Selective deployment of attention to time and modality and its impact upon behavior and brain oscillations

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Für meinen Großvater Wolfgang Mühlberg. Danke dass du immer für mich da warst - ich vermisse dich.

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Sincerely,

Stefanie.

Summary

This thesis investigates the relationship between attention to time and modality at the levels of behavior and pre-stimulus brain oscillations, measured with EEG. Participants were presented with target stimuli from one of two possible modalities, which could appear at one of two different time points. The factors time and modality were interlaced with each other by the fact that each of the modalities was more likely to appear at a different point in time and additionally one of the modalities being more likely overall. We observed that attention to each modality followed its respective temporal likelihood, independently which combination of modalities was used, suggesting a general mechanism for cross-modal temporal decoupling in time. This result is in contrast with cross-modal attention in space, which occurs in a coupled way. At the physiological level, the decoupling effect in time also seems to modulate ongoing neural oscillations in different frequency bands. Based on the results obtained in the time-frequency analysis, we put forward the following tentative hypotheses: alpha oscillations appear to encode switches in modality expectation over sensory cortices, while the beta band might encode the expected modality of the next upcoming stimulus and for the effect of temporal attention itself.

Resumen

Esta tesis investiga la relación entre la atención al tiempo y a la modalidad al nivel de comportamiento y oscilaciones cerebrales pre-estímulo. En los estudios que se presentan aquí, los participantes debían responder a estímulos que se presentaban en una de dos modalidades distintas, y podían aparecer en uno de dos momentos distintos. Los factores de tiempo y modalidad fueron entrelazados el uno con el otro a través la manipulación de su probabilidad, según la cual una modalidad era más probable en un momento u otro y una de las modalidades era más probable en general. Los resultados mostraron que la atención a cada modalidad seguía su respectiva probabilidad temporal, independientemente de la combinación de modalidades, lo cual sugiere un mecanismo general para el desacoplamiento inter-sensorial en la atención temporal. Este resultado es interesante porque contrasta con la atención inter-sensorial en el dominio espacial, donde las distintas modalidades parecen funcionar de manera acoplada. El efecto de desacoplamiento en atención temporal también parece modular las oscilaciones cerebrales antes del momento en anticipación al estímulo, en bandas de frecuencia distintas. Según los resultados obtenidos mediante el registro de estas oscilaciones, elaboramos las siguientes hipótesis: las oscilaciones alfa parecen codificar expectativas sobre cambios de modalidad en las cortezas sensoriales, mientras que la banda beta parece codificar las expectativas sobre la modalidad del siguiente estímulo, y el efecto de atención temporal en sí.

Prologue

In many ways have the technical progresses in the last two centuries granted beneficial effects for humanity, but they also face us with new challenges in everyday life, especially in terms of management of the incoming sensory information. Our brain has a limited capacity for processing sensory information, and it has developed mechanisms to optimize the use of these resources, such as attention, that helps prioritize and filter relevant from irrelevant events. Many professions, such as air traffic controllers, require nowadays the monitoring and managing of large amount data and even seemingly easier, yet complex tasks, such as driving, require the processing of large amount of sensory information, to some extend even presented across different senses, like vision and audition. If the complexity and amount of information will increase further, in a similar manner, in the future, which is likely, given the rapid changes in society and everyday life within the past two decades, this could pose a challenge for more and more people, requiring us to find ways to improve interfaces of information delivery. To develop such strategies to improve attentional orienting, one has to improve and extend the current understanding of attention first.

For a long time, a large amount of the attention literature has focused on spatial attention, and later, on its interplay across sensory modalities. The study of temporal attention started to become popular in the late 90s and a new focus seems to develop by studying the effect of temporal attention across modalities. The topic of this thesis is a special case of temporal attention, the distribution of temporal attention across modalities. The paradigm used in this thesis pursues to reveal the interplay of attention to time and attention to modality by probabilistically manipulating the sensory context of our participants, to set an orthogonal, conflicting relationship with each type of attention.

In the first chapter of this thesis I review the current state of the attention literature with a special focus on temporal attention and crossmodal attention, as well as the possible underlying mechanism in terms of brain oscillations.

In the second chapter, I present three different, independent studies that investigate the relationship of orthogonal temporal and modality attention with respect to its behavioral effects and the modulation of the underlying pattern of brain oscillations.

In the last chapter, I discuss the possible meaning and implications of the observed results and conclude with a brief presentation of future directions necessary to further advance in the investigation of the relation between attention to time and modality.

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1. INTRODUCTION

1.1.Attention – a general overview

The term ‘attention’ seems to have an intuitive meaning, yet at the same time; is difficult to describe with words when one needs a precise definition (Pashler, 1998). The famous words of William James provide thereby a very popular description of the subjective experience that seems to carry the meaning of the word attention.

> “Every one knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others, and is a condition which has a real opposite in the confused, dazed, scatterbrained state which in French is called distraction, and Zerstreutheit in German.” (James, W., 1890, pp.403-404)

As many have pointed out, these words and many subsequent attempts at defining attention fail to provide an exact scientific description (e.g. Luck & Vecera, 2002; Pashler, 1998) and thus the term attention has to be used with caution (Broadbent, 1982). Sometimes, a too casual use of the word attention, together with our intuitive concept of it, restricts ones mindset by regarding cognitive phenomena as a result of attention while disregarding other possible interpretations (Pashler, 1998).

In the context of this thesis, attention will be viewed as an internal filter mechanism, prioritizing important sensory inputs to be processed first and/or more thoroughly. Our world is full of sensory information, often more so than the human brain is ever able to process. Like when reading a book, one not only sees the written text in front of oneself, but also has a glimpse of the surrounding area out of the corner of the eye, and can feel and smell the parchment, hear the rustle when turning the pages, on top of the sensation of the clothing over ones skin, or the distant roar of cars in the street, amongst further sensory stimulation. Yet, most of this sensory information is irrelevant and one needs mechanisms that help focusing on the processing of what is important, such as the words written in the book in this example. Attention incorporates such process, helping us to filter sensory information (Treue, 2003).

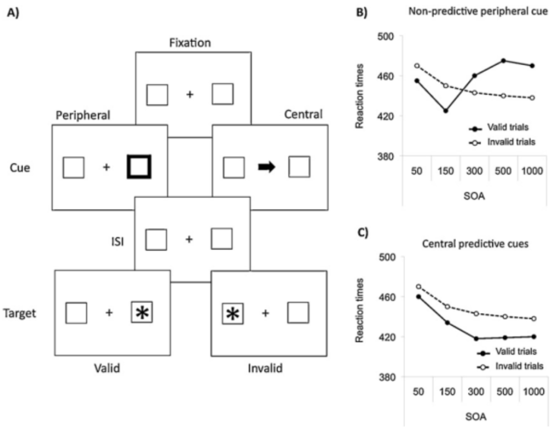

Figure 1.1.1: Overview of endogenous and exogenous attention. **A)** Endogenous attention can be captured through symbolic cues, such as a color, encoding for certain stimulus positions. Exogenous attention can be captured by salient, often peripheral events, such as flashes. **B)** The effect

of exogenous orienting occurs very fast, yet its duration is very short. **C)** While endogenous attentional orienting is slower, one can observe its effect over a longer period of time. Figure adapted from (Chica et al., 2013).

Attention is probably best understood as a set of different processes (e.g. Parasuraman & Davies, 1984), and hence its mechanisms can be classified in different ways. One well known classification is the distinction between exogenous and endogenous attention (Figure 1.1.1.; e.g., Carrasco, 2011; Chica et al., 2013). Exogenous attention refers to an automatic capture of processing resources, occurring outside of our voluntary control (Kahneman & Treisman, 1984). Exogenous orienting of attention is usually triggered by highly salient stimuli (Figure 1.1.1.A ; Posner, 1980), occurs very shortly after the given event (Figure 1.1.1.B; Müller & Rabbitt, 1989) and is very resilient to interference (Jonides, 1981). Exogenous attentional orienting is also closely related to bottom-up information processing in the brain, as is evident by the strong modulation of early event-related potentials (ERP), such as the P100 through exogenous attention (Hopfinger & Ries, 2005). Endogenous attention, on the other hand, refers to a voluntary act of orienting of resources (Figure 1.1.1.A; Posner, 1980). Endogenous attentional orienting takes usually more time than exogenous orienting and is more sensitive to disruption by highly salient external events, but its behavioral effects last longer (Figure 1.1.1.C; Müller & Rabbitt, 1989). Endogenous attention is related to top-down processes in the brain (Corbetta et al., 2008; Corbetta & Shulman, 2002) and has a stronger impact on later ERP components, such as P300 (Hopfinger & West, 2006). Endogenous and exogenous attention mechanisms are not fully independent from each other (e. g. Chica et al., 2013; Corbetta et al., 2008; Corbetta & Shulman, 2002). For example an interaction between endogenous and exogenous attention leads to a modulation of very early ERP components, such as the C1 component (60 - 80 ms) generated in the primary visual cortex, a modulation which cannot be observed by either endogenous or exogenous attention alone (Hopfinger & West, 2006). Yet the distinction between automatic (exogenous) and voluntary (endogenous) attention is important and useful. In light of the content of this thesis, the studies presented here investigate voluntary attentional orienting.

1.1.1. Temporal attention

Despite the division between endogenous and exogenous orienting mechanism, different varieties of attention can also be distinguished after the type of information used for orienting. Perhaps the most emphasized dimension in studies and models in psychology is spatial attention (e.g. Corbetta et al., 1993; Desimone & Duncan, 1995; Kastner et al., 1999; Klein, 1977; Posner et al., 1980; Posner, 1980; see Macaluso & Doricchi, 2013 or Chica et al., 2014 for recent reviews). Yet, one of the most basic dimensions towards which attention can also be oriented is time (Nobre, 2001).

Time is a very relevant factor for our behavior (Nobre & O’Reilly, 2004). The estimation of event timing is an important process to accomplish effective movement control (Georgopoulos, 2000). Many natural events in the environment also operate in a rhythmic fashion and provide a person with a measure of time (e.g. night and day, seasons, moon phase; Buzsáki, 2006), not to mention the different types of rhythmic activity within the body itself, such as fluctuations of neural activity (Buzsáki, 2006), heart rate (Klimesch, 2013; Park, Correia, Ducorps, & Tallon-Baudry, 2014) or the rhythmic contractions of gastrointestinal tract (Park & Tallon-Baudry, 2014). Also, many behavioral relevant stimuli, such as speech, contain rhythmic components (Arnal & Giraud, 2012; Arnal et al., 2015; Gross et al., 2013; Poeppel, 2014; van Wassenhove et al., 2005). Thus, it is no surprise that time plays a paramount role for perception. Several phenomena observed in psychophysical experiments are related to time, such as the attentional blink, were a person fails to perceive a brief visual stimulus presented within 90 to 540 ms after a previous, task relevant, visual event (Shapiro et al., 1997). Another related phenomenon is the inhibition of return, were the attentional benefits reverse to costs (lower speed and accuracy) within 300 ms after a location has been exogenously cued (Posner & Cohen, 1984).

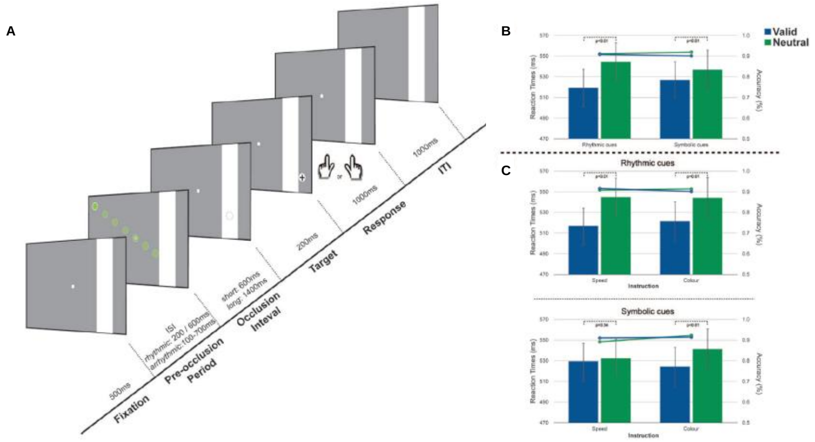

Figure 1.1.2: Overview over endogenous and exogenous orienting in temporal attention. **A)** Overview over the task design. Participants had to discriminate if a circle, after moving across the screen, contained an upright or tilted cross. Exogenous temporal attention was allocated by moving a circle in rhythmic steps across the screen. Endogenous orienting was allocated by assigning different colors to different time intervals in which the circle was hidden. **B)** Both, rhythmic and symbolic cues lead to a behavioral improvement, but as **C)** shows, participants use rhythmic cues independent if they had been instructed or not, while improvements through symbolic cues only occur when participants were instructed to use the symbolic cue. Figure adapted from (Rohenkohl et al., 2011).

Given the tremendous role that time plays for our perception, we can use temporal information also directly to guide attentional resources to points in time were we expect a relevant event (Nobre & O’Reilly, 2004). Like selective attention in general, temporal attention can thereby operate in an exogenous or endogenous fashion (Figure 1.1.2.; Coull & Nobre, 2008; Rohenkohl et al., 2011). Exogenous temporal attention is evidently captured when targets are presented always after a fixed time interval (and thus possess absolute temporal certainty), when stimuli are presented within 100 ms after a cue or, in studies using targets embedded in rhythmic streams of stimuli (Figure 1.1.2.A; Doherty et al., 2005; Lawrence & Klein, 2013). Endogenous temporal attention on the other hand, can be engaged by using informative cues to guide attention towards a certain point in time (Miniussi et al., 1999). The effects of exogenous and endogenous attention in time are to some extent dissociable from each other and, so far, the effects of both have been shown to be additive at the behavioral level, but not directly interacting (Figure 1.1.2.B & C; Rohenkohl et al., 2011). Exogenous and endogenous temporal orienting of attention are often triggered within the same paradigm, although the influence of one or the other can be diminished, like the effects of exogenous temporal orienting can be reduced by introducing uncertainty in the task design (Griffin et al., 2001) and by presenting stimuli after intervals longer than one second after the cue (Lawrence & Klein, 2013).

Temporal attention leads to a variety of behavioral benefits, such as faster reaction times (Correa et al., 2004), higher accuracy (Correa & Nobre, 2008) or lower perception thresholds (Cravo et al., 2013) when targets appear at the attended moment, compared to an unattended time. The effect of temporal attention can also be observed with electrophysiological measurements in terms of the modulation of event-related components. ERP modulations have been found for the early, sensory processing related components, such as an enhancement of P100 (Correa et al., 2006) and N100

(Lampar & Lange, 2011). At the same time, temporal attention does also modulate the later ERP stages through enhancements of the N200 (Sanders & Astheimer, 2008) or enhancements of the P300 component (Lampar & Lange, 2011).

Temporal attentional orienting is related to changes of activity in a network of different areas of the brain, classically identified by using functional magnetic resonance imaging (fMRI) or positron emission tomography (PET). Especially noteworthy is thereby a study of Coull and Nobre (1998), who compared activity changes elicited by temporal attention and spatial attention. They found common activation in a set of frontal, parietal and subcortical regions, such as the bilateral medial premotor cortex (equivalent with Broca Area 6, BA6), the bilateral ventrolateral prefrontal cortex (BA 11), the bilateral inferior parietal lobule (BA 40) and right posterior intraparietal sulcus or the bilateral cerebellum. This activity pattern suggests that orienting temporal attention, like other types of attention, engages a frontoparietal network. Additionally, within the same study, it was shown that temporal attention led to some left-lateralized activity within the left intraparietal sulcus and the left lateral inferior premotor area (BA 6/44), which is in so far interesting since it suggests a stronger left hemispheric engagement in temporal attention tasks, in contrast to spatial attention where the right hemisphere is more strongly activated (Coull & Nobre, 1998).

Taken together, temporal attention is an important type of selective attention, leading to behavioral benefits and to modulations of neuronal activity at various stages in stimulus processing. To do so, temporal attention engages the frontoparietal attention network; however, its activity pattern can be distinguished from other types of attention, such as spatial attention, by leading to stronger left hemispheric modulations (Coull et al., 2000; Coull & Nobre, 1998; Coull, 2004; Davranche et al., 2011).

1.1.2. Intersensory attention

So far, this thesis has reviewed attentional effects within one sensory modality or, in other words, unisensory attention. However, unlike under controlled experimental conditions, sensory information in everyday situations is received across various senses. In some situations, different types of sensory information encode for the same event and thus their integrated processing leads to benefits (Stein & Meredith, 1993). A very prominent example in that context is speech, which consists of auditory information, but also various types of visual information, like lip movements (Senkowski et al., 2008; Sumby & Pollack, 1954) or hand movements (e.g., Biau & Soto-Faraco, 2013). Integrating information across the senses often helps our perception, leading to faster and more reliable responses (Senkowski et al., 2011) and the effect of multisensory integration upon brain activity can already be observed at the single cell level, through changes in the firing rate of the encoding neurons (Stein & Stanford, 2008).

a) Rivalry between the senses

While multisensory integration is a very useful and important process for behavior in some occasions, integrating across different senses does not always make sense. Instead, in many other situations, the inputs from different senses rival for limited processing capacities, forcing a person to attend one of several possible modality streams. The process of attending one modality over the other is thereby called intersensory or cross-modal attention. Usually, when focusing attention to a certain sensory modality, behavioral responses toward that modality improve and one observes faster response times and higher response accuracy (Spence et al., 2001). Interestingly, while obtaining this behavioral benefits for an attended modality, one can also observe decreased performances towards stimuli presented in an unattended modality, which can be even greater in magnitude (albeit, in the reverse direction) than the benefits for the attended modality (Spence et al., 2001). Various studies also report imbalances between the cost-benefit trade-off in the different combinations of attended-unattended sensory modalities. For example, responses towards an unattended visual stimulus are slower when touch is attended, than when audition is attended. Touch seems to be a special case in general, not only because it generates the highest competitive costs for vision and audition in general (as mentioned by the previous example), but because responses towards unattended tactile stimuli are often much slower than responses towards unattended visual or auditory targets. Since responses towards unattended tactile stimuli and responses away from attended tactile stimuli are producing the highest behavioral costs, touch is sometimes considered as a “sticky modality”, because it is difficult to orient towards, and hard to orient away from it (Spence et al., 2001).

Naturally, orienting attention across different modalities also has an impact on the brain activity, since attention to one modality leads to increased evoked responses within its corresponding sensory cortex when a target is presented in that modality (Eimer & Driver, 2000; Eimer et al., 2002; Teder-Sälejärvi et al., 1999). In addition, some indicators of the modulation of brain activity show different topographies for attending different sensory modalities. For example, within audiovisual tasks, a modulation of the ERP over occipital channels can be observed when vision is attended and over central and frontocentral channel when audition was attended (Alho et al., 1994; Lenartowicz et al., 2014).

b) Cross-modal spatial attention

Of particular interest is how cross-modal attention affects other types of attention. For example, the allocation of attention by an auditory event leads also to an automatic reorienting of overt visual attention, in terms of saccadic eye movements or whole head orienting (Whittington et al., 1981). A first evidence for an interaction between modality attention and spatial attention upon endogenous attentional orienting was illustrated by Buchtel and Butter (1988), showing that visual attention can be oriented in space even when using a cue in a different sensory modality than the target. Based on this finding, Farah et al. (1989) suggested a supramodal spatial attention system in which spatial attention maybe acting entirely independent of the target modality. This fully supra-modal account was disputed by other studies showing that, despite the existence of a link between modalities in attention orienting, the consequences of cross-modal attention where different (often an attenuated version) from within-modality spatial attention (Calvert et al., 2004; Spence & Driver, 2004; Spence, 2010)

One particular interesting study conducted by Spence and Driver (1996), who addressed the relation between spatial attention and modality attention on the behavioral level by cleverly interweaving spatial and modality probabilities (Figure 1.1.3. A). Participants performed a discrimination task on auditory or visual stimuli (an elevation judgment task), which could be presented on either the left or the right side of space. A symbolic cue informed the participant on which side the target stimulus was most likely to appear (about 80% validity), but not of the relevant target modality, albeit, overall, one of the target modalities was more likely to appear than the other one. The factors spatial probability and modality probability were pitched against each other so that the most likely modality overall was also the far most likely modality at the cued side, however, the less likely modality was, instead, relatively more likely to appear at the uncued side (hence, the majority of uncued side targets belonged to this less likely modality). Thus, attention to modality and attention to space were orthogonal to each other, which allowed testing if spatial attention and modality attention can be deployed independently or if they are obligatorily linked to each other. Over a series of experiments, the authors found that responses to both modalities were faster at the attended side, even though the less likely modality was very unlikely to appear at this side (Figure 1.1.3.B). This result shows that spatial attention and modality attention are closely linked with each other.

Despite this demonstrations of cross-modal synergies in spatial attention, it is however possible to direct spatial attention in two different directions sometimes. For example, effective divided attention can be achieved when participants are explicitly instructed to attend to each sensory modality at a different side (experiment 7; Spence & Driver, 1996). Thus, spatial attention cannot be entirely supramodal as had been suggested before (e.g., Farah et al., 1989), albeit a close coupling between spatial attention and modality attention exists. This finding of cross-modal spatial coupling has been replicated also with other modality combinations, such as vision and touch (Spence et al., 2000). There are, however, a few studies which failed to find cross-modal spatial coupling, most important Lloyd et al. (2003). Within the study of Lloyd et al., using a similar design as Driver and Spence (1996), participants were instructed to orient their attention for the most likely target modality (either audition or touch) in space, while remaining a spatially diffuse expectation for the less likely modality. While they found the typical spatial attention benefits for their most likely target modality, no effect of spatial orienting was observed for the less likely modality. There is a small assortment of reasons which might explain the finding of Lloyd et al. First, the study used auditory and tactile targets, which are hypothesized to be less reliable for spatial information than vision (Welch & Warren, 1980) and thus may trigger a less dominant spatial orienting than visual stimuli. Another potential reason is that Lloyd et al. used a sustained attention paradigm, which may weaken the effects of spatial attentional orienting, while Spence and Driver used trial-by-trial cueing. Either of those factors or an interaction of both could have lowered the level of cross-modal coupling. Nevertheless, Lloyd et al. conducted a second experiment in the same study in which they instructed the participants to divide their attention upon different sides for each modality and found that voluntary orienting of spatial attention in different directions for different modalities produces behavioral costs, which is in line with the results Spence and Driver (1996) and suggests some cross-modal spatial coupling even between audition and touch.

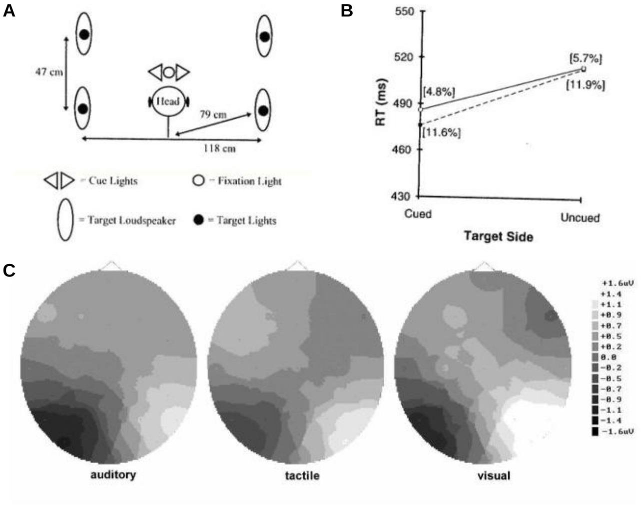

Figure 1.1.3: Effects of cross-modal spatial attention upon behavior and EEG scalp topography. **A)** Overview over the task design of Spence and Driver (1996). Participants had to attend either visual or auditory stimuli that could be presented at different spatial positions. A cue told them on which side the target was most likely to appear. While this was true for one of the modalities, the other modality was most likely at the opposite side. **B)** Result of Spence and Driver (1996). Participants are the fastest for both modalities at the same target side, independent at which side each modality was most likely, suggesting strong cross-modal link in spatial attention. **C)** Topography changes for different modalities in a cross-modal spatial attention paradigm. Evident is the great similarity of ERP topography changes for all three modalities, further cementing cross-modal links in spatial attention. A and B adjusted after (Spence & Driver, 1996), C adjusted after (Eimer et al., 2002).

Cross-modal spatial coupling also modulates the stimulus evoked potentials in ERPs. One of the first studies to investigate the cross-modal links in spatial attention using ERPs was published by Eimer and Schröger (1998). The authors of this paper conducted two experiments with visual and auditory stimuli. Participants were instructed to respond when either a high pitch tone (auditory) or the letter ‘M’ (visual) was presented. Participants were required to respond if the target appeared in a particular combination of location (left or right, cued trial to trial) and modality (instructed prior to each experiment block) and only a total of 8.3% of all trials required a response. Hence, ERPs uncontaminated by the response could be measured on most of the trials of the experiment, at attended/unattended locations and modalities. Visual and auditory stimuli were presented from different spatial positions in experiment 1 and spatially aligned, as well as further from the cue in experiment 2. Eimer and Schröger found that visual stimuli affect the evoked potentials of midline sensors even when vision was the secondary modality, while auditory stimuli lead to a modulation of the evoked potentials of midline sensors when audition was the primary modality, but not if it was the secondary modality. The observed modulations of the midline ERP sensors was stronger when the stimuli where spatially aligned (experiment 2).

