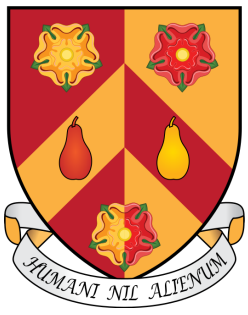
Temporal expectations in the context of spatial expectations and stimulus competition

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Abstract

With this thesis, I investigated the effects of combined temporal and spatial expectations. In addition, I examined temporal expectations in the context of spatially and temporally competing distractors. In a parallel line of research, I studied the effects of aging on these functions. In Chapter 1, I introduce the subject of temporal expectations, review how they interact with other top-down biases, and argue why they should be investigated in the context of distraction. I also review theories of cognitive aging and motivate the investigation of age-related changes in the context of the main subjects of this thesis. In Chapter 2, I show that both behavioural performance and neural markers of pre-target processing can be modulated flexibly and beneficially by combined temporal and spatial expectations. I also show that neural markers of expectation seem to have behavioural relevance, and that temporal and spatial expectations can interact both neurally and behaviourally, when lateralised effects are investigated. I further demonstrate that aging compromises lateralised effects of spatio-temporal expectations. In Chapter 3, I show that perceptual effects of temporal expectations on stimulus competition depend on the stimulus context. Temporal expectations act independently of competition when stimuli are presented in different hemifields but can impair performance with intrahemifield competition. I further show that aging can spare the ability to suppress irrelevant information, and that older adults benefit from temporal expectations. In Chapter 4, I explore the effects of temporal expectations for a target stimulus when stimuli compete over time. I show that target-related behavioural performance can be increased, and pre-target distractor representations relatively decreased. In Chapter 5, I draw commonalities and differences across experimental Chapters 2-4, discussing temporal expectations in the context of isolated and competing stimuli, the relevance of lateralised effects of temporal expectations, age-related findings, and future questions and directions for research.

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Chapter 1: General introduction

Temporal expectations

Selective attention refers to the set of cognitive functions enabling us to prioritise and select relevant events to guide adaptive behaviour according to specific goals. So far, most of attention research has focussed on the prioritisation of location (Carrasco, 2014; Nobre & Mesulam, 2014) and feature properties (Scolari, Ester, & Serences, 2014) of relevant items. However, we live in a dynamic world. A stream of countless events is constantly reaching our senses. As a result, making sense of and navigating within our environment can only be attained by dealing with these dynamics. There is a growing body of literature acknowledging that our environment is not static, but constantly unfolding. This research incorporates the fourth dimension. It deals with the temporal aspects of attention (Nobre & Rohenkohl, 2014).

We can extract various temporal contingencies and regularities from the environment and build temporal expectations for adaptive and goal-directed behaviour accordingly. In principle, every change carries temporal information. A recurring temporal contingency between two items signifying a change and resulting into a temporal association between the two items, is the minimal pre-condition for the generation of a temporal expectation. Temporal expectations can also be generated where more items are repeated according to a temporally structured pattern resulting in rhythms or more complex temporal sequences. The dynamic modulation of temporal expectations for a given item with the passage of time is expressed by a so-called hazard function.

Real-world situations contain a variety of different temporal structures. Imagine a tennis player preparing to serve. She may bounce the ball regularly five times (rhythm) before presenting it on the racket. During the course of the match, the audience has learnt that this can be interpreted as a cue for the player to start executing the serve toss in about 2 seconds (cued temporal association). The execution of the toss itself features a complex movement pattern, where the relative position of different body parts in relation to each other changes according to specific yet stereotyped temporal pattern (cued temporal associations, temporal sequence). When the ball has reached maximum height, we anticipate that it is going to reverse its direction of movement because of gravity, falling back towards the ground. We further expect that the player is going to hit the ball and this expectation increases the more time has passed and the further the ball has fallen (increasing hazard). Once the ball has reached the height of the player's head, she may want to have the ball fall on the ground and re-execute her movement. It becomes very unlikely that she will still hit the ball. Accordingly, our expectation for a serve decreases (decreasing hazard).

Nobre and Rohenkohl (Nobre & Rohenkohl, 2014) separated temporal expectations into different categories: rhythms, cues, and hazards based on previous literature and neural and behavioural dissociations. Rhythms, or, more broadly defined, repeating temporal sequences are the most pervasive phenomena linked to temporal expectations in our environment. As already exemplified above, movements often feature well-paced temporal coordination. Further examples are walking, writing, chewing, breathing, speaking, or saccading toward relevant events, to name only a few. As a consequence, sensory sampling is often also parsed into rhythmic units, and it has been proposed that entraining perception to regular contexts is a

fundamental aspect of attention, sharpening perception for relevant events (Besle et al., 2011; Jones, 1976; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Lakatos et al., 2013). Indeed, it could be shown that valid, rhythmic temporal expectations can improve the quality of perception as well as response speed (Barnes & Jones, 2000; Cravo, Rohenkohl, Wyart, & Nobre, 2013; Jones, Johnston, & Puente, 2006; Mathewson, Fabiani, Gratton, Beck, & Lleras, 2010; Praamstra, Kourtis, Kwok, & Oostenveld, 2006; Rohenkohl, Cravo, Wyart, & Nobre, 2012; Sanabria, Capizzi, & Correa, 2011). In addition, rhythmic expectations have been shown to facilitate anticipatory perceptual and response-related ERP (event-related potential) and oscillatory measures (Cravo et al., 2013; Praamstra et al., 2006; Rohenkohl & Nobre, 2011). Unlike cued temporal associations, rhythmic temporal facilitation seems to be automatic, exogenously driven, independent of task instructions, partly resistant to brain damage and competing task demands, and, to some degree, outside of cognitive control (Breska & Deouell, 2014; de la Rosa, Sanabria, Capizzi, & Correa, 2012; Rohenkohl, Coull, & Nobre, 2011; Sanabria et al., 2011; Triviño, Arnedo, Lupiáñez, Chirivella, & Correa, 2011), suggesting that temporal expectation benefits may be mediated by different, also regionally separate mechanisms.

Temporal cueing exploits learnt temporal associations between stimuli. Cued temporal expectations are invoked flexibly after a cue stimulus and can improve performance according to specific goals by active voluntary control. In this sense, they are complementary to classical endogenous spatial cueing (Posner, 1980). With temporal cueing, performance is typically contrasted for valid versus invalid or neutral temporal expectations. Valid temporal expectations can facilitate perceptual sensitivity and response speed (Correa, Lupiáñez, & Tudela, 2005; Coull & Nobre, 1998). Recent

findings emphasize the selective nature of cued temporal expectations, pointing to perceptual processing trade-offs across time for temporally expected vs. unexpected stimuli (Denison, Heeger, & Carrasco, 2017). Cued temporal expectations can also benefit neural perceptual and motor-related measures, as shown by ERPs and neural oscillations (Correa, Lupiáñez, Madrid, & Tudela, 2006; Heideman et al., 2018; Miniussi, Wilding, Coull, & Nobre, 1999; Zanto et al., 2011).

Hazard rates - the conditional probabilities for the occurrence of an event given that it has not yet occurred (Luce, 1986) – are rarely orthogonal to rhythms or cues. Instead, hazard-based temporal expectations may develop in most experimental tasks with fixed stimulus onsets. Importantly, they can emerge even without rhythmic stimulation or explicit cueing, where experience has formed a temporal association. Research using temporally predictable intervals between events (foreperiods) has shown that perceptual sensitivity and response times follow hazard functions (Cravo, Rohenkohl, Wyart, & Nobre, 2011; Rolke & Hofmann, 2007; Schoffelen, Oostenveld, & Fries, 2005). Magneto- and electroencephalography (M/EEG) studies, as well as single-cell measures, also point to improved perceptual and motor processing with increasing hazard rates (Cravo et al., 2011; Ghose & Maunsell, 2002; Janssen & Shadlen, 2005; Schoffelen et al., 2005).

Different temporal expectations can also exist in parallel. Where different temporal biases co-occur, independent (Breska & Deouell, 2014; Rohenkohl et al., 2011) and interactive (Correa & Nobre, 2008; Coull, Frith, Büchel, & Nobre, 2000) relationships have been observed.

Temporal expectations and other expectation biases

Temporal expectations do not occur in isolation. We do not sample "time" from the environment. Instead, temporal expectations are connected to other attributes of events (, e.g. their location or identity). In the brain sensory events are represented relative to neuronal receptive fields. Furthermore, processing in receptive fields can be biased by object-based, feature-based (Scolari et al., 2014), and spatial expectations (Carrasco, 2014; Nobre & Mesulam, 2014). In order to understand the dynamics of selective cognition, it is vital to investigate how temporal biases work in relation to these other biases.

Interactions of feature-based expectations with temporal expectations have been observed with the tracking of rhythmic sequences of tones (Lakatos et al., 2013). Two sequences were presented in parallel, where each sequence featured a specific repetitive tone and rhythm. Monkeys were cued to one of the sequences and were required to respond to deviant tones in the cued sequence, while multiunit activity was recorded in area A1. Neural activity entrained to the temporal structure of the sequences. Counter-phase entrainment was observed for differently tuned A1 neuronal ensembles. Importantly, high-excitability phase was connected to the attended sequence of tones and low-excitability phase to the unattended sequence of tones. The representation of attended tones was thus sharpened, and the authors concluded that temporal (rhythm) and feature-based (tone pitch) expectations acted as a spectro-temporal filter. In human participants and ERP research, interactions between temporal and feature biases have also been shown. ERP prediction error signals could be provoked by omitting tones of an auditory stream when both tone identity and presentation interval were predicted. When presentation interval, but not

tone identity could be predicted, no error signal was observed (Sanmiguel, Saupe, & Schröger, 2013). Using MRI, feature-based and temporal bias interactions were shown for visual cortical responses (Warren, Yacoub, & Ghose, 2014).

Investigating temporal expectations together with spatial expectations, Ghose and Maunsell (Ghose & Maunsell, 2002) recorded single-cell activity in monkeys. Behaviourally relevant Gabor gratings were presented peripherally inside the receptive field of V4 neurons. Monkeys were required to spatially attend to these gratings and detect a stimulus orientation change. Irrelevant gratings were presented in the diagonally opposite visual quadrant. Spatial attention to stimuli inside the receptive field of a neuron increased the firing rate of that neuron. Importantly, attentional modulation followed the conditional probability (hazard rate) of stimulus orientation change, presumably reflecting monkeys' temporal expectations.

Rhythmic temporal expectation can also interact with spatial expectations. Doherty et al. (Doherty, Rao, Mesulam, & Nobre, 2005) presented a disk in the left side of the visual field. The disc moved spatially predictably or unpredictably in a regular or irregular pace to the right of the screen, finally disappearing behind an occluding barrier. After that, the disc reappeared to the right of the barrier and participants were required to discriminate if the disc contained a small black dot in its centre. Depending on the experimental condition, participants could or could not anticipate the occurrence of the disc in space and time. Early visual evoked potential P100 relating to perceptual processing was increased with only spatial but not only temporal expectations. Crucially, temporal expectations synergistically combined with spatial expectations to boost P100 amplitude above the P100 amplitude level relating to the spatial expectation condition. Interestingly, spatial and temporal biases improved

response speed independently, suggesting that neural interactions between temporal and spatial biases do not need to manifest in behaviour.

Rohenkohl and colleagues (Rohenkohl, Gould, Pessoa, & Nobre, 2014) orthogonalised cued temporal and spatial expectations behaviourally. Arrow cues presented in the centre of the visual field indicated if a target stimulus was likely to occur in the right or left visual hemifield. Cue colour indicated the likely temporal interval of target occurrence. Perceptual sensitivity increased for valid versus invalid spatial expectations. Perceptual performance was not different for valid versus invalid temporal expectations. However, similarly to Doherty et al.'s findings (2005), valid temporal and spatial expectations worked together and generated larger perceptual benefits than spatial expectations alone.

The experimental study in Chapter 2 follows on from that research, investigating the interplay between cued temporal and spatial expectations in the neural domain (see also: Heideman et al., 2018). Behavioural performance and pre-target neural measures of attentional biasing were studied using psychophysics in combination with electroencephalography (EEG).

Temporal expectations and stimulus competition across space

The vast majority of studies on temporal expectations has been conducted in the context of isolated stimuli (But see: Rolke, Festl, & Seibold, 2016; Seibold & Rolke, 2014). This is quite surprising. Our environment holds countless events at every instance in time, as well as unfolding in close temporal proximity. It can certainly be beneficial to perceive better and react more quickly to a single stimulus. However,

arguably, it is more important to select a relevant stimulus from a multitude of competing stimuli.

Simultaneously presented stimuli interact with one another at the single-cell level (Gilbert, Ito, Kapadia, & Westheimer, 2000; Moran & Desimone, 1985; Reynolds, Chelazzi, & Desimone, 1999). When two stimuli are presented together inside the receptive field of a neuron, related response profiles are not represented additively. Instead, neuronal firing can best be explained by a weighted average of individual response rates (Luck, Chelazzi, Hillyard, & Desimone, 1997; Reynolds et al., 1999). Importantly, if spatial attention is directed to one of the two stimuli, the response profile of the neuron is biased such that it resembles the responses evoked by the attended stimulus alone (Moran & Desimone, 1985; Recanzone & Wurtz, 2000; Reynolds et al., 1999). Along the same line, competitive stimulus interactions have also been shown in humans using functional magnetic resonance imaging (Kastner, De Weerd, Desimone, & Ungerleider, 1998). Kastner and colleagues presented a set of complex colourful stimuli in the periphery of the visual field in close proximity to each other. Stimuli were either presented simultaneously or sequentially, and participants were required either to ignore the peripheral stimuli in order to perform a centrally presented task or to attend to one of the stimuli to perform a target-detection task at one of the peripheral locations. Higher-level visual-cortex activity was weaker when stimuli were presented simultaneously versus sequentially, suggesting stimulus competition. Attending to one of the peripheral stimuli increased visual cortex activity, regardless of stimulus-presentation condition. Crucially, stimulus activity was specifically increased with attention to simultaneously presented stimuli, suggesting that spatial attention decreased stimulus competition.

These findings accord well with the theory of biased competition (Desimone & Ducan, 1995). The theory states that stimuli mutually compete with each other for representation due to limited processing resources. One major function of attention is to resolve competitive interactions at the level of the receptive field by biasing processing resources to attended stimuli. Attended stimuli are then able to prevail against unattended stimuli. Temporal expectations can work on task-relevant sensory areas (Cravo et al., 2013; Ghose & Maunsell, 2002). In fact, timing may be an intrinsic property of neural circuits (Goel & Buonomano, 2016; Mauk & Buonomano, 2004). Temporal expectations may therefore be specifically useful in the context of stimulus competition and team up with other e.g. spatial biases to help overcome competitive conflict.

The empirical study in Chapter 3 examines the behavioural effects of concurrent spatial and temporal expectations on visual stimulus competition. Target and distracting stimuli were presented simultaneously in different or the same hemifields to investigate the consequences of temporal expectation within the context of indirect, interhemispheric or direct, receptive-field competition.

Temporal expectations and stimulus competition across time

Stimulus competition is not restricted to the spatial layout of a receptive field. As described before, perception unfolds within continuous and dynamic environmental stimulation. Thus, stimuli also compete for representation across time.

Building on previous research (Broadbent & Broadbent, 1987; Reeves & Sperling, 1986; Weichselgartner & Sperling, 1987), Raymond et al. (Raymond, Shapiro,

& Arnell, 1992) conducted a series of experiments that illustrate competitive interactions among stimuli over time. Letters were presented in rapid temporal succession at a single, attended location. They found that identification of a salient target letter leads to significant costs in identifying temporally proximal subsequent stimuli. Identification of the subsequent stimulus followed a U-shaped curve, with the letter immediately following the target and letters presented at later stimulation positions being comparably less affected than letters presented at subsequent proximal post-target stimulation positions. Distant subsequent targets were progressively unaffected. Furthermore, they found that the deficit was specific to conditions requiring detection of the first target. Target saliency alone was insufficient and did not result in a post-target deficit. Raymond et al. argued that the effect had a strong attentional component, where attention could not be deployed for intermediate time ranges after target presentation. The authors called the effect "attentional blink" and later postulated that stimuli might actually compete for representation (Shapiro, Raymond, & Arnell, 1994). A lot of research has been conducted on the attentional blink phenomenon and its mechanism is still debated (Dux & Marois, 2009). However, and importantly, temporal expectation to a post-target probe stimulus can interact with the processing dynamics of stimuli presented in rapid temporal succession, ameliorating the attentional blink (Martens & Johnson, 2005).

