Voluntary direction of attention through alpha oscillations

Electrophysiological signatures of adaptive and maladaptive attentional orientation

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Research beginning nearly two decades ago has suggested that alpha activity has an inhibitory influence on stimulus processing within the context of attention being coordinated across space, with an increase in the power of alpha activity occurring in spatially irrelevant regions (Foxe et al., 1998). According to this framework, the excitability of a sensory region can be modulated through top-down control of alpha power and thereby promoting or inhibiting processing of stimuli. In this thesis various aspects of the role of alpha oscillations in voluntary direction of attention are discussed.

Suppression versus enhancement

Alpha activity is thought to actively suppress distracting input. However, with respect to cross-sensory attention (distribution of attention to different sensory modalities) an increase in alpha activity from baseline has not yet been definitively linked to active inhibition of distraction. In chapter 2 we were interested in isolating inhibitory processes during cross-sensory attention. Therefore two versions of a cross-sensory paradigm were utilized in which attention was cued between the auditory and visual modality. In the first paradigm distractors were presented in the opposing modality of target presentation, while targets were presented alone in the second paradigm. Presentation of trials with and without distraction in different sessions provides the opportunity to separate preparatory processes related to expectation of a distractor from activity during the absence of distraction expectation.

We were able to identify alpha activity in the posterior region of the brain that showed an increase in power prior to expected visual distractor presentation, suggesting a deliberate process to actively inhibit distraction. However, two findings make the interpretation of the increase more complicated. First, the absolute levels of pretarget alpha activity did not differ between the distractor-present and distractor-absent condition. Instead, the increase in alpha power during distractor expectation evened out a difference between conditions that was present at baseline. Second, reaction times were not influenced by the amount of alpha activity in the distracting sensory modality while correlations were found for the attended modality.
The absence of behavioral benefit or distractor-specific increases in absolute alpha power could indicate that modulations are not as important for the distracting modality as for the attended modality. This is in line with the assumption that separate attentional resources exist for visual and auditory processes. In a dual-task paradigm participants were able to carry out tasks in the auditory and visual domain simultaneously without deterioration of performance on either one (Alais et al., 2006), discarding the need to selectively direct attention to one modality while suppressing another. Additionally, spatial cues presented in one modality can reorient spatial attention in other modalities (i.e. cross modal cuing, Driver & Spence, 1998; Fens et al., 2014), suggesting that collaboration between sensory modalities is possible. In contrast, no evidence of parallel processing during spatial attention exist, suggesting that this type of attention is automatically focused (Jans et al., 2010). According to a dominant model of visuospatial attention the ‘biased competition model’ (Desimone & Duncan, 1995) all information in a receptive field (RF) of a neuron will be averaged and RF size increases every step in the hierarchy of visual processing. In order to retain detailed visual information remaining input needs to be suppressed from further processing. Here a mechanism such as gating by inhibition (Jensen & Mazaheri, 2010) could be beneficial. Different requirements for spatial and cross-sensory attention makes it inappropriate to compare results and explains differences in conclusions drawn about the inhibitory influence of alpha activity from different attentional paradigms.

Additional evidence for the absence of functional relevance of alpha modulations in the distracting sensory modality could be obtained by replication of the distraction-present paradigm using cues presented in the auditory domain. Alpha power in the occipital cortex should not change when both the cue and target are presented in the auditory modality given that the modality remains irrelevant. If alpha power does however increase prior to visual distractor presentation it would point towards active suppression of distraction.

Against our expectation, the presentation of distraction in an irrelevant region did not lead to an increase in alpha above that of ‘idling’ (i.e. no distractor expectation). Instead, a general difference in posterior alpha power was present between the distraction present and distraction absent paradigm. This suggests a difference in default resource allocation between the easier and more difficult paradigm. That is, instead of larger modulations in alpha activity when task difficulty is increased, the total level of alpha activity is reduced. This implies that trial-specific increases and decreases of alpha are not perfectly related to
inhibition and excitation. Perhaps the balance between alpha activity in the relevant and irrelevant region determines which information is given priority. Since activity in auditory cortex are difficult to measure, intracranial measurements in nonhuman primates could give more insight.