This result suggests that there are cross-modal links in spatial attention on ERPs which are partially dependent on the stimulus modality and increase with spatial alignment of the stimuli, as it was suggested by the previous results from behavioral studies. In another, study Eimer (1999) found that early sensory-related ERP components such as P1 are modulated in audiovisual cross-modal spatial attention paradigms when participants are instructed to attend both modalities at the same side, but not if participants are required to attend each modality at a different side, adding further evidence for close cross-modal synergies in spatial attention. Cross-modal links have also been found for experiments using visual and tactile stimuli (Eimer & van Velzen, 2005), although it seems that touch again might play a special role. In this case, ERP components over somatosensory scalp sensors seem to be only affected when tactile stimuli play a potentially relevant (even if indirect) role in the task (Eimer & Driver, 2000). Additionally, the scalp topography elicited by stimuli of different modalities in cross-modal spatial attention paradigms show great similarities, suggesting further strong links in cross-modal spatial attention (Figure 1.1.3.C; Eimer et al., 2002)

c) Cross-modal temporal attention

With the increasing interest upon temporal attention, the interplay between temporal and cross-modal attention became a relatively recent focus of study in the field of cognitive sciences. A very interesting and important study for this thesis was conducted by Lange and Röder (2006). In their elegant design, participants had to discriminate between single and double-pulse auditory or tactile stimuli which could be presented either 600 or 1200 ms after an initial, bilaterally presented tactile warning signal. The expected target onset time and modality was thereby manipulated in a probabilistic manner. Stimuli within one modality, called the primary modality, were twice as likely as in the other modality, called the secondary modality. Stimuli within the primary modality were also mostly appearing at one of the two possible onset times, hence called attended onset time. The majority of stimuli at the other, unexpected time point belonged to the less likely secondary modality instead. The design attempts to translate the idea behind Driver and Spence's (1996) cross-modal spatial attention design, but in the time dimension. However, behaviorally Lange and Röder could only analyze the data obtained from early onset targets, because the changing hazard rates over time violated the assumption of uncertainty by the later onset time (Griffin et al., 2001). They found that responses towards both modalities were fastest when the (early) time point was attended, therefore adding evidence for a cross-modal coupling in temporal attention as well. Additionally, Lange and Röder investigated the interplay between attention to time and modality also in regard of their modulation of ERPs. They found that the task modulated early ERP components such as the auditory N1 and the tactile N140, independent of the attended modality, supporting cross-modal links in temporal attention. As mentioned, one caveat in the study of Lange and Röder however, is the lack of temporal uncertainty at the late onset. Without the comparison of behavioral responses to targets delivered at both time points, it is difficult to judge the full extent of cross-modal links in temporal attention, thus the exact interplay between attention to time and modality is still up to debate.

1.1.3. The frontoparietal attention network

While the previously described modulations of activations in the sensory cortices and effects upon the behavior are important aspects of attention orienting, they only describe a part of the process. What is not described by this is the control of attentional orienting itself, and how factors such as saliency or task relevance influence attention. In order to gain a more complete understanding of attentional orienting, one thence has to consider the additional activations of a wider range of brain regions elicited by attention and evaluate their role in attentional orienting. In an attempt to explain the different control mechanisms involved by orienting attention Corbetta and Shulman (2002) proposed the existence of two frontoparietal networks. Several other publications (e.g. Buschman & Kastner, 2015; Corbetta et al., 2008; Katsuki & Constantinidis, 2014; Petersen & Posner, 2012; Petersen & Sporns, 2015) have since extended and updated the idea of this fronto-parietal attention networks. Within this proposed framework, attention is both controlled by top-down factors, such as knowledge and experience, and bottom-up factors, such as the sensory input itself. Additional factors like stimulus novelty are further driving the different attentional patterns. To account for the different modes of attention orienting, Corbetta and Shulman suggested the existence of two attentional networks, roughly matching the idea of the exo- and endogenous systems proposed based on behavioral studies. One is a ventral frontoparietal system with a strong right hemispheric lateralization and the other one is a dorsal frontoparietal system.

The ventral frontoparietal network or ventral stream is considered to be closely related to exogenous attention processes (Corbetta & Shulman, 2002). Classically, the ventral stream is activated when a stimulus of high behavioral relevance is presented and thus able to capture our attention, especially if this target appears at an unattended spatial location or was unattended in any other regard (Kincade et al., 2005). Corbetta and Shulman proposed that this right ventral frontoparietal network will be activated when the current brain state is interrupted to allow reorienting to unexpected, yet salient events. This leads to an activation of areas such as ventral frontal cortex (VFC) and the ventral temporoparietal junction (TPJ), although some studies (e.g. Kincade et al., 2005) fail to find TPJ activation in exogenous attention paradigms.

The dorsal frontoparietal system or dorsal stream, in contrast, is related to endogenous attentional orienting (Corbetta & Shulman, 2002). Prominent regions of the dorsal stream include the intraparietal sulcus (IPS) and the frontal eye field (FEF). In contrast to the ventral stream, activation in the dorsal stream is usually bilateral, albeit often stronger on the side contralateral to the attended location (Hopfinger et al., 2000). The engagement of the dorsal attentional network begins often already in preparation of an upcoming event, as is evident in animal models showing increased firing rate in areas putatively analogous to the human FEF

(Goldberg & Bushnell, 1981). Thus, the activity in the dorsal frontoparietal attention network can be correlated to prestimulus modulations in oscillatory activity (Marshall et al., 2015).

In summary, similar as one can observe two different mechanisms of attention in behavior, one can also distinguish two different networks of attentional control in the brain itself.

1.1.4. The difference between attention and expectation

A concern in many attention studies, especially the ones addressing temporal attention, is that attention is often closely interlaced with expectation (Lange, 2013). Yet attention and expectation are two independent, or at least dissociable, processes in the brain. Expectation reflects our prior knowledge (Summerfield & Egner, 2009). If a person is walking through a familiar room, like one's living room for example, there is an expectation about the position of each piece of furniture and no attention is necessary to navigate through this familiar environment. Should someone however, have moved a table since the last visit to this room, the expectation of the position of this table would be violated, thus capturing the attention of the person. Many studies of attention orienting are in fact modulating attention and expectation at the same time, a very common way to intermix attention and expectation is thereby the usage of probabilistic cues (Posner, 1980).

On the behavioral level, the effects of attention and expectation are similar, with both leading to faster and more accurate responses and lower perception thresholds for attended/expected events (Nobre, 2001; Oswal et al., 2007; Sharma et al., 2014), thus a distinction between attention and expectation in behavioral studies is often unnecessary, or at least, inconsequential. On the neural level, attention and expectation are two separable mechanisms, that root upon seemingly orthogonal processes (Derosiere et al., 2014; Kok et al., 2012a; Summerfield & Egner, 2009). Attention serves the facilitation of the processing of an attended event via amplification, and it usually leads to increased neural activity (Schroeder & Lakatos, 2009). Expectation leads to a decreased response towards the expected stimulus by decreasing the activity of neurons encoding for unexpected events, resulting in an overall more focused or sharpened firing pattern (Kok et al., 2012b). A reduction of neural activity can thereby also be observed through a reduced ERP components such as N1 (Lange, 2009) or reduced fMRI activity (Kok et al., 2012b). Despite attention and expectation being different processes in terms of their expression in brain activity, they interact with each other. Evidence for this comes from a recent MEG study, which suggests that expectation sharpens neural activity in absence, but not in presence of attentional facilitation (Todorovic et al., 2015).

In conclusion, attention and expectation are different cognitive processes routing upon different neural mechanisms. Despite their similar implications for behavioral studies, a considerate usage of the words attention and expectation seems advisable, especially owing to their effects in terms of brain responses.

1.2. Prestimulus brain correlates of attentional orienting

So far, this thesis reviewed the consequences of attention in behavior and brain activity when a stimulus, attended or unattended, was presented. Yet, (endogenous) attentional orienting is a process of preparation or anticipation, and hence it leads also to changes in the brain before the stimulus is (potentially) presented (Bushnell et al., 1981). The brain correlates of attentional orienting in anticipation of an upcoming event has been observed with PET (Corbetta et al., 1993), fMRI (Kastner et al., 1999), as well as in studies using neuronal recording within animal models (Goldberg & Bushnell, 1981).

While the aforementioned studies provide evidence for prestimulus attentional modulations across an assortment of different measures, the most prominent prestimulus modulations are changes in the ongoing neuronal oscillations observed with MEG and EEG. The changes of prestimulus oscillations have been a topic of strong interest in attentional orienting for the last two decades (Worden et al., 2000) and this section of the thesis will review the possible mechanism and its importance.

1.2.1. Modulation of ongoing neuronal oscillations

Neuronal electrical oscillations reflect the periodic fluctuations in overall excitability of neuronal populations (Buzsáki, 2006). They were first reported by Hans Berger (1932) and are based upon the excitation properties of neurons. The concentration of ions inside and outside a neurons membrane is different (Hodgkin & Huxley, 1952), resulting in an electric resting trans-membrane potential of about -70 mV. Via neural discharges, neurotransmitters are able to change the transmembrane potentials through excitatory postsynaptic potentials (EPSP) or inhibitory postsynaptic potentials (IPSP) of target neurons. These can eventually lead to a rapid change of the neurons electric potential, resulting in an action potential. The transmembrane potential is thus an indirect measure of the underlying neuronal activity and can be measured through local field potentials (LFPs) over small neuronal populations and eventually with EEG and MEG for larger populations (Buzsáki, 2006).

a) The classification of neuronal oscillations

Within every spatial scale, measures of the transmembrane potential reflect periodic fluctuations of electrical activity, corresponding to the fluctuations in excitability of the underlying neuronal populations. These periodic fluctuations are called neuronal or brain oscillations and are often associated with different cognitive processes (Table 1.2.1.). Classically, neuronal oscillations are divided into five different frequency ranges: delta (1 – 4 Hz), theta (5 – 7 Hz), alpha (8 – 14 Hz), beta (15 – 30 Hz) and gamma (30 – 120 Hz). Everything below delta is often simply classified as slow wave activity, as well as oscillations faster than gamma are usually simply called fast or ultra-fast (>200 Hz) oscillations (Buzsáki & Draguhn, 2004).

The exact frequency borders vary between different authors and also their exact relation with cognitive function is not always clear, since often different types of oscillations can correlate with the same cognitive process, and each oscillatory regime is involved in various cognitive functions. Sometimes the different frequency ranges are also even further divided and may also represent different functions. A common distinction is thereby between high and low gamma (Canolty et al., 2006) and a recent paper suggest also a division between high and low beta oscillations (Herding et al., 2016).

Table 1.2.1: Overview over the different frequency bands and some of their main cognitive functions.

Frequency Band	**Range (Hz)**	**Related Cognitive Processes**
Delta	1 – 4	Sleep (Steriade et al., 1993), Motivation (Knyazev, 2012), Speech perception (Giraud & Poeppel, 2012a)
Theta	5 – 7	Memory allocation (Klimesch et al.,

		1996), Spatial navigation (Buzsáki, 2005), Imagery (Byrne et al., 2007), Speech perception (Giraud & Poeppel, 2012b)
Alpha	8 – 14	Attention (prestimulus; Worden et al., 2000), Sensory gating (Jensen & Mazaheri, 2010), Consciousness (Mathewson et al., 2012)
Beta	15 – 30	Movement preparation (Zhang et al., 2008), Expectation (van Ede et al., 2010), Temporal attention (prestimulus; Pomper et al., 2015)
Gamma	30 - 120	Stimulus processing (Womelsdorf & Fries, 2007), Attention (poststimulus; Jensen et al., 2007)), Speech perception (Giraud & Poeppel, 2012b)

Interestingly, neuronal oscillations seem to be a phylogenetically conservative feature, since similar types of oscillations related to similar functions can be observed across different mammalian species (Buzsáki et al., 2013), which suggests that any oscillatory firing pattern observed within one vertebrate species is most likely to be found within a different vertebrate species as well, thus results from invasive methods on animal models are most likely transferable upon humans. In some cases coupling between different frequency bands exists, a prominent case is the coupling of the power of slow (30 - 50 Hz) and mid-frequency gamma (50 - 90

Hz) power to the phase of the theta cycle in the rat hippocampus (Belluscio et al., 2012).

When measuring oscillatory activity, one is often interested in the amplitude of an oscillation in a certain frequency range. The amplitude defines the overall strength of an oscillation and is measured in terms of power. In humans, power modulations in advance of an expected event have been found in a variety of tasks for visual (Hanslmayr et al., 2007), tactile (Haegens et al., 2011) or auditory stimuli (Fu et al., 2001). Another measure of interest is the phase of an ongoing oscillation. Phase refers to the current state in the cycle of an oscillation and is often defined in terms of degrees of angle (value between 0 and 2π, or –π and π). For neuronal oscillations, the phase reflects the current average excitability of the underlying neuronal population. Sensory events will often be more readily perceived if they fall into a certain oscillatory phase (Busch & VanRullen, 2010). An example is the observation that in detection tasks with threshold stimuli, detected and missed sensory events often happen at different phases of the alpha cycle (Busch et al., 2009). This accumulation of similar phase angle per trial can be measured with the phase locking value (PLV, (Busch et al., 2009)). Like attentional orienting leads to modulations of prestimulus power, it can also modulate the prestimulus phase, such that attended events fall into a phase angle that facilitates stimulus processing and unattended events in the opposite, inhibiting phase angle (Bonnefond & Jensen, 2012, 2013). The phase of an ongoing oscillation can be reset by the onset of a stimulus. If events are presented in a rhythmic fashion, this can lead to a strong locking between the successive stimuli and the ongoing oscillations within the same frequency in which the stimuli are presented, which is called entrainment (Lakatos et al., 2008).

b) Prestimulus oscillations and attention

A huge body of literature has shown that oscillations of various frequency bands are modulated during attentional orienting. A very prominent role seems to be attributed to the alpha band frequencies (Worden et al., 2000). The alpha band rhythm was the first rhythm to be discovered with the EEG (Berger, 1932) and can even be identified by simple visual inspection of EEG data. Fluctuations in the alpha band represent the ongoing (rolandic) rhythm of the visual (alpha; Drewes & VanRullen, 2011) and auditory cortex (tau; Weisz et al, 2011) and are part of the rolandic rhythm of the somatosensory cortex as well (mu; Hari, 2002). Since the power of the visual alpha band rhythm typically increases when a participant closes its eyes, and decreases under active tasks, alpha was considered as a marker for cortical idling for a long time (Pfurtscheller et al., 1996), but in recent years the interpretation of the role of the alpha band rhythm has undergone profound changes with respect to its role in attention.

One usual finding in attention paradigms is that alpha power increases within the corresponding sensory cortex on the side ipsilateral of an expected stimulus and/or decreases on the side contralateral of an unexpected stimulus (Sauseng et al., 2005). This pattern, which is often also measured by using a lateralization index between the hemispheres, was observed when attention was directed towards visual stimuli (Kelly et al., 2006), auditory stimuli (Weisz et al., 2011) or somatosensory stimuli (van Ede et al., 2011). Attention towards somatosensory stimulus leads often to a modulation of alpha band power and beta band power, which might be related to the beta band rhythm being the second part of the somatosensory mu rhythm (Hari, 2002). Importantly, the prestimulus modulations in the alpha band are directly correlated to task performance (Hanslmayr et al., 2007). The stronger the lateralization between the two hemispheres in the prestimulus period is, the better a participant responds towards the upcoming stimulus. The prestimulus alpha band power was also found to be negatively correlated to the poststimulus gamma band power. Studies show that within trials where the gamma activity is high, responses towards stimuli are faster and they are perceived at a lower intensity compared to trials with low gamma activity (Fries et al., 2007).

While EEG and MEG provide correlation evidence for the important relation between the power of various frequency bands to task performance, one can also address their causal relation, at least for lower frequency bands, with transcranial magnetic stimulation (TMS; e.g. Romei et al., 2012; Ruzzoli & Soto-Faraco, 2014; Thut et al., 2011) and transcranial direct/alternating current stimulation (tDCS/tACS; Zaehle et al., 2010). With TMS and tDCS/tACS one can increase the power of ongoing oscillations. One example is a study conducted by Romei et al. (2012), were 5 repetitive TMS pulses over 500 ms were applied (consistent with a stimulation at 10 Hz alpha frequency) over the right IPS, while participants performed a Navon hierarchical letter task, where a large letter (global letter) consisted of a series of smaller letter (local level) and participants had to detect the presence of a target on either this global or local level. They found that an increase of alpha in the right IPS led to impaired target detection on the global level, while an alpha increase in the left IPS impaired target detection on the local level and thus this result provides evidence for a causal relationship between high prestimulus alpha power and decreased performance in attentional orienting tasks.

Similarly, some other studies suggest that also the phase of an ongoing oscillation can be altered by, and affect, attention. In tasks with predictable stimulus onset times, one does often observe not only changes in power, but also an alignment of the prestimulus activity such that the stimuli fall into their optimal phase for stimulus perception (Bonnefond & Jensen, 2013). Like one can modulate the power of ongoing oscillations with TMS and tDCS/tACS, one can also modulate the phase to observe causation between low frequency phases and task performance. An example for this is provided by Neuling et al. (2012). In this study, participants performed an auditory signal detection task with and without the application of alpha tDCS. The authors divided the data in 6 different categories dependent on the phase of the tDCS at stimulus onset and found that the target detection was improved in some alpha phases, while the performance decreased in other phase angles compared to a non-phase aligned condition (no tDCS block). This result implies that indeed a causality between the phase of ongoing alpha oscillations and the performance upon sensory events.

c) Prestimulus oscillations in cross-modal attentional paradigms

The impact of prestimulus oscillations has also been studied for cross-modal spatial and cross-modal temporal attention. Concerning cross-modal spatial attention, the MEG study of Bauer et al. (2012) deserves special mention. In this study, visual and tactile stimuli were presented on either the left or right side (of the visual field, or the body). Participants had to attend one of the sides and one of the modalities, to monitor the presentation of rare oddball stimuli occurring at the attended side and modality. Which side the participants had to attend was thereby cued on trial-by-trial basis, while the attended modality was blocked. Within this paradigm, Bauer et al. found that focusing attention to one side and modality led to a widespread alpha lateralization, with decreased alpha power contralateral to the attended side and increased alpha ipsilateral to the attended side (Figure 1.2.1). A similar lateralization pattern was found for the beta band over central sensors, therefore replicating the typical finding for spatial attention. For modality attention, they found that alpha or alpha/beta power increased over sensors corresponding to the sensory cortex of the unattended modality (central sensors for vision and occipital sensors for touch) and vice versa. Interestingly, Bauer et al. failed to find an interaction between attention to space and modality, with the modulation pattern of spatial attention being dominant over the pattern of modality attention, suggesting limited impact of modality attention upon spatial attention, hence adding evidence to the hypothesis of the close cross-modal links for spatial attention.

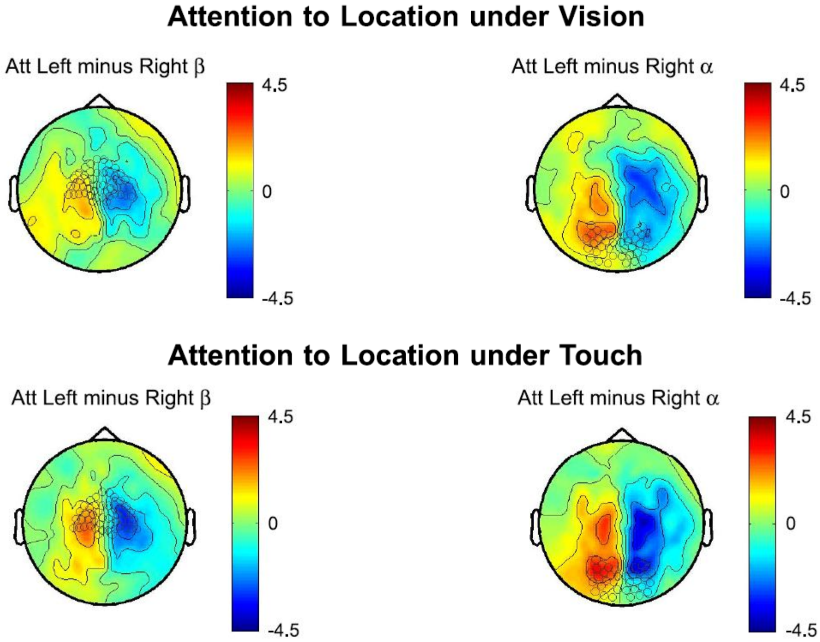

Figure 1.2.1: Effect of cross-modal spatial attention upon prestimulus brain oscillations. Participants performed a spatial oddball task on either visual or tactile targets. Independent which modality was attended, both modulated oscillations in the alpha and beta frequency range across the same range of sensors. Figure adapted from (Bauer et al., 2012).

Some more recent studies have investigated the effect of cross-modal temporal attention in the prestimulus period. The first study to mention in this context was conducted by Pomper et al. (2015). Within this study, participants performed a go-/no go-task in which they had to respond when a stimulus appeared in the target (attended) modality, either vision or touch. In order to manipulate temporal attention, targets could either appear after a variable interstimulus interval or after a fixed interstimulus interval, depending on the experimental block. Pomper et al. found that modality attention modulated alpha or alpha/beta oscillations over the corresponding sensory regions of interest (ROI), leading to the typical low frequency power decreases over sensory ROIs in anticipation of a target in the corresponding modality (Figure 1.2.2.A & B). Interestingly enough, a modulation of combined alpha and beta oscillations was observed only in the visual ROI over occipital sensors, while modality attention in the somatosensory ROI appeared to be purely driven by changes in beta power. This is interesting since usually a modulation of alpha and beta oscillations is observed over central sensors (Bauer et al., 2012; van Ede et al., 2011), while only alpha oscillations are modulated across occipital sensors (Bauer et al., 2012).The effect of temporal attention was observed in the somatosensory ROI and in a ROI corresponding to the motor cortex (Figure 1.2.2.B & C). In both ROIs, temporal attention led to a modulation of beta and delta oscillations. No interaction between modality attention and temporal attention was found with either power or inter-trial phase coherence. The authors concluded that alpha band and delta band oscillations would encode for separate task demands, with alpha encoding for orienting towards modality and delta for orienting towards time. Since they could not find an interaction between these two attentional processes, they further conclude that attention towards time and modality are mostly independent, which would mean a basic difference between cross-modal temporal and cross-modal spatial attention.

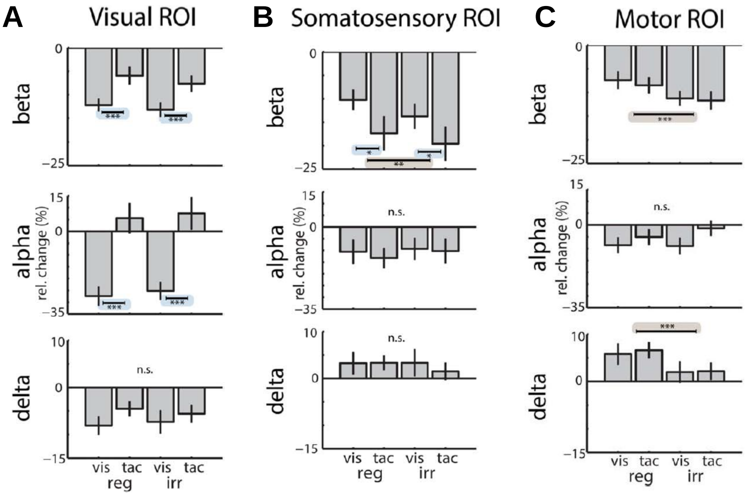

Figure 1.2.2: Results of the cross-modal temporal study of Pomper et al. (2015). **A)** A modality dependent alpha and beta power modulation was found at a visual ROI, with a decrease for both when a visual stimulus was attended. **B)** In the somatosensory ROI, a further modulation of beta oscillation was observed. The overall amount of beta power was thereby modulated by temporal attention. **C)** In the motor ROI, a temporal attention dependent modulation of power was found within the beta and delta band. Figure adapted from (Pomper et al., 2015).

In another recent study, Keil et al. (2015) investigated the interplay between attention to time and modality further by using the same task as in Pomper et al., 2015, and comparing the effects of temporal and modality attention upon power and functional connectivity. Functional connectivity serves to identify which brain areas show a correlated activity pattern of the experimental factors, here attention to time and modality, through the measured type of neuronal activity, here oscillatory power. While they replicated Pomper et al.'s findings for oscillatory power, Keil et al. found an interaction between attention to time and modality in the theta frequency range, in the functional connectivity between the right parietal cortex and the inferior frontal gyrus. Both, the studies of Pomper et al. and Keil et al., suggest that temporal attention and modality attention are mostly independent processes, expressed in different cortical regions and in different frequency bands, which would be in contrast to the close cross-modal links found for cross-modal spatial attention and also in contrast to the findings of Lange and Röder (2006), whose conclusions suggested temporal links for cross-modal temporal attention.