Interestingly, Denison et al. (Denison et al., 2017) recently showed processing trade-offs across time. When a stimulus was temporally cued, behavioural performance relating to that stimulus could benefit, whereas performance relating to preceding or succeeding stimuli could be decreased. Unlike attentional-blink

modulations by temporal expectations, this finding still suggests that more flexible, pre-target preparatory processing modulations can be induced by temporal expectations.

The aim of the empirical study in Chapter 4 was to investigate the neural, perception related stimulus processing across time in the presence of temporal expectations. Using a combination of behavioural, ERP and stimulus-decoding analysis techniques, I characterise the processing of task irrelevant pre-target distractors when the target is more or less expected in time.

Theories of cognitive aging, temporal and spatial expectations and stimulus competition

This thesis investigates cued temporal expectations in the context of spatial expectations and how temporal expectations can act in the presence of stimulus competition. In a second line of research I studied the influence of aging on these processes.

Cognitive aging is usually discussed as cognitive decline, or, if cognition is maintained, in the context of compensatory mechanisms. Theories of aging include the discussion of general slowing of brain function (Salthouse, 1996), which may also have to do with structural decline (Rabbitt et al., 2007; Turken et al., 2008) and less precise neuronal coding (Reuter-Lorenz & Lustig, 2005). Put simply, slower processing would result in less information being available for successive levels of processing, amounting at some point to the emergence of a deficit (Salthouse & Madden, 2013).

The prefrontal cortex is thought to play a major role in cognitive aging. Dysfunctional prefrontal processing, potentially associated with an impairment to represent task-relevant information, is hypothesised to impair cognitive control, including lower levels of inhibitory processing and higher levels of distractibility (Braver et al., 2001; Dempster & Vegas, 1992; Wecker, Kramer, Wisniewski, Delis, & Kaplan, 2000; West & Schwarb, 2006).

However, aging has also specifically been related to impaired sensory processing (Monge & Madden, 2016; Park et al., 2004), so that evaluations of frontal function should also account for possible sensory processing deficits propagating along the hierarchy. The posterior-to-anterior shift in aging (PASA) theory (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008) accounts for that by proposing that age-related prefrontal activation increase leads to improved performance and compensates for posterior sensory cortex activation deficits.

In addition, it has become clear that cognitive aging does not simply mean functional and structural decline. Functional reorganisation and compensation are thought to play a key role in healthy cognitive aging. This is at the core of the compensation-related utilisation of neural circuit (CRUNCH) hypothesis (Reuter-Lorenz & Campbell, 2008). With this theoretical approach, it is particularly crucial to relate increased neural activation to performance measures in order to dissociate beneficial compensatory effects from overactivation which rather points to age-related dedifferentiation, inefficient processing or disinhibition. Similarly, the scaffolding theory of aging and cognition (STAC; Park & Reuter-Lorenz, 2009) states that increased especially prefrontal activation develops gradually across the live span in order to build a “compensatory scaffold” in response to neural decline. Older adults may perform on

a par with younger adults in many tasks. Only with particularly demanding tasks their neural scaffolding may become insufficient and performance deficits apparent.

Prefrontal cortex is generally considered the be a critical node in the selection of relevant targets and suppression of irrelevant information, and therefore to play an important role in top-down modulation (Gazzaley & D'Esposito, 2007). Not surprisingly, cognitive aging has also been related to a top-down modulation deficit (Chao, 1997; Gazzaley, 2013). The selection of relevant information can be afforded by various expectation biases. By employing combined spatial and temporal expectations, the study in Chapter 2 investigates the interplay of two different domains of cognitive flexibility. By testing a large cohort of older participants, I studied whether aging is predictive of neural and behavioural variability. Examining combined spatial and temporal expectations in the context of aging is particularly interesting. Most effects of pre-target spatial expectation seem to be relatively well preserved in aging (Chapter 2 introduction). However, it is less clear how far older participants can employ temporal expectations to facilitate neural processing and behaviour (Chapter 2 introduction). Studying spatial and temporal biases in parallel should help to characterise the specific modulations related to each bias, thereby potentially resolving conflicting findings from earlier research where temporal and spatial biases have been studied separately. The study in Chapter 3 examines spatial and temporal top-down modulation in aging with an emphasis on the suppression of distracting information, where relevant and irrelevant stimuli can occur in opposite hemifields.

Chapter 2: Temporal and spatial expectations

Abstract

Expecting a relevant stimulus in time or space improves performance and facilitates neural processing related to that stimulus. In the experiment of this chapter, using psychophysics and electroencephalography I investigated the effects of combined temporal and spatial expectations on the processing of a relevant stimulus. Supporting previous research, both response speed and perceptual sensitivity were enhanced by temporal and spatial expectations. Neurally, common event related potential measures of pre-target temporal (CNV) and spatial (ADAN, LDAP) expectations were observed. Topographical representation of these measures was clarified using scalp current density transformation. CNV, ADAN and LDAP could also be correlated with behaviour, suggesting their behavioural relevance. Importantly, it could be shown that a temporal CNV can correlate positively with both response speed and perceptual sensitivity. Furthermore, spatial expectation-related left ADAN and LDAP were increased by temporal expectations, emphasising their role in flexible top-down modulation. Similarly, spatial expectation-related lateralisation of posterior alpha oscillations was also sensitive to temporal expectations. In particular, right but not left posterior alpha oscillations were sensitive to temporal expectations. This neural finding was also reflected in behaviour, where left versus right visual hemifield seemed to be more sensitive to temporal expectations.

Investigations were conducted in a large group of older participants. Neural and behavioural variance within this group were correlated with age. Interestingly, temporal expectation-related modulation of posterior alpha lateralisation was decreased in relatively older versus younger participants. Behaviourally, effects of aging could specifically be related to the left visual field.

The present findings support the important role of temporal and spatial expectations in guiding pre-target neural activity and facilitating behaviour. Lateralisation of temporal expectation-related effects should be further investigated, as temporal expectations may exert their modulatory influence specifically well in the context of spatial expectations.

Introduction

In a world that provides an abundance of sensory input, being able to select relevant information is vital for meaningful, goal-directed and successful behaviour. Most generally, the selection of relevant information is defined as attention, which in turn generally needs to operate along the spatial and temporal dimensions. Investigations in spatial expectation by far outnumber temporal expectation research. Both spatial and temporal expectations can modulate neural processing and provide behavioural benefits. However, investigations of combined spatial and temporal expectations are relatively limited. The aim of the present study was to characterise well-established neural and behavioural markers of top-down control in a spatial and temporal context. Using scalp current density transformed electroencephalographic potentials, these markers were studied with high temporal and reasonable spatial resolution in a large set of healthy older participants. In order to investigate potential changes of expectation-related mechanisms with aging, neural and behavioural markers were correlated with age. In the following sections, the most important markers of spatial and temporal expectation as well as their potential modulation with aging are briefly reviewed.

Behaviour

The effects spatial expectations on perception have been a subject of research long ago (Helmholtz, 1866), and it has been shown that spatial expectation enhances visual processing as measured by reaction time (Posner, 1978, 1980). In addition, there is

ample evidence that spatial expectation can modulate perceptual processing by increasing contrast sensitivity and spatial resolution (Carrasco, 2014). Temporal expectations have also been related to both response-related and perceptual benefits (c.f. Chapter 1, Nobre & Rohenkohl, 2014; Nobre & Van Ede, 2018). Interestingly, there is even a report for an improvement of visual perceptual performance through synergistic effects of combined spatial and temporal expectations as measured by behaviour (Rohenkohl et al., 2014), although depending on the type of temporal manipulation and perceptual challenge, neural interactions do not necessarily need to manifest in behavioural interactions (Doherty et al., 2005).

Event-related potentials (ERPs), derived from EEG recordings, have provided a powerful method to investigate spatial and temporal expectations. ERPs depict the average voltage fluctuations triggered by particular stimuli, responses, or cognitive events in a task, which in turn reflect the summed voltage fields generated by the extracellular synaptic potentials over large populations of co-active neurons. They thus provide a direct read-out of brain activity with excellent, millisecond resolution, with which it is possible to observe the influence of spatial or temporal expectation on neural activity in anticipation of relevant targets or after targets or distractors are presented.

CNV

One of the most reliable event-related potentials elicited in anticipation of an imperative stimulus is the contingent negative variation (CNV). If a warning stimulus

(S1) is paired with an imperative stimulus (S2) requiring a response and following in close temporal proximity, a slow negative amplitude deflection can be observed. This negative deflection is most commonly recorded over fronto-central electrodes from several hundred milliseconds before and until the presentation of S2. The CNV was first described by Walter and co-workers (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). Walter et al. presented two stimuli in temporal succession with an inter-stimulus interval (ISI) of approximately 1s. A stimulus could either consist of a click or a flash and participants were instructed to respond by button press after the presentation of S2. After several trials, a CNV was observed, regardless of stimulus modality. Interestingly, when S2 was withdrawn, the CNV was still observed, but declined gradually within 30 trials, where its peak amplitude occurred when S2 would have been presented. When, after successful establishment of the CNV, participants were told that S2 would be omitted with upcoming trials, the CNV was immediately abolished. In a further experimental condition, in which participants were required to press a button 1s after presentation of S1 which was not followed by S2, a CNV was again established. These results suggest that the CNV is associated with the anticipation of a behaviourally relevant (external or internal) event which is contingent on a sensory-motor association.

Connor & Lang (Connor & Lang, 1969) began to employ longer S1-S2 intervals, where two negative components after the presentation of S1 could be observed. It was proposed that the CNV would reflect the summation of an early, more frontally located negative potential related to uncertainty processing, and a later more centrally located negative response related potential (Järvilehto & Fruhstorfer, 1970) which was identified with the previously described Bereitschaftspotential (BP; Kornhuber &

Deecke, 1965). Following the above reasoning, it was suggested that the early component may regulate sensitivity to subsequent stimuli (Loveless & Sanford, 1975), whereas the late component would be determined by motor preparation (Gaillard, 1977).

However, later studies point against a simple decomposition of the CNV. Brunia and Vingerhoets (Brunia & Vingerhoets, 1981) recorded a BP and a CNV within same trials. Different waveforms lead the authors to speculate that the late CNV actually contained a BP which was but superimposed on a different continuing negativity. A late CNV has also been reported for motivationally relevant stimuli in the absence of a motor response (Ruchkin, Sutton, Mahaffey, & Glaser, 1986). As the latency and amplitude of the CNV instead depended on the time point when a relevant stimulus was likely to occur, the authors concluded that the CNV they recorded would reflect expectancy or anticipation. Frost et al. (Frost, Neill, & Fenelon, 1988) reported a late CNV for task-relevant stimuli, where motor responses had to be delayed and contrary to Ruchkin (Ruchkin et al., 1986) stimulus foreperiod duration was randomly alternated. Accordingly, Frost suggested that the CNV depended on cognitive factors in anticipation of task-relevant information as conveyed by succeeding stimuli.

It thus seems that composition and functional significance of the CNV depend on task context, especially where event and time uncertainties come into play. Slow negative drifts preceding task relevant stimuli may relate to motor preparation, preparation or anticipation for the content or occurrence of upcoming stimuli, or a composite of all these factors, depending on specific task characteristics. If a task emphasises speeded responses or employs easily detectable stimuli, the CNV will mainly be composed of motor related activity (Gaillard, 1977). On the other hand, if

task-relevant stimuli are hard to discriminate, a stronger perceptual component might be expected.

Response speed (Brunia & Vingerhoets, 1980; Cohen, 1973; Hillyard, 1969; Trillenberg, Verleger, Wascher, Wauschkuhn, & Wessel, 2000) and perceptual factors (Cohen, 1973; Hillyard, 1969; Hillyard, Squires, Bauer, & Lindsay, 1971; Loveless, 1975) have been related positively to CNV amplitude. However, simple associations of CNV amplitude with behaviour have also explicitly been rejected or partly rejected (Hillyard, 1973; Ng & Penney, 2014; Perdok & Gaillard, 1979; Rebert & Tecce, 1973), where also more complex e.g. multidimensional relationships have been suggested (Kononowicz & Penney, 2016). The behavioural significance of the CNV is thus far from settled, but conflicting results may again point to its multifaceted, task dependent nature.

One consistent aspect of the CNV is its relation to the predicted timing of task-relevant events. Miniussi et al. (Miniussi et al., 1999) have shown that the CNV can be modulated on a trial-by-trial basis depending on the specific temporal interval predicted until target appearance by temporally informative cues. Cues that oriented temporal attention to shorter, more proximal temporal moments caused a larger pre-stimulus negativity compared to cues that oriented attention to longer, more distal temporal moments for target appearance. Using blocked temporal expectations, Trillenberg and colleagues (2000) instead showed that the CNV follows the conditional probability of target occurrence ("hazard rate"; Trillenberg et al., 2000). The timing of the CNV peak has also been connected to explicit and implicit memory and judgements about specific temporal intervals (Los & Heslenfeld, 2005; Macar & Vidal, 2003; Pfeuty, Ragot, & Pouthas, 2005). With a time-estimation task, Macar et al. had participants judge the duration of probe stimuli, which could be longer or shorter than standard

stimuli. If a probe stimulus was shorter than the standard stimulus, the CNV developed typically until a response was made. However, if a probe stimulus exceeded the duration of a standard stimulus, the CNV peaked and subsequently declined around the time a standard stimulus would have been offset. A more recent study parametrically varied the degree of attention participants should devote to time intervals versus stimulus identity (Liu et al., 2013), finding that more attention dedicated to stimulus duration resulted in larger CNVs. Together, these diverse sets of findings converge on showing the high degree of sensitivity of the CNV to temporal factors.

ADAN, LDAP

Studies of spatial orienting have identified a highly reliable set of lateralised ERPs associated with shifting attention to different locations in space (Harter, Miller, Price, LaLonde, & Keyes, 1989; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000; Yamaguchi, Tsuchiya, & Kobayashi, 1994). Three cue-related neural markers of spatial anticipation of targets have been described. When spatial attention is deployed by attending to either visual hemifield after central cue presentation, these markers can be obtained by contrasting potentials for left vs. right cues. There is an initial early directing attention negativity (EDAN) component starting approximately 200 ms after cue onset over posterior (parietal and occipital) electrodes (Harter et al., 1989; Nobre et al., 2000; Yamaguchi et al., 1994). The component usually manifests as a posterior contralateral negativity, where a left hemisphere focus has been reported (Hopf & Mangun, 2000; Kelly, Gomez-Ramirez, & Foxe, 2009; Nobre et al., 2000). It has been

proposed that EDAN reflects the initiation of an attentional shift. However, studies in which physical features of the cue have been controlled more strictly have raised the possibility that the EDAN may actually relate to the selection of non-central physical features of the cue itself (Van Velzen & Eimer, 2003). The degree to which the EDAN also reflects spatial orienting independently of the physical parameters of the cue is still unresolved. One suggestive finding in favour of this possibility is the fact that the magnitude of the EDAN is predictive of the benefits of spatial attention on performance (Murray, Nobre, & Stokes, 2011).

The second component, an anterior directing attention negativity (ADAN) emerges at around 300 ms after cue onset (Hopf & Mangun, 2000; Nobre et al., 2000). Greater anterior negativity is observed contralaterally to cue direction. ADAN may be related to the programming and initiation of attentional shifts (Eimer, 2004; Nobre et al., 2000), where a more pronounced right hemisphere lateralisation has been reported (Hopf & Mangun, 2000; Nobre et al., 2000).

Finally, there is a late directing attention positivity (LDAP; Harter et al., 1989; Hopf & Mangun, 2000). It is observed from around 400 ms after cue onset as a posterior contralateral positivity and may functionally represent a preparatory change in excitability of occipital and temporal areas (Harter et al., 1989; Hopf & Mangun, 2000). Interestingly, it has been reported that LDAP can be modulated as a function of temporal predictability, with larger LDAP for temporally predictive versus non-predictive cues (Green & McDonald, 2010).

Connections of pre-target event-related signals of spatial attentional deployment with behavioural measures are rare but have been shown for reaction time (Kelly et al., 2009; Murray et al., 2011; Talsma, Mulckhuyse, Slagter, & Theeuwes,

2007). In a cued spatial attention paradigm, Kelly and colleagues (Kelly et al., 2009) investigated the relation of EDAN, ADAN and LDAP with reaction time and d'. They only found a connection of LDAP with reaction time, and this connection was dependent on cues pointing to the left hemifield.

