of alpha power over posterior areas is associated with the focus of spatial attention, i.e. alpha power increases ipsilaterally and decreases contralaterally to the attentional