To summarize, prestimulus oscillations have a great impact upon attentional orienting, as it is suggested by a variety of methods. This is especially true for lower frequency oscillations, such as alpha band oscillations. Attending to an upcoming event at a location leads usually to a contralateral decrease and/or an ipsilateral increase of alpha or alpha/beta oscillations in advance of the stimulus presentation. Some studies also show an impact of the prestimulus phase upon behavioral measurements, since stimuli falling at a certain phase angle often lead to better behavioral responses compared to trials where stimuli fall within other phase angles. The increased body of literature concerning the prestimulus modulation of alpha and beta modulations in terms of power and phase let also to a more precise picture of the role of alpha oscillations in attentional processing, as discussed in the next section.

1.2.2. The gating-by-inhibition hypothesis

With the increase of the body of literature upon the modulation of prestimulus alpha oscillations through attention, the perception of the role of alpha band oscillations has changed. Considered initially as an indicator cortical idling, this hypothesis could not hold anymore in light of the new findings. In consequence, amongst others (Başar et al., 1997; Foxe & Snyder, 2011; Klimesch et al., 2007; Klimesch, 2012; Palva & Palva, 2007), Jensen and Mazaheri (2010) proposed a new hypothesis to explain the operating mechanism behind alpha modulations, the gating-by-inhibition hypothesis. This framework proposes that an increase of alpha activity functionally inhibits underlying cortical activity to block out unnecessary sensory stimuli. In other words, an increase in alpha activity is correlated with a decrease of spiking activity in the same cortical region (Haegens et al., 2011).

The level of prestimulus alpha oscillations is directly correlated with the level of poststimulus gamma oscillations (Bauer et al., 2006; Fries et al., 2001), which usually increases contralateral to an attended stimulus (Müller et al., 2000). The relation between alpha and gamma is a reverse one, a strong contralateral alpha decrease in advance of a stimulus leads to a high contralateral gamma power when a stimulus is presented (Bauer et al., 2006; Fries et al., 2001). Gamma oscillations are classically considered to encode the neuronal processing of stimuli (Womelsdorf & Fries, 2007). Therefore, since high alpha power seem to inhibit the overall cortical activity, it also reduces the activity of the neurons that can encode for the stimulus in the rapid gamma frequency.

Oscillations are periodic events and not only their amplitude (power), but also their phase has an impact in behavior. To account for the periodic nature of neural oscillations (Landau & Fries, 2012), the initial theory of Jensen and Mazaheri (2010) was extended into the pulsed-inhibition theory (Mathewson et al., 2011). Pulsed-inhibition theorizes that during high alpha activity, cortical excitability changes rhythmically, with stimulus processing and gamma firing being suppressed during phases of low cortical excitability (e.g., peaks of the oscillatory cycle). This theory was refined by Jensen et al. (2014), proposing that when entering a phase of high cortical excitability, neurons with highest response will break through the inhibition earlier, and the representation they are part of, be processed first. This is how the most salient stimuli will be first noticed and it would establish a processing priority order, from the highest to the lowest salient stimulus until this phase of high cortical excitability ends (Figure 1.2.3.A). High alpha power would reduce the width of the window of high cortical excitability, enabling fewer stimuli to be processed (Figure 1.2.3.B).

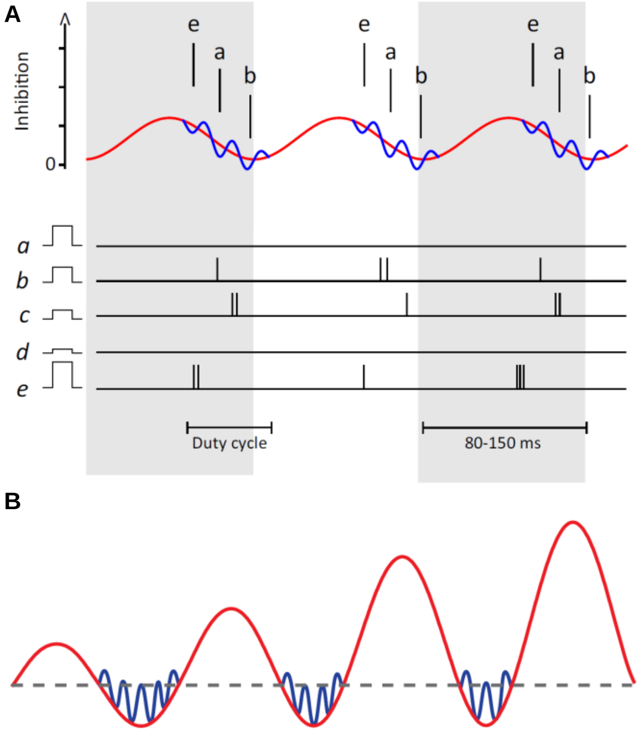

Figure 1.2.3: Current model of pulsed inhibition. **A)** The alpha rhythm is providing a temporal framework for gamma firing bursts. Cortical excitability is decreased in some phases of the alpha oscillations. When the alpha cycle changes from a phase of low excitability towards high excitability, the stimulus processing via gamma oscillations is enabled, with the most relevant stimulus being processed first. **B)** The number of duty cycles is dependent on alpha power. The higher the level of alpha

power is, the fewer gamma cycles can be fulfilled. Figure adapted from Jensen et al. (2014).

While the hypothesis of gating-by-inhibition can explain many behavioral results obtained in the current literature, the model at its current state is dependent on the periodic properties of the oscillations. This however, can be a considerable problem in tasks with unknown stimulus onset time. When the possible onset asynchrony is large enough, then the chance increases for the attended stimulus to fall into a phase of low cortical excitability. Schroeder and Lakatos (2009a) suggest therefore the existence of two modes in which lower frequency oscillations can function. One is a rhythmic mode, where the phase of high cortical excitability gets aligned to the expected onset of the stimulus, and is therefore consequential to behavior. This mode relies on rhythmic environments such as regularly spaced stimulus presentation, periodic events, or predictable inter-stimulus time intervals. Yet, when the environment does contain these temporal regularities, the system can enter a continuous mode of operation relying on the sustained power imbalance between the contralateral (decrease) and ipsilateral side (increase). This continuous mode generates much higher metabolic costs than the rhythmic mode, but it would provide a better attentional control within tasks where the exact onset of the target is unknown, such us in vigilance tasks (Schroeder & Lakatos, 2009).

To conclude, lower frequency oscillations, especially within the alpha frequency range, seem to serve an inhibitory role for irrelevant sensory information through an increase in power and consequently decreased cortical activity. Low frequency oscillations seem to operate in a phasic manner and are tightly coupled to gamma activity during stimulus processing. The brain modulates the phase or power of ongoing oscillations, dependent on the temporal certainty of an attended event. In this respect, it is worth noting that the 'gating-by-inhibition' hypothesis of Jensen and Mazaheri (2010) and the 'rhythmic-vs-continuous modes' hypothesis of Schroeder and Lakatos (2009) are not mutually exclusive; rather both frameworks offer an important tool to explain the effect of low frequency oscillations upon perception

1.3. Scope of this thesis

The previous sections reviewed the current state-of-the-art about attention and low frequency neural oscillations. A special focus was the interaction between different types of attention, namely cross-modal spatial attention and cross-modal temporal attention.

While strong cross-modal links for spatial attention seem to be established on the level of behavior (Spence & Driver, 1996), ERPs (Eimer, 2001) and prestimulus oscillations (Bauer et al., 2012); the relation between attention to time and modality in cross-modal temporal paradigms is less clear. Lange and Röder (2006) found in their ERP study strong cross-modal correspondences between time and modality at the level of behavior and in ERPs, whereas Pomper et al. (2015) and Keil et al. (2015) found temporal attention and modality attention to be mostly independent from each other in terms of oscillatory power, although Keil et al. found an interaction between attention to time and modality that reflected in terms of inter-trial coherence, putatively reflecting changes in functional connectivity.

This thesis presents three original studies investigating the relation between attention to time and attention to modality on the levels of behavior and prestimulus neuronal oscillations. To do so, the task that Spence and Driver (1996) used to study spatial cross-modal attention was adjusted here to our experimental needs in order to establish a direct dependence between attention to time and modality and to compare the results to the ones obtained in other cross-modal temporal attention paradigms, as well as with the results obtained for cross-modal spatial attention.

1.3.1. Goals and hypotheses

The goal of this thesis was to investigate the relationship between attention to time and modality (see Figure 1.3.1.). We conducted three studies, reported in the form of scientific papers. In our first study, the goal was to measure the interaction between attention to time and modality in behavior, using visual and tactile stimuli (Mühlberg et al., 2014). In a second study, we tested the generality of the pattern of effects observed with vision and touch by using a different modality combination, audition and touch (Mühlberg & Soto-Faraco, 2016). Finally the goal of the last study of this thesis was to investigate the modulation of low frequency oscillations in the prestimulus period for the cross-modal temporal attention task, using EEG (Mühlberg et al., 2016). An overview over the three experiments is presented in Figure 1.3.1., followed by a quick summary and specific formulation of hypotheses, for each.

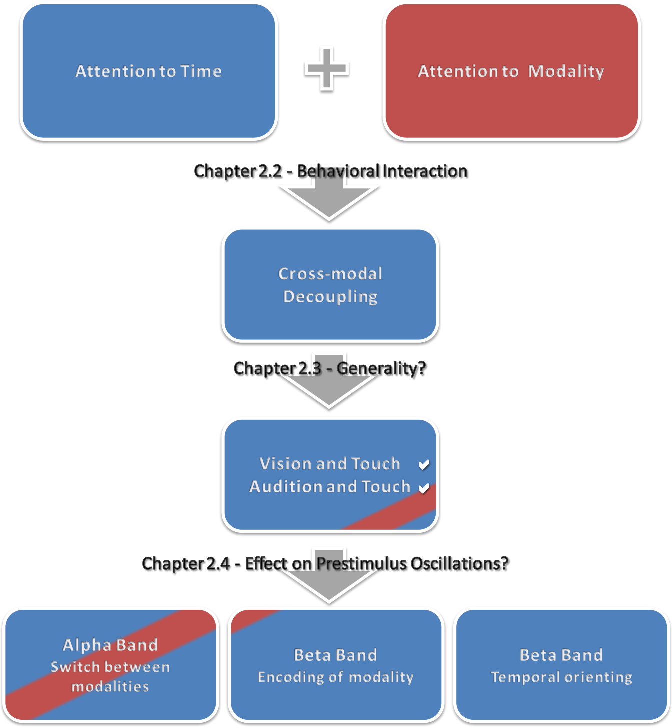

Figure 1.3.1: Overview over the three studies and their outcomes. Chapter 2.2 investigates the behavioral interaction between attention to time and attention to modality. The second paper (Chapter 2.3)

investigates the generality of the effects observed in the first study. Chapter 2.4 investigates the interaction between attention to time and modality on the level of prestimulus oscillations.

Within the first study, we investigated the interplay between attention to time and modality by using a discrimination task between single and double pulse stimuli in the visual or tactile modality. The target could appear after 1.2 seconds or after 2.5 seconds of a cue to the upcoming stimulus side. Through probabilistic cueing, we manipulated the participants' attention such that they expected the most likely (primary) modality at the most likely (expected) time point and the less likely (secondary) modality at the less likely (unexpected) time point. Of course such probabilistic cueing affects both, the participants' attention and expectation, yet it was not the purpose of this study to distinguish between these two, especially since both lead to similar behavioral consequences. Since a clear distinction between attention and expectation cannot always be made within our paradigm, we will jointly use these two words within the following studies. By maintaining temporal uncertainty throughout the trial using catch trials, we were able to analyze the behavioral effects at both possible onsets. Through this, we wanted make our data directly comparable with Spence and Driver (1996) and to the findings of Lange and Röder (2006). Through the data analysis at both time points, we planned to observe furthermore the whole temporal pattern of cross-modal attention and may uncover further links or decoupling in temporal attention. This experiment can attribute between two hypotheses: On the one side, if the hypothesis of cross-modal coupling is true, based on the findings of Lange and Röder (2006), we expected to find strong cross-modal links between attention to time and modality, such that responses towards every modality would be the fastest at the overall expected time point, despite their relative probabilities. On the other side, if we should fail to do so, than this would be evidence that temporal attention and spatial attention might operate different across modalities, up to the point that both modalities are maybe oriented fully independently. This would support the cross-modal decoupling hypothesis.

Independent of our findings in study 1, which clearly indicated cross-modal decoupling in temporal attention, the few different experimental findings so far in the literature vary in their interpretation. One obvious possible cause is the variation in the particular modality combination used. We hypothesized that, if our results of study 1 may reflect a general mechanism, than one should also observe a similar pattern with a different combination of modalities. Our experiment presented in the first study of this thesis used visual and tactile stimuli. Yet, visual stimuli are generally considered to be less temporally reliable than auditory or tactile stimuli (VanRullen et al., 2014). Thus, even if we failed to find cross-modal links between time and modality in that study, these links might still exists, when using auditory stimuli, since audition is generally considered to be the dominant modality in time (Kubovy, 1988). Following up this assumption, in our study 2 we repeated the task of study 1 with auditory and tactile stimuli. We expected to be able to replicate our findings of study 1 and thus might add evidence that our conclusion that cross-modal attention decoupling might reflect a general mechanism in temporal attention. Indeed, our results confirmed this conclusion.

In the third and last study presented in this thesis (Mühlberg et al., 2016), using the EEG to try and unravel the pattern of underlying changes in pre-stimulus oscillations in a cross-modal temporal paradigm, using an adaptation of the task used in study 1. In contrast to other studies investigating the combined effect of attention to time and attention to modality, both types of attention are strongly interlaced in our paradigm. We were inspired by a previous unimodal study conducted by van Ede et al. (2011), who investigated the interplay of attention to time and space using tactile stimuli. Instead of analyzing the ipsilateral and contralateral power against the baseline separately, van Ede et al. combined these two measurements into a common lateralization index, here a contra-over-ipsi ratio. The lateralization index reflects a power imbalance between the two hemispheres, without distinguishing if the imbalance is driven by changes in the ipsilateral hemisphere, the contralateral hemisphere or both. Lateralization index values below one reflect higher ipsilateral than contralateral power, and above one reflect the opposite imbalance. One advantage is that the lateralization index allows averaging the effects of power modulation over stimulation side, increasing the amount of trials per condition and thus statistical power. In the study of van Ede et al., the target stimuli could appear at two different time points or at three different time points with fixed hazard rates for these two different experimental conditions. They found that the typical pattern of alpha modulation could be observed with a decreased contra-over-ipsi ratio in advance of the moment of likely stimulus appearance (around its possible onset time), but not in the time window in between. This effect was especially evident within the beta band (although some effect could also be observed for alpha oscillations).

We hypothesized that cross-modal attention in time would express in a similar way, only our interest was to identify to which extent this effect would express in the interaction between attention to time and modality. Using the same contra-over-ipsi ratio as van Ede et al., we suspected that temporal attention would express in the time windows around stimulus onset, with the power in the alpha and/or beta band being more lateralized in advance of likely stimulus onset times, but not in the time window between possible onsets. Additionally, we expected that modality attention would be expressed in changes in the localization of the power modulations, with an increase over central sensors (reflecting activity in the somatosensory cortex) and a decrease over occipital sensors (reflecting activity in the occipital cortex) when a visual stimulus was most likely and the opposite pattern when participants had to orient towards a tactile event.

In the following section of the thesis, I will present these three studies and their results in detail and I will discuss their implications upon the field of cross-modal temporal attention, as well as their position in the general attention literature, in the subsequent discussion.

2. EXPERIMENTAL SECTION

2.1. Overview of the experiments

Chapter 2 of this thesis consists of three independent studies that are either published in international journals or submitted for publishing.

Study 1 (Mühlberg et al., 2014) investigates the behavioral interplay between attention to time and modality, using a single/double discrimination task. Stimuli could be presented at two different time points (1.2 or 2.5s) and be presented within two different modalities (vision or touch). One of the time points and one of the modalities were more likely to appear. Attention to time and modality were manipulated orthogonal in a probabilistic manner. The most likely, primary, modality was mostly presented at the most likely, expected, time point, while at the unexpected time point, the majority of targets belonged to the secondary modality. Behavioral reactions were measured in terms of reaction times, accuracy and inverse efficiency. The study was published in the European Journal of Neuroscience.

Study 2 (Mühlberg & Soto-Faraco, 2016) investigates the interplay between attention to time and a different combination of modalities. Again a target could be presented at two different time point (1.2 or 2.4 s) and within two different modalities (audition and touch). Keeping the relation between attention to time and modality similar to study 1, the goal was to test the generality of the previously observed effect. Behavioral reactions were recorded through reaction times, accuracy, median reaction times and inverse efficiency. The study was submitted to the Journal of Experimental Psychology: Human Perception and Behavior.

Finally, study 3 (Mühlberg et al., 2016) investigates the interplay of attention to time and modality upon the level of prestimulus neuronal oscillations. As previously, attention to time and modality were manipulated orthogonally and stimuli could appear at two different time points (1.2 or 2.4 s) and within two different modalities (vision or touch). The behavior was measured through reaction times and accuracy and the neuronal expression was measured through a contra-over-ipsi ratio (a measure of lateralization) in sensor and source space. The study was submitted to Cortex.

2.2. Cross-modal decoupling in temporal attention

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Cross-modal decoupling in temporal attention

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Cross-modal decoupling in temporal attention between audition and touch

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(This article is submitted for review to the *Journal of Experimental Psychology: Human Perception and Performance*)

Abstract

Similar to spatial selective attention, endogenous orienting of attention in time leads to various behavioural benefits for sensory events occurring at the attended moment. However, when temporal allocation of attention happens in a cross-modal context, its consequences do not seem to follow the same rules as cross-modal spatial attention. Whilst spatial attention and modality attention seem to be closely coupled, with space dominating over modality, there exists some controversy regarding the interaction of temporal attention and modality attention. Recent findings suggest that temporal expectations in vision and touch can unfold independently of one another (i.e. decoupled), whereas prior studies using an audio-tactile paradigm have reported that, like in spatial attention, there is a tight cross-modal coupling in temporal attention. In the present study, we address the generality of cross-modal decoupling for auditory and tactile stimuli. If cross-modal decoupling is a general property of temporal attention, we would expect to reproduce it in this study, whereas if decoupling depends on the particular modality pairing, then we will find cross-modal coupling (temporal attention would prevail over modality attention). The results from two experiments support the former account. In both experiments, we found an interaction between attention to time and modality. Furthermore, our results suggest that cross-modal decoupling might be modulated by task difficulty.

Introduction

Within most everyday life situations, our sensory organs receive more information than our brains are possibly able to process. Selective attention is thereby an essential mechanism (or set of mechanisms) to manage this information stream, boosting the processing of relevant sensory information and filtering out irrelevant one (Treue, 2003). The focus of attention can be captured automatically towards salient, novel stimuli or be oriented voluntarily, in a strategic fashion, according to goals and intentions (Jonides, 1981, Posner & Cohen, 1984; Chica et al., 2013). Although attention orienting has been most studied in terms of spatial selection, one of the most basic dimensions towards which one can orient attention is time. Temporal attention helps improve performance for events occurring at attended moments, compared to non-attended moments in time, by granting faster responses (e.g. Correa et al., 2004; Coull&Nobre, 1998; Griffin et al., 2001; Miniussi et al., 1999), increased accuracy (Correa &Nobre, 2008) and lower perception thresholds (Cravo et al., 2013; Rohenkohl et al., 2012). Additionally, temporal attention has been found to modulate the N100 component elicited in sensory ERPs (Lange et al., 2003; Lange et al., 2006; Lange, 2012; Miniussi et al., 1999; Sanders &Astheimer, 2008), a component which is often also modulated by spatial attention (Eimer& Driver, 2000; Eimer&Schröger, 1998). Temporal attention also modulates later ERP components, such as the P300 (Lampar& Lange, 2011; Miniussi et al., 1999) and the N200 (Sanders &Astheimer, 2008).

However, while most of the existing literature focuses on unisensory temporal attention, our world is multisensory by nature and thus the system must constantly face the problem of cross-modal selection, in addition to spatial or temporal selection. That is, to allocate processing resources to information arising from different sensory systems. A classical question here is whether orienting attention in one modality affects other sensory modalities or else, resources can be managed independently for each sense (Driver & Spence, 1998a, 1998b; Spence & Driver, 1997).

Whilst work in the last 20 years has led to a generalized agreement about the existence of strong cross-modal coupling of attention in spatial orienting (eg. Driver & Spence, 1994; Eimer& Driver, 2000; Eimer et al., 2002; Eimer, 1999; Macaluso& Driver, 2005; Macaluso et al., 2000; Macaluso, 2010; Sambo & Forster, 2011; Santangelo et al., 2010; Spence & Driver, 1997, 1996; Spence et al., 2000; Tang et al., 2015; Trenner et al., 2008), the consequences of cross-modal orienting in time has been far less studied and results are still controversial (Lange &Röder, 2006; Mühlberg et al., 2014). There are some rare cases of spatial cross-modal decoupling reported as well. Of importance in the present context is thereby the study from Lloyd et al. (2003), because they investigated the case of audition and touch, addressed in the present study (see also Soto-Faraco et al., 2005, for another failure to find cross-modal synergies in an audio-visual sustained spatial attention task). Within the experiment of Lloyd, participants had to orient their spatial attention for the most likely target modality (audition or touch), while remaining a spatially diffuse expectation for the less likely modality, which were, however, slightly more likely at the opposite side. The authors reported spatial benefits for the most likely modality, while no effect of spatial cueing was found for the less likely modality. Yet, in a second experiment within the same study though, Lloyd et al. also found that it is more difficult to track auditory and tactile stimuli coming from different sides than from the same side of space. Hence, they concluded that while spatial decoupling is possible, it comes at a cost, which would still align well with the spatial synergy results of Spence and Driver (1996). A potential confound to explain the absence of (or weakened) cross-modal coupling in Lloyd et al. (2003; also in Soto-Faraco et al. 2005) could be the need for attentional re-orienting on trial-to-trial basis, as opposed to the possibility to sustain attention throughout a block of trials. It seems that, at least in spatial attention, the need for trial to trial transient orienting may induce less cross-modal coupling (Lloyd et al., 2003, pp. 917).

One important paper to address the relation between attention to time and modality was published by Lange andRöder (2006). The authors recorded behavioural and electrophysiological ERP responses to tactile and to auditory stimuli that could appear, with different known probabilities, at one of two different time points after a warning cue. Lange andRöder found a time-dependent coupled reaction time decrease for both modalities at the overall most expected time point and a modulation of the N100 component for both modalities, suggesting cross-modal synergy in temporal allocation of attention, similar to previous cross-modal spatial attention results (Spence & Driver, 1996). However, the authors in this paper were able to investigate responses at only one (the early) time point, because the changing hazard rates in their protocol led to absolute temporal certainty at the late onset, violating the assumption of uncertainty (Coull&Nobre, 1998; Griffin et al., 2001). In order to investigate both responses towards an early and towards a late target, Mühlberg, Oriolo and Soto-Faraco (2014) adjusted a paradigm previously used by Spence and Driver (1996), where two modalities, vision and touch, possessed different likelihoods at two possible onset times, early and late, and added catch trials without stimuli in order to prevent temporal certainty. In contrast to the results of Lange andRöder (2006), Mühlberg et al. found a clear decoupling of cross-modal temporal attention, meaning that responses towards every modality were the fastest at their respective times of maximal likelihood. These findings are in stark contrast to the earlier results obtained by Lange andRöder, hence a paramount question arises as how general the cross-modal coupling/decoupling effects in temporal attention are.

One possibility is that the disparity between Lange andRöder (2006) results and Mühlberg et al. (2014) results simply reflects that different cross-modal combinations are subject to different degrees of coupling/decoupling of temporal attention. In this case, touch-audition would happen to be more strongly coupled in time than touch-vision. Such an account could be supported by the fact that vision is less temporally reliable than both, audition and touch

(Kubovy, 1988; VanRullen et al., 2014). Such modality asymmetries have been reported before, for example in the case of cross-modal spatial attention (Klein, 1977; Posner et al., 1976), or when it comes to quickly switching attention expectation towards or away from touch (Spence, Nicholls, & Driver, 2001). Another possibility, however, is that temporal orienting of attention is fundamentally different from spatial orienting of attention in terms of how strongly different sensory modalities follow each other.

We argue that there is a basic difference between temporal and spatial constraints on attention selection that could possibly underlie differences in their behavioural expression (see Mühlberg et al. 2014). Spatial attention usually involves a pressure for processing several events at the same time, which are competing for resources, and emphasizes the parallel nature of attentional selection based on spatial and non-spatial features (Desimone& Duncan, 1995). In contrast, within temporal attention, orienting episodes to events occur serially, allowing for a more flexible allocation of processing resources at relevant (and irrelevant) moments in time (Mühlberg et al., 2014). This tentative hypothesis is indirectly supported through various differences in neural expression, from ERPs and fMRI studies, between spatial (Eimer& Driver, 2000; Störmer et al., 2009; Yang & Mayer, 2013) and temporal attention (Coull&Nobre, 1998; Davranche et al., 2011; Lampar& Lange, 2011; Miniussi et al., 1999; Sanders &Astheimer, 2008). If temporal and spatial attention are indeed intrinsically different, then cross-modal temporal decoupling might represent a general property of the mechanism.