Alpha-band activity

In addition to brain activity strictly time-locked to cues, it is also possible to examine changes in oscillatory patterns induced by cues in preparation for target stimuli. In human EEG, neural oscillations in the alpha frequency band (8-12Hz) serve as a robust marker of pre-target anticipatory spatial attentional deployment. It has been suggested that low alpha power and a reduction of alpha synchrony relate to increased cortical excitability and information processing, and, conversely, that high alpha power and alpha synchrony reflect a state of relative cortical inhibition (Jensen, Bonnefond, & VanRullen, 2012; Klimesch, Sauseng, & Hanslmayr, 2007; Lindsley, 1952). Empirical findings and theory have also been supported by biophysically detailed neural models (Becker, Knock, Ritter, & Jirsa, 2015; Lundqvist, Herman, & Lansner, 2013). Alpha modulation during anticipatory states has been observed in the visual (Fries, Reynolds, Rorie, & Desimone, 2001; Sauseng et al., 2005; Worden, Foxe, Wang, & Simpson, 2000), somatosensory (Haegens, Handel, & Jensen, 2011; van Ede, de Lange, Jensen, & Maris, 2011), and auditory domains (Weisz, Hartmann, Müller, Lorenz, & Obleser, 2011).

Human visual cortical excitability in relation to alpha range oscillatory activity has also been probed more directly by transcranial magnetic stimulation (TMS; Romei

et al., 2008; Romei, Gross, & Thut, 2010; Samaha, Gosseries, & Postle, 2017). In particular, Romei et al. (Romei et al., 2008) used TMS to excite the visual cortex of blindfolded participants and investigated the relationship between TMS-induced illusory visual percepts called phosphenes and pre-TMS alpha power. Interestingly, for trials where participants reported phosphenes, pre-TMS alpha power was lower compared to trials where no phosphenes were reported. In a further study, Romei (Romei et al., 2010) stimulated participants' visual and parietal cortices with TMS pulses in the alpha frequency range (10Hz). Detection performance for ipsilaterally presented visual stimuli increased, whereas contralaterally presented visual stimuli were detected less frequently compared to 5Hz and 20Hz control stimulation conditions. Although the effect was only short-lived (3s), and the mechanistic relationship of experimentally and cortically induced alpha remains to be determined, TMS-induced alpha oscillations functionally support a role of alpha as a mediator of the cortical excitation-inhibition balance.

Alpha phase and alpha-phase coupling have been shown to predict visual stimulus perception (Busch, Dubois, & VanRullen, 2009; Hanslmayr et al., 2007; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). In addition, low pre-stimulus alpha power has been connected to increased target-related neural processing, faster reaction times and improved visual perceptual performance (Ergenoglu et al., 2004; Hanslmayr et al., 2007; Kelly et al., 2009), although a couple of recent studies have related improved behavioural perceptual performance to a change in decision variables as opposed to increased precision of sensory processing (Busch et al., 2009; Samaha, Iemi, & Postle, 2017).

In the field of spatial attention, hemispheric lateralisation of pre-stimulus alpha power has been established as a marker of hemifield-specific attentional deployment (Kelly et al., 2009; Sauseng et al., 2005; Thut, 2006; Worden et al., 2000). Typically, there is a central arrow cue pointing to the left or right visual hemifield and participants are instructed to covertly direct their attention to the cued visual hemifield. Then, a few hundred milliseconds before target onset, there is a relative decrease in alpha power over posterior cortical regions contralaterally to the cued visual hemifield. In addition, it was shown that larger contralateral alpha decreases predict faster reaction times and better target discriminability (Kelly et al., 2009), as well as larger perceptual processing related ERP modulation (Gould, Rushworth, & Nobre, 2011). Decreased alpha in anticipatory states also seems to be under flexible control depending on task demands. Gould et al. (Gould et al., 2011) used a set of central spatial cues with varying spatial predictability. Larger spatial predictability resulted in comparably larger contralateral alpha decrease. Interestingly, alpha power can also lateralise in the absence of spatial cueing as a function of time-on-task, where larger pre-target alpha power was observed over the right hemisphere with increasing time-on-task, which in turn could be related to a rightward shift of a behavioural spatial bias (Newman, O'Connell, & Bellgrove, 2013).

When studying the effects of spatial attention on alpha lateralisation, early studies have in fact not only investigated spatial attention. By employing a fixed (Kelly et al., 2009; Thut, 2006; Worden et al., 2000) or only minimally jittered (Sauseng et al., 2005) cue-target interval, these studies inadvertently also tapped into the effects of combined spatio-temporal processing. Although the effects of temporal processing cannot be studied in isolation, if alpha band modulation is a more general mechanism

of attentional deployment, temporal anticipation (Nobre & Van Ede, 2018) should also have an influence on alpha processing. In fact, rhythmic cueing studies have shown a decrease in alpha power at the time of (Praamstra et al., 2006) and shortly before (Rohenkohl & Nobre, 2011) the expected occurrence of an omitted stimulus. For example, Rohenkohl and Nobre (2011) presented a white dot stimulus in the upper left corner of the screen which moved in several discrete steps diagonally downward during one trial. The dot could move in a predictable isochronous rhythm or in variable temporal intervals. The last occurrence of the dot marked a perceptual discrimination task, whereby a "+" or "x" was overlaid on the dot. The occurrence of the second to last dot was occluded by a stationary white band, and thus could not be perceived but only imagined. With rhythmic versus variable temporal stimulation and during the times just before the imagined occurrence of the second to last dot and before the actual occurrence of the last dot, there was a relative decrease in alpha power. In addition, subsequent broadband visual and motor related target processing was enhanced, supporting a role of alpha in modulating cortical excitability. A cortical excitability increase in connection with a decrease in alpha power as a result of temporal processing has also been suggested in the tactile domain (van Ede et al., 2011) and in a study recording local field potentials in monkeys (Lima, Singer, & Neuenschwander, 2011). Specifically studying cued temporal expectations in humans, Zanto et al. (Zanto et al., 2011) reported a posterior alpha power decrease before the onset of a predictive short target compared to when a target was unpredictable in time. This finding was supported by a recent study employing spatiotemporal cues (Heideman et al., 2018). The authors found bilateral posterior alpha power suppression before target onset when the target was expected in time compared to

when it was expected to appear only at a later time point. Finally, there is also evidence that temporal and spatial expectations can interact in the alpha oscillatory frequency range, although findings relate to experimentally induced alpha entrainment (Kizuk & Mathewson, 2017).

Posterior oscillatory alpha dynamics have also been connected to prefrontal control. Sauseng et al. (Sauseng et al., 2005) showed stronger alpha-phase coupling between prefrontal and posterior parietal sites contralateral to the attended hemifield. Kelly et al. (Kelly et al., 2009) reported a larger frontal broadband positivity in association with a stronger posterior alpha bias. More direct evidence for prefrontal control comes from a TMS study. Capotosto et al. (Capotosto, Babiloni, Romani, & Corbetta, 2009) applied repetitive TMS to temporally lesion frontal eye field and intraparietal sulcus during the cue-target interval of a cued spatial attention task. They found a disruption of posterior pre-target alpha desynchronisation and hemispheric spatial sensitivity, suggesting that the dorsal frontoparietal attention network is crucial for posterior alpha power modulation. Although most investigations on attentional control and alpha focus on cortico-cortical interactions, it should be noted that also subcortical regions like the thalamus may play a crucial role (Saalmann & Kastner, 2011), not least with the thalamus being involved in the generation of cortical alpha oscillations (Hughes & Crunelli, 2005).

Age related changes

Studies on age-related changes to attentional control are often conflicting. Among other things, this may relate to many different attentional sub-processes which may

not have been separated or addressed clearly in different studies. It may also relate to a generally high heterogeneity in cognitive function with aging. Whereas age-related changes mostly become apparent with cognitively highly demanding tasks, behaviour and neural processing often seem to be spared when accounting for general slowing or sensory deficits (Zanto & Gazzaley, 2014).

Aging seems to relatively spare behavioural outcomes of the spatial allocation of attention (Gottlob & Madden, 1998; Hartley, Kieley, & Slabach, 1990; Nissen & Corkin, 1985; Tales, Muir, Bayer, & Snowden, 2002), although there may be a deficit with orienting to the left visual hemifield in older adults (Nagamatsu, Carolan, Liu-Ambrose, & Handy, 2011). With temporal expectations, it has been proposed that older participants do not benefit from explicit temporal expectations in detection and discrimination tasks (Zanto et al., 2011). However, a more recent study reported speeded-response and perceptual discrimination benefits in older participants (Chauvin, Gillebert, Rohenkohl, Humphreys, & Nobre, 2016).

As described above, the CNV may arise as a function of different processes in anticipation of a relevant stimulus. Not surprisingly, different effects of aging on CNV magnitude have been shown with different tasks. Whereas CNV reductions in frontal but not central or posterior regions have been shown with S2-choice go-/no-go and distraction tasks (Dirnberger et al., 2000; Michalewski et al., 1980), in a cued spatial attention task Hong et al. (Hong, Sun, Bengson, Mangun, & Tong, 2015) reported an even larger CNV over centro-frontal electrodes in older versus younger participants. Where targets were temporally predictable or non-predictable, Deiber and co-workers (Deiber, Ibañez, Missonnier, Rodriguez, & Giannakopoulos, 2013) also seem to find a larger CNV with older compared to younger participants. However, Deiber did not

explicitly investigate or statistically compare CNVs. In addition, temporally predictive and non-predictive trials were poorly matched with only predictive trials featuring cues. By contrast, Zanto et al. (Zanto et al., 2011) compared trials with temporally predictive and temporally neutral cues. He observed a CNV only with younger but not older participants.

Nagamatsu et al. (Nagamatsu et al., 2011) investigated spatial orienting-related EDAN and ADAN. As EDAN did not differ between younger and older participants, she concluded that cue evaluation is spared by aging. On the contrary, left visual hemifield-related ADAN was reduced in older participants. In connection with poorer left hemifield-related behaviour, this was interpreted as an age-related problem in shifting attention to the left visual field. Hong and co-workers (Hong et al., 2015) showed spared EDAN, ADAN and even increased LDAP with aging in connection with reduced alpha oscillatory processing. However, they averaged across contra- and ipsilateral trials, so that hemisphere-related effects could not be examined.

Not much work has been done regarding the effects of temporal cueing on alpha modulation. Zanto et al. (Zanto et al., 2011) reported a decrease in alpha power modulation with older adults. A recent study by Heideman et al. (Heideman et al., 2018) did not find temporal alpha modulation in aging at all. There is mixed evidence in how far pre-stimulus spatial alpha oscillatory dynamics are preserved in aging. Deiber et al. (Deiber et al., 2013) reported decreased pre-target alpha desynchronisation. Hong et al. (Hong et al., 2015) and van der Waal (van der Waal, Farquhar, Fasotti, & Desain, 2017) used a Posner-like spatial cueing paradigm and did not find alpha lateralisation in older participants. In contrast, Leenders et al. (Leenders, Lozano-Soldevilla, Roberts, Jensen, & De Weerd, 2016) and Heideman et al. (Heideman

et al., 2018) reported preserved spatial alpha lateralisation in aging, suggesting that also in older participants, alpha oscillations can prepare for upcoming events under certain conditions.

In the current study, I investigated combined spatio-temporal orienting of attention in older participants. My study enabled me to extend the knowledge base about behavioural and EEG markers of spatial and temporal orienting by asking whether individual markers of spatial and temporal orienting occur in the case of combined spatio-temporal orienting, and by helping provide evidence where findings have been mixed. By testing a large number of older participants, it was possible to capitalise on the increased performance-related variability in this population to look for whether and how specific attentional markers are predictive of behavioural outcomes. Behavioural and neural makers were also correlated with age. Using variability within one cohort of older participants sidesteps cohort-related effects that can complicate interpretation when comparing neural effects between different cohorts of participants (e.g. older versus younger).

Methods

Participants

The study protocol received approval by the Central University Research Ethics Committee (CUREC) at the University of Oxford. The study was part of a larger multimodal study, in which neuropsychology, MRI, and EEG data of 45 healthy older

participants were acquired. Four participants exhibited structural abnormalities as determined independently by 2 clinically experienced researchers and were excluded from the study, leaving 41 participants (age range: 54 – 84 years, mean age: 67.08 years with SD 5.78 years, 24 females) for the analysis.

Presentation

Visual stimuli were presented on a 27-inch monitor with a 100-Hz refresh rate and a 1920 x 1080 resolution. Auditory stimuli were presented via two 2-Watts desktop computer speakers. Participants responded using a standard United Kingdom layout computer keyboard. Stimulus presentation and response collection were controlled by psychophysics Toolbox Version 3 (Kleiner et al., 2007) for MATLAB (The MathWorks).

A schematic of the task is shown in figure 2.1. Participants needed to discriminate peripherally presented target letters, which were preceded by a compound audio-visual cue indicating the spatial location and the likely temporal interval of target presentation.

Visual stimuli were presented on a grey background (RGB: 102 102 102). During every trial, participants were required to keep their eyes fixed on a small white square (RGB: 255 255 255, 0.08° each side), which was presented centrally. At the same time, in order to reduce spatial uncertainty (Smith & Ratcliff, 2009), luminance pedestals were presented horizontally to the left and right of fixation (fixation-centre-to-pedestal-centre eccentricity: 6.99°), where letter stimuli could appear. After a random interval of 750 +/-250 ms (standard uniform distribution sampling) two horizontally aligned pink arrows (size: 1.86°) were presented centrally for 200 ms. The direction of

the arrows indicated where a target stimulus would appear. Informative spatial cues comprised arrows pointing in the same direction, to the left or right of central fixation (<< or >>). Neutral cues consisted of arrows pointing in opposite directions (<>), to the left and right of central fixation. Arrow presentation was always paired with the presentation of one of two electronically generated pure tones (pitch: 440 Hz or 880 Hz). The tones predicted if a target stimulus would more likely be presented after a short (600 ms) or long interval (1800 ms) after the offset of the audio-visual cue stimulus. A target stimulus consisted of either a black (RGB: 0 0 0) letter 'L' or 'T' and was presented for 50 ms behind a translucent circular white-noise patch (size: 1.86°) atop one of either peripheral pedestals. When a target stimulus disappeared, the noise patch stayed on the screen for 280 ms.

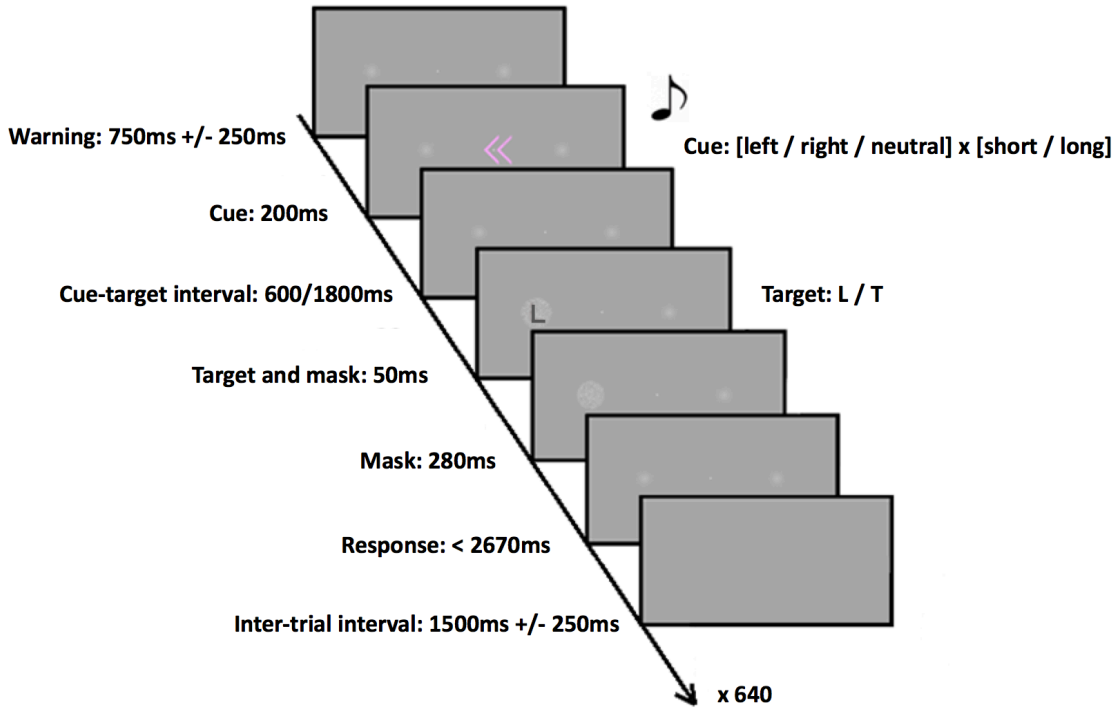


Fig. 2.1. Schematic depiction of an example trial: Arrows convey laterally directed (arrows pointing to the left or right, 100% validity) or neutral (arrows pointing to the left and right) spatial information. Simultaneously presented pure tones (high or low pitch) cue short or long cue-target intervals (75% validity), conveying temporal information. Participants need to discriminate target letter identity (T or L) by button presses.