**Top-down modulation of phase-angle**

Previous research has found that the detectability of a stimulus depends, not only on the power of an alpha oscillation, but also on the phase angle at target presentation (Mathewson et al., 2009). This raises the intriguing possibility that in addition to the power modulation found in chapter 2, a modulation of alpha phase could improve the strength of inhibition during this task. Because targets were presented with a constant cue-to-target interval the arrival of the targets was predictable. By speeding up or slowing down oscillations in the alpha band, the preferred phase angle for optimal inhibition of firing could be reached during target presentation. Chapter 3 shows no evidence of such a phase angle modulation. The most important reason for this conclusion was that none of the subjects showed a clear pattern of significant inter-trial phase-locking (ITPC). In chapter 4 and in the next paragraph we discuss why this measures is assumed to be the most appropriate measure to demonstrate phase adjustment.

A methodological limitation of the results in chapter 3 is the fact than an absence of a difference cannot be statistically proven. Unless two conditions show exactly the same results, no conclusion about inequality can be made. Replication of the current finding could improve reliability of the null-result. This requires the tendency of journals to reject studies with null-findings to be eliminated.

There is the possibility that a type II error was made. Here a few options exist to increase power to reject the null-hypothesis. Increasing the number of participants could increase the power to detect (small) differences in ITPC. This could be beneficial for detection of an increase in phase-locking compared to baseline. However, it would not increase the chance of finding significant inter-trial phase-locking per condition, the finding we consider to most important to support the rejection of top-down modulation of phase. Furthermore,
increasing the number of trials could improve accuracy and lower the threshold for statistical significance. However, one should keep in mind that ITPC values tend to get smaller once more observations are added to the calculation. Moreover, task parameters could be adjusted; for instance Mathewson et al. (2012) found that detectability changed with phase angles by using subliminal targets. Thus, it could be argued that we failed to get any top-down modulation of alpha activity given that our targets were not subliminal. However, this would then suggest that the ability to control visual cortex alpha phase is subtle and depends on finely tuned task characteristics, and as such an unlikely mechanism by which the brain processes information outside the laboratory.

The absence of a type II error could mean that a mechanism to control the phase of oscillation does not exist, or that such a mechanism is only valuable during other types of attention than cross-sensory attention. Two other experiments yielded results indicating that top-down control of the phase-angle of alpha oscillations is possible. In an experiment of Bonnefond and colleagues (2012) the phase-angle was adjusted in order to inhibit processing of a temporally predicted visual distraction. Importantly, targets were also presented in the visual modality. This means that attention was not regulated between modalities such as in our experiment, but attention was regulated over time. Samaha et al. (2015) found a modulation of the phase of alpha oscillations in an experiment including predictable targets that were presented without distraction. Top-down modulation of the phase-angle was not related to increasing the effectiveness of the inhibitory influence of alpha oscillations, but to enhance target processing at a specific points in time. Together these results suggest that alpha phase modulations are used as a mechanism for temporal attention, rather than during suppression of distraction in irrelevant sensory regions. If cross-sensory attention indeed relies comparatively little on suppression of distraction (as discussed in the previous section) no top-down control in order to realize more effective inhibition is necessary. An alternative possibility is that results supporting the presence of top-down phase-adjustment are based on false positives caused by suboptimal measures of phase-adjustment. In chapter (4) we have discussed why comparisons of ITPC between conditions should be interpreted with caution.
No influence of power changes in the absence of phase adjustments

The absence of a modulation of the phase-angle of alpha oscillations could be the reason that no correlation was found between alpha power and reaction times as described above. Because the inhibitory influence of high power alpha is larger at certain phase angles than others, higher alpha power is not strongly related to fast reaction times. Testing this hypothesis is difficult: we show in Chapter 4 that estimating phase angles close to target presentation can be problematic because of temporal leakage of evoked responses. Phase-estimations were therefore performed on trials in which a target was expected but not actually presented. Because targets need to be presented in order to obtain reaction times, there is no possibility to relate instantaneous phase angle (together with preparatory alpha power) to RT.