Therefore, one should be able to find evidence for decoupling between other pairs of modalities including audition and touch, just like Mühlberg et al. had previously found with touch and vision.

The particular case of audition and touch, used here, is interesting because it allows comparison with the previous work of Lange andRöder (2006). If decoupling turns out to be true, one then should attribute the discrepant findings of Lange andRöder to methodological differences. In order to discern between these two possibilities, we designed a protocol to measure possible coupling-decoupling in cross-modal temporal attention based on a previous task used in Mühlberg et al., but with audition and touch as target modalities. This paradigm allows one to dissociate endogenous attention to modality (high- vs. low-probability target modality) and time (high- vs. low-probability onset time) by setting opposite relative temporal probabilities in each modality. Cross-modal coupling will express as the most likely (primary) modality dominating temporal expectation of the less likely (secondary) modality, producing a main effect of time expectation regardless of modality prevalence (primary or secondary). Temporal decoupling, instead, will express as each sensory modality following its own expectation pattern, producing an interaction between time expectation and modality prevalence (primary vs. secondary). Reaction times and accuracy are used to measure expectation in the observers.

Experiment 1

Methods

Participants

A total of 29 participants volunteered for this experiment (2 left-handed; 20 female; mean age 25.92 years, age-range 18-61 yeas) in exchange for 8€ per hour. They all reported normal or corrected to normal vision and gave written informed consent to participate in the study, which was in accordance to the Declaration of Helsinki and approved by the ethics committee CEIC Parc de Salut Mar (University Pompeu Fabra, Barcelona, Spain).

Stimuli

The stimuli used as targets in the study could be auditory or tactile, and presented as single or double pulse stimulation. Auditory stimuli consisted of auditory tones with a frequency of 1000Hz, delivered via headphones at a comfortable loudness. Single pulse stimuli lasted 50ms, whereas double pulse stimuli consisted of two pure tone bursts of 10ms duration, separated by a 30ms gap. Tactile stimulation was presented on the left and right index finger pad of the participant's hand and was delivered by a solenoid tapper (round tip, 8 mm, Miniature Solenoid Tapper Controller Mk3, MSTC3-10M, M&E Solve, UK). For single pulse stimulation, the tapper was lifted for 10ms; double pulse stimuli consisted of two 2 ms stimulations, separated by an 8 ms gap. The tactile stimulation did not cause any pain or annoyance to the participant. These parameters of the auditory and tactile stimuli were adjusted based on prior informal pilot testing, so that the accuracy for both would exceed chance level.

Experimental design and procedure

The experiment protocol and response collection protocols were custom programmed using MatLab 8.3.0 (The MathWorks Inc.; Natick, MA, USA). The goal of this study was to investigate if cross-modal decoupling in time (Mühlberg et al., 2014) extends a different set of modalities such as audition and touch. In order to do so, we adjusted the task design from Mühlberg et al. to suffice the aforementioned experimental purpose.

Participants performed a one vs. two pulse discrimination task over tactile and auditory stimuli in a paradigm where we manipulated the participants' expectations about the onset time and modality of the upcoming target. The experiment was conducted in a sound attenuated room with dim illumination. Participants sat in a chair with their arms relaxed on each side, on the chair armrests. A monitor placed in front of the participants displayed a black fixation cross on a grey background and two grey arrows, left and right side of the fixation cross, respectively pointing left and right. In order to start a trial, participants had to simultaneously press two foot pedals, placed underneath the heel and the toes of their dominant foot, and remain pressing the pedals at all times until the response. Each trial started with a colour change of one of the arrows from grey to black, indicating the side of the upcoming stimulus with 100% validity. The onset of the cue was accompanied by masking white noise over headphones, which was presented throughout the whole length of the trial in order to block out the slight noise produced by the solenoid tappers. Either 1.2s (early) or 2.4s (late) after this spatial cue, a target stimulus could appear which could either be auditory or tactile, and could also be single or double pulse stimulation. Participants had to discriminate if the target stimulus had been a single or double and in order to do so, participants had to release (depress) one of two foot pedals (response mapping counterbalanced across participants). If participants failed to press both pedals during the trial or during the first 100ms after target presented, the trial got discarded and was repeated at a later time point within the block. Participants were informed before every block about the most likely time point of target appearance and the most likely modality, and instructed to answer as fast and as accurately as possible. After the response (or after the response timeout of 3s), an intertrial interval of 1s led to the beginning of the next trial.

In order to manipulate the participants' expectation about onset time and target modality in a cross-modal manner, we adjusted the likelihoods these two factors in a probabilistic manner (Fig. 2.3.1). Temporal expectation about onset time was manipulated in a block wise manner. Targets would appear at the expected onset time in 54% of the trials, compared to only 23% of trials containing the target at the unexpected onset time. The remaining 23% of trials would be catch trials where no target would appear at all.

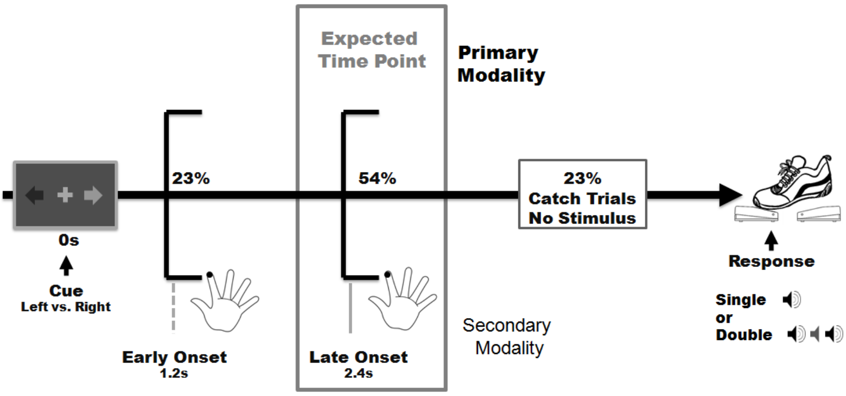

Figure 2.3.1: Schematic description of the task. Every trial started with a colour change of a visual arrow cue left or right from the fixation cross. After 1.2s or 2.4s an auditory or a tactile target could appear. The likelihood of appearance of each combination of time point and modality differed in order to drive attention to time and modality in a certain direction. One of the two modalities was far more likely to appear (fixed between participants) and the target was more likely to appear at one of the time points (fixed between blocks). Importantly, while targets of the more likely, primary modality would be mostly presented at the more likely, expected time point, they would be the minority at the unexpected time point, where most targets were of the secondary modality. In order to prevent complete temporal certainty, some trials contained no target at all.

To manipulate modality prevalence, we made one of the two target modalities, called primary modality, more likely to appear than the other, accounting for a total of 70% of all targets, whereas only 30% of all targets belonged to the other, secondary modality. Which modality would be the primary modality and which the secondary modality, was thereby fixed for each participant and encoded in the factor primary modality. Since one of the participants was excluded from the analysis due to chance accuracy in one of the experimental conditions, resulting in a total of 28 participants in the analysis, the factor of primary modality was counterbalanced between participants and each of the groups contained a total of 14 participants.

Most importantly, in order to measure any decoupling between modality and time, the factors modality prevalence and temporal expectation influenced each other in the following way. At the expected time point the majority of targets (86%) where primary modality targets and only the remaining 14% of targets were in the secondary modality. At the unexpected time point the likelihoods reversed, so that 67% of targets were in the secondary modality and the remaining 33% were in the primary modality.

Every participant ran a total of six experimental blocks of 108 trials each (total of 648). Within three of the experimental blocks the early onset would be the expected onset (1.2s) and within the remaining three blocks the late onset (2.4s), with the order of conditions, AAABBB, being counterbalanced between participants. One experimental session lasted approximately 45min. During the experiment, reaction times and response accuracy were recorded. Trials in which the participants failed to provide a response or in which the foot pedals were not correctly pressed were automatically discarded and repeated at the end of the block.

In order to learn the probabilities of the different experimental conditions, participants performed the task on a training set of 36 trials. The training consisted only of half of the primary targets at the expected onset and half of the secondary targets at the unexpected onset of the first three experimental blocks. In order to learn the temporal properties further visual temporal information was given throughout the training. After the initial cue, the arrow corresponding to the cued side would flicker every 400ms for 50ms, resulting in two flickers before an early target and five flickers before a late target. Participants were made aware of this supporting temporal information and instructed to use it. Additionally, a second training set, consisting of 24 trials, was presented after the first three blocks in order to enable the participant to adapt upon the changed temporal expectation. The data from the training sets were not analysed.

Analysis

All incorrect responses and RTs two standard deviations away from the individual mean were discarded from the analysis (<5% of all trials were excluded). In addition to mean RTs and accuracy, we calculated the median RT and the inverse efficiency score (IE=RT/Proportion of correct responses). IE is accounting for trade off effects between RTs and accuracy and, according to Bruyer and Brysbaert (2011), makes sense especially at low error rates, which was the case in this study.

A repeated measures ANOVA was performed for mean RTs, accuracy, IEs and median RTs with modality prevalence (primary, secondary), onset time (1.2s, 2.4s) and expected time point (early, late) as within participant factors and primary modality (audition, touch) as between participant factor. Statistics were performed with IBM SPSS Statistics 19 (IBM Corp., Armonk, NY, USA).

Results

Mean RTs

We found a significant main effect of modality prevalence ($F_{1,26}=21.31$, $p<0.01$), with participants responding faster towards primary modality targets than towards secondary. Furthermore, we found an interaction between the primary modality and the modality prevalence ($F_{1,26}=12.01$, $p<0.01$) showing that the main effect of modality prevalence is mainly driven by the audition group, where we have a strong difference between the primary (audition, 807ms) and secondary modality (touch, 992ms; $p<0.01$), whereas there was no significant difference between the responses towards primary and secondary modality targets within the touch group (touch, 878ms vs. audition, 904ms; $p=0.42$).

No other main effect reached significance. We found two close-to-significance interactions, one between modality prevalence and time expectation ($F_{1,26}=3.98$, $p=0.056$) and another between modality prevalence, time expectation and primary modality ($F_{1,26}=3.93$, $p=0.058$). In light of the theoretical importance (as per our hypotheses, above) of these interactions involving temporal expectation and modality prevalence, we decided to follow up the higher order, three way interaction. Indeed, this pattern reflects that, in the touch group the RTs were modulated following the relative time/modality likelihoods (modality prevalence by time expectation interaction within the touch group; F1,12=5.54, p=0.037), hence reflecting decoupling, whereas in the audition group there was a very dominant effect of modality prevalence (F1,12=0.00, p=0.99) without temporal modulation, hence reflecting neither coupling nor decoupling in the audition group.

Accuracy

The overall accuracy during the experiment was very high, with on average 92.4% correct responses. We found a significant interaction between modality prevalence and primary modality (F1,26=40.02, p<0.01), with more accurate responses towards the primary modality for the audition group (p<0.01) and more accurate responses towards the secondary modality for the touch group (p<0.01). Please note that this pattern simply reflects that, overall, responses to auditory targets were more accurate than to tactile targets. This effect was further modulated by the onset time, leading to a three way interaction between onset time, modality prevalence and primary modality (F1,26=7.51, p=0.01). However, post-hoc t-tests revealed that the aforementioned effect (audition being more accurate than touch) was highly significant at every onset time (p<0.01 for all conditions). Thus, this analysis proves that participants responded more accurate towards auditory targets (97.02%), than towards tactile targets (87.91%). No other main effect or interact reached significance and no trends were observed.

Inverse Efficiency

We found significant main effect of modality prevalence (F1,26=8.77, p<0.01). As for reaction times, responses towards primary modality targets were significantly more efficient than towards secondary modality targets (p<0.01). Again, this effect was modulated by the primary modality (F1,26=25.35, p<0.01), so that this modality prevalence effect was highly significant for the audition group (p<0.01) but not present in the touch group (p=0.15). Additionally, just like in the mean RT analyses, we found a trend towards an interaction between the modality prevalence, time expectation and primary modality (F1,26=3.51, p=0.07). The pattern behind this marginal interaction is the same as in the RT analysis; IE scores reflect the modulation of each sensory modality to its relative likelihoods in time for the touch group (F1,12=3.98, p=0.069, for the modality prevalence by temporal expectation interaction in the touch group), indicating decoupling. In the auditory group, instead, the data revealed a strong modality prevalence effect (F1,12=33.02, p<0.01) independent of time likelihoods (F1,12=0.30, p=0.59, for the interaction between modality prevalence and time expectation in the audition group). No other significant main effects or interactions and no further trends were observed.

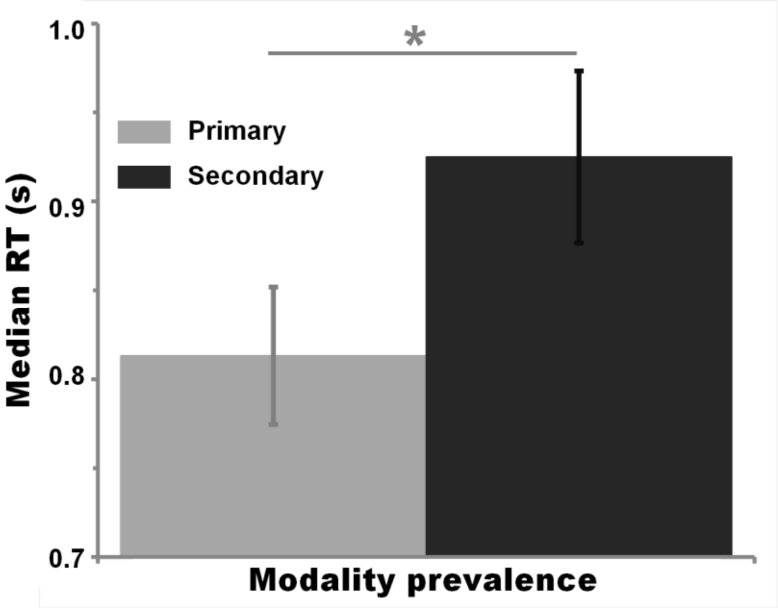

Figure 2.3.2: Main effect of modality prevalence. Responses towards primary modality targets (0.813s) were significant faster than towards secondary modality targets (0.925s). Similar significant effects were observed for mean RT and IE.

Median RTs

As for mean RT and IE, we found a significant main effect of modality prevalence (Fig.2.3.2, F1,26=19.80, p<0.01) and a significant interaction between modality prevalence and primary modality (F1,26=8.04, p<0.01), with the effect of faster responses to primary modality targets (p<0.01) being entirely driven by the audition group (p<0.01), whereas there was no significant difference between primary and secondary modality targets for the touch group (p=0.26). Also, we found a significant interaction between modality prevalence, time expectation and primary modality (Fig.3, F1,26=5.04, p=0.033). In addition to the observed effects, we found further trends towards a main effect of time expectation (F1,26=3.54, p=0.071) and towards a two-way interaction between modality prevalence and time expectation (F1,26=3.35, p=0.079), which are explained within the larger order, significant interaction. No further significant results or trends were observed. Like above, we decided to follow up the triple interaction effect in further detail by running separate ANOVAs for the audition and touch group. Please note that this significant interaction supports the consistent trends with the same pattern (albeit only marginally significant interactions), found on mean RTs and IEs. In the touch group, we did find a trend towards a main effect of temporal expectation (F1,13=4.52,p=0.053) and, most importantly, a significant interaction between temporal expectation and modality prevalence (F1,13=4.98,p=0.044). This interaction reveals a decoupling pattern; Participants showed a significant median RT speed up (84 ms) for the primary modality at the expected time point vs. the unexpected time point (Fig. 2.3.3B, p<0.01), whereas a numerical trend in the opposite direction (-23 ms) without significant time expectation modulation was seen in the secondary modality targets (Fig. 2.3.3B, p=0.39). In the audition group, we found a main effect of modality prevalence (F1,13=16.59,p<0.01), yet no other significant main effect or interactions and no other trends (0.05<p<0.1). In particular, the interaction between temporal expectation and modality prevalence was clearly far from significance (Fig. 2.3.3A, F1,13=0.26,p=0.62). So, participants were faster to respond to primary (auditory) targets than to secondary (touch) targets, but response times were statistically equivalent between the expected and unexpected time points within primary modality targets (p=0.85) and within secondary modality targets (p=0.55).

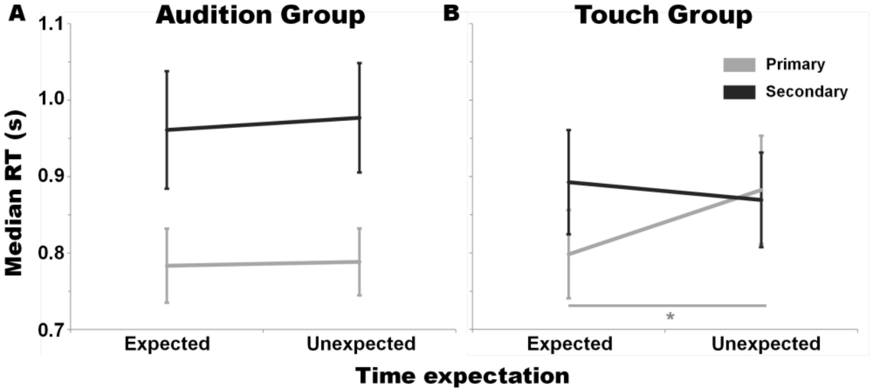

Figure 2.3.3: Interaction between modality prevalence, time expectation and primary modality. While not significant, similar trends had been observed for RTs and IEs. **A)** Interaction between modality prevalence and time expectation for the audition group. Neither for the primary, nor for the secondary modality can a temporal modulation of modality attention be observed. **B)** Interaction between modality prevalence and time expectation for the touch group. Responses towards the primary modality are significantly faster at the expected time point (0.798s) than at the unexpected time point (0.882s, p<0.01). For the secondary modality there was no significant difference for the secondary modality at the expected time point (0.893s) compared to secondary responses at the unexpected time point (0.869s, p=0.39).

Discussion

According to the hypothesis of cross-modal coupling in temporal attention, one would expect that at moments of strong expectation for one sensory modality, other sensory modalities would also be facilitated (Lange &Röder, 2006). In Experiment 1, we pitched relative time expectancies of two different modalities against each other, and failed to find any evidence for cross-modal temporal coupling. Instead, we found evidence for decoupling in some modality pairings, like it happens with touch and vision (Mühlberg et al.), or lack of evidence for either. Such decoupling revealed itself as strong trends towards an interaction of temporal expectation and modality prevalence. Strong expectation about a tactile target at a particular time point, did not express as an advantage for auditory targets presented at that time point. Instead, if something, responses to auditory targets tended to follow their own likelihoods. This pattern was consistent across mean and median RTs and IE scores, though it was most strongly revealed in statistical terms for median RTs, a measure more robust to individual variability inherent in RT distributions.

Although the failure to find coupling, plus the existence of this decoupling pattern in the touch group is sufficient to rule out the generality of the coupling hypothesis, our results also show a clearly different pattern in the auditory group (hence the interaction between temporal expectation, modality prevalence and primary modality). Indeed we found a significant interaction for temporal expectation and modality prevalence for the touch group, but not for the audition group, questioning the generality of the decoupling effect as well. At this point, one clear possible explanation of the failure of decoupling pattern to arise in the auditory group would be that the discrimination of the auditory targets was simply too easy, so that participants had no need to resort to selective attention to be able to respond to auditory targets (Spitzer et al., 1988). It is possible that due to the low auditory task difficulty and perhaps also due to an auditory temporal dominance (Kubovy, 1988; Welch & Warren, 1980), possible temporal effects of the primary (auditory) and secondary (tactile) were just washed away when audition was the favoured modality by attention. Please note that strictly speaking, the coupling hypothesis would predict a strong temporal orienting effect for the primary modality, together with a trend in the same direction for the secondary modality. Instead, what happened in this group is that temporal orienting failed to occur altogether[2].

Within a past study we revealed evidence for decoupling between touch and vision (Mühlberg et al., 2014), and here we report evidence for decoupling when participants monitor for touch targets and get occasional auditory targets. In addition, the case for the auditory primary group does not clearly lean towards coupling or decoupling pattern due to a failure to reproduce temporal orienting altogether. This pattern allows us to conclude that cross-modal coupling is, by no means, a norm in temporal attention. On the contrary, most cases seem to point to the idea that allocation of resources across modalities can be flexibility and strategically

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[2] In other words, like we have a high spatial resolution for vision and therefore visual dominance in crossmodal spatial attention paradigms (e.g. ventriloquist effect; Jackson, 1953; Slutsky & Recanzone, 2001; Spence, 2010; Welch & Warren, 1980), the resolution for audition in the temporal domain is higher than for vision or touch (Bresciani et al., 2005; Fendrich & Corballis, 2001; Morein-Zamir et al., 2003) and therefore audition would lead in temporal attention paradigms, dominating over all possible modulations in other modalities.

adapted in time. It, however, remains to be observed in how far the task difficulty was biasing these results, since the high auditory accuracy might render the orienting of the temporal attention unnecessary, an explanation which would perfectly fit the results of both experimental groups. In Experiment 2, we address this possibility, and try to extend decoupling to the case where audition difficulty is moderate.

Experiment 2

Methods

Participants

A total of 14 new participants volunteered for this experiment (3 left-handed; 12 female; mean age 22.86 years, age range 18-35 years) in exchange for 8€ per hour. They all reported normal or corrected to normal vision and gave written informed consent to participate in the study, which is in accordance to the Declaration of Helsinki and approved by the ethics committee CEIC Parc de Salut Mar (University Pompeu Fabra, Barcelona, Spain).

Stimuli

The goal of this experiment was to test the hypothesis that the task difficulty had affected the results for the audition group in Experiment 1. In order to test this hypothesis, we adjusted the loudness of the auditory stimuli in comparison to the background white noise for each individual separately until participants reached an auditory training performance of around 80% correct responses and subjectively reported that the orientation of attention was necessary in order to perceive the auditory stimulus correctly.

Experimental Design

The experimental design was mostly identical with Experiment 1. However, since our hypothesis about this experiment was made in reference to the results of the auditory group of the first experiment, all of our participants had audition as their primary modality and touch as their secondary modality, removing the factor of primary modality from our analysis.

Analysis

Our goal was a direct comparison of the data of experiment with the data obtained within this experiment. Thus, the analysis was conducted following the procedures of Experiment 1.

Results

Mean RTs

We found a significant effect of modality prevalence (F1,13=5.62, p=0.034) with faster responses for the primary (auditory, 893ms) than for the secondary modality targets (touch, 963ms; please note that this 70 ms difference, is less than half of the difference seen in Experiment 1; 185ms; p=0.021). Importantly, we found significant interaction between modality prevalence and temporal expectation (F1,13=6.37, p=0.025). Post-hoc t-tests revealed that responses to primary modality stimuli were significantly faster at the expected than at the unexpected time point (Fig. 2.3.4, 59ms, p<0.01), whereas responses towards secondary modality showed the opposite, albeit non-significant, directionality (Fig. 2.3.4, -22ms, p=0.44). No other main effect or interaction reached significance or showed a trend.

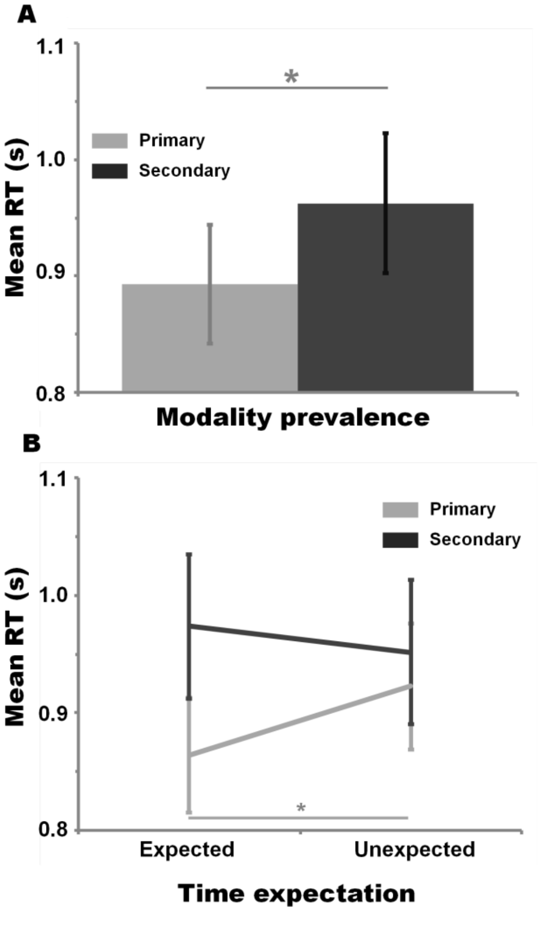

Figure 2.3.4: Mean reaction time results of Experiment 2. **A)** Main effect of modality prevalence. Participants responded significantly faster (p=0.034) towards primary stimuli (893ms) than towards secondary stimuli (963ms). The same effect was also for IE, but not for median RT data. **B)** Interaction between modality prevalence and time expectation.