Participants were required to indicate by button press (number '1' or '3' on the keyboard number pad), if they had seen a letter 'L' or 'T' stimulus. They responded with their index and middle finger of their right hand respectively and were given up to three seconds for their response. A button press was followed by an inter-trial interval of 1500 +/-250 ms (standard uniform distribution sampling) during which nothing but a uniformly grey screen was presented.

Cue-target interval duration and temporal cues, target presentation side and spatially directed and neutral cues, and target identity were counterbalanced across the experiment. Temporal cues were blocked, always informative and had 75% validity. In blocks with all high/low-pitch temporal cues, 75% of targets occurred at the validly cued short/long interval, and a 25% minority occurred at the other, invalidly cued interval. Simultaneously presented spatial cues were 100% valid and presented in blocks of spatially neutral and directed cues, where left and right directing cues were equally intermixed and randomised on a trial-by-trial basis within blocks of directed spatial expectation. Target identity was unpredictable on a trial-by-trial basis. Response mapping and auditory cue-pitch cue-target interval assignments were counterbalanced across participants.

Procedures

Participants were seated comfortably at a viewing distance of approximately 100 cm and used a chin rest. Computer speakers were placed at the same depth to the side and 20 cm in front of the computer screen. Prior to the experiment, participants received a practice session with half predictive valid spatial cues (100%) and half

neutral spatial cues, both paired with valid temporal cues (100%). They were instructed to keep their eyes on the central white square, whenever it was present, and to use the spatial and temporal information provided by the cue to predict the location and onset of the target stimuli. Next, participants completed a staircasing procedure to standardise task difficulty across participants. Procedures were analogous to the practice session, in which a minimum of 40 trials were presented. Every five trials, target visibility was adjusted by increasing (less than 4 of 5 trials correct) or decreasing (5 of 5 trials correct) the transparency level of the noise mask by 5% of full mask contrast. If participants responded correctly in four of five trials, mask transparency was kept constant, so that participants' performance reached 80% correct responses. When stimulus visibility levels ceased to fluctuate, the staircasing was stopped. This was usually achieved after a minimum of 40 trials and less than 4 minutes.

During the actual experiment, participants completed 20 blocks of 32 trials, amounting to 640 trials. Rest breaks could be taken after each block. There were 60 valid and 20 invalid temporal-cue trials for both the short and long condition for both left and right spatial cues. For neutral spatial cues, there were 120 valid and 40 invalid temporal-cue trials for both the short and long condition. Participants completed the task in approximately 70 minutes.

Behavioural analyses

The data were analysed with custom written functions using MATLAB. Responses faster than 200 ms were generally discarded. For reaction-time (RT) analysis, only

correct responses within +/- 3 SDs of mean individual RTs were processed. Response accuracy (percent correct, PC) was calculated by dividing the number of correct responses by the total number of all possible responses. D prime (d') was calculated to determine perceptual sensitivity: Z score (hits) - Z score (false alarms).

Repeated-measures analyses of variance (ANOVAs) were calculated for RT, PC and d' across 3 factors. There was a factor of temporal cue validity (Temporal Validity), where a target could appear at a validly or invalidly cued interval (Valid/Invalid). There was a further factor of spatial cue information (Spatial cue), where spatial cues could be directed to one hemifield or neutrally directed to both hemifields (Spatial/Neutral). Finally, there was a factor of target hemifield (Hemifield), where a target could appear in the left or right visual field (LVF/RVF). Statistical tests were two-sided and with a critical alpha level of 0.05. Analyses concentrated on targets appearing at short intervals. In any trial, with the passage of a short interval, the target must appear at the long interval, regardless of the temporal cueing. Long interval trials are thus unsuitable for showing differential temporal expectations (Coull & Nobre, 1998; Griffin, Miniussi, & Nobre, 2002).

EEG acquisition

Electroencephalogram (EEG) data were acquired continuously with NeuroScan SynAmps RT amplifiers (Model 9032, Compumedics NeuroScan, North Carolina, USA) using Scan 4.5 acquisition software (Compumedics NeuroScan, North Carolina, USA) from 60 Ag/AgCl surface electrodes according to the International 10-10 system with a 1000-Hz sampling rate. Brain potentials were acquired from the following electrodes:

FP(1,2), AF(z,3,4,7,8), F(z,1-8), FC(z,1-6), FT(7,8), C(z,1-6), T(7,8), CP(z,1-6), TP(7,8), P(z,1-8), PO(z,3,4,7,8), O(z,1,2). Electrode impedance was kept at or below 5 kilo-Ohm, wherever possible. The vertical electrooculogram (EOG) was obtained by subtracting the recording of a left-sided electrode placed infraorbitally from the FP1 recording. The horizontal EOG was acquired by subtracting the recording of an electrode placed to the left of the lateral canthus of the left eye from the recording of an electrode placed to the right of the lateral canthus of the right eye. Data were referenced online to the left mastoid recording and later re-referenced offline to an average of the left and right mastoid recording. An electrode placed on the left upper arm served as the ground.

EEG processing

Data processing was performed in Matlab with custom written code and FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). Raw data were band-pass filtered between 0.1 and 40 Hz (two-way, zero phase-shift Butterworth filter) and epoched into 20 blocks representing the 20 experimental blocks. Data were then manually screened, and signals with artefactual data, reflecting poor electrode contact, were replaced by the plain average signal of all immediately neighbouring electrodes. An independent-component analysis (ICA) using the FastICA fixed-point algorithm (Hyvarinen, 1999) was performed on the data. Artefactual components were identified by their spatial topography and their correlation with EOG signals. Up to 3 artefactual components were removed per participant. Non-artefactual components were back-projected on the original data. Data were then re-epoched around the cue onset (-500

to 1800 ms). Excessively noisy trials, or trials containing eye movements within a critical window of -300 to 800 ms were removed based on visual inspection of their variance across channels and trials, and based on vertical and horizontal EOG traces. For time-frequency analyses, data were then down-sampled to 300 Hz.

In order to improve the spatial resolution, signals were transformed into scalp current density measures using the second-order spatial derivative (Laplacian surface transformation) of the EEG potential distribution (Vidal et al., 2015). This linear transformation maintains the invariant aspects of the EEG signal and data can be analysed using the same analysis techniques that have been established for simple surface potentials (Kayser & Tenke, 2015). Specifically, scalp current density transformation was conducted with a spherical spline interpolation method (Perrin, Pernier, Bertrand, & Echallier, 1989) as implemented with the FieldTrip analysis toolbox.

For event-related potential (ERP) analyses, epoched data were baseline-corrected by subtracting for each electrode the baseline from the whole signal of the epoch. The mean signal within an interval preceding cue onset (-200 ms to 0 ms) served as a baseline.

Attentional control processes have previously been studied by investigating differential cue-related ERPs. In order to isolate lateralised potentials associated with spatial attention, ERPs were derived according to the target side (Left, Right) indicated by the spatial cue. Main effects of temporal cueing were assessed by comparing potentials elicited by cues predicting short vs. long temporal intervals. To test for interactions, differences between lateralised spatial potentials according to the cued temporal intervals were compared.

Two lateralised cue-related potentials were analysed for spatial attention, resulting from contrasting potentials elicited by left vs. right spatial cues: (1) An 'anterior directing attention negativity' (ADAN) at about 300 ms, with greater contralateral negativity over anterior sites (Hopf & Mangun, 2000; Nobre et al., 2000), and (2) a 'late directing attention positivity' (LDAP), reflecting a relative positive shift over contralateral posterior electrodes starting around 400 ms after cue onset (Harter et al., 1989; Hopf & Mangun, 2000). An 'early directing attention negativity' (EDAN; Harter et al., 1989; Yamaguchi, Tsuchiya, & Kobayashi, 1994) was not observed. However, EDAN is not always observed in paradigms of cued spatial attention and it has been suggested that EDAN might not be a true component of spatial orienting, but might reflect attention allocation to lateralised features of the cue (Van Velzen & Eimer, 2003).

For cue-related temporal orienting, modulation of the centrally distributed contingent negative variation (CNV; Walter, Cooper, Aldridge, McCallum, & Winter, 1964) has been observed, with more negative potentials elicited by cues indicating short compared to long cue-target intervals (Miniussi et al., 1999).

In order not to restrict statistical comparisons to specific time points or electrodes, main effects were examined by employing cluster-based permutation tests (Maris & Oostenveld, 2007) across all scalp electrodes (minimum number of neighbouring electrodes required for clustering: 2) and all time points sampled within the whole cue-target interval (0 – 800 ms relative to cue onset).

Interactions of spatial and temporal expectations were assessed by comparing potentials for left versus right spatial expectations according to the cued temporal intervals. Cluster-based permutation tests were employed across all time points of the

cue-target interval. For each component, electrodes were chosen on the basis of main effects, where electrodes which showed a significant difference with the left versus right contrast in more than 80% of cluster time points were chosen and averaged.

In principle, for cluster-based permutation testing, samples of neighbouring time points (and electrodes) which survive univariate two-sided t-tests ($p < 0.05$) are clustered (their t-values are summed up). If clustering occurs across time points and electrodes, a minimum number of neighbouring electrodes which is required for a sample to be included in the clustering algorithm can be specified. The largest cluster is selected and serves as the test statistic. This test statistic is compared to the same test statistic obtained after random permutations of the data using a Monte Carlo method. Participant-specific condition averages are permuted between conditions, and t-values of significant neighbouring samples are again summed up. This permutation procedure is repeated 1000 times, where with every permutation the largest cluster value is selected. A permutation distribution is constructed with these 1000 cluster values. The originally observed test statistic is then evaluated with respect to the permutation distribution. The proportion of cluster values from the permutation distribution showing a larger value than the test statistic is calculated. In order to achieve that the alpha level is distributed over both tails, this proportion is multiplied by a factor of two and then thresholded with a critical alpha level of 0.05.

Target-related ERPs were not the focus of the present study of the mechanisms of pre-target spatial and temporal expectations. In addition, target-related processes were assessed by behavioural outcomes. For completeness, main ERP effects of spatial and temporal expectation allocation to the target stimulus are presented in the appendix (Appendix: A1).

Analysis of alpha power

To complement the analyses of ERPs, alterations in the induced patterns of alpha-band activity were also considered using time-frequency analyses. The broadband signal was separated into its frequency constituents with the Fieldtrip Toolbox (Oostenveld et al., 2011) over all electrodes using Hanning tapers (300-ms fixed time window, step size 30 ms). Frequency power was estimated in steps of 0.5 Hz between 4 and 40 Hz. Alpha-band activity was calculated by averaging the spectral power between 8-12 Hz within participants. As a consequence of the sliding time-window technique, the decomposed signal at a given time point is estimated by evaluating broadband signal around that time point in a range of half the size of the sliding time window. This decreases the number of time points within the cue-target interval that are uncompromised by visual cue or target displays. In order to ensure that the analysis during the cue-target period was uncompromised by immediate visual stimulation, comparisons between conditions were restricted to time points within 350 to 650 ms after cue onset.

For spatial orienting, an anticipatory spatial bias is typically associated with a cue-induced lateralisation of alpha-band activity. Specifically, a relative decrease in alpha power has been observed contralaterally to the attended visual hemifield over posterior electrodes, and the strength of the oscillatory bias has been connected to behavioural processing (Kelly et al., 2009; Sauseng et al., 2005; Thut, 2006).

Temporal orienting has also been shown to modulate posterior alpha-band power. There was a relative decrease in alpha power with cues predicting a short interval compared to temporally non-predictive cues (Zanto et al., 2011).

In order to evaluate the main effects of spatial and temporal orienting, trials were averaged within participants and several contrasts created. Contrasts initially

included cues predicting short (Short) versus long (Long) cue-target intervals, averaged across and separately for the three spatial attention cues (Left, Right, Neutral). Further contrasts evaluated hemifield-specific processing: cues for directed versus neutral spatial information, separately for the left (Left vs. Neutral) and right (Right vs. Neutral) hemifield. A measure of hemisphere-specific processing combining both hemifields was obtained by contrasting Left vs. Right cues. In addition, all spatial contrasts were conducted separately for Short and Long cues. The spatio-temporal effect was derived by contrasting Short vs. Long for the different spatial orienting conditions. All 1^{st} – level contrasts (e.g. condition 1 vs. condition 2) were normalised by dividing them by the sum of the contrasted conditions (Thut, 2006). Statistical comparisons were carried out with cluster-based permutation tests across all scalp electrodes (minimum number of neighbouring electrodes required for clustering: 2) averaged between 350 and 650 ms ($p < 0.05$, two-tailed). Significant electrode clusters were further visualised topographically. In addition, in order to investigate if significant clusters show band-limited effects, time-frequency representations averaged across cluster electrodes were plotted for the whole cue-target interval.

Correlations

In order to reveal the relationships between neural modulations and variability in performance, correlation analyses were performed. For all participants, ERP contrast measures for time points where clusters were significantly different at the group level were extracted and z-scored. In order to decrease the influence of short-lived spatial dynamics, only electrodes which were, at the group level, part of a cluster in more

than 80% of cluster time points were selected. Finally, data were averaged across time points and electrodes to obtain a single neural measure for every participant.

Alpha contrast measures integrating activity related to both hemifields (Left vs. Right; Left vs. Right Short; Left vs. Right Long; Left vs. Right x Short vs. Long) were extracted from two symmetrical sets of posterior electrodes (Hong et al., 2015) of the left (O1, P3, P7) and right (O2, P4, P8) hemisphere during the cue-target period not immediately affected by visual stimulation (350 - 650 ms). Contrast measures were then averaged across sets of electrodes and time points. These measures of left and right hemisphere alpha modulation were further combined to a measure of alpha lateralisation by subtracting the right hemisphere from the left hemisphere measure.

Extracted ERP and alpha measures were then Pearson-correlated with effects of reaction time and d'. Reaction time effects were normalised by calculating the ratio between conditions (Invalid/Valid, Neutral/Spatial). As d' measures are already normalised, d' effects were obtained by simple subtraction between conditions (Invalid-Valid, Neutral-Spatial).

Age-related changes in behaviour and neural measures were calculated accordingly by correlating age with behavioural and neural effects.

For all correlation analyses, Cook's distance was used to identify outliers at the participant level. Data points were excluded if they exceeded a threshold of 3 times the mean of all Cook's distance values of an analysis.

Results

Behaviour

For reaction time (Fig. 2.2 a), there were main effects of Spatial Cue ($F(1,40)=17.15$, $p=0.0002$) and Temporal Validity ($F(1, 40)=13.82$, $p=0.0006$), indicating that participants were responding faster with directed spatial and valid temporal information. No interactions were observed.

For perceptual measures of accuracy and d' (Fig. 2.2 b,c), there was a main effect of Spatial Cue (accuracy: $F(1, 40)=9$, $p=0.0046$; d': $F(1, 40)=10.01$, $p=0.003$). Participants responded more accurately and were perceptually more sensitive with directed spatial information. With d' there was also a main effect of Temporal Validity ($F(1,40)=7.58$, $p=0.0088$), pointing to greater perceptual sensitivity with valid temporal information.