Caveats of comparing inter-trial phase-locking between conditions

Currently the findings of studies examining top-down modulations of phase-adjustment are inconsistent. It is possible that the inconsistencies are caused by differences in task design: some paradigms might profit more from phase modulations than others. However, it is also possible that some designs suffer from methodological issues because the measure of inter-trial-phase-locking is used inappropriate. In chapter 4 we demonstrate that the two phenomena can influence the estimation of phase angles of ongoing oscillations and thereby the measure of ITPC. First, when a phase angle is estimated at a time-point temporally close to stimulus presentation, evoked responses can affect the phase angle due to temporal leakage. We show that when ITPC is calculated for two conditions that show a difference in latency or amplitude of the evoked response, ITPC values are influenced to such an extent that significant differences arise that are fallacious. Second, a decrease in power could lead to a reduction in accuracy with which the phase is estimated. This introduces more variation in the phase estimation during low power oscillations, which in turn decreases ITPC values. We show that a systematic difference in power could consequently lead to significant differences in ITPC.
Instead of using ITPC as a measure to identify if a phase-adjustment takes place one could also look at whether oscillations speed up or slow-down in expectation of a temporally predictable target or distractor. How much an oscillations must accelerate or decelerate to obtain the optimal phase for processing or inhibition depends on the phase of the ongoing oscillation prior to a temporal prediction. The phase of the oscillation prior to cue presentation should therefore be related to the trial-to-trial peak-frequency prior to stimulus expectation if top-down adjustment of the phase of ongoing alpha oscillations indeed takes place.

**Alpha as a reactive mechanisms of attentional selection**

Previous studies mainly focused on the modulation of alpha oscillatory activity prior to presentation of targets and distractors. This mechanism is not applicable when one does not know beforehand which stimulus is relevant. We therefore studied post-target alpha activity in a feature based-attention task in chapter 5. In this task a target was to be distinguished from a distractor presented in the opposing hemifield based on stimulus shape. Task difficulty was varied by changing the color of a distractor to be more or less similar to the target color. We found a lateralization in alpha power after stimulus presentation when the target was easily distinguished from the distractor. The lateralization was behaviorally relevant: the extent to which people showed the lateralization was associated with smaller distraction cost in RT. Because the alpha lateralization appeared relatively late (500 - 900 ms) after target onset it is unlikely a reflection of initial target selection (or evoked responses) but rather a mechanism in support of ongoing stimulus processing. This finding is intriguing since feature based attention is thought to operate in parallel across the visual field (Folk et al. 1992). Our results show that a mechanism previously only associated with spatial filtering of information also comes into play after feature-based selection. Less striking but still noteworthy was the lateralization of alpha activity when the spatial location of the target was cued prior to presentation, which was present independent of distractor strength. These results show that alpha modulations can be viewed as a general mechanism to enhance target processing and suppress distracting information, both pro-active and reactive.
(In)voluntary direction of attention in misophonia patients

Finally in Chapter 6 we observed the first evidence suggesting that it is possible to distinguish misophonia patients from healthy controls through their early auditory evoked responses. Specifically, we found that a lower than normal N1 response could be a neurophysiological marker for misophonia. However, it still remains to be investigated if this diminished N1 is a distinctive characteristic for misophonia and whether the underlying symptoms of misophonia are due to altered auditory perception. We propose that in addition to altered low level attentional processing, patients might exhibit a failure to re-orient attention. Such a failure will cause a prolonged focus on stimuli that are generally considered annoying (such as chewing). A failure to re-orient attention could be demonstrated using a similar cross-sensory attention paradigm employed in chapter 2 and will be apparent as a diminished modulation in alpha activity. If future research indeed shows this failure in patients with misophonia a therapy could be designed to improve voluntary direction of attention.
References