For the primary modality, responses are faster at the expected time point (864ms), compared to responses at the unexpected time point (923ms, p<0.01). The difference between responses for secondary targets at the expected (974) compared to the unexpected time point (952ms) is insignificant. This interaction is not observable in IE data, however a similar trend was found for the median RTs.

Accuracy

Again the average accuracy within the experiment was very high (89.64%) and we observed a significant effect of modality prevalence (F1,13=20.42, p<0.01), where responses towards primary targets were more accurate (95.01%), than for secondary targets (84.26%).

No other significant effect or trend could be observed.

Inverse Efficiency

Similar to the mean reaction times, we observed again a significant main effect of modality prevalence (F1,13=11.45, p<0.01) with more efficient responses for the primary modality (949ms) than for the secondary modality (1181ms). Additionally, we observed a significant effect of time expectation (F1,13=6.28, p=0.026). Responses towards targets at the expected time point (1041ms) are thereby faster than responses towards targets at the unexpected time point (1089ms). No other main effect or interaction could reach significance or trend level. While the directionality of the responses for an interaction followed the mean reaction times, the interaction itself remained insignificant as well (F1,13=1.38, p=0.261).

Median RTs

For a complete comparison with Experiment 1, we also again added the results of the median RTs. In contrast to the mean reaction time data and the inverse efficiency data, none of the main effect reached significance or chance level. We did, however, observe a near-significant trend for the interaction between modality prevalence and time expectation (F1,13=4.51, p=0.053). The directionality of this trend followed the same pattern as the mean reaction times, with responses towards the primary modality being fastest at the expected time point (50ms speed-up) and the slower secondary modality responses at the expected time point (-33ms). No other interaction reached significance or displayed a trend.

Note that, whether significant (mean RTs) or near-significant (Median RTs), the pattern of effects in this new version of the auditory attention group, closely matches the pattern found in the tactile group of Experiment 1.

Discussion

In Experiment 1, we observed a difference in cross-modal temporal decoupling. Whereas we observed cross-modal temporal decoupling when touch was the dominant modality, (the primary tactile and secondary auditory targets followed each their own temporal properties); we did not see decoupling (neither coupling) within the audition group. Two accounts seemed likely to explain the pattern of our results, first a general auditory dominance in time (e.g. Bresciani et al., 2005; Fendrich&Corballis, 2001) and second an effect of lower difficulty of auditory stimuli and thus reduced need to reorient attention. In Experiment 2, we levelled off the difficulty of auditory targets by decreasing the loudness of the auditory stimulus. Responses towards the primary auditory targets were indeed slower, and accuracy levels marginally lower (we assume, due to practice), than in Experiment 1, suggesting a successful increase of difficulty. Critically, this time a clear decoupling effect emerged within the mean reaction time and similar near-significant interactions in the same directionality for the median RT data. While responses towards the primary auditory targets were significantly faster at expected time point, the secondary tactile stimuli did not follow the same pattern. This is evidence that cross-modal temporal decoupling is dependent of the task difficulty and that it is not intrinsically influenced by auditory dominance in the temporal domain.

General Discussion

Within the experiments reported here, we tested if temporal attention involving different modalities operates in a coupled fashion. The question is whether orienting follows a temporal expectation pattern dominated by one (more likely) modality, as some studies (Lange &Röder, 2006) suggest or if cross-modal temporal decoupling (Mühlberg et al., 2014), were each modality can unfold its own temporal expectation, is more generally observable. Because the two previous contradictory results had been obtained using different modality combinations, an outstanding interpretation problem was whether cross-modal coupling and decoupling may manifest selectively for different pairings of modalities. Here we modified the experiment of Mühlberg et al. (2014) to use auditory and tactile stimuli, to address which of these two possibilities is more likely. Following the assumption that audition is dominant in time (Bresciani et al., 2005; Fendrich&Corballis, 2001; Morein-Zamir et al., 2003), such as vision is generally considered spatially dominant (Spence, 2010; Welch & Warren, 1980), one could assume that the deployment of auditory (dominant modality) would lead to cross-modally coupled processing (like in Lange &Röder, 2006). However, here we observed that despite the involvement of the auditory modality, behaviour was more consistent with cross-modal temporal decoupling, suggesting that decoupling would indeed seem to be a general property arising from the mechanism of temporal attention. This provides another piece of evidence for a general difference between temporal and spatial attention, when operating in cross-modal contexts.

One could argue that within our experiment the auditory tactile stimuli were not presented in close spatial proximity, as the auditory stimuli were presented over head phones and the tactile stimuli over solenoid tappers at the index fingers. Within the study of Lange andRöder (2006) however, the stimuli were presented in close spatial proximity. Is there a possibility that our participants had used spatial location for selection, and hence, the decoupling is not between modality attention and temporal attention, but between spatial and temporal attention? This is technically possible, but unlikely. Please note that the spatial cues at the beginning of a trial in this experiment were 100% spatially valid, therefore the spatial disparity between the location of touch and sound is restricted to only a few degrees in depth and elevation, within the same hemifield. Auditory and tactile receptive fields are more flexibly located than visual receptive fields and can be changed e.g. through a change in body posture (Anderson & Bueno, 2002; Maravita et al., 2003). Audio-tactile stimulation can lead to similar activation patterns and behavioural interactions in absence of spatial alignment (e.g., Murray et al. 2005). Most importantly, Lloyd et al. (2003) did present auditory stimuli at four different spatial positions, two aligned with the spatial position of the tactile stimuli and two spatially incongruent and they found no effect of spatial congruency within their paradigm. They even repeated their experiment with crossed hands and found that changing the hand posture, did not only lead to a tactile remapping, but the auditory stimuli were remapped in a similar fashion than the tactile stimuli. Therefore, we believe this difference is here inconsequential to the interpretation of the decoupling result (please, also note our previous study, Mühlberg et al. (2014), also reported decoupling with much more closely matched spatial locations), though it must remain an open issue.

Behaviourally, it well known that in cross-modal spatial attention it is the most frequent case that different sensory modalities follow a common spatial orienting pattern, independent of their own spatial likelihoods (see Driver & Spence, 1994; Spence & Driver, 1996; Spence et al., 2000; Teder-Sälejärvi et al., 1999, please regard however Lloyd et al., 2003 and Soto-Faraco et al., 2005 for possible exceptions), suggesting a dominance of spatial attention over modality attention. This finding is supported by the investigation of prestimulus oscillations, showing the same lateralization pattern of alpha and beta oscillations in the occipital and central cortex independent if a visual or tactile stimulus was attended (Bauer, Kennett, & Driver, 2012). The interaction between modality attention and temporal attention is more flexible on the other hand (Keil et al., 2015). The authors found that different frequency ranges and brain areas were activated during the orienting of modality or temporal attention and they also found an interaction of the modality and temporal attention in the theta band range. While the studies of Bauer et al. (2012) and Keil et al. (2015) are not directly comparable in task design, their basic finding would be aligned with our hypothesis of different cross-modal interactions for spatial and temporal attention and thus indirectly supports cross-modal temporal decoupling as a general mechanism. Indeed, a different study of the same group (Pomper et al., 2015) used the same go- no go task with visual and tactile stimuli, who could appear after a fixed or random time interval. The study of Pomper et al. focussed thereby on the analysis of prestimulus modulations in the lower frequency bands and upon intertrial coherence. They found modality and temporal attention to be independently distributed in different frequency bands and scalp regions, with modality attention leading to modulations in the alpha and beta band within sensory cortices and temporal attention leading to activation of the motor cortex in the beta and delta band. Thus, this study would support temporal and modality attention to be dissociable from each other in their neural bases. In general, spatial attention is associated with a lateralization in the alpha frequency range (for vision or audition) or alpha/beta frequency range (for touch), in particular through contralateral decreases and or ipsilateral increases in amplitude in the alpha band (see e.g. Jensen &Mazaheri, 2010). A correlation between these changes in the alpha band and the modulation of prestimulus oscillations has been shown repeatedly (Hanslmayr et al., 2007; Romei et al., 2010; Thut et al., 2006). Temporal attention is usually leading to modulations in the beta band, which holds true for different modalities such as touch (van Ede et al., 2011) and audition (Todorovic et al., 2015). Spatial and temporal attention, despite sharing some similar activation patterns in the fMRI, also lead to non-overlapping activations at the cortical level. Spatial attention, but not temporal attention, usually activates areas such as the frontal eye field (Liu et al., 2014; Yang & Mayer, 2013), whereas activations such as in the superior occipital gyrus or the cerebellum seem to be rather related to temporal attention (Davranche et al., 2011; Li et al., 2012). All these studies suggest that there might be important differences in the mechanisms underlying temporal and spatial attention, and our results would support such a hypothesis.

In order to weight the relevance of our current results, it is important to note that in this paradigm we do not only modulate attention, but also expectation (see Summerfield &Egner, 2009). Expectation (or prediction) and attention are intimately related but probably dissociable processes, which can sometimes lead to the same behavioural expression but fairly opposite neural effects (e.g. Lange, 2013). While temporal attention usually leads to increased neural activity (Schroeder &Lakatos, 2009), temporal expectation often leads to decreased or rather sharpened neural activity (Bendixen et al., 2012; Schwartze et al., 2013)[3]. Due the subtle, probabilistic cueing used within our experiment, we definitively engage temporal expectation, yet in order to use the probabilities in the most sufficient way, one has to actively orient attention based on combining the temporal probabilities. In short, we are aware that our experiment modulates both, expectation and attention, but since both seem to lead to similar behavioural modulations, we do not believe this is a possible confound in our study (just like it has not been in many other behavioural studies REFs). Still, it will be important to disentangle, possibly using neural measurements, the

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[3] Responses towards expected stimuli are eliciting a weaker N100 component than unexpected stimuli (Lange, 2009) and reduced fMRI activity (Kok et al., 2012). The reduced activity is thereby caused due to suppression of neurons encoding for unexpected events, while the activity of neurons encoding for expected events remains unaffected in comparison to neuronal activity in absence of attention (Kok et al., 2012), thus expectation is sharpening the neuronal activity.

attention orienting versus expectation components of cross-modal coupling and/or decoupling.

The conclusion to emerge from the present study is that cross-modal temporal decoupling seems to be a rather general property of temporal attention, and hence, is independent of the modalities used in the task design. In turn, this suggests that cross-modal decoupling in time might be a differential feature of the expression of attention orienting mechanism between temporal and spatial attention. A secondary, but important finding is that cross-modal coupling/decoupling effects are modulated by imbalances in modality difficulty, with low difficulties wiping out any expression of temporal orienting, including decoupling.

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2.3. Alpha switch and beta swap: Cross-modal decoupling of temporal attention reflected in low frequency oscillations

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Abstract

When, in a cross-modal environment, attention is allocated to time and sensory modality one can often observe efficient decoupling; meaning that temporal attention adapts the processing of targets within each different modality flexibly in time and independent of the other modalities. Here, we were interested in the oscillatory correlates underlying switches in cross-modal temporal attention. We manipulated participants' expectation about the upcoming target modality and onset time by using a discrimination task in which visual or tactile stimuli could eventually occur at one of two possible time points. We collected behavioural and electrophysiological responses. While we confirmed cross-modal decoupling behaviourally, the EEG revealed prestimulus changes in alpha and beta low frequency oscillations which seemed to serve distinct functional roles. Alpha oscillations might encode for upcoming switches in modality expectancy, and beta oscillations for the directionality of the change, thus for a swap from one modality to another, as well as for temporal expectation itself. These findings start to unravel the complex interplay between oscillatory regimes that embody the act of attentional selection in complex, multisensory environments.

Introduction

Attention allows us to select relevant information and to filter out irrelevant information (Treue, 2003), which is a critical function because processing resources in the brain are limited. Selective attention can be allocated to various types of information, such as spatial regions, moments in time or a particular sensory modality. Extensive research shows that attention leads to an improved behavioural performance (Müller & Rabbitt, 1989; Posner, 1980 (space); Cravo et al., 2013; Rohenkohl et al. , 2012 (time)), and to modulations of physiological responses in event-related potentials (ERPs) (Eimer et al., 2002 (space); Lange & Röder, 2006; Miniussi et al., 1999 (time)) and the BOLD signal in fMRI (Coull et al., 2000; Coull & Nobre, 1998 (time); Corbetta et al., 1998; Yantis et al., 2002 (space)). The physiological correlates of this enhancements are frequently specific of the brain area that represents the attended feature (e.g., colour, spatial location, sensory modality), but often the act of orienting attention itself leads to an activation of similar areas of the brain regardless of the stimulus feature used for selection, the frontoparietal attention network, hypothesized to control attentional processes (Corbetta et al., 2008; Corbetta & Shulman, 2002).

Of particular interest is the interaction between distinct types of selective attention, because it reflects how attentional selection may play out in complex, real environments. A well-known example is cross-modal spatial attention. Within a series of experiments, Spence & Driver (1996) investigated how participants allocate attentional resources across different sensory modalities in space. Presenting targets from one of two different modalities with different spatial likelihoods, they found that responses towards targets in both modalities were fastest at the most likely spatial location overall, suggesting a coupling between modalities in spatial orienting. Although a few studies suggest that there are exceptions to this pattern (Lloyd et al., 2003), there is a general agreement that sensory modalities tend to be linked, in a synergistic fashion, within spatial attention (Driver & Spence, 1994; Spence & Driver, 1996; Spence et al., 2000; Teder-Sälejärvi et al., 1999). This cross-modal spatial coupling is also reflected in the ERPs, where orienting spatial attention in one modality affects the ERPs of stimuli in both the relevant as well as irrelevant modalities (Eimer et al., 2002).

Another important case of interaction between attention types is cross-modal temporal attention, the focus of this paper. Addressing such an interaction, Lange & Röder (2006) found, similarly to cross-modal spatial attention, a cross-modal temporal coupling in time, both in terms of behaviour and in the modulation of the N100 component of the ERPs. More recently, however, Mühlberg et al. (2014) manipulated participants' attention towards time and modality (vision or touch) in a similar manner as Spence & Driver (1996) and obtained disparate results. In Mühlberg et al.'s paradigm, the results showed that each modality seemed to unfold its own temporal expectation according to their individual probabilities of appearance, suggesting a cross-modal decoupling effect in temporal attention. This behavioural pattern has been also observed in another study of the same group, this time between audition and touch (Mühlberg & Soto-Faraco, 2016).

One way to further understand attention is to study its neural expression. Traditionally, neural correlates were measured by comparing the brain responses towards attended vs. unattended events (Eimer & Driver, 2000; Eimer & Schröger, 1998; Müller & Hillyard, 2000; Sambo & Forster, 2011). However, another perspective is to look at pre-stimulus, ongoing activity (Fu et al., 2001; Hanslmayr et al., 2007; Herrmann & Knight, 2001; Jones et al., 2010; Sauseng et al., 2005). According to recent evidence, brain oscillations picked up from EEG or MEG play an important role for attentional orienting (Arnal & Giraud, 2012; Bosman et al., 2012; Sauseng et al., 2005; Schroeder & Lakatos, 2009; Wang, 2010; Womelsdorf & Fries, 2007). One of the most important frequency ranges is thereby the alpha band (8-14 Hz), which seems to play a key role of orienting attention towards an upcoming event through power imbalance between relevant and irrelevant brain representations. When using spatial attention, as it is often the case, the power imbalance is reflected as a lateralized power imbalance (Romei et al., 2010; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000). Enhanced alpha oscillations typically decrease the cortical excitability and thus, the allocation of participants' attention to one side of space is reflected through a contralateral power decrease and/or an ipsilateral power increase, as proposed by gating-by-inhibition hypothesis (Jensen & Mazaheri, 2010; Klimesch et al., 2007). This alpha gating is proposed to act in a cyclic way, as shown by several findings of phase-dependent performance (Busch & VanRullen, 2010; Landau & Fries, 2012; Mathewson et al., 2011; Torralba et al., 2015; VanRullen et al., 2011). Importantly, the relevance of prestimulus alpha oscillations for attentional orienting was not only observed in vision, but also in other modalities such as audition (Banerjee et al., 2011; Neuling et al., 2012) and touch (Haegens et al., 2011; Ruzzoli & Soto-Faraco, 2014). Touch is thereby a special modality because not only the alpha band, but also the beta band (15-30 Hz) is engaged in attentional orienting (Haegens et al., 2011a; Haegens et al., 2012; Haegens et al., 2011b; Haegens et al., 2011c; Jones et al., 2010; van Ede et al., 2011; van Ede et al., 2010; Zhang & Ding, 2010).

Some studies have investigated the interplay of different types of attention on the level of prestimulus oscillations. Of particular interest here is the study of Bauer et al. (2012) et al., where the authors used an oddball task with visual and tactile stimuli to investigate cross-modal spatial attention. The authors found prestimulus power lateralization in the alpha and beta bands, across parieto-occipital and central sensors, independent of the attended modality, supporting the view of strong cross-modal links in spatial attention. Concerning modality attention, they observed that attending to vision lead to a decrease of alpha band activity in parieto-occipital sensors and to an increase of alpha and beta band activity within central sensors; the opposite pattern was elicited when attending to touch. Another interesting study was conducted by van Ede et al. (2011), where the authors investigated the interplay between attention to space and time, in a unisensory (tactile) paradigm. Using two different hazard rates in a somatosensory discrimination task, the authors observed a lateralization of alpha and especially beta oscillations in advance of the possible target onsets, suggesting that prestimulus oscillations are modulated dependent on the onset time of a stimulus the spatial attention as a proxy to measure lateralization. Concerning cross-modal temporal attention, recently Pomper et al. (2015) used a go/no go-task to investigate the interplay between attention to modality and temporal attention in terms of pre-stimulus brain oscillations. Participants pressed a button if a target appeared in the attended modality (either vision or touch), either after a fixed interstimulus interval or after a variable delay. They found modulations of modality attention within the corresponding sensory region of interest (ROI), occipital or somatosensory, in the alpha and beta bands and, a modulation of temporal attention within the somatosensory and motor ROI in the beta and delta bands (1-4 Hz). Importantly, no interaction between the two types of selective attention was found, suggesting a largely independent encoding of modality and temporal attention, which would fit to the idea of cross-modal decoupling of temporal attention (Mühlberg et al., 2014). Another EEG study of the same group (Keil et al., 2015) added further evidence towards a separate processing of modality and temporal attention, although they found an interaction between the two when measuring functional connectivity in the theta band (5 – 7 Hz).

Previous studies investigating temporal and modality attention on the level of prestimulus oscillations presented both types of attention in a mostly independent manner. To further investigate the interplay between these two types of attention, the present study focuses on the modulation of prestimulus oscillations when attention to time and modality must be deployed in a context where they are interwoven and dependent on each other. Using a similar behavioural paradigm as in Mühlberg et al. (2014), the goal of the present study was to measure the prestimulus power lateralization of lower frequencies as a consequence of orienting selective attention throughout time using EEG. Our expectation was that modality attention should be expressed by a modulation of alpha (and eventually beta) band power at the moments of likely target appearance within the channels over the respective sensory cortex of the attended modality (occipital channels for visual targets and somatosensory channels for tactile targets). The reversed pattern should emerge within the channels over the sensory cortex of the unattended modality. Furthermore, effects of temporal attention should reflect as a modulation of this pattern in advance of the two possible onset times, as is suggested by several papers about temporal attention (Pomper et al., 2015; van Ede et al., 2011; van Ede et al., 2010).

Methods

Participants

A total of 25 participants with normal or corrected to normal vision volunteered for this experiment in exchange for 10€ per hour. They gave written informed consent to participate in the study, which was in accordance to the Declaration of Helsinki and approved by the local ethics committee CEIC Parc del Mar

(University Pompeu Fabra, Barcelona, Spain). One subject was excluded due to poor behavioural performance (below 50% correct responses in one of the experimental conditions) leaving a total of 24 remaining participants (1 left-handed; 16 female; mean age 25 years, age-range 18-37 years).

Stimulus design

Stimuli could either be visual or tactile and be presented as a single pulse or double pulse stimulation. Visual stimuli consisted of flashes of yellow LEDs placed left or right (visual angle 10°) of a central red LED (fixation), all mounted upon a black cardboard box (32.5 x 20 x 11 cm). The intensity (LED brightness) was individually adjusted with a variable resistor until participants reached equal and above chance training performance for visual and tactile stimuli. The single pulse visual stimulus lasted for 100 ms; the double stimuli consisted of two 40 ms flashes, separated by a 30 ms gap. Tactile stimuli were delivered through solenoid tappers (8 mm ∅ coil, blunt, round tip for painless stimulation; Miniature Solenoid Tapper, MSTC3-10M; M&E Solve), placed on the left and right index finger pads. Single stimuli consisted of a lift of the tapper tip for 40 ms and double stimuli consisted of two lifts of 2 ms duration each, separated by a 36 ms gap. Like for visual stimulation, the intensity (voltage) and duration of tactile stimuli was adjusted if needed, to ensure an above chance training performance and a roughly equal performance upon both stimulus types.

Experimental design and procedure

Participants performed a discrimination task between single and double stimuli (Fig. 2.4.1), as in Mühlberg et al. (2014). Participants sat in an armchair with their hands positioned on a wooden tray and covered by the black cardboard box with the fixation and the two stimulation LEDs attached. The positions of subjects' index fingers were aligned with the stimulation LEDs, so that tactile and visual stimuli were in approximate spatial correspondence. Each trial started with a warning event consisting of the illumination of the fixation LED and an auditory cue (100 ms duration, 60 dB), delivered via headphones. The cue could either be a low pitch tone (200 Hz) or a high pitch tone (1000 Hz) encoding with 100% validity for the side of the upcoming stimulus (the cue-side mapping was counterbalanced between participants), followed by masking white noise throughout trial duration. Trials could be classified into early onset trials (target presented 1200 ms after the cue), late onset trials (target presented 2400 ms after the cue) or catch trials (no target). Participants were asked to discriminate between single and double pulse stimuli via the release of one of two feet pedals (heel for single pulse; toes for double) as quickly and accurately as possible. The next trial started 500 ms after the response or, if no response was provided, after the end of the response interval (2500 ms after target presentation).

The paradigm (Fig. 2.4.1) aimed at modulating participants' temporal expectation and modality expectation in a probabilistic manner, indicating that the target events would be more likely to occur at one of the two possible time points, i.e. the expected time point (time expectation: early vs. late) and in one of the two sensory modalities, i.e., the expected modality (modality prevalence: primary vs. secondary), which could be visual or tactile depending on the participant. Overall, the expected time point contained a target in 54% of the trials and the unexpected time point contained a target in 23% of the trials, whereas the rest (23%) were catch trials, thus fulfilling the assumption of uncertainty (Coull & Nobre, 1998; Griffin et al., 2001; see Mühlberg et al., 2014). Time expectation was manipulated in a block-wise manner within the same participant, with a counterbalanced order between participants. Modality prevalence was manipulated in all participants as a within participant variable (modality prevalence: primary vs. secondary modality), although the particular sensory modality that was used as primary or secondary was counterbalanced across subjects (modality group: vision or touch). Hence, the majority (70%) of targets belonged to the more likely (primary) modality, whereas only 30% of the targets were presented in the less likely (secondary) modality. For half of the participants vision was primary (vision group) whereas for the other half touch was primary (touch group). Most importantly, modality prevalence and time expectation were orthogonally coupled in the distribution of trials, so that at the expected time point, the primary modality was the most likely, with 86% of targets vs. only 14% in the secondary. At the unexpected time, the secondary modality was more likely (67%), compared to 33% of targets occurring in the primary modality.

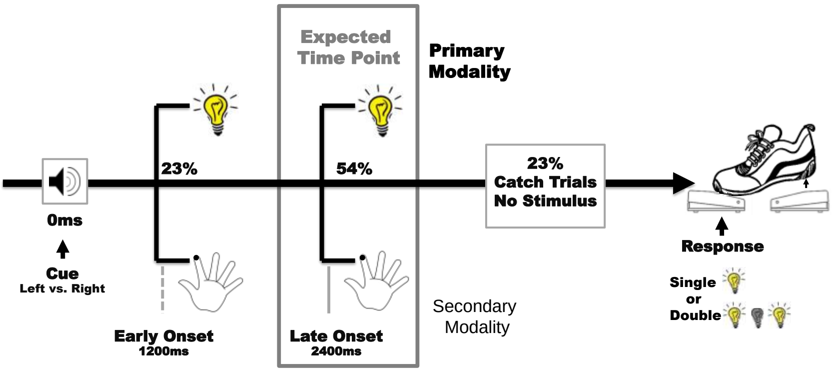

Figure 2.4.1: Schematic description of the task. Participants performed a single/ double pulse discrimination task on visual and tactile targets. Each trial started with an auditory cue, signalling the side of the upcoming stimulus with 100% validity. A target could appear either 1200 ms (early) or 2400 ms (late) after the cue onset. One of the modalities was thereby more likely to appear, making it the primary modality and one of the onset times was more likely to contain a target than the other, making it the expected time point. Additionally, the primary modality was the most likely modality at the expected time point, with 83% of all targets being primary there, however, the majority of targets at the unexpected time point belonged with 66% to the secondary modality. In some trials, no target was presented to avoid temporal certainty. Responses were delivered via foot pedals.