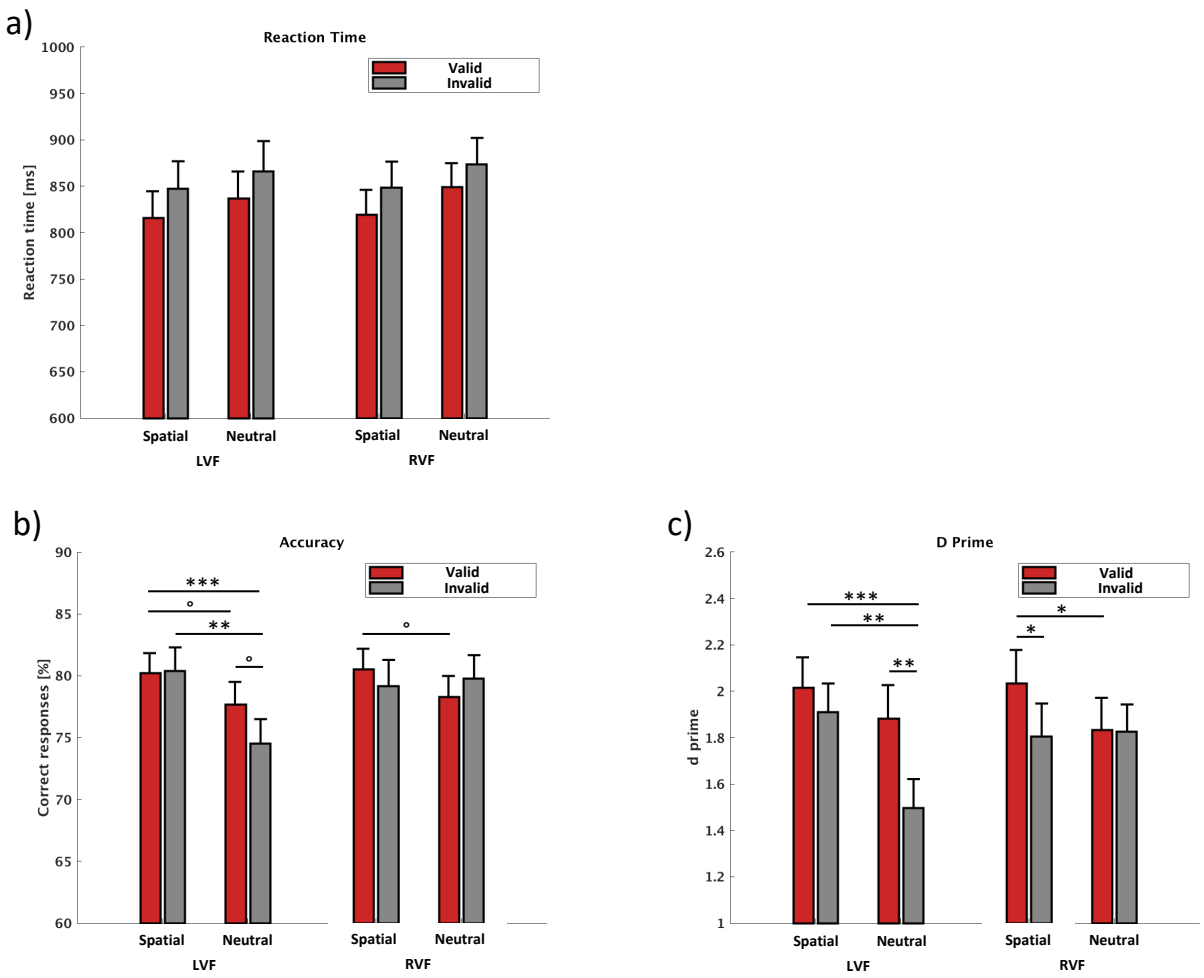


Fig. 2.2. Reaction time (a), accuracy (b) and d' (c) as a function of the different cue types for the left (LVF) and right (RVF) visual field. a) Effect of Spatial Cue: p=0.0002; effect of Temporal Validity: p=0.0006. b) Effect of Spatial Cue x Hemifield: p=0.039; effect of Spatial Cue x Temporal Validity x Hemifield: p=0.036. c) Effect of Spatial Cue x Temporal Validity x Hemifield: p=0.02. Whiskers denote SEM. ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, °: p=0.06.

For accuracy, there was a 2-way interaction between Spatial Cue x Hemifield ($F(1,40)=4.55$, p=0.039). Importantly, there was a 3-way interaction of Spatial Cue x Temporal Validity x Hemifield for both accuracy and d' (accuracy: $F(1,40)=4.71$, p=0.036; d': $F(1,40)=5.88$, p=0.02).

Post-hoc t-tests for accuracy with left visual field stimuli indicated that participants responded less or marginally less correctly after spatially neutral and temporally invalid cues compared to all other conditions (Spatial / Valid: $t(40)= -$

3.6581, p=0.0007; Spatial / Invalid: t(40)= -3.0275, p= 0.0043; Neutral / Valid: t(40)= -1.9247, p= 0.0614). With left and right visual field stimuli they responded marginally less correctly for Neutral / Valid compared to Spatial / Valid (LVF: t(40)= -1.9458, p= 0.0587; RVF: t(40)= -1.9122, p= 0.063).

Post hoc t-tests with d' for left visual field stimuli showed a similar pattern as accuracy analyses. Participants were perceptually less sensitive with Neutral / Invalid compared to all other conditions (Spatial / Valid : t(40)=-4.8516, p=0.00002 Spatial / Invalid: t(40)=-3.2952, p=0.0021; Neutral / Valid: t(40)= -3.3479, p=0.0018). With the right visual field, participants were perceptually marginally more sensitive for Spatial / Valid compared to Spatial / Invalid (t(40)= 2.0548, p= 0.0465) and Neutral / Valid (t(40)=2.0713, p=0.0448). The difference between Spatial / Valid and Neutral / Invalid did not reach significance (t(40)=1.6240, p=0.1122).

Post-hoc statistics were not corrected for multiple comparisons. For perceptual sensitivity d', all significant effects in the left visual hemifield are still significant after Bonferroni correction, assuming an adjusted alpha level of $p < 0.008$ (0.05 / 6 possible comparisons per hemifield).

Event-related potentials

Cue-related potentials were examined with cluster-based permutation tests across electrodes and time points. A time window from cue onset (0 ms) to target onset was analysed (800 ms). Contrasting activity with cues indicating a short versus long cue-target interval yielded two electrode-time clusters with a central negative topography. Cluster electrodes are listed in table 2.1. An early negative cluster (p=0.01; Fig. 2.3 a,b)

appeared from 235 ms to 332 ms, featuring a central left topography. A second negative cluster (p=0.002; Fig. 2.3 c,d) could be observed from 541 ms until target onset. This second cluster showed a central topography and was identified as a CNV (Walter et al., 1964).

Table 2.1. ERP electrode-time cluster electrodes for the Short versus Long contrast

Early negative cluster, 235 ms - 332 ms, p=0.01		
Electrode	Time [ms]	∑ (time points) / cluster duration
FCz	235-332	1
FC1	235-244, 248-332	0.97
Cz	248-331	0.86
C1	235-244, 260-332	0.85
FC2	238-251, 270-302, 326-331	0.54
C2	239-261, 280-294	0.39
FC3	295-303, 310-324	0.24
CPz	252-268	0.17
FC4	238-249	0.12
Fz	294-304	0.11
F1	318-326	0.09
F2	238-243	0.06
FC5	310-315	0.06
C5	310-315	0.06
CNV, 541 ms - 800 ms, p=0.002		
Electrode	Time [ms]	∑ (time points) / cluster duration
C1	541-551, 563-772, 777-800	0.94
C2	555-601, 607-797	0.92
FCz	565-601, 612-800	0.87
Cz	560-594, 611-800	0.87
FC2	560-601, 607-628, 640-796	0.85
FC1	543, 576-784	0.81
CP1	541-582, 597-634, 657-691, 784-792	0.48
C4	607-628, 638-662, 693-728, 774-791	0.39
CPz	557-584, 624-633, 653-692, 780-796	0.37
CP2	555-568, 590-594, 598-601, 607-616, 638-667, 695-709, 772-785	0.35
C3	543-553, 588-615, 643-677, 692-697, 715-721	0.33
FC3	602-611, 639-659, 673-687, 697-715, 736-742, 767-772, 777-781	0.32
CP4	555-562, 610-625, 650-658, 700-713	0.18
FC4	643-653, 678-688, 773-789	0.15
P1	555-582	0.11
Pz	561-582, 598-601	0.1
CP3	541-557	0.07
P3	547-554, 575-582	0.06
CP5	549-556	0.03
P5	551-556	0.02

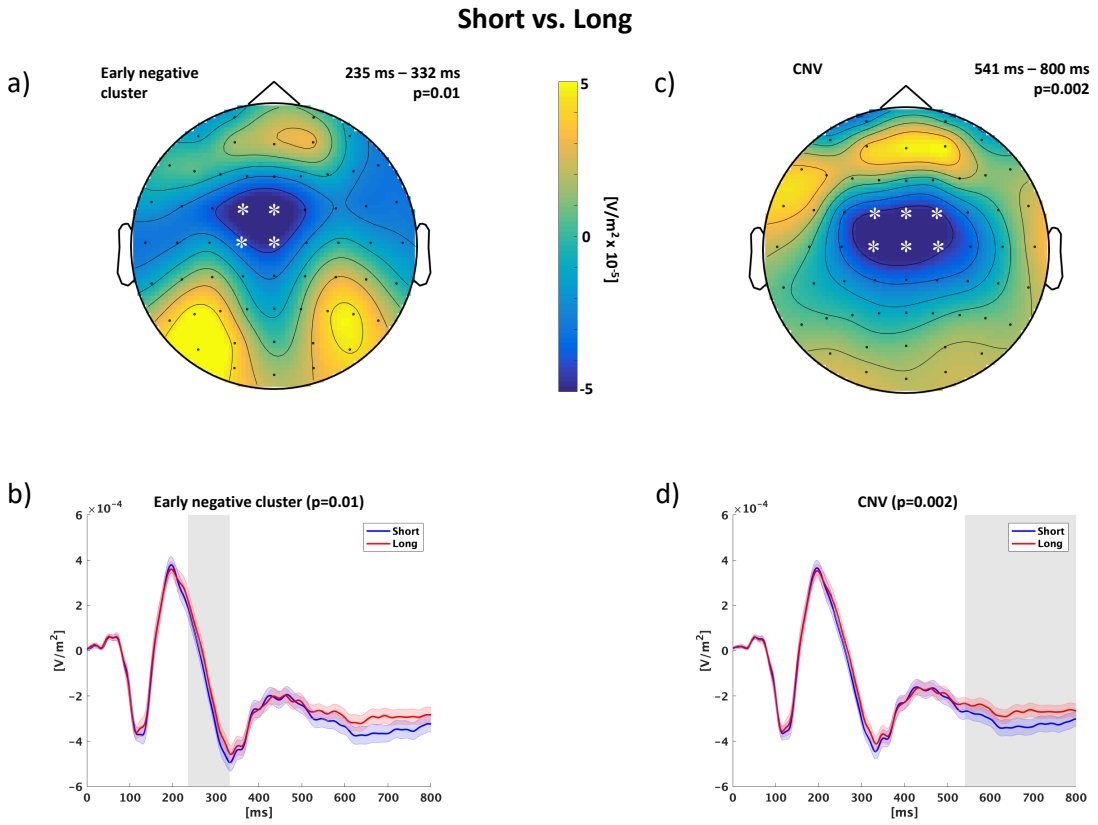


Fig. 2.3. Event-related potential electrode-time clusters for the Short vs. Long contrast. A central early negative cluster (a) was followed by a CNV (c). Time courses were plotted for electrodes marked with stars, which showed a difference between conditions in more than 80% of cluster time points. Time courses for the early cluster are shown with b). Time courses related to the CNV are shown with d). Grey shading indicates intervals when the significant electrode-time clusters were observed. Red and blue shading of time courses represents SEM.

When left versus right cue-related time courses were contrasted, left and right hemisphere ADAN (Hopf & Mangun, 2000; Nobre et al., 2000) and LDAP (Harter et al., 1989; Hopf & Mangun, 2000) could be observed (Fig. 2.4). Cluster electrodes are listed in table 2.2. Left ADAN comprised an anterior-medial, left-sided positivity (p=0.002; 330 ms to 639 ms). Right ADAN consisted of a right-sided medial negativity (p=0.002; 405ms to 517 ms). Left LDAP was present as a left posterior negativity (p=0.002; 486 ms to 614 ms) and right LDAP as a right posterior positivity (p=0.002; 434 ms to 641 ms).

There were two additional positive clusters. One cluster (p=0.004) emerged very early from 142 ms to 213 ms with a left posterior topography. The other cluster (p=0.004) had a left medial posterior topography and lasted from 649 ms to 772 ms.

Table 2.2. ERP electrode-time cluster electrodes for the Left versus Right contrast

Left ADAN, 330 ms - 639 ms, p=0.002		
Electrode	Time [ms]	∑ (time points) / cluster duration
C3	330-639	1.00
C1	330-639	1.00
FC1	332-530, 546-611	0.85
CP1	335-373, 413-493, 511-553, 570-635	0.74
CP3	330-373, 391-483, 502-552, 610-639	0.70
FC3	333-483, 497-527, 554-572, 595-601	0.67
CP5	335-349, 356-372, 394-429, 522-527, 621-638	0.30
F3	334-350, 370-383, 430-434, 471-483, 561-568	0.18
C5	365-374, 411-419, 456-458, 497-499, 521-532, 621-637	0.17
Cz	569-605	0.12
CPz	577-608	0.10
F1	335-349, 464-477	0.09
P3	353-363	0.04
F5	347-350, 381-382, 482-483	0.03
P1	431-440	0.03
Right ADAN, 405 ms -517 ms, p=0.002		
Electrode	Time [ms]	∑ (time points) / cluster duration
FC2	415-517	0.91
C2	415-517	0.91
C4	415-517	0.91
CP2	409-427, 436-515	0.88
FC4	421-464, 476-485, 494-505	0.58
CP4	429-467, 493-500	0.42
C6	425-434, 451-467	0.24
F2	431-445	0.13
Pz	409-416	0.07
P2	409-416	0.07
POz	405-411	0.06
FT8	451-456	0.05
T8	451-456	0.05
O1	405-408	0.04
Oz	405-408	0.04
Left LDAP, 486 ms - 614 ms, p=0.002		
Electrode	Time [ms]	∑ (time points) / cluster duration
P7	486-614	1.00
P5	486-614	1.00
PO7	486-614	1.00
PO3	488-614	0.98
O1	488-614	0.98
P3	497-503, 565-586	0.22
TP7	501-512, 603-613	0.18
POz	516-531	0.12
Oz	516-531	0.12
Right LDAP, 434 ms - 641 ms, p=0.002		
Electrode	Time [ms]	∑ (time points) / cluster duration
P6	434-641	1.00
P8	434-641	1.00
PO8	434-641	1.00
PO4	434-610	0.85
O2	434-610	0.85
P4	494-507, 549- 576	0.20
TP8	549-557, 611-614	0.06

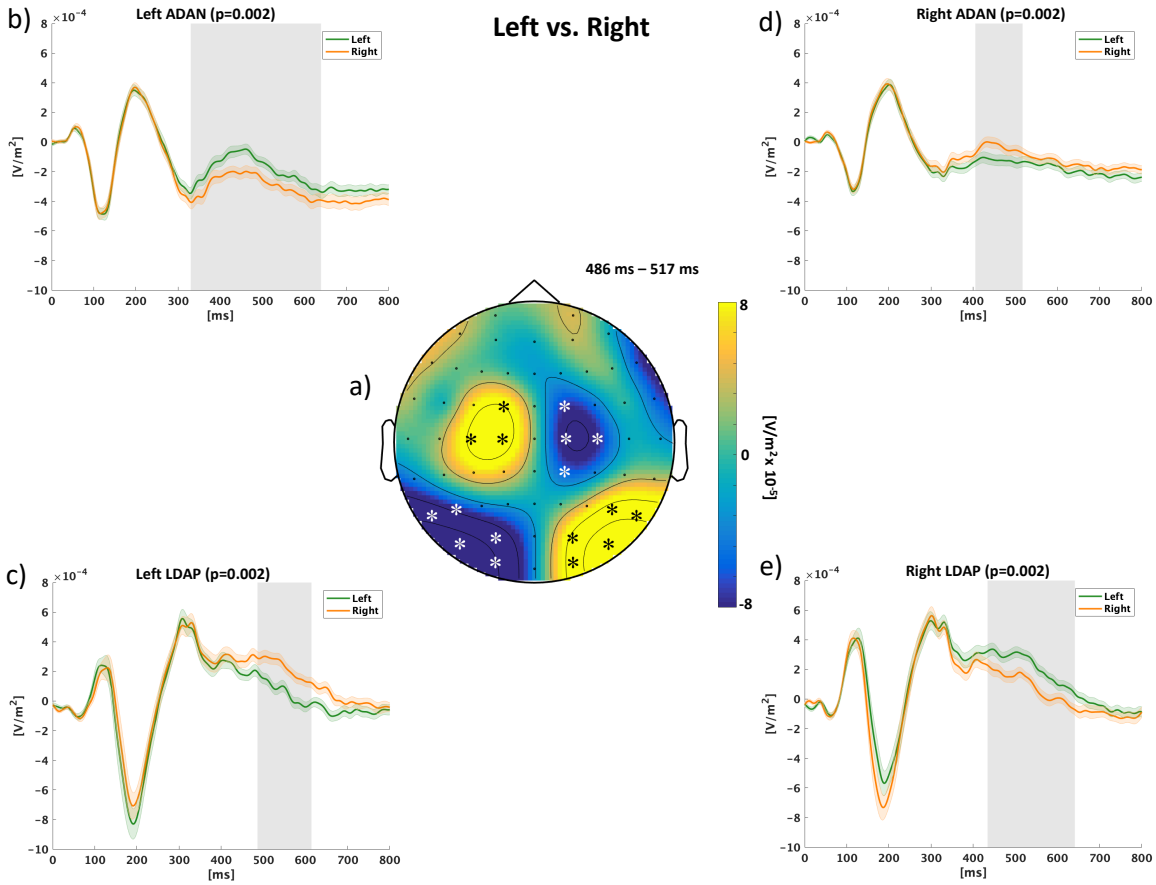


Fig. 2.4. Event-related potential electrode-time clusters for the Left vs. Right contrast. a) shows the topographies for left ADAN (upper left positive cluster), left LDAP (lower left negative cluster), right ADAN (upper right negative cluster) and right LDAP (lower right positive cluster) during a time interval where all four components were observed. Time courses were plotted for electrodes marked with stars, which showed a difference between conditions in more than 80% of cluster time points. Time courses for left ADAN, left LDAP, right ADAN and right LDAP are shown with b), c), d) and e). Grey shading indicates intervals when the significant electrode-time clusters were observed. Green and orange shading of time courses represents SEM.

To examine whether lateralised ADAN and LDAP components can be modulated by differential temporal expectations, time courses for right directing cues were subtracted from time courses for left directing cues separately for cues indicating short versus long cue-target intervals. Electrodes were selected based on previously obtained main effects, where electrodes which demonstrated a significant difference with left versus right spatial expectations in more than 80% of cluster time points were selected and averaged for each component. For ADAN, electrodes FC1, C3, C1 (left)

and FC2, C2, C4, CP2 (right) were selected. For LDAP, electrodes included P7, P5, PO7, PO3, O1 (left) and P6, P8, PO4, PO8, O2 (right). Resulting time courses were then compared by cluster-based permutation analyses for the whole cue-target interval. Left ADAN (Fig. 2.5 a,b) showed temporal expectation sensitivity from 591 ms to 616 ms (p=0.016), where expecting a target earlier in time lead to a relative increase of the component. Left LDAP (Fig. 2.5 c,d) showed such sensitivity from 402 ms to 447 ms (p=0.016) and 587 ms to 615 ms (p=0.034).

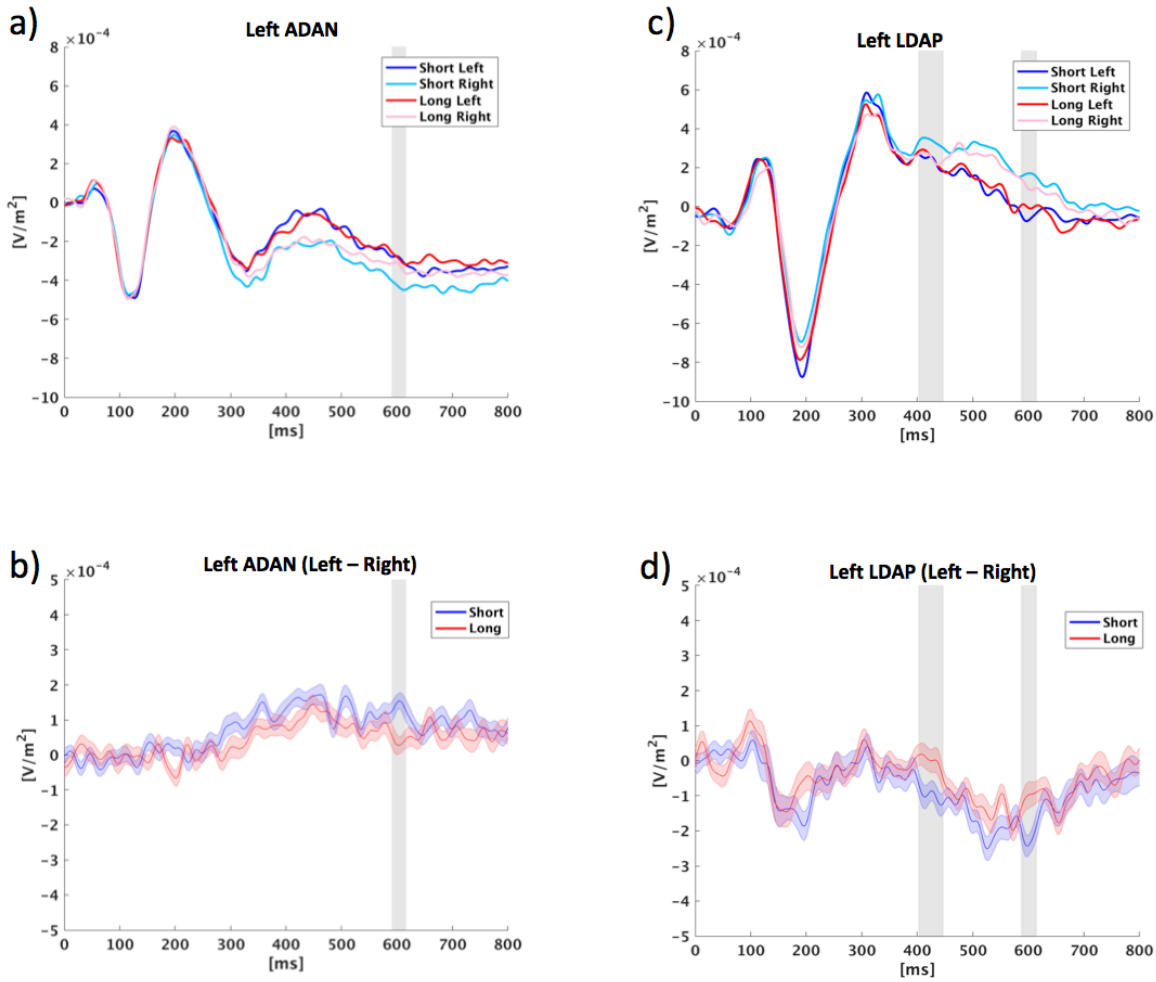


Fig. 2.5. Modulations of left ADAN (a,b) and left LDAP (c,d) by temporal expectations. Time courses are shown for separate conditions (a,c) and where time courses for orienting to the right hemifield were subtracted from time courses for orienting to the left hemifield (b,d). Grey shading indicates intervals when the significant modulation of ADAN respectively LDAP by time was observed ($p < 0.05$). Blue and red shading of time courses indicates SEM.

Alpha processing

Alpha processing within the cue-target interval uncompromised by immediate cue or target stimulation was analysed for various contrasts. Statistics and significant electrode clusters are shown with Table 2.3. In particular, there was lower alpha power in medial and frontal regions, when participants expected a target after a short versus long interval (Fig. 2.6). Analysing the contrast separately for conditions of different spatial expectations, left sided spatial expectations showed a marginally significant left medial negativity and neutral spatial expectations a frontal negativity. No difference in temporal alpha processing was found when a target was expected to occur in the right hemifield. Time-frequency representations (Fig. 2.7) relating to significant clusters did not show spectral specificity to the alpha band during the time window uncompromised by visual stimulation (350 ms - 650 ms).

Table 2.3. Electrode clusters for alpha processing

Contrast	Cluster polarity	P-value	Electrodes
Short vs. Long	Negative	0.016	Fp1, AF7, AF3, F7,F5, F3, FC5, FC3, C1, CP1, CPz
Short vs. Long, Left	Negative	0.0539	FC3, C3, C1, CP1, CPz
Short vs. Long, Right	-	-	-
Short vs. Long, Neutral	Negative	0.004	Fp2, AF3, AF4, AF8, F3, F1, Fz, F2, F4, F6, F8, FC5, FC3, FC6, FT8, T8
Left vs. Neutral	Negative	0.002	FC2, FC4, C3, C1, Cz, C2, C4, CP3, CP1, CPz, CP2, CP4, P1, Pz, P2, P4, P6, P8, POz, PO4, PO8, Oz, O2
Left vs. Neutral, Short	Negative	0.002	C3, C1, Cz, C2, C4, CP3, CP1, CPz, CP2, CP4, Pz, P2, P4, P6, P8, POz, PO4, PO8, O2
	Positive	0.0639	AFz, F1, Fz, F2
Left vs. Neutral, Long	Negative	0.004	C3, C2, C4, CP3, CP1, CPz, CP2, P3, P1, Pz, P2, P4, P6, POz, PO4, PO8, Oz, O2
Left vs. Neutral x Short vs. Long	-	-	-
Right vs. Neutral	Negative	0.004	C3, C1, Cz, C2, CP3, CP1, CPz, CP2, P7, P5, P3, P1, Pz, P2, PO7, PO3, POz, O1, Oz
Right vs. Neutral, Short	Negative	0.002	C3, C1, Cz, C2, CP5, CP3, CP1, CPz, CP2, P7, P5, P3, P1, Pz, P2, PO7, PO3, POz
	Positive	0.034	AF3, AFz, F3, F1, Fz, F2
Right vs. Neutral, Long	Negative	0.006	C3, C1, Cz, CP3, CP1, CPz, CP2, P5, P3, P1, Pz, P2, P4, PO7, PO3, POz, O1, Oz
Right vs. Neutral x Short vs. Long	Positive	0.05	AFz, AF4, Fz, F2, F4, F6
Left vs. Right	Negative	0.006	C2, C4, CP2, CP4, P4, P6, PO4, PO8, O2
	Positive	0.014	P5, P3, P1, PO7, PO3, O1
Left vs. Right, Short	Negative	0.002	C2, C4, C6, T8, CPz, CP2, CP4, CP6, P4, P6, P8, PO4, PO8, O2
	Positive	0.0659	P3, P1, PO3
Left vs. Right, Long	Positive	0.0739	P3, P1, PO3
Left vs. Right x Short vs. Long	Negative	0.044	CP6, TP8, P6, P8, PO8

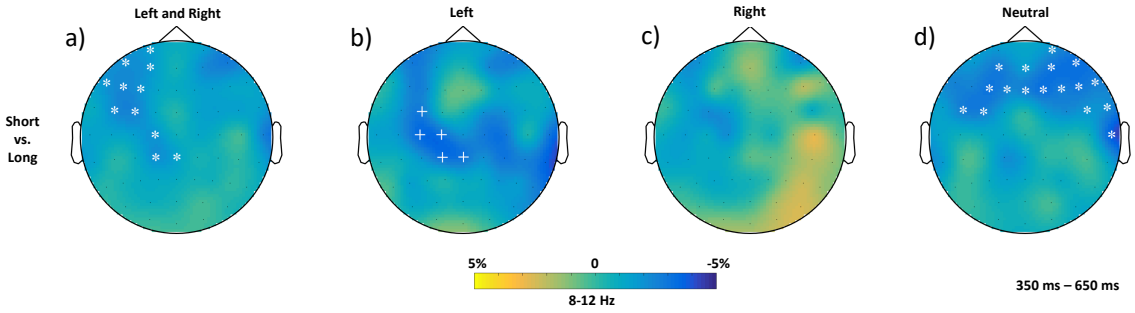


Fig. 2.6. Topographies for modulation of alpha power by temporal expectations in the pre-target interval (350 ms – 650 ms). Topographies are depicted for combined (a) and separately for left (b), right (c) and neutral (d) spatial expectations. Significant electrodes are marked by stars. Crosses signify electrodes with a trend toward significance.

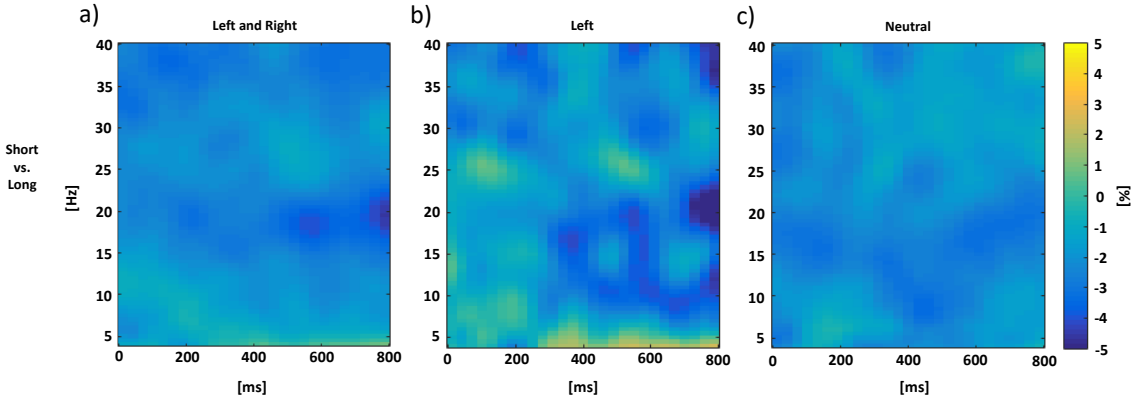


Fig. 2.7. Time-frequency representations relating to significant electrode clusters of alpha power modulation by temporal expectations. Representations for combined (a), left (b) and neutral (c) spatial expectations.

With directed compared to neutral spatial expectations (Fig. 2.8, a-h), there was a contralateral, posterior decrease in alpha power when participants expected a stimulus to appear in the left or right hemifield. This pattern was preserved regardless of temporal expectations. A frontal alpha power increase was found when participants had right side versus neutral spatial expectations specifically in connection with expecting a target after a short but not after a long interval. A comparable bordering significant frontal increase was observed when participants had left side versus neutral spatial expectations in connection with expecting a target after a short interval. When comparing short versus long interval expectations explicitly, there was a marginally

significant right frontal alpha power increase for right versus neutral spatial expectations. Time-frequency representations (Fig. 2.9) for significant posterior clusters revealed decreases in power for the alpha and beta frequency band.

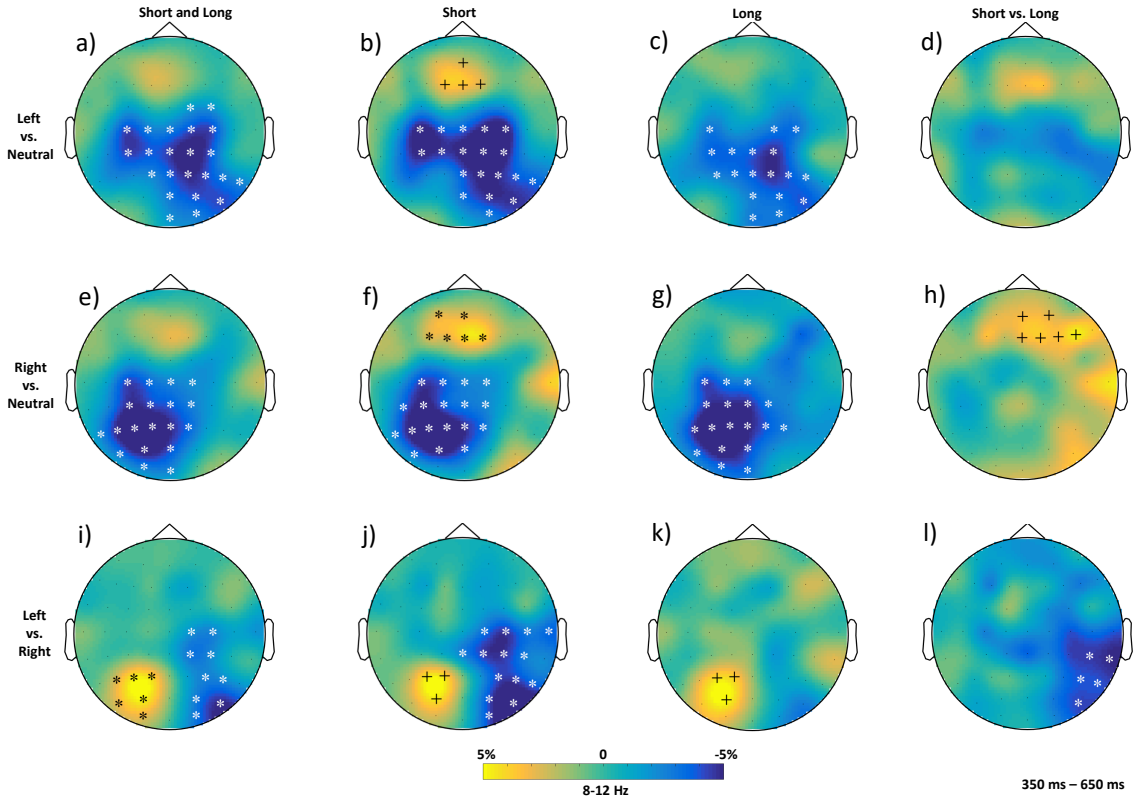


Fig. 2.8. Topographies for modulation of alpha power by spatial and temporal expectations in the pre-target interval (350 ms - 650 ms). The first row (a-d) depicts left versus neutral, the second row (e-h) right versus neutral, and the third row (i-l) left versus right spatial expectations. With the first column, expectations for long and short intervals are combined. The second and third column represent short respectively long interval expectations. The fourth column shows the interaction for short versus long interval expectations. Significant electrodes are marked by stars. Crosses signify electrodes with a trend toward significance.