Each participant ran a total of six experimental blocks of 108 trials each. Trials in which the participants failed to provide a response or in which the foot pedals were not correctly pressed were automatically discarded and repeated during the block. One experimental session lasted approximately 45 min in total. Participants were encouraged to respond as fast and accurate as possible, to keep the fixation on the central LED, and to blink after response delivery when possible. Reaction times (RT) and accuracy were recorded as behavioural measures.

Two training sessions of 36 trials each were performed before the actual experiment. In order to encourage participants to orient attention in time, the first training session capitalized on auditory entrainment presenting beeps (frequency either 1000 Hz or 200 Hz and identical to trial cue, 50ms duration) in 400 ms steps until the target onset (2 beeps in case of the first onset; or 5 beeps in case of the second onset). The training was considered successful when participants perceived the difference between the early and late onset and performed above chance level. Then, participants performed a second training session without auditory entrainment, but an auditory beep was placed in case no target occurred at the first onset. Also for this case, the training was considered successful when participants perceived the difference between the early and late onset and when they performed the discrimination task above chance level.

EEG Recording

EEG was recorded using 60 active electrodes (actiCAP, Brain Products GmbH, Munich, Germany) placed after the 10-20 international system, with the tip of the nose as online reference and AFz as ground electrode. Two external electrodes were used for recording vertical and horizontal ocular movements. Additionally, left and right mastoids electrodes were used for off-line re-referencing. The signal was recorded via BrainVision Recorder (Brain Products GmbH, Munich, Germany) at a sampling rate of

500Hz. To improve the accuracy of the source analysis, the position of each electrode was recorded in advance of the experiment using SoftTaxic Optic 2.0 (EMS, Bologna, Italy) for each participant.

Data Analysis

Behaviour

Incorrect responses and RTs two standard deviations away from the individual mean were discarded from the analyses (<5% of all trials were excluded). A repeated measures ANOVA was performed on RTs and accuracy, with onset time (1200 ms, 2400 ms), modality prevalence (primary, secondary) and time expectation (early, late) of the primary modality as within participant factors, and the modality group (vision, touch) as between participants factor. Statistics were performed with STATISTICA 8.0 (StatSoft Inc.; Tulsa, OK, USA). Post-hoc analyses were performed using the Fisher LSD test ($p<0.05$).

EEG Preprocessing

The EEG analysis was conducted using the fieldtrip toolbox (Nijmegen, Netherlands, Oostenveld et al., 2011) in MatLab 8.2.0.701 (The MathWorks Inc., Natick, MA, USA). The EEG data were filtered between 2-30Hz and an independent component analysis (ICA) was performed in order to remove eye movement or heart artefacts (on average 3 components per participant). In order to avoid stimulus-evoked response in power modulation throughout the course of a trial, only catch trials and trials where the target was presented at the late onset were considered for the analysis. In this way we ensured the possibility to isolate the time evolution of power modulation as a function of modality and time expectations. Epochs were time-locked to the cue (-2000 to 3400 ms). For the analysis, the time interval of interest was the cue target period, from 0 ms (cue onset) to 2400 ms (late target onset). Data were demeaned and offline re-referenced to the left and right mastoid. Non-functional channels or channels presenting massive artefacts (0-3 channels per participant) were excluded and their signal restored via interpolation of the neighbouring channels.

Channel and Frequency Band Selection in sensor space

For each group and expected time point, we separately identified the regions of interests (ROIs) considering the period of 800 ms before each possible onset, contrasting the modality prevalence (primary, secondary) at the early and late time point. We calculated a contra-over-ipsi power ratio (see van Ede et al., 2011) for each channel pair (power in the contralateral channel divided by the power in the ipsilateral channel in respect to the cued side) and frequency range 2-30 Hz (1 Hz resolution) and corrected for multiple comparisons (1000 repetitions, cluster correction, $p<0.05$). No baseline correction was performed. Electrode-frequency clusters containing three neighbouring electrodes with the highest significant contra/ipsi power ratios for the vision and the touch group separately were selected as ROI. We thus obtained the occipital (PO9/10, PO3/4, O1/2) and somatosensory (FT7/8, FC5/6, C3/4) ROIs (Fig. 2.4.2A) and the two frequency bands of interest: alpha (8-10 Hz) and beta 18-20 Hz)[4] .

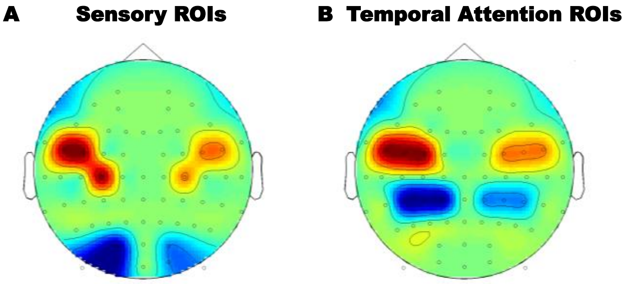

Figure 2.4.2: Topography of the ROIs for the sensor analysis. **A)** Modality dependent ROIs, roughly corresponding to the underlying somatosensory (red) and occipital cortex (blue). **B)** Modality independent ROIs, over frontocentral (red) and centroparietal sensors (blue).

Additionally, to detect any modality independent effects of temporal attention (contrast of time expectations at each onset; expect early vs. expect late at the early and late onset time), we collapsed the two modality groups and repeated the aforementioned procedure. We identified a frontoparietal (FT7/8, FC5/6, FC3/4) and a centroparietal (CP5/6, CP3/4, CP1/2) ROI (Fig. 2.4.2B), with activity modulated in the same two frequency bands: alpha and beta.

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[4] We also found a significant modulation of the contra-over-ipsi ratio within the theta band. However, the observed modulations within the theta band overlap partially with the modulation of the alpha band and thus, we will consider the observed theta modulation caused through a spread of alpha activity within the theta band and will not discuss the modulation of theta activity any further.

Calculation of Contra over Ipsi Power Ratios

A short-time Fourier transform (STFT) with a sliding Hanning window (500 ms length, 2 Hz resolution) in steps of 20 ms over the whole time interval of interest (-100 ms to + 2500 ms relative to cue onset) was applied (without baseline correction) for the frequency range between 2-30 Hz. The calculation of the contra-over-ipsi ratio was performed following the procedure from van Ede et al. (2011). First, we averaged the power over the channels in the ROI and over the width of the frequency band (time range between -100 and 2500 ms) separately for the left and right channels of our selected ROIs for each modality group, time expectation, frequency band and cued side and then we calculated the contra-over-ipsi ratio. Afterwards, we collapsed the ratios of left and right sides, to obtain contra-over-ipsi ratios for each modality group, time expectation and frequency band. For statistical comparison we conducted students t-tests of the ratios against each other or against a baseline of non-lateralized activity, and corrected for multiple comparisons (Guthrie & Buchwald, 1991).

Source Analysis

To investigate if the sensor modulation is reflected in the source space, we investigated the modulation of alpha and beta power based on source estimations in the primary visual cortex (referred to as occipital ROI) and the primary somatosensory cortex (referred to as somatosensory ROI). The focus was upon the lateralization of source activity, to obtain a direct comparability with the sensor data. In particular, the primary somatosensory cortex and the primary visual cortex were chosen as regions of interest according to the a-priori hypothesis of this study. We selected the Talairach coordinates for the left [-4.0, -3.0, 5.4] and right [4.8, -2.8, 5.4] primary somatosensory areas based on Conte et al. (2012). The Talairach coordinates for left [-1.3, -6.3, 0.3] and right [0.9, -6.7, 0.5] primary visual cortex were selected from Belliveau & Kennedy (1991). The headmodels of the participants were obtained after realigning a standard Boundary Element Model (BEM) of 8 mm resolution to the registered electrode positions. Afterwards, the ROI Talairach coordinates were projected on the realigned headmodels to define four ROIs (somatosensory and occipital, each left and right) centred for the selected coordinates (8 mm radius each). Oscillatory activity within the ROIS was estimated through a frequency-domain spatial filter obtained by the Dynamical Imaging of Coherent Sources (DICS) method (Gross et al., 2001) based upon the cross-spectral density (CSD) matrices of each condition (modality group, time expectation), time window (early, intermediate, late) and frequency of interest (alpha, beta) separately. The data were bandpass-filtered (2Hz bandwidth), segmented in the three aforementioned time windows early (800 – 1300 ms post cue), intermediate (1400 – 1900 ms) and late (2000 – 2500 ms) and zero-padded to 1000 ms length. A STFT over each of the time windows (Hanning taper, 500 ms length) was used for obtaining the power and CSD estimation used for the calculation of the spatial filters in the frequency domain.

Contra over Ipsi Source Activity Ratios

Similar to the sensor space analyses, we calculated the contra-over-ipsi ratio for the source space data. We multiplied the pre-processed data with the three different kinds of spatial filters (early, intermediate, and late). We conducted a time-frequency analysis (STFT, 500 ms Hanning window, 20 ms sliding steps, 2 Hz resolution) for the frequency bands of interest and segmented the trials in the time windows of the previously used filters. We calculated the mean of each of the source time evolutions and calculated the contra-over-ipsi ratios in a similar way as for the sensor power data before (van Ede et al., 2011).

Results

Behaviour

Accuracy

The overall response accuracy in the experiment was 83.47%. The accuracy for visual targets (87.11%) was higher than for tactile targets (79.84%), in the vision group (p=0.014) and, marginally, in the touch group (p=0.062). In other words, visual accuracy was superior to tactile accuracy in both groups (for primary modality vision and primary modality touch groups), although the tendency was less strong when touch was primary. Because of this pattern, the interaction modality prevalence x modality group was significant (F1,22=9.16, p<0.01). No other significant interaction or trend in the accuracy data was observed.

Reaction Times

We observed a significant effect of modality prevalence (F1,22=20.40, p<0.01) with faster responses for the primary (826 ms) than the secondary modality (912 ms). However, an interaction between modality prevalence and modality group (F1,22=11.28, p<0.01) revealed that this difference was mostly driven by the vision group, where participants responded 150 ms faster to the primary modality (vision) than to secondary modality (touch; p<0.01), whereas this difference levelled off when touch was primary (32 ms; p=0.40). This pattern is similar to what happened in accuracy. However, in RTs we also found a significant interaction between modality prevalence and time expectation (Fig. 2.4.3A). Participants responded significantly faster to the primary modality at the expected time point (803 ms), compared to the unexpected time point (849 ms, p<0.01), whereas the difference was in the opposite direction for the secondary modality (933 ms vs. 891 ms, p<0.01). The effect was independent of the primary modality (modality prevalence x time expectation x modality group; F1,22=0.05, p=0.83). This pattern confirms (and replicates) previous findings (Mühlberg et al., 2014; Mühlberg & Soto-Faraco, 2016) arguing for cross-modal decoupling, and against a cross-modal synergy, in temporal attention. Additionally, we observed that this effect was reliable only at the early onset, as revealed by the interaction between onset time x modality prevalence x time expectation (F1,22=5.47, p=0.029; Fig. 2.4.3B). Early target responses in the primary modality were faster when that time point was expected (791 ms) than when the early time point was unexpected (845 ms; p=0.034). For the secondary modality the pattern reversed, meaning that at the expected time point the reaction times (959 ms) were slower (p<0.01) than at the unexpected onset (871 ms). At the late time point, responses towards the primary modality were still following the previous, albeit here non-significant, directionality at the expected time point (816 ms vs. 853ms; p=0.17), whereas no difference was found for the secondary modality (907 ms vs. 912 ms; p=0.85).

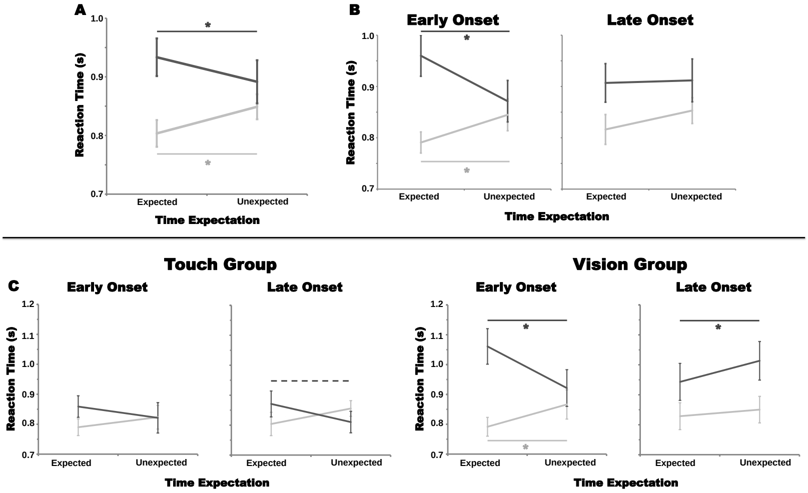

Figure 2.4.3: Behavioural results of the experiment. **A)** Interaction between modality prevalence and time expectation. Participants responded significantly faster towards primary targets at the expected time point (44 ms benefit), whereas responses towards secondary targets were faster at the unexpected time point (42 ms cost). **B)** Interaction between onset time, modality prevalence and time expectation. Whereas the observed effect for both modalities are significant for early onset targets (54 ms benefit for primary targets and 88 ms cost for secondary targets), there was no significant difference in response times for both, primary (34 ms benefit)

and secondary targets (5 ms benefit), if the target was presented at the late onset. **C)** Interaction between onset time, modality prevalence, temporal expectation and modality group. The previously observed modulation is mostly driven by the vision group (right) for both primary (791 ms vs. 866 ms) and secondary targets (1061 ms vs. 921 ms), while the touch group (left) displayed a similar, yet insignificant pattern. At the late onset, the pattern remains the same for the touch group, which shows marginal faster responses for the secondary targets at the unexpected onset (871 ms vs. 810 ms). For the vision group, the previously observed pattern for the secondary modality reversed (943 ms vs. 1013ms).

Last, we observed an interaction between onset time, modality prevalence, time expectation and modality group (F1,22=10.31, p<0.01; Fig. 2.4.3C), revealing that the previously described interaction at the early onset was mostly driven by the vision group (primary modality targets, expected 791 ms vs. unexpected 861 ms, p=0.074; secondary modality targets, expected 1061 ms vs. unexpected 921 ms, p=0.046). We observed only trends of time expectation for the touch group, though it is important to note that the pattern was the same as the overall data (primary modality targets, expected 790 ms vs. unexpected 824 ms, p=0.33; secondary modality targets, expected 859 ms vs. unexpected 821 ms, p=0.27). At the late onset, the vision group showed a reversed pattern for secondary modality targets with faster responses when that onset time was attended (943 ms) vs. unattended (1013 ms, p=0.048). The touch group showed the opposite trend (871 ms vs. 810 ms, p=0.085). No significant differences were observed for late targets of the primary modality. In summary, the overall pattern of results reproduces the effect of cross-modal decoupling in temporal attention, albeit its reliability is somehow weaker for the case of the late onset (compared to early) and tactile targets (compared to visual).

EEG

We analysed the effects of attention to time and modality over two separate sensor ROIs (occipital and somatosensory) within the alpha and beta band. Additionally, since the effect of temporal attention is not necessarily expressed over channels representing the primary sensory cortices, we identified two time expectation ROIs (frontocentral and centroparietal; see methods) for the same frequency bands. All ROIs were selected by contrasting the activity 800ms before the primary or secondary target for each group (occipital and somatosensory ROI) or contrasting the activity 800 ms before the early and late onset across groups (frontocentral and centroparietal ROI).

Alpha

We compared the time evolution of alpha power imbalance in the occipital and the somatosensory ROIs. In the touch group, early onset expectation trials led to differences between somatosensory and occipital ROIs in the alpha frequency band (Fig. 2.4.4A), in a time window just before the late onset (2400 ms; $t_{11}=3.81, p<0.05$). Comparing the time-resolved alpha power ratios for each ROI against the baseline, we found that only the occipital activity was significantly modulated ($t_{11}=2.64$, $p<0.05$). In the touch group, when the late onset was expected (Fig. 2.4.4B), a significant modulation of alpha contra-over ipsi ratio was observed, right after the early onset (t11=2.79, p<0.05). For both ROIs the alpha contra-over ipsi ratio differed significantly compared to baseline (occipital: t11=2.34, p<0.05; somatosensory: t11=-2.91, p<0.05).

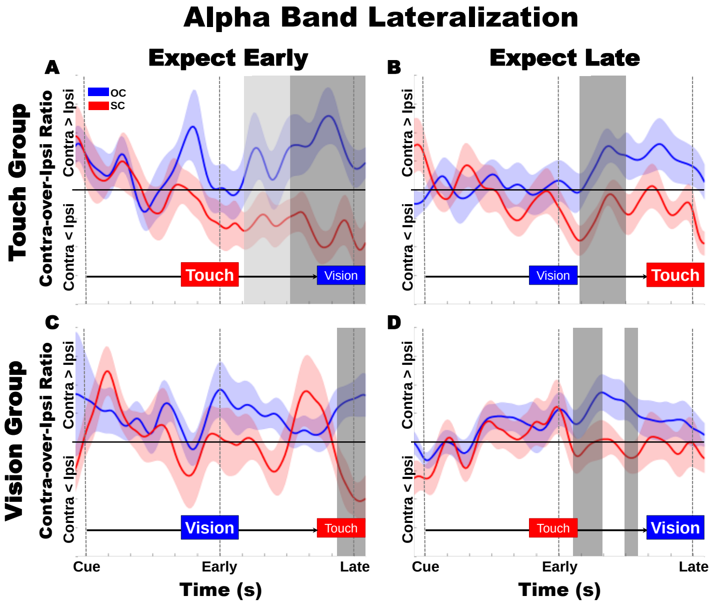

Figure 2.4.4: Results of the prestimulus alpha lateralization (8-10Hz). Images depict the differences in lateralization between the somatosensory ROI (SC, red) and occipital ROI (OC, blue) averaged across participants, blue and red shaded areas display the standard error of the mean. Contra-over-ipsi ratios are plotted in the range between 0.8 - 1.2. Contra < Ipsi is thereby a ratio below 1 or more ipsilateral than contralateral power and Contra > Ipsi a value above 1 or more contralateral than ipsilateral power. Significant differences are shaded in dark grey (p<0.05), whereas a light grey shading is marking trends (p<0.1) after multiple comparison correction. The onsets of the cue, non-occurring early target and possible

late targets are marked through grey dashed lines. **A)** Prestimulus alpha lateralization for the touch group when an early tactile target was expected. Participants show a significantly different alpha modulation in the ROIs after the early onset. **B)** Prestimulus alpha lateralization for the touch group when a late tactile target was expected. Participants show a significant difference between the ROIs after the early onset, driven by both, higher contralateral occipital alpha power and lower contralateral somatosensory alpha power. **C)** Prestimulus alpha lateralization for the vision group when an early visual target was expected. Participants show a significant difference in the alpha modulation pattern before the late onset. **D)** Prestimulus alpha lateralization for the vision group when a late visual target was expected. Participants show a modulation in alpha lateralization after the early onset.

For the vision group, when the early onset was expected (Fig. 2.4.4C) alpha power ratio modulation was significantly different between occipital and somatosensory ROIs right before the late onset ($t11=4.69$, $p<0.05$). For both ROIs the alpha contra-over ipsi ratio modulation was significant compared to baseline (occipital: $t11=2.43$, $p<0.05$; somatosensory: $t11=-2.89$, $p<0.05$). When a late target was expected (Fig. 2.4.4D), a significant power difference between ROIs was observed, right after the early onset ($t11=2.57$, $p<0.05$), mainly caused through more contralateral than ipsilateral power in the occipital cortex ($t11=2.42$, $p<0.05$).

In summary, for the sensory ROIs we observed a similar pattern in the alpha time evolution for both modality groups. The modulation took place roughly after the first possible time point of target presentation (regardless of whether it was expected or unexpected) and prior to the second time point (regardless of whether it was expected or unexpected). The effects were stronger for the occipital ROI. This pattern of alpha modulations seems to be independent of modality attention, but slight variations in the time windows of significant differences across early and late expectation made us suspect some modulation by temporal expectation. In order to address possible temporal expectation effects, we contrasted the alpha power ratio of the two temporal expectancy conditions (early vs. late) against each other. However, the data failed to show any significant differences in terms of time expectancy for either group in the occipital ROI, and only for the touch group we found a significant difference before the second onset in the somatosensory ROI.

We also compared the modulation of alpha power in the frontoparietal and centroparietal ROIs identified as target regions for modality-independent temporal attention effects, thereby contrasting the two different time expectations (expect early vs. expect late) against each other. Again, no modulation was observed over the course of time.

Beta

For the touch group, when an early target was expected (Fig. 2.4.5A), we found a significant modulation directly after cue onset and up to 300ms post cue. The beta power ratio was thereby higher in the occipital than in the somatosensory ROI. A comparison against baseline revealed this early modulation of beta power ratio was driven by a decrease over the somatosensory ROI. In addition, we observed a second significant difference window between the ratio of the two ROIs directly before the late onset (t11=2.59, p<0.05). The ratio was higher in the occipital than in the somatosensory ROI, though none of them were significant against the baseline (occipital: t11=1.38, p=0.21; somatosensory: t11=-1.58, p=0.17). For expect late trials (Fig. 2.4.5B), still within the touch group, we found a significant difference between the ROIs (with a higher somatosensory, than occipital ratio) in a time window directly before the late onset (t11=-3.09, p<0.05). Yet, either ROI was not significantly different against baseline activity (occipital: t11= 1.07, p=0.35; somatosensory: t11=0.68, p=0.53). It is important to note that the lateralization difference between ROIs in expect late trials was of opposite directionality than for expect early trials, within the same group of participants.

For the vision group, the data were less clear. When an early (visual) target was expected (Fig. 2.4.5C), the data showed a trend towards a higher occipital than somatosensory power ratio after the early onset (; t11=2.22, p<0.1). The comparison of the power ratios against baseline shows that there was indeed a significant increase in the occipital ROI (t11=2.67, p<0.05), that is higher contralateral than ipsilateral occipital power. When participants of the vision group expected a late target (Fig. 2.4.5D), we observed a trend towards a higher occipital ratio in advance of the early onset (t11=2.28, p<0.1). A comparison of the power ratios against the baseline revealed that this effect was driven by a significant occipital ratio increase (t11=2.65, p<0.05).

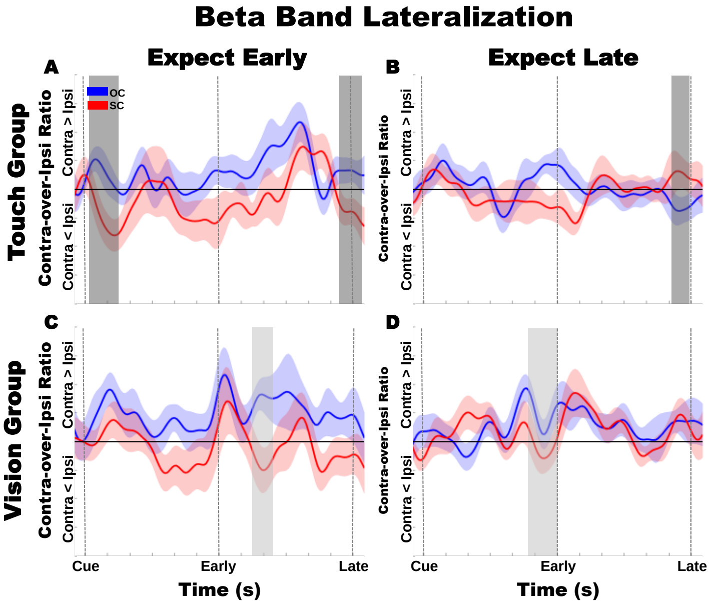

Figure 2.4.5: Results of the prestimulus beta lateralization (18-20Hz). Images depict the differences in lateralization between the somatosensory ROI (SC, red) and occipital ROI (OC, blue) averaged across participants, blue and red shaded areas display the standard error of the mean. Contra-over-ipsi ratios are plotted in the range between 0.8 - 1.2, Contra < Ipsi is thereby a ratio below 1 or more ipsilateral than contralateral power and Contra > Ipsi a value above 1 or more contralateral than ipsilateral power. Significant differences are shaded in dark grey ($p<0.05$), whereas a light grey shading is marking trends ($p<0.1$) after multiple comparison correction. The onsets of the cue, non-occurring early target and possible late targets are marked through grey dashed lines. **A)** Prestimulus beta lateralization for the touch group if an early target was expected. Participants show beta modulation directly after cue onset, driven by a somatosensory contralateral decrease in beta power. Furthermore, participants show a significant ROI difference in advance of the late onset. **B)** Prestimulus beta lateralization for the touch group if a late tactile target

was expected. Participants show a beta modulation difference between the ROIs before the late onset. **C)** Prestimulus beta lateralization for the vision group if an early visual target was expected. Participants display a beta modulation pattern after the early onset, driven by higher contralateral, than ipsilateral power in the occipital ROI. **D)** Prestimulus beta lateralization for the vision group if a late target was expected. Participants show a small, yet significant beta power difference before the early onset.