Alpha lateralisation has also been measured (Thut, 2006) by subtracting cortical alpha processing for left versus right hemifield spatial expectations. Even though this measure does not immediately afford insight into the direction of alpha power changes, by combining attentional processing of both hemifields, it is a useful measure for sharpening and enquiring spatial expectation related alpha modulation. A posterior

lateralised alpha power modulation was observed (Fig. 2.8 i-l). This posterior lateralisation was also present, when analysing trials for short target expectation separately, although left hemisphere modulation only reached a trend toward significance. When participants expected a target after a long interval, there was only a marginally significant left hemisphere modulation. Explicitly comparing trials for expecting a target after short versus long interval showed a right hemisphere alpha power decrease, suggesting that the right but not the left hemisphere is modulated differentially by temporal expectations. Time-frequency representations (Fig. 2.10) of observed clusters showed power modulations in the alpha and low beta frequency band.

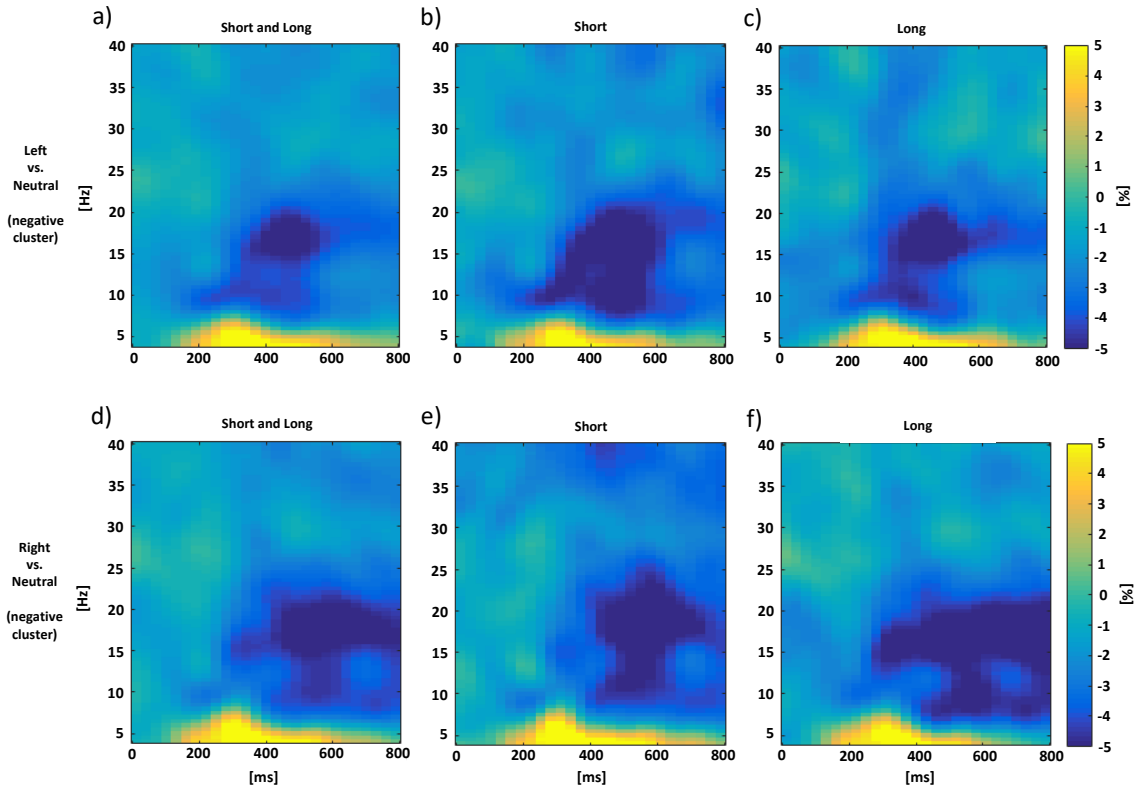


Fig. 2.9. Time-frequency representations relating to significant posterior electrode clusters of alpha power modulation by left versus neutral (a-c) and right versus neutral (d-f) spatial expectations according to combined (a,d), short (b,e) and long (c,f) temporal expectations.

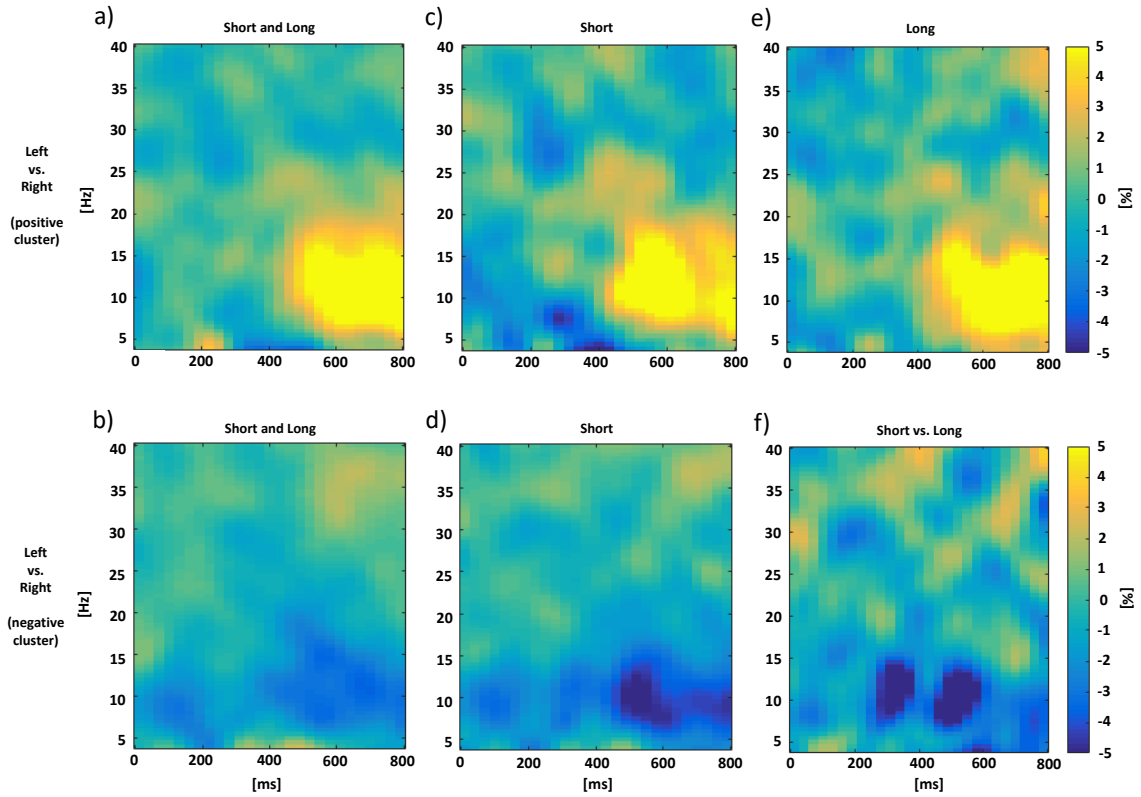


Fig. 2.10. Time-frequency representations relating to significant posterior electrode clusters of alpha power modulation by left versus right spatial expectations according to combined (a,b), short (c,d), long (e) and short vs. long temporal expectations (f).

Correlations

There were significant correlations of the CNV effect with temporal effects of behaviour (Fig. 2.11 a,b). The CNV correlated with reaction time (r=-0.3321, p=0.0478), where larger temporal reaction time effects were associated with larger (negative) CNVs. Most importantly, the CNV also correlated with d' (r=0.5639, p=0.0003), suggesting that larger CNVs are associated with larger perceptual benefits with temporal expectations.

Right ADAN (Fig. 2.11 c) correlated marginally significantly with the spatial effect of d' (r=0.32, p=0.0502). Right LDAP correlated also with the spatial effect of d' (r=-0.4032, p=0.0148; Fig. 2.11 d). Both larger right hemisphere ADAN and LDAP were

connected to larger spatial perceptual behavioural effects. In contrast, larger left LDAP effects were related to faster reaction times (r=-0.4312, p=0.0077; Fig. 2.11 e).

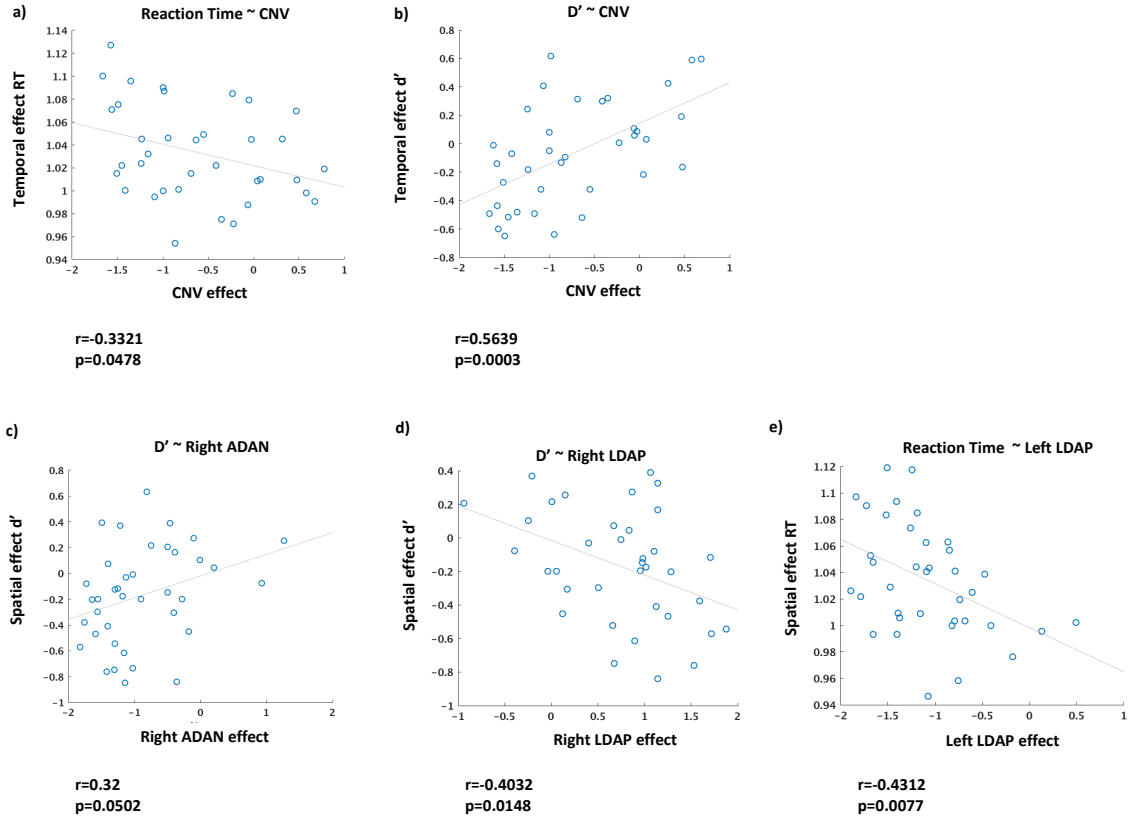


Fig. 2.11. Correlations of behavioural measures with neural measures. Depicted are correlations of CNV with temporal effects of reaction time (a) and d' (b), right ADAN with spatial effect of d' (c), right LDAP with spatial effect of d' (d), and left LDAP with spatial effect of reaction time (e).

Different neural measures were also correlated with age. With broadband neural measures, there was only a significant correlation with left ADAN (Fig. 2.12 a); younger participants had larger left ADANs (r=-0.4138, p=0.0098). For alpha lateralisation (Fig. 2.12 b), the younger the participants, the more lateralisation there was with expecting a short compared to long cue-target interval (r=-0.4464, p=0.005). This result was supported by simple right hemisphere alpha modulation (Fig. 2.12 c,d). Younger participants showed more alpha modulation for expecting a short versus long interval,

although there was only a trend toward significance (r=0.2918, p=0.0755). In addition, for the right hemisphere, with expectations for short target presentations younger participants showed larger alpha modulation (r=0.3215, p=0.0491).

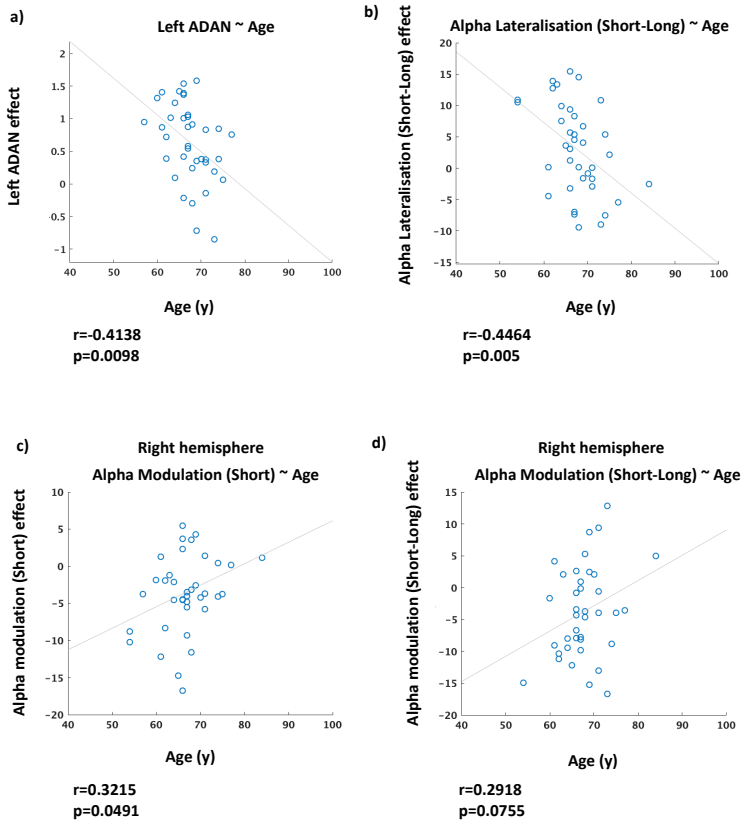


Fig. 2.12. Correlations of age with neural measures. Depicted are correlations of age with left ADAN (a), alpha lateralisation for short versus long interval expectations (b), right hemisphere alpha modulation for short interval expectations (c), and right hemisphere alpha modulation for short versus long interval expectations (d).

Surprisingly, older participants had a larger behavioural spatial effect d' (r=-0.4513, p=0.0051; Fig. 2.13 a). The same result was obtained when only left hemifield responses were considered (r=-0.3895, p=0.0189; Fig. 2.13 b). Younger participants showed a larger temporal orienting effect with left hemifield related reaction times (r=-0.4423, p=0.0048; Fig. 2.13 c).

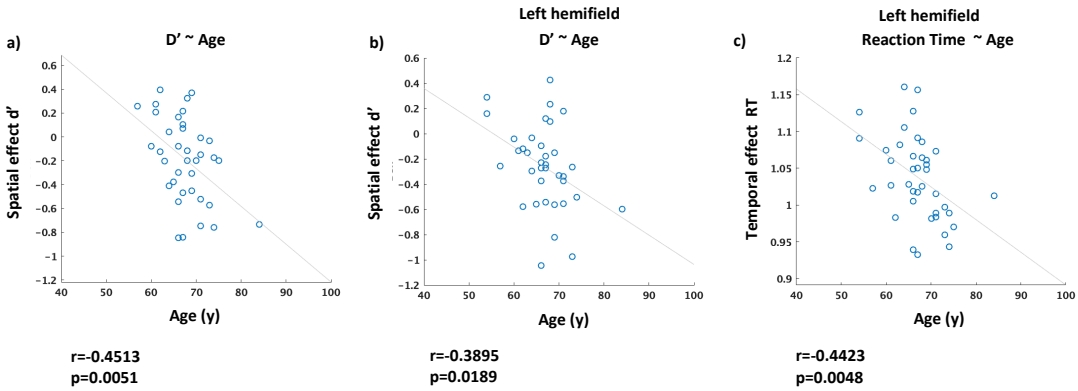


Fig. 2.13. Correlations of age with behavioural measures. Depicted are correlations of age with spatial effect of d' (a), left hemifield spatial effect of d' (b) and left hemifield temporal effect of reaction time (c).

Discussion

The present study showed clear effects of combined spatial and temporal expectations in a large cohort of healthy older participants. While non-linearities in the expression of the relevant markers across age beyond the age range tested are possible, larger performance-related variability in older participants should have benefitted the characterisation of the relationship of neural and behavioural effects. Effects of aging were shown by correlating behavioural and neural effects with age, sidestepping cohort-related effects.