Like we did for the alpha band, we computed the beta modulation pattern in temporal attention ROIs (frontocentral and centroparietal), to identify possible modality independent effects of time expectation. In the frontocentral ROI (Fig. 2.4.6A), we found a beta power ratio difference between expect early and expect late trials in two time windows, right after the early onset ($t_{11}=-2.39$, $p<0.05$) and directly before the late onset ($t_{11}=-2.44$, $p<0.05$). In both cases, the contra-over-ipsi ratio increased significantly against the baseline when a late target was expected (first significant window: $t_{11}=2.32$, $p<0.05$; second significant window: $t_{11}=2.63$, $p<0.05$). In the centroparietal ROI (Fig. 2.4.6B), significant beta power ratio differences in the same time windows as before appeared (post early onset: $t_{11}=2.58$, $p<0.05$; before late onset: $t_{11}=3.14$, $p<0.05$), but in the opposite direction as the frontocentral ROI. This time, the difference consisted of an increase in the beta power ratio when expecting early targets ($t_{11}=2.67$, $p<0.05$). Additionally, we found a trend towards a ratio difference in advance of the early target, marked through a decrease in contra power ratio when expecting an early target ($t_{11}=-2.21$, $p<0.1$). The ratio for expecting a late target showed weaker tendencies, but again in the opposite direction.

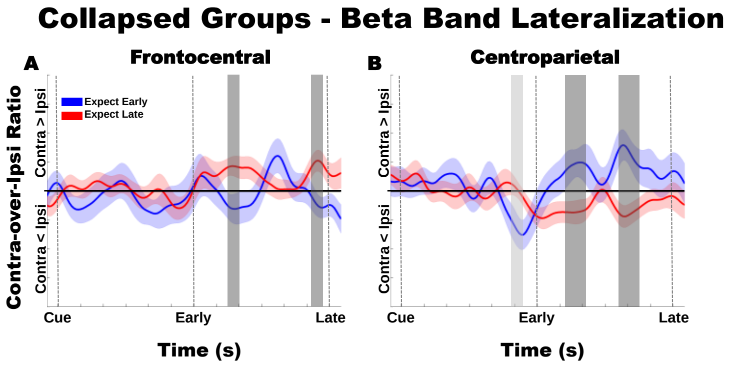

Figure 6: Results of the contra-over-ipsi ratios of the collapsed groups (time attention effect, averaged across all participants). Images contrast the ratio generated by expecting an early (blue) and expecting a late (red) target in two distinct ROIs, blue and red shading is thereby depicting the standard error of the mean. The values are plotted in the range between 0.8 – 1.2. Dark grey shading is marking for corrected significant differences ($p<0.05$) and light grey shading for corrected trends ($p<0.1$). The onsets of the cue, non-occurring early target and possible late targets are marked through grey dashed lines. Due to no significant differences between expecting early and expecting late for the alpha band, only the ratios for the beta band (18-20Hz) are shown. **A)** Beta ratio contrast in the frontocentral ROI. The curves are significantly different from each other after the early onset and before the second onset. **B)** Beta ratio contrast in the centroparietal ROI. Significant differences can be observed after the early onset and before the late onset. Additionally, we observed a trend in advance of the early onset.

In summary, we observed various sources of contra-over-ipsi beta power ratio modulations. On the one hand, beta modulations affected the sensory ROIs. In the touch group (Fig. 2.4.5A &B), beta was modulated before the late onset with a higher occipital than somatosensory ratio when an early tactile target was expected and, a lower occipital than somatosensory ratio when a late tactile target was expected. In the vision group (Fig. 2.4.5C & D) we observed trends towards higher occipital than somatosensory beta power ratios around the early onset in both, expect early and expect late trials. On the other hand, additionally, beta power was also modulated by temporal attention overall, independently of modality (Fig. 2.4.6). In the frontocentral ROI, we observed a ratio difference after the early onset and before the late onset, possibly indicating a decrease in expectancy past the early onset when an early target was expected, whereas expectation was still building up for expecting a late target. The pattern was much clear in the centroparietal ROI, especially if an early target was expected.

Source analysis: Sensory ROIs

Alpha

Starting with the expect-early condition of the touch group, we found source modulation within all three time windows analysed (early, intermediate, and late). In particular, we found a higher ratio in the occipital than somatosensory ROI around 1000 ms past cue ($t_{11}=2.87$, $p<0.05$), between 1400 – 1700 ms past cue ($t_{11}=3.86$, $p<0.05$) and around 2300ms past cue ($t_{11}=3.39$, $p<0.05$). When a late tactile target was expected, we only found a significant difference in the source ratio in the intermediate window between 1400 – 1600 ms past cue (t11=2.69, p<0.05), with a higher occipital than somatosensory source activity ratio. For the vision group we could not observe any significant differences between the source ratios of the two ROI within either condition. In general, the power analyses at the source level confirmed, in a weaker fashion, the results seen at the sensor level.

Beta

For the touch group, we did not find any significant differences between the ratios in the two ROIs within the expect-early or the expect-late conditions. For the vision group, we only found a significant difference between the source ROI ratios when a late visual target was expected. The source activity power ratio was higher in the occipital ROI than in the somatosensory ROI (t11=3.82, p<0.05). Again, the significant differences went in the same direction as the sensor level analysis, but did not replicate the whole pattern of significances.

Discussion

The present experiment was designed to investigate the modulations of neuronal oscillations in the prestimulus period underlying changes in cross-modal temporal attention. While we largely replicated our previous finding of cross-modal decoupling at behavioural level (Mühlberg et al., 2014; Mühlberg & Soto-Faraco, 2016), we also found modulations of oscillations in the alpha and beta frequency range. Since we used spatial orienting as a proxy for modality/time allocation of attention, we sought for (and found) modulations of the alpha lateralization index (contra-over-ipsi power ratio) expressed through an increase over occipital channels. When participants expected an event at a late time point, the alpha increase occurred well in advance (hence, shortly after an early time point, when no target was expected, passed). Instead, when expectation concentrated at an early time point, the alpha increase occurred later on, closely before the late, unexpected time point. These modulations were not specific of modality or expected stimulus onset time, as they always occurred in between the two possible target onsets, and might suggest a general preparation of a modality switch. Beta modulations were mostly found in the touch group and were modality dependent. We observed beta (contra-over-ipsi ratio) increases in the somatosensory ROI in advance of an upcoming tactile target and a higher ratio in the occipital compared to the somatosensory ROI in advance of an upcoming visual target. We assume that modality expectancy was encoded in the beta band, albeit the evidence for this was mostly assembled in the touch group. Additionally, when focusing on modulation through temporal expectancy, regardless of the particular modality, we found specific sensor clusters showing modulations in the beta band responding with opposite patterns as a function of early vs. late target expectation, suggesting some encoding of temporal expectancy in the beta frequency range.

Behavioural cross-modal decoupling

As in previous studies (Mühlberg et al., 2014; Mühlberg & Soto-Faraco, 2016), participants responded faster for the primary modality at the expected time and faster for the secondary modality at the unexpected time point, thus showing a general pattern of cross-modal decoupling in temporal attention. The effects are more consistent for the vision than for the touch group, yet both groups show the same effect directionalities. A possible reason for this difference is the difficulty to focus towards and away from touch (Lloyd et al., 2003; Spence et al., 2001), which increased behavioural effect upon secondary tactile targets (vision group) and reduced the effects for vision when it was secondary modality (touch group). Reaction time costs for secondary tactile targets were higher than for secondary visual targets, as well as the benefit for secondary tactile targets at the unexpected time point were higher than for secondary visual targets. These findings, however, are in line with previous findings of other groups reporting benefits of attention to be larger for tactile than visual targets (e.g. Keil et al., 2015; Spence et al., 2001). One common explanation therefore would be our familiarity of visual stimuli, leading to visual dominance (Posner et al., 1976; Spence et al., 2001) and thus might lead to decreased benefits of focused attention to that modality.

Prestimulus oscillations – a priori hypothesises

Our main goal was to identify the underlying neural expression of cross-modal temporal decoupling at the level of prestimulus brain oscillations. We hypothesized to observe prestimulus power modulations (expressed through the lateralization index; contra-over-ipsi ratio) in the alpha and beta frequency ranges. Within previous paradigms for both, temporal and spatial attention, changes in the alpha and beta band have been found over the corresponding sensory cortices (Bauer et al., 2012; Pomper et al., 2015; Snyder & Foxe, 2010; van Ede et al., 2011). Following these results, we expected to observe a power decrease for occipital alpha before a visual stimulus was expected and a decrease of central (somatosensory) alpha and beta power when a tactile stimulus was expected. Since participants are able to decouple different modalities in time at a behavioural level, one should see both an occipital decrease and a somatosensory decrease within the same trial, but at distinct points in time, reflecting the participants' strategic allocation of modality expectation. Since decoupling also means that temporal and modality attention are largely independent, one should observe additionally an overall effect of temporal attention, which we hypothesized to observe outside of the sensory ROIs and within the beta band. This temporal beta modulation should be reflected by a power decreased in advance of both possible target onsets in our two temporal attention ROIs (frontocentral and centroparietal). These expectations were met only partially, as will be discussed below.

Alpha band changes in advance of expectancy switches

The alpha band modulations for both groups showed a similar pattern. The occipital alpha power ratio increased shortly before the late onset, when participants expected an early target, and shortly after the early onset, when participants expected a late target. The similarity of the pattern across both groups, suggests some kind of temporal modulation of alpha oscillations. However, contrasting expect early vs. expect late trials did not lead to a significant difference in alpha modulation for either of the two sensory ROIs, suggesting that alpha band oscillations were not directly modulated by temporal expectation. Furthermore, the power ratio always increased in the occipital ROI, independent which modality was expected, in varying temporal windows that occurred between the early and the late expected time points. Hence, we can exclude a direct alpha modulation through modality expectation within this paradigm. The findings in source space confirmed the results in sensor space, though in a weaker fashion (e.g., we found similar modulations in the touch group, but we could not find significant source modulation in the vision group).

It is particularly curious that our observed alpha band modulations led always to occipital increases in the contra-over-ipsi ratio, with no modality or modality by time modulation. This in contrast to our expectations, based on the gating-by-inhibition hypothesis (Jensen & Mazaheri, 2010), which proposes that sensory gating through alpha oscillations leads to lower contralateral than ipsilateral alpha power in the expected modality/side, a pattern which was observed in another study investigating the temporal orienting of tactile unimodal attention with probabilistic expectancies of the possible stimulus onsets (van Ede et al., 2011). However, the attentional demands within our experiment are much higher than in other paradigms manipulating spatial or temporal attention. Participants have not only to reorient their attention over space and time, but also towards one of two possible modalities and, within the course of the trial, reorient in time towards a different modality.

Albeit the alpha modulations did not fit to the expected pattern, they did seem to express some sensitivity to our cross-modal temporal attention manipulation. In particular, the observed periods of occipital ratio increases in alpha power occurred well in advance of a late expected target (hence, shortly after the early but unlikely onset time had gone by without target). In contrast, when an early target was expected, the contralateral alpha increase occurred shortly after the passing of the early onset. This alpha pattern could reflect a general modulation signalling the modality switches throughout the course of a trial. In order to explain this, we propose that, instead of gating the information flow directly, in this paradigm alpha band oscillations served as a “switch mediator”. In other words, the timing of the necessary modality switch or the beginning of a reorienting process is encoded though changes in the alpha band, leading to the observed increases in alpha power over occipital sensors. When an early target is expected, this expectation of an early target may only be given up well after the possible window of target appearance has passed, quite close to the second possible onset (hence, the switch occurs later). However, the attention switch may instead act quickly, early after the first possible onset time has passed, when targets are unlikely at that early time, and well in advance to a likely late target. This alpha pattern, which appears in both modality groups, is nevertheless more extensive and wide spread for the touch group than for the vision group. This could reflect target difficulty. Behavioural responses towards tactile targets were less accurate and slower than towards visual targets; therefore a more resource-consuming reorienting of attention might have been necessary. Additionally, some literature claims that switches from touch towards vision or vice versa generate higher behavioural cost than switch from or towards other modalities. Indeed, Spence et al. (2001) suggest that the processing of visual information is the default state of the brain (Mantini et al., 2007). Seeing the large temporal window of a significant occipital ratio increase for the touch group after an expected early tactile target did not occur, our data would support touch being a modality difficult to orient towards.

In conclusion, our finding so far is that alpha band modulation did not seem to encode directly for temporal expectation or modality expectation, and projecting these expectations over the corresponding sensory cortices. This partially fits into literature which ties temporal expectations to changes in the beta band (Cravo et al., 2011; Todorovic et al., 2015; van Ede et al., 2011), to be discussed below. We also found no difference in alpha modulation between the vision and touch group and between the expectation of a visual or tactile target. This finding is perhaps more surprising, since contralateral decreases of alpha oscillations, especially in the occipital cortex, are generally associated with orienting attention towards vision (Banerjee et al., 2011; Capilla et al., 2014; Händel et al., 2011; Mazaheri et al., 2014; Worden et al., 2000) and contralateral beta and alpha changes over somatosensory channel when orienting attention towards touch (Bauer et al., 2012; van Ede et al., 2011; van Ede, et al., 2013). We do not find this pattern even compared to other studies using a multisensory paradigm (Bauer et al., 2012; Keil et al., 2015), however, this might be explained due to various subtle differences between experimental paradigms, such as the instruction to ignore stimuli of the unattended modality in Keil et al. or the use of a fixed vs. jittered temporal onset to guide participants' temporal attention. In light of these discrepancies towards other studies about alpha oscillations, we propose a different role for alpha band oscillations in our paradigm, which capitalized more strongly on switching modalities throughout time. In particular, we propose that the observed pattern of alpha band modulations does not reflect sensory gating, but might reflect modality switches in attention, independent of direction.

Beta as indicator of modality change and encoder of temporal expectation

Our results suggest that beta power modulations embody a double role. In terms of the combination of temporal and modality attention, we find significant beta modulations for the touch group. Noticeably, our data reveal a significant difference in beta power between the occipital and somatosensory ROIs in advance of the late onset, with the direction of the modulation opposite for expecting a late tactile vs. expecting a late visual event. When a tactile target was expected, the power ratio was higher in the somatosensory ROI than it was in the occipital ROI, while the opposite was observed when vision was expected late.

This pattern of modulation is counterintuitive since one would usually expect a contralateral alpha/beta decrease over somatosensory sensors if a tactile stimulus is expected and our results are pointing upon the opposite. This means that, like our results for the alpha band, our pattern of beta modulation cannot be explained by the classical approach of the gating-by-inhibition hypothesis (Jensen & Mazaheri, 2010). We propose that this pattern is caused due to switches towards the modality occurring at the late onset, at least in the touch group. The vision group does not follow the same pattern as the touch group, and also only displays modulation trends, which cannot be taken for too strong assumptions. Given the fact that the data in the vision group are only marginal significant, we will not further interpret the modulations in the vision group.

Our behavioural results suggest (at least partial) independence of modality and temporal attention. When collapsing the experimental groups to analyse the modality independent effects on neural oscillations of temporal expectation, we found modulation of beta power in two sensor ROIs (frontocentral and centroparietal). The beta laterality index decreased before an expected target and decreased before moments of low target expectation. This pattern is stronger for the expect-early trials, possibly due to less accurate subjective time estimation in expect-late trials, leading to less temporal certainty. This finding is in accordance with the existing literature, where temporal expectation is reflected in modulations within the beta frequency band (Todorovic et al., 2015; van Ede et al., 2011). After collapsing the two participants’ groups to obtain a modality independent pattern of attentional modulation, we observed two regions of interest (frontocentral and centroparietal). The frontocentral ROI is thereby partially overlapping with the somatosensory ROI for modality dependent temporal modulation. Considering that Pomper et al. (2015) found a modulation of beta oscillations by temporal attention in the somatosensory ROI as well, the topography of our data would fit very much in the pattern observed so far for experiments combining temporal and modality attention. Yet, the frontocentral and the somatosensory ROI are not completely overlapping and furthermore both, the frontocentral and the centroparietal ROI fit roughly to the expected topography elicited by the underlying frontoparietal attention network (Brunetti et al., 2008; Corbetta & Shulman, 2002; Liu et al. , 2014), usually associated with spatial attention. The frontoparietal network is usually observed in fMRI studies, showing attentional modulation across a network of anterior and posterior brain areas such as the frontal eye fields and the intraparietal sulcus. Its activity could be linked to the typical prestimulus changes of alpha and beta oscillations (Liu et al., 2014), meaning that our unusual patterns of alpha and beta modulation still engage the classical attention network, engaged also for gating-by-inhibition. Keeping that in mind, then our results would not only confirm that temporal expectation is encoded in the beta frequency range, but that it is also possibly encoded through the orchestration of the frontoparietal attention network.

Prestimulus modulations of source activity

Next to sensor space, we also observed the modulation of alpha and beta power in source space; following the assumption orienting attention towards a certain modality does also change the prestimulus low frequency power in the corresponding sensory cortex. For the alpha band, we found only a significant source modulation for the touch group, which however, fit perfectly to the obtained results in sensor space, displaying increases in the alpha contra-over-ipsi ratio within the primary occipital cortex in advance of the unexpected late onset or directly after the unexpected early onset.

The story is different for the beta band. For beta activity, we only found a significant source modulation for the vision group, thus the source results cannot confirm the results obtained in sensor space. Interesting however is, that we observe a source modulation before the early onset when a late target was expected, expressed through a higher occipital than somatosensory ratio and aligns to the trends for vision results in sensor space. Thus, one can assume that the marginal modulation of the vision group, which would fit to the modulation of the touch group and which is supporting our interpretation of beta as encoder of the upcoming modality, is indeed true, since the source data support the pattern observed in sensor space.

It is evident that our ROI for the primary sensory source cannot grasp the source activity for both groups at equal measure. For the alpha band modulation, one explanation could be the general weaker nature of alpha modulation in the vision group, leading to alpha modulation below significance. Another explanation could be that the individual differences of the participants brains lead to a better match of our selected coordinates for the occipital ROI for the touch group than for the vision group. Lastly, our paradigm might have led to a more central power modulation in the vision group (e.g. the broad spread of prestimulus alpha modulation in Mazaheri et al., 2014), compared to the touch group, but since we focus here on power lateralization, we are unable observe such central power increases. For beta, the difference in source modulation might be explained to the fact that we based the ROI for source analysis on anatomical, not functional, criteria. Given the variety of somatosensory regions involved in the generation of beta activity, such as S1, but also motor-cortical regions such as M1 (Hari, 2002), it might be possible that the cortical source for the somatosensory beta modulation seen in sensor space did not correspond to the source we used. In a similar way, we have to note that we found beta source modulation for the vision group in advance of the early onset when a late visual target was expected, a result which we do not observe in sensor space. Thus, it is possible that the ROIs for beta modulation were not precisely corresponding to the functionally relevant brain areas, at least for the touch group.

Modulation of prestimulus oscillations – attention vs. expectation

One might argue in how far our modulation reflects attentional orienting and not temporal expectation. Indeed, we use probabilistic cueing, which is in general related to expectation, yet our participants had to actively reorient their attention to use the probabilities in the most optimal manner, leading to a clear modulation of both, temporal attention and expectation. Evidence suggests that attentional modulation is dominating over expectation, which can only be observed in absence of attention (Todorovic et al., 2015), leading to assume that our observed effects here are likely to be an attention modulation. Instead, our paradigm could be clearer representation of temporal attention, than other cross-modal temporal paradigm investigating oscillations (Keil et al., 2015; Pomper et al., 2015). Within these studies, participants were previously informed about the two types of blocks (regular or irregular interstimulus interval), but an active use of this knowledge is not necessary, thus the observed effects might be due to temporal expectation instead of temporal attention. In contrast, one has to actively use the intrinsic knowledge about the temporal and modality probabilities in order to optimize behavioural responses in our paradigm. In conclusion, we argue that our results indeed reflect low frequency modulation caused by attention instead of expectation, though dissociation between these two mechanisms is beyond the scope of this study.

Conclusions

To conclude, one can say that cross-modal temporal orienting of attention, which behaviourally leads to decoupling, expresses through alpha and beta modulations in neural oscillations in an intricate mechanism, which seems to differ from the classical gating-by-inhibition pattern typically found in simpler, spatial orienting paradigms. Alpha band oscillations seem to fulfil the role as a switch mediator, signalling when the observers switches their expectation from one modality towards another, while beta might encode for the modality towards which this switch occurs. Both, alpha and beta modulations were more pronounced for the touch group, in contrast to the behavioural data, which were clearer for the vision group. This however, can be a reflection of an increased task difficulty for touch, leading to higher behavioural variance and engaging the underlying neuronal network in a stronger fashion. While the interplay of the alpha switch and the beta swap (towards the modality at the later time point) is to some extent modulated by temporal attention, both, modality attention and temporal attention seem to express independently, as suggested by cross-modal decoupling. The pure effect of temporal attention was observed over a frontocentral and centroparietal channels, in alignment with the existing attention literature suggesting the involvement of the frontoparietal attention network.

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3. GENERAL DISCUSSION

3.1. Summary of the experimental results

This thesis aimed at exploring the nature of the relationship between attention to time and attention to modality. To investigate their relation, three experimental studies were performed focusing on the interplay of attention to time and modality on behavior and prestimulus brain oscillations.

In the first study (Chapter 2.2), we manipulated the participants' expectation of time and modality of an upcoming event in order to guide their attention towards different modalities at different time points. We used vision and touch with the goal to investigate whether cross-modal temporal attention has similar tight links as cross-modal spatial attention, where responses towards an event in any modality are often fastest at the side of expectation of one modality. Yet, we found that the opposite is true for cross-modal temporal attention, with each modality showing the most efficient response pattern at its most likely time point and thus suggesting a cross-modal decoupling in time.

In the second study (Chapter 2.3), we investigated the generality of the decoupling effect found in the first study. If decoupling of cross-modal temporal attention is a general phenomenon, then one should be able to observe similar decoupling patterns when using different combinations of modalities. If, instead, cross-modal temporal attention is a phenomenon that depends on the particular modality combination, then using a different modality combination may lead to cross-modal temporal coupling. We used auditory and tactile stimuli in our paradigm, in part because we reasoned that, unlike vision, used in the first study, audition is a temporally dominant modality, as is touch. Given this combination, cross-modal coupling, if possible, may be more likely to arise. Yet, we found similar behavioral effects as in study 1, which suggest that cross-modal temporal decoupling is indeed, likely to be a general phenomenon.

Finally, in the third study (Chapter 2.4), we addressed how cross-modal temporal decoupling is expressed in the power of prestimulus brain oscillations. This study used an adapted version of the task in study 1 to investigate the prestimulus effects of cross-modal temporal decoupling in low frequency oscillations, while replicating behavioral results consistent with decoupling, as in study 1 and 2. The EEG analysis focused on modulations of prestimulus oscillations in the alpha band (8-10 Hz) and beta band (18-20 Hz) expressed through power lateralization (contra-over-ipsi ratio), within sensor and source space. We found that the power in the alpha band does not correspond to either, purely modality attention or purely temporal attention, yet we observed a consistent pattern of modulation at approximately the same points in time with an increase of the alpha band contra-over-ipsi ratio over occipital sensors, in a time window between the two possible target onsets. Beta power was modulated separately by modality attention and temporal attention at different time points and ROIs. In terms of modality attention, the beta contra-over-ipsi ratio was modulated in advance of the late onset. The beta lateralization ratio was higher over somatosensory than occipital channels when a tactile target was expected to appear at the late onset and the ratio was higher over occipital than somatosensory channels when a late visual target was expected. However, this pattern was only significant for the touch group, with some similar trends for the vision group; hence this pattern has to be considered with caution. Beside the effect of beta on modality attention, over sensory ROIs, the effect of temporal attention upon beta power expressed over frontocentral and centroparietal ROIs. A modulation of the contra-over-ipsi ratio was observable after the first onset and directly before the second possible onset times, but not in the time period in between. Additionally, we also observed some modulations in the theta band, yet the theta pattern showed great similarities with the alpha band pattern and since we therefore could not observe the exact contribution of the theta band to the interaction of temporal and modality attention, we did not discuss the theta modulation any further and this thesis will not focus on the role of theta either.

3.2. Implication of the results

The studies conducted in this thesis provide evidence that attention to different modalities can be flexibly deployed at separate time points, thus cross-modally decoupled. The effect appears to be of general nature and adds evidence for a potential fundamental difference between the allocation of spatial and temporal attention across modalities. Furthermore, cross-modal temporal attention does not only affect behavior, but also the underlying pattern of brain oscillations in the prestimulus period. Modulations were observed in the alpha and beta band across the sensors over sensory cortices and, for temporal attention, across frontal and parietal sensors. This final chapter of the thesis will discuss the different results and put them into the perspective of the existing literature.

3.2.1. The difference between crossmodal spatial and crossmodal temporal attention

Modality expectation in time seems to follow its own unique temporal profile for each sense, hence be cross-modally decoupled. To be more specific, for the more likely, primary modality, we found a reaction time benefit at the expected time point, were events of the primary modality were also the most likely to occur. This confirms the well-known benefit of temporal orienting in general (Correa et al., 2004; Griffin et al., 2001; Miniussi et al., 1999). Interesting though is that the secondary modality did not follow the pattern of the primary modality; instead responses towards secondary stimuli were faster at the overall less likely, unexpected time point, which contained, however, the highest amount of secondary modality targets.

In contrast to the pattern described above, in a very similar task but investigating cross-modal spatial attention (Spence & Driver, 1996), events of both, the primary modality and secondary modality showed the fastest responses at the overall most likely side, although the secondary modality was more likely to appear at the opposite side. This pattern in spatial attention suggests close cross-modal links, which have been observed in many other occasions across different combinations of modalities (Kennett et al., 2001; Spence & Driver, 1996; Spence et al., 2000; or see Spence, 2010 for more recent review), save for a few noticeable exceptions (e.g., Lloyd et al., 2003; Soto-Faraco et al. , 2005). In other words, spatial attention seems to dominate over modality attention, by reallocating all processing resources upon the most likely stimulus location, foregoing the selectivity for target modality (Eimer, 1999; Macaluso, 2010). This hypothesis would also explain why one can observe a prestimulus lateralization of low frequency oscillations in the alpha and beta frequency range even across different sensory cortices, as shown by Bauer et al. (2012).

Temporal attention and spatial attention are at least in part two segregate processes (Doherty et al., 2005), which, despite leading to similar behavioral effects, are reflected in different ERP components (early components such as P1 for spatial attention (Hillyard et al., 1998 Mangun, 1995) vs. later components for temporal attention (Griffin et al., 2001; Miniussi et al., 1999)). Also when one observes the activation pattern elicited by the two types of attention with PET and fMRI, both modulate in part different areas of the brain, although some overlap exists (Coull & Nobre, 1998).

As such, the difference between spatial attention and temporal attention might be caused due to a difference in their basic nature. In spatial attention paradigms, stimuli are usually presented, or at least expected, in parallel (within the same time window), and hence participants usually struggle to allocate the same processing resources between different spatial locations at the same time (Treisman, 1982). Temporal attention instead, is rather serial in nature (Bowman & Wyble, 2007; Olivers & Meeter, 2008), since stimuli have to be presented at distinguishable time points in order to focus attention upon one of the possible onset times. This would mean that in spatial attention paradigms, participants have difficulties to direct attention in two different directions at the same time, which is also evident due to the spread of spatial attention in same direction across modalities (Bauer et al., 2012). For temporal attention, this problem may simply not exist in most experimental paradigms, since the temporal spacing between the stimuli allows abundant time for our brain to reallocate processing resources through a reorientation of attention. One support for this hypothesis is provided by the attentional blink phenomenon, also referred to as the attentional dwell time (Duncan et al., 1994), were participants fail to perceive a second stimulus presented rapidly after a first stimulus (Shapiro et al., 1997). In this paradigm, the time intervals between the stimuli have been shortened tremendously enough to not allow a reorienting of attention and thus a serial processing of temporal attention. Instead processing resources are still busy on the processing of the first stimulus and the second one cannot be processed in equal fashion, making attentional blink a rare case of almost parallel processing in temporal attention, comparable to the parallel processing in spatial attention.

Some previous evidence gathered for temporal cross-modal attention is in contrast to this simple, but apparently reasonable theoretical sketch. Lange and Röder (2006) found results consistent with temporal cross-modal coupling, that is, once one time point is attended in one modality, other modalities will also follow. This is in clear contrast with our results, and our conclusions. So how can these discrepant results be explainable with our hypothesis of seriality of temporal attention? One possibly important difference between the study of Lange and Röder and ours is that the time intervals in the cited work are shorter than in our study, which is one possible source of differences of cross-modal links in temporal attention (fully detailed discussion in the Discussion section of Chapter 2.2). However, given that the intervals used in both studies are still longer than the interval causing attention blink (Shapiro et al., 1997), which could indicate a temporal processing limit, this explanation alone may not seem sufficient to explain the whole difference. The other possibly relevant factor is that the discrepancy is caused due to the restrictions in Langes and Röders design, which do not allow for an analysis of the late time point without violating the assumption of uncertainty (Griffin et al., 2001).

In conclusion, in a cross-modal temporal attention paradigm, we observed that for each modality, participants performed best at the time point when this modality was most likely to appear, independent of the overall likelihood of this time point. This result suggests that it is possible to decouple the processing of different modalities in time and it is different from cross-modal spatial attention, where one usually observes a coupled processing. The most likely explanation is thereby that the difference is caused through the basic nature of spatial and temporal attention, with the first often oriented towards parallel events and the later upon serial events.

3.2.2. Crossmodal temporal decoupling – a general mechanism?

As discussed in the previous section of the thesis, the cross-modal temporal decoupling we had observed is at variance with earlier findings of Lange and Röder (2006), who found at least some cross-modal links in temporal attention. One possibility for the disparity between Lange and Röder (2006) and Mühlberg et al. (2014), reported in study 1 of this thesis, could have been the difference in modalities (audition and touch for Lange and Röder and vision and touch for Mühlberg et al.). Since audition is generally considered to be a more temporally dominant modality than vision or touch (Bresciani et al., 2005; Fendrich & Corballis, 2001; Morein-Zamir et al., 2003), cross-modal temporal decoupling might only be observable in absence of auditory targets. We tested this in the second study, using a similar task as in study 1, but with audition and touch as possible target modalities. Again, we observed a cross-modal decoupling in temporal attention, providing evidence that cross-modal temporal decoupling is a rather general process independent of the target modality.

Within this study, we exclude the possibility that cross-modal temporal decoupling is merely a niche phenomenon caused by the specific modality combination of study 1. Rather it seems that cross-modal temporal decoupling is indeed a more general phenomenon, and that the difference between the first study presented in this thesis and Lange and Röder (2006) can thus not be caused by the modality combination. Instead, it seems most likely that the differences are caused through a combination of the shorter intervals used in Langes and Röders study, and through the missing analysis of the behavioral data at the late time point. One might have to test if the cross-modal temporal decoupling also holds true for vision and audition (the most temporally accurate and inaccurate modalities) and if decoupling can also be found in other paradigms. Yet, the second study in this thesis is the first step in showing that decoupling is more than just a side effect driven by a certain modality combination and brings us closer to understand the interplay between attention to time and modality.

3.2.3. The role of prestimulus modulations of brain oscillations upon crossmodal temporal decoupling

The first two studies of this thesis introduce the novel concept of cross-modal decoupling in time and illustrate that this mechanism of selective allocation of processing resources is observable with different combinations of target modalities. After addressing the cross-modal interplay of attention to time and modality on the behavioral level, the third study presented in this thesis was designed to explore the expression of cross-modal temporal decoupling in the modulation of prestimulus neural oscillations.

The task in the third study combined the behavioral protocol used in study 1 with EEG measures from a 60 electrode montage (10-20 system). Behaviorally, the findings of study 1 could, for the most part, be replicated in study 3; since we again observed that each modality (vision or touch) followed their distinct temporal likelihood, leading to faster responses of the different modalities at different time points. Yet, the main focus of this study was the interplay of these two types of attention on the prestimulus oscillations in sensor and source space measured with EEG. In terms of sensor space, two regions of interest (ROI) were identified, one over central sensors roughly corresponding to the underlying position of the somatosensory cortex and one over occipito-parietal channels, roughly at the position corresponding to the underlying visual cortex. Within these two regions of interest, we found prestimulus modulations in the alpha and beta frequency bands. In terms of source space, we analyzed the level of modulation of alpha and beta oscillation at the estimated location of the primary visual and primary somatosensory cortex, based on a-priory hypothesis. We found that source power modulation in the alpha and beta frequency range corresponded well to the observed modulation in sensor space, although we observed differences between the groups. For the touch group, we observed strong similarities in source and sensor space for the alpha band, while the vision group showed a stronger correspondence between the (marginally significant) pattern of beta modulation in sensor space and its significant correlate in source space.

Next to this general effect of interlaced temporal and modality attention, we also identified two other regions of interest displaying a modality-independent modulation of temporal attention over frontocentral and centroparietal cortex. Within these regions, we mainly observed a modulation of prestimulus oscillations in the beta frequency band. This section of the thesis will offer explanations for the different oscillatory modulations and the putative roles of the different frequency bands involved.

a) The role of alpha: switch signal vs. gating-by-inhibition

In the third study, we observed a modulation of alpha lateralization in the period in between the two possible target onset times. Alpha oscillations were modulated both right before unexpected late onsets (that is, well after an expected early onset had passed without target; see Fig. 3.2.1.A), and shortly after an early unexpected onset (that is, well in advance of an expected late onset; see Fig. 3.2.1.B). The pattern was consistent across modality groups and let always to a higher contra-over-ipsi ratio in the occipital region of interest, compared to the somatosensory cortex. Since the alpha modulation pattern was always driven by a contra-lateral increase over occipital sensors, independent of which modality was attended, this alpha modulation cannot be an encoder for modality attention. Indeed, the fact that alpha increased, instead of decreased, contra-lateral to the attended side runs against the usual finding linking alpha upregulation with inhibition of irrelevant locations (Haegens et al., 2012; Jensen & Mazaheri, 2010; Kelly et al., 2006; Worden et al., 2000).

Furthermore, we observed that this changes in the alpha band ratio always occurred around the same points in time in comparable conditions of the touch and vision group, suggesting some sort of time-dependent modulation. Yet, a direct comparison between expect early and expect late trials showed no significant time windows of alpha modulation, suggesting that alpha oscillations cannot be directly encoding for temporal focusing of attention either.

Instead we propose a different role in which alpha band oscillations would reflect modality switches, regardless of the direction of the switch. One piece of support to this interpretation is that, in all cases, contralateral alpha-power increases happened between the two possible target onset times. This is further supported by the observation that the increases in alpha lateralization peaked at slightly different times depending on whether the expected onset time was early or late. Please note that, in the trials used for EEG analysis, a target never occurred at the early time point, even if in some blocks, many early targets appeared, to build up the expectation. In these type of trials, when early targets were expected, the alpha contralateral increase peaked only shortly before the late onset. That is, the expectation of a target seemed to be held for longer, and hence the switch (putatively marked by alpha) released late, upon the impending occurrence of a target in the other modality at a late time. On the other hand, in blocks where most targets occurred at a late time point, the switch (from an unlikely early event towards a likely late event) seemed to occur much earlier in time, marked by an alpha peak just after the first onset time had passed (without a target).

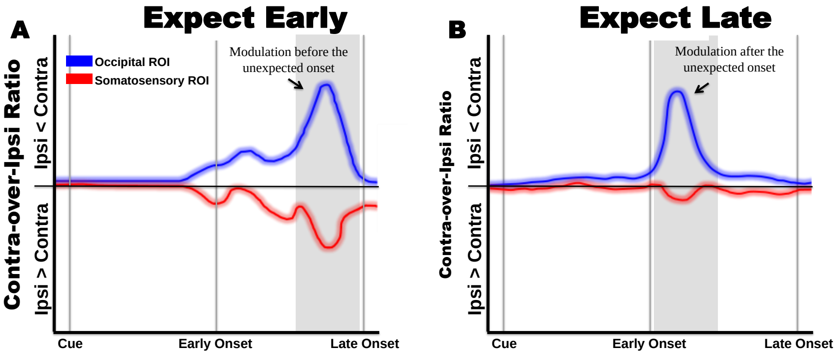

Figure 3.2.1: Illustration of the observed pattern of alpha band modulation. **A)** When an early target was expected, participants showed a late modulation of alpha band activity, directly before the late, unexpected time point. **B)** When a late target was expected, participants showed a modulation of alpha band activity directly after the early, unexpected time point.

It is interesting that our observed alpha modulation pattern was usually expressed through an increase in the alpha power ratio in the occipital ROI, partially accompanied by a significant ratio decrease in the somatosensory ROI. While the alpha modulation over occipital sensors/channels is often present for vision (Banerjee et al., 2011; Gould et al., 2011; Hanslmayr et al., 2007; Kelly et al., 2006; Sauseng et al., 2005; Snyder & Foxe, 2010; Thut et al., 2006), attentional orienting towards touch usually leads to a modulation of alpha and beta activity in more central channels and sensors, corresponding to our somatosensory ROI (Haegens et al., 2011; Jensen et al., 2005; van Ede et al., 2011; van Ede et al., 2010). As we mentioned before, the similar alpha modulation pattern in both groups suggests the modulation of alpha power in our paradigm was independent of the target modality and the topography of our modulation further adds to this hypothesis. One could try to counter the modality independence of alpha activity in our paradigm by pointing out that Pomper et al. (2015) also investigated an interplay between attention to time and modality where the authors found alpha band modulation only in the visual ROI as well. Concerning that the previously mentioned studies either focused on spatial attention paradigms (Banerjee et al., 2011; Kelly et al., 2006; Sauseng et al., 2005; Thut et al., 2006) or on the interplay between temporal and spatial attention (van Ede et al., 2011), one might raise the question if occipital alpha could be a general pattern for temporal paradigms, whereas it is expressed across different sensory cortices in spatial attention. Yet, although offering an explanation to our pattern of results, this account would not be in accordance with our hypothesis of alpha as a switch signal and one might also explain the data of Pomper et al. in a similar fashion, by arguing that their observed alpha was not encoding for modality either, but for a switch towards the modality, if necessary in time. However, this account at the moment is based mostly on speculation and further evidence has to be assembled in order to develop the exact role alpha in cross-modal temporal paradigms further.

An important question is how our hypothesis of alpha as a mediator of a modality switch aligns with the existing theories of alpha power. The most dominant hypothesis about the role of prestimulus alpha oscillations is probably the gating-by-inhibition hypothesis (Bonnefond & Jensen, 2013; Jensen et al., 2014; Jensen & Mazaheri, 2010; Mathewson et al., 2011), which suggests that increases in local alpha band oscillations serve to gate the processing of sensory information towards attended events by blocking out information presented at unattended locations, modalities, etc., which decreases the excitability of the underlying cortical regions. Gating-by-inhibition is additionally hypothesized to act in a periodic manner (Jensen et al., 2014; Landau & Fries, 2012; Mathewson et al., 2011). However, our data suggest temporal orienting of attention across different modality increases the prestimulus alpha power instead of decreasing it. Therefore, our observed alpha pattern is not explainable by the gating-by-inhibition. One explanation might be that our proposed switch is actually an inhibition of our current expectation. To clarify, this would mean that in order to reorient attention about another modality in time, one needs to be “gated away” from the current expectation. Since the timing in our task is known to the paradigm, participants might be able to switch their attention by suppressing their previous expectation about onset time and modality. If this would behold true, then our results would not be at odds with the gating-by-inhibition hypothesis. However, van Ede et al. (2011), investigated the orienting of tactile spatial attention at two or three possible onset times (2-point vs. 3-point hazard rate, blocked). There, participants always showed a decrease in the alpha (and even more the beta) contra-over-ipsi ratio in advance of a possible onset. The result of van Ede is completely compatible with gating-by-inhibition and opposite of our finding. Maybe the cross-modal nature of our paradigm with visual and tactile stimuli has led to this disparity. As we already stated for our behavioral results, touch seem to be a very special modality, since it to focus towards or away from touch (Lloyd et al., 2003; Spence et al., 2001). As such, the alpha switch might be reflection of the difficulty of switching modality expectations, and in particular, the difficulties of orienting towards or away from touch. This might also explain why the alpha pattern in source space was more pronounced for the touch group, where the behavioral need to focus towards touch was greater than in the vision group. Why a reorienting towards or away from a modality should mainly be encoded over occipital channels, however, is at present unclear and overall, one would need to test this hypothesis further. For example, one such test would be to measure prestimulus EEG in a cross-modal temporal attention paradigm with visual and auditory stimuli, in order make more profound assumptions about the discrepancy between van Ede et al. and the results of our third study.

b) The double role of beta: encoding for temporal attention and upcoming modality

The role of the beta band seems to be a complex one in our study. With respect to the interaction between attention to time and modality, we observed a significant beta modulation only for the touch group in advance of late targets. When the late event was expected to be visual, the contra-over-ipsi ratio was higher in the occipital than in the somatosensory region of interest. In contrast, when the late event was expected to be tactile, the contra-over-ipsi ratio was higher in the somatosensory compared to the occipital region of interest. We hypothesize that this could possibly mean that beta oscillations change the expectation towards the modality, when a switch was mediated by the alpha band. Beta also played a role in the pure temporal attention itself (that is, when pooling over modality expectation), leading to modulations over frontocentral and centroparietal sensors when comparing early vs. late expectation trials. The temporal modulation over centroparietal sensors was especially strong in expect early trials, a pattern that makes sense since orienting immediately after the cue may be easier (and temporally more precise) than towards the late onset, further away from the temporal anchor of the cue onset.

Beta oscillations seem to be directly involved in the encoding of modality attention. We observed that the contra-over-ipsi ratio increased selectively for the ROI corresponding to the modality it encodes for. Note that this is different from the lack of modality selectivity of alpha. Again, this pattern seems to be at odds with the gating-by-inhibition hypothesis; however the question why beta oscillations are reflected in such a way is currently pure speculation. Maybe analyzing the relationship between the prestimulus beta phase and the observed behavior would give some more tangible evidence, since one might assume that some form of phase alignment led to the disagreement between our observed beta modulation pattern and gating-by-inhibition.

Despite this effect of beta power modulation was only observed in a significant fashion for the touch group, the trends for the vision group point in a similar direction. Of course, it is difficult to interpret a non-significant trend, but one possibility is that the weaker beta expression of the vision group compared to the touch group was due to the higher temporal accuracy of touch (Boulter, 1977). The vision group had a much higher amount of visual targets and their decreased spatial accuracy might have also decreased the modulation of beta band oscillations. Another possibility for the weaker effects in vision (or stronger effects in touch) would be a general difficulty to focus attention away from touch (Lloyd et al., 2003; Spence et al., 2001). If it is more difficult to focus attention away or towards touch, then one might also perceive stronger modulations in the underlying oscillatory pattern. Since the vision group has fewer tactile targets overall, the oscillatory pattern would also be weaker than for the touch group. Which of these possibilities is more accurate remains speculation and need further evaluation in future studies. Interesting enough, the beta effect for the touch group is not reflected in source space, yet the beta trends of the vision group are. This might add evidence that a modulation pattern exists also for the vision group and that individual differences in terms of source alignment exist between the vision and the touch group, leading here to decreased source accuracy for the touch group.

In contrast to the role of beta oscillation in the encoding of modality attention, the role of beta as encoder of temporal attention seems very much aligned with the existing literature. Many studies show that temporal attention, even in light of gating-by-inhibition, is stronger encoded in the beta band than in the alpha band (Keil et al., 2015; Pomper et al., 2015; Todorovic et al., 2015; van Ede et al., 2010). Some of these studies find also contributions of other low frequency bands to temporal attention, such as delta (Keil et al., 2015; Pomper et al., 2015), yet others do not find such contributions (van Ede et al., 2011). The absence of further temporal modulation in other low frequencies in our study and in some of the other temporal attention studies suggests that the exact spectral distribution of oscillations in the low frequency range might be task dependent. Interesting enough is the position of the region of interest for the temporal attention effect across sensor space. We observe temporal attention modulation independent of modality in the frontocentral and centroparietal sensors. Other studies show partial overlapping patterns of modulation of temporal attention (Buchholz et al., 2014; Todorovic et al., 2015; van Ede et al., 2014). This might suggests a general engagement of the frontoparietal attention network (e.g. Coull & Nobre, 1998), which cannot be confirmed without an in-depth source analysis of the temporal attention spread though. Overall though, the beta modulation for temporal attention seems to validate previous findings in temporal attention due to its good fit into the existing literature.

3.3. Conclusions

The goal of this thesis was to investigate the interaction between attention to time and modality. To do so, we conducted three different experiments investigating the behavioral responses within a cross-modal temporal paradigm and its underlying neural expression in the prestimulus period.

We expected that temporal cross-modal attention would be expressed different than spatial cross-modal attention, since attention to space and to time are distinct processes partially encoded in independent networks in the brain. Indeed, in study 1 we observed that, if attention to time and modality are strongly interlaced with each other, such that different modalities would follow different temporal likelihoods, with one modality and time being the most likely, then cross-modal temporal attention would lead to a decoupled processing, which is different from cross-modal spatial attention, where all modalities show the best behavioral responses at the overall most likely spatial position, independent where the modality itself is most likely to be presented.

While study 1 suggested a different mechanism for cross-modal spatial and temporal attention, some existing literature found some cross-modal temporal links, raising the question of how general the pattern we observed actually is. We tested this by repeating our previous experiment with a different combination of stimulus modalities, using the temporally dominant auditory modality and touch this time (in contrast to vision and touch in study 1). We expected to observe a similar behavioral pattern as in study 1 and indeed, this is exactly what we observed, adding evidence that cross-modal temporal decoupling might be a general pattern.

At last, we investigated the neural expression of the interaction of temporal and modality attention in our third study, by using an adapted version of study. While we found a prestimulus modulation of the alpha and beta band in sensor ROIs, corresponding roughly to the somatosensory and occipital cortex, as expected, the pattern of alpha and beta modulation was different than the pattern expected according to the gating-by-inhibition hypothesis. Instead, alpha oscillations seem to signal when to switch from one expectation towards another. Similar to alpha oscillations, also the modulation of beta oscillations in the sensory ROIs did not follow the classical pattern and we suspect that, like alpha is encoding for the expectation switch, beta might encode for the modality towards which the participant switches its attention to. Beside the modality-dependent attention effect of beta, a second, temporal attention effect in the beta band was observed outside the sensory ROIs. This modality-independent beta pattern confirmed our hypothesis of temporal attention being encoded in the beta band in a possible modality independent matter.

To summarize, the results of this thesis advance current knowledge about how attention is allocated across different modalities over time, with the following main conclusions.

1. Sensory modalities can orient attention and/or follow expectations in an independent matter, in other words be decoupled, in cross-modal temporal attention.
2. This cross-modal temporal decoupling is, in principle, independent of the modalities involved in the task.
3. Cross-modal temporal attention leads to prestimulus modulation of alpha and beta oscillations, which is, however, different from the pattern observed in spatial attention paradigms.
    - 3.1. Alpha oscillations might encode for the reorienting process itself or, in other words, the switch from one expectation to another.
    - 3.2. Beta oscillations might encode for which modality participants switch their attention to.
    - 3.3. Temporal attention is encoded in the beta band in a modality-independent matter, in regions possibly related to attention control.

3.4. Outlook on possible future directions

This thesis aimed to explore the relationship between attention to time and modality, yet many open questions, and new questions emerging from the findings of the studies presented here, remain. For example, if cross-modal temporal decoupling is indeed a general mechanism, as our studies suggest, then one should also be able to observe when using more modality combinations like auditory and visual, in a similar paradigm, and one should observe cross-modal temporal decoupling in other temporal attention paradigms. Also, the temporal limitations of cross-modal temporal decoupling are currently unknown. The results of Lange and Röder (2006) suggested that some interval timings between possible sensory events will not enable us to process modalities independently and to explore the exact borders of the necessary time intervals of each modality would be an interesting and important question.

Even less well known is the role of the underlying brain oscillations in cross-modal temporal decoupling yet. To our knowledge, this is the first attempt at the question, together with the recent studies of Pomper et al. (2015) and Keil et al. (2015), published during the writing of this thesis. Whilst the third study of this thesis analyzed EEG modulations in terms of power, some of the results and prior literature might suggest a prominent role of prestimulus phase. While the amount of trials and paradigm presently used were simply not sufficient to investigate this relationship in this study, it remains an important question to address phase dependency in temporal attention, in the future. MEG might be a more suitable method to address the question of the role of phase, since the substantially lower preparation time, compared to the EEG, allow extending the duration of the experiment itself before the participants will show signs of exhaustion. Additionally, the increased spatial accuracy of the MEG should provide a better localization of the underlying sources of cross-modal temporal decoupling and thus a more thorough exploration of the relation of temporal and modality attention in source space. Interesting is also the question in how far the observed modulation are correlated to the behavior, by comparing the levels of prestimulus alpha, beta and theta power of the fastest response trials to the levels of prestimulus alpha, beta and theta power of the slowest trials.

Completely unexplored is yet the causal relation between the underlying brain oscillations and cross-modal temporal decoupling. If the modulation of prestimulus power and lateralization can be proven to be correlated to behavior, then one should also be able to influence the behavioral response by modulation the power in the different frequency band. Considering the absence of noise, especially tACS/tDCS seem to be a good choice of method to test possible causation, in the future.

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