Behaviour

The present paradigm successfully replicated effects of cued spatial (Carrasco, 2014; Posner, 1980) and temporal (Nobre & Rohenkohl, 2014) expectations with both reaction time and perceptual processing. Participants were generally faster and

perceptually more sensitive with spatially informative cues and with valid versus invalid temporal information. In a similar paradigm, Rohenkohl et al. (Rohenkohl et al., 2014) reported synergistic interactions of combined spatial and temporal expectations on d'. With reaction time (Fig. 2.2 a), the present study clearly showed independent effects of spatial and temporal modulations. Rohenkohl et al. did not report raw reaction time measures and in addition contrasted valid against invalid spatial expectations. It is therefore possible that spatio-temporal interactions generally rather occur at a more perceptual as opposed to response-related processing level (Doherty et al., 2005) or that neutral as opposed to invalid spatial expectations fail to induce a spatial effect sufficiently strong to interact with temporal expectations. In the perceptual domain (Fig. 2.2 b, c), more complex 2 and 3-way interactions between spatial and temporal expectations and hemifield were observed, which cannot be compared directly to the results of Rohenkohl et al., where trials were averaged across hemifields. Most importantly, hemifields differed in the way spatially neutral cued targets were processed in the presence of temporal expectations. A relative cost with invalid as opposed to valid temporal expectations was observed only with the left visual field. Possible implications of such a finding are discussed further below in connection with alpha oscillatory processing.

CNV

Contrasting trials in which participants expected a target after a short versus long interval, an earlier central negativity from 235 ms lasting for about 100 ms (Fig. 2.3 a, b) and a later central negativity from 541 ms lasting until the occurrence of the target

stimulus were observed (Fig. 2.3 c, d). Importantly, the later component correlated positively with response speed and perceptual sensitivity across participants.

As pointed out in the introduction, the CNV is a well investigated marker of stimulus anticipation. An early and a late component have been described. However, a separation of both components is usually observed from cue-target interval durations of several seconds and investigations of the early component focus on a time range from at least 400 ms post cue (Gaillard, 1977; Gómez et al., 2001; Loveless & Sanford, 1974). The early component with the present paradigm may thus not necessarily be connected to previous CNV investigations. The early time range and shape of the time course also suggest that the component is superimposed on later stages of cue related visual processing. Interestingly, there is a mild central-left-sided topography. This may be connected to early stages of response preparation, where participants were always responding with their right hand relating to left lateralised pre-motor cortex activation. Specifically, the supplementary motor area (SMA) has been connected to temporal processing (Coull, Vidal, & Burle, 2016; Liu et al., 2013; Merchant & Yarrow, 2016), which would be compatible with the observed central topography. In addition, a left SMA (Brodmann area 6) bias with temporal processing has been reported in functional imaging (Coull & Nobre, 1998). Finally, in a central target detection task with temporal expectations for short versus long intervals Miniussi and colleagues (Miniussi et al., 1999) also observed a relatively early left hemisphere bias, although the effect was located more posteriorly compared to the present one and the authors suggested that parietal cortex engaging in early attentional orienting might be involved.

The second component, a central negativity coincides topographically and temporally with a CNV. As outlined in the introduction, a CNV can emerge in various

contexts (Brunia, van Boxtel, & Böcker, 2012; Tecce, 1972) potentially relating to various cognitive functions and neural generators, which share as a common feature a cognitive mode of expectancy or anticipation. This of course inevitably includes the temporal dimension and there is a body of research investigating the CNV particularly in terms of temporal processing (Ng & Penney, 2014). In the field of temporal expectations, it was shown that temporal orienting in a target detection task can flexibly modulate behaviour and CNVs (Miniussi et al., 1999). Moreover, different temporal conditional probability distributions for target occurrence were shown to modulate CNVs differently and response times accordingly (Cravo et al., 2011; Trillenberg et al., 2000) in go/no-go tasks. The present study replicated the modulation of a CNV by temporal expectation in a combined spatio-temporal expectation discrimination task. Using unbiased electrode-time cluster correction statistics after scalp current density transformation, the CNV could be described with refined temporal and topographical precision.

Interestingly, the temporal effect of CNV modulation correlated with temporal effects of behaviour (Fig. 2.11 a, b). Relationships of response-related and perceptual measures with CNV amplitude have been reported, but also questioned (Cohen, 1973; Hillyard, 1969; Perdok & Gaillard, 1979; Rebert & Tecce, 1973). With temporal processing related CNV modulations, relationships are also unclear (Ng & Penney, 2014). Faster reaction times have been connected to larger CNV amplitudes in tasks where response speed is emphasized (Cravo et al., 2011; Miniussi et al., 1999; Trillenberg et al., 2000). The present study supports such a relationship in a perceptual discrimination task showing that temporal reaction time effects correlate with CNV effects across subjects. Most importantly, for the same task, there was also a

correlation of the temporal effect of perceptual sensitivity (d') with the CNV effect, and this effect was even more pronounced.

An older study by Perdok and Gaillard (Perdok & Gaillard, 1979) investigated stimulus discriminability in relation to CNV amplitude. They did not find a relationship between the two measures. However, Perdok and co-worker employed a much longer ISI compared to the present study (4 s versus less than 1 s). Temporal estimation abilities and CNV amplitudes have been shown to decay considerably from intervals of more than 3s (Elbert, Ulrich, Rockstroh, & Lutzenberger, 1991). In addition, Perdok and Gaillard did not explicitly investigate the effects of differential temporal expectations.

It can only be speculated how large CNVs mechanistically relate to better perceptual sensitivity in the present task. It has been proposed that the sources of the CNV are distributed across different brain areas (Gómez, Flores, & Ledesma, 2007). However, motor involvement has been described consistently (Gómez et al., 2007; Nagai et al., 2004; Rektor, 2002). Although EEG topographies afford relatively limited regional information, the present results nevertheless suggest a pre-motor, potentially SMA source of the temporal CNV effect. It has been suggested that the estimation of time is a complex process which can happen at different levels of the processing hierarchy and in more separate or centralised modules (Merchant et al., 2014). Across different tasks and modalities, a core set of brain regions comprising a basal ganglia-thalamo-cortical circuit including pre-SMA and SMA is activated in motor timing and time perception tasks (Coull & Nobre, 2008; Schubotz, Friederici, & Yves Von Cramon, 2000; Wiener, Turkeltaub, & Coslett, 2010). As meaningful action is intimately connected to timing, it has been suggested that pre-motor regions play a more general, supra-modal role in timing (Coull et al., 2016; Merchant & Yarrow, 2016). It

could therefore be argued that the present CNV effect signifies a supra-modal temporal modulation which feeds into more specialised visual areas, eventually improving target processing and perceptual sensitivity.

However, different explanations for the observed relation between a CNV and d' are still possible. The present relationship is a correlation. Although there is no immediate electroencephalographic evidence for it, it is possible that a third more general factor, e.g. alertness, has similar modulatory influences on both CNV and perceptual sensitivity (Fan, McCandliss, Sommer, Raz, & Posner, 2002; Matthias et al., 2010).

ADAN / LDAP

Contrasting left versus right directing cues, bilateral ADAN and LDAP components were observed (Fig. 2.4). Importantly and furthering previous research, these components were obtained independently by electrode-time cluster-based analyses and after scalp current density transformation of the signal, improving spatial topographical resolution (Vidal et al., 2015).

Previous research has found ADAN and LDAP components from approximately 300 ms, respectively 400 ms (Harter et al., 1989; Hopf & Mangun, 2000; Nobre et al., 2000). Component peaks at around 400 ms (ADAN) and 600 ms (LDAP) have been reported (Praamstra, Boutsen, & Humphreys, 2005). This is in line with the temporal distribution of the effects of this study. As ADAN follows spatial directional cues and partly overlaps with medial frontal regions which have been linked to spatial attention (Corbetta & Shulman, 2002; Nobre et al., 1997), it has been proposed that ADAN

represents an event-related potential manifestation of the preparation for attentional shifts (Hopf & Mangun, 2000; Nobre et al., 2000; Praamstra et al., 2005).

In the present study, ADAN was observed bilaterally. Further on and interestingly, right ADAN was marginally correlated with the spatial attention effect of perceptual sensitivity (Fig. 2.11 c). Although ADAN has been shown to predict visual short-term memory performance as measured by d' (Murray et al., 2011), to the best of the author's knowledge correlations of ADAN with perception have not been reported before. Improved topographical representation through scalp current density transformation and both spatially and temporally unbiased statistics may have facilitated this finding. The finding may provide further evidence that pre-target spatial orienting can translate into improved behavioural performance measures (Kelly et al., 2009).

LDAP was clearly observed bilaterally, so that scalp current density results are well in line with previous findings using non-spatially transformed ERPs (Harter et al., 1989; Hopf & Mangun, 2000). Scalp current density topographies were very symmetrical covering mostly occipital cortices, where right LDAP was a bit more long lasting, starting around 50 ms earlier and ending around 30 ms later than left LDAP. The symmetrical posterior topography supports previous claims that LDAP is localised in lateral occipital gyrus respectively the ventral part of the temporal lobe (Praamstra et al., 2005; Praamstra & Kourtis, 2010). It may reflect visual cortical excitability modulation in anticipation of the target (Harter et al., 1989; Hopf & Mangun, 2000). It has also been claimed that LDAP is generated in occipital and parietal areas, so that it may rather relate to supra-modal attentional control processes operating on visual spatial representations (Green, Teder-Sälejärvi, & McDonald, 2005). Interestingly, with

the present study right LDAP amplitude correlated positively with perceptual sensitivity and left LDAP amplitude correlated negatively with response time (Fig. 2.11 d,e). The only other report of a connection of LDAP with behaviour comes from Kelly et al. (Kelly et al., 2009), who subtracted right from left hemisphere measures separately for cue left and right conditions and sorted trials into bins with increasing LDAP effects. With cue-left trials, they found a linear trend for larger neural effects being associated with faster reaction times. Whereas Kelly investigated an LDAP - behaviour relationship with respect to the side of attentional deployment averaging across hemispheres, the present results relate to hemisphere specific effects. It is difficult to interpret why left and right LDAP are only connected to response time and perceptual sensitivity respectively. However, it should be noted that right but not left ADAN was also connected to perceptual performance, potentially pointing to a right hemisphere sensitivity specifically for perceptual processing.

Focusing on electrodes where left and right ADAN and LDAP were observed, ADAN and LDAP modulations were further investigated in the context of different temporal expectations. Both left ADAN and LDAP were modulated by temporal expectations, where expecting a target after a short compared to long interval lead to a larger left ADAN and LDAP (Fig. 2.5).

Green et al. (Green & McDonald, 2010), in a cued visual spatial and temporal attention paradigm, also found a modulation of LDAP with temporally predictive cues. However, findings were based on limited pre-specified electrodes (PO7/PO8) and time points (400 ms – 600 ms) and averaged across contra- and ipsilateral presentation, which does not allow for more refined, hemisphere resolved investigations. More importantly, there was no direct comparison of trials with different temporal

expectations. The authors merely showed that a study cohort with temporally non-predictive cues does not exhibit an LDAP, whereas another cohort with temporally predictive cues does. The present study clarifies this finding by providing a spatially and temporally resolved comparison between two conditions of temporal expectation within the same dataset. It also extends Green's report by evidence for medial frontal modulation (ADAN). Effects of spatio-temporal orienting with the present study were lateralised to the left hemisphere. LDAP showed an earlier temporal effect from around 400 ms for about 50 ms, and both ADAN and LDAP showed later effects around 600 ms which were temporally very much overlapping. The pattern of results is compatible with imaging studies showing a left-dominant network of parietal and frontal areas involved in the control of temporal orienting (Coull & Nobre, 1998, 2008).

With the present study, participants responded with their right hand only. Could lateralised effects of spatial expectation be due to right-hand responding? In general, bilateral ADAN and LDAP have also been reported with spatial expectation paradigms where the response hand was balanced (Hopf & Mangun, 2000; Nobre et al., 2000), although for ADAN a right hemisphere bias has been observed. Moreover, as for LDAP, the more posterior occipital and parietal topography is not consistent with more central and frontal motor related processing (Eimer, 1998; Heideman, van Ede, & Nobre, 2017). Finally, the Left versus Right contrast should principally cancel out response related potentials, as participants needed to prepare for a response with left and right hemifield targets. It is theoretically possible that left ADAN was confounded by an interaction of response hand and lateralised spatial expectations. However, this seems unlikely, as hemifield specific effects of behaviour were only found in perceptual and not response related measures.

To summarise, both ADAN and LDAP were sensitive to temporal orienting. How does that connect to the proposed functions of ADAN as a signature for the preparation of attentional shifts, and LDAP as a signature of cortical excitability modulation or more general attentional control? In general, their modulation by the expected onset time of a target stimulus further emphasises their flexible anticipatory character. However, both ADAN and LDAP seemed to be most pronounced between 400 and 500 ms (ADAN), respectively 500 and 600 ms (LDAP), whereupon they rather decreased before the onset of the first target. This is true for both expecting a target after short and long intervals (Fig. 2.5 b,d). A decrease of ADAN until target onset is well compatible with its proposed function of initiating attentional shifts. The shift may be initiated well before target onset, whereupon ADAN decreases again. If a target is expected to occur earlier, the shift may be executed more forcefully and quickly and ADAN increases. LDAP has been connected to attentional control and cortical excitability modulations. Regarding attentional control, the same argumentation as with ADAN applies – shifts could be initiated early after the cue and temporal expectations may facilitate these shifts. Temporal expectations could also facilitate cortical excitability. However, a simple and continuous excitability modulation is rather unlikely as LDAP generally decreases before target onset where excitability should be maximal. If LDAP should relate to excitability modulations, one would therefore expect a more complex pattern of cortical preparatory activity. A state of high sensitivity could be set up before target onset. At this stage it would be accessible through EEG. During the following, mainly anticipatory stage cortical activity could be highly sensitive to external stimulation without leaving readily observable EEG traces (e.g., Stokes, 2015).

Alpha

There was a relative left medial frontal decrease in alpha power for short versus long temporal interval expectations (Fig 2.6, a). A medial, left-side biased decrease was observed when only left-cue trials were respected (Fig. 2.6, b). A frontal, more right-side biased decrease was observed with cues featuring neutral spatial information (Fig. 2.6, d). No difference was obtained with only right-cue trials (Fig. 2.6, c). Decreases in alpha and beta band power as a function of increased temporal expectancy have been observed in different modalities and with different methods (Heideman et al., 2018; Lima et al., 2011; Rohenkohl & Nobre, 2011; van Ede et al., 2011; Zanto et al., 2011). In these previous studies, the topographies of the effects were suggestive of a modulation of modality specific cortical areas. With the present visual attention paradigm, a comparatively posterior parietal occipital topography would have been expected. A measure of globally distributed alpha power has been connected to attentional control (Sadaghiani et al., 2010). However, investigating the spectral distribution for the present contrasts (Fig. 2.7) and significant electrodes showed little spectral specificity with more general oscillatory power decreases with frequencies of more than 5 and up to 40 Hz.

Supporting previous findings (Gould et al., 2011; Kelly et al., 2009; Sauseng et al., 2005; Thut, 2006), alpha power was observed to decrease at posterior sites contralaterally to the cued direction of attention (Fig. 2.8, a-h). Following common conceptions of alpha processing (Jensen et al., 2012; Klimesch et al., 2007; Lindsley, 1952) it is proposed that the relative decrease in posterior alpha power relates to a state of increased cortical excitability for contralaterally presented visual stimuli enhancing their active processing (Fries et al., 2001; Sauseng et al., 2005). Although

the present data did not replicate a direct connection of alpha power with behaviour (Ergenoglu et al., 2004; Hanslmayr et al., 2007; Kelly et al., 2009), participants responded faster and were perceptually more sensitive with directed versus neutral spatial cues.

Investigating spatial modulations in the context of different temporal expectations (Fig. 2.8, b,c,f,g) showed contralateral decreases for both cue directions and temporal conditions. For right vs. neutral cues, relative contralateral left hemisphere alpha decreases were comparable between different temporal expectations. In addition, although statistically not significant, it seems as if there may have been a mild relative right hemisphere ipsilateral increase in alpha power for short temporal interval expectations. Increased alpha power with unattended spatial locations has been linked to low cortical excitability relating to a state of inhibition (Klimesch et al., 2007; Worden et al., 2000). Leftward directing vs. neutral cues elicited an overall larger right hemisphere contralateral decrease with short compared to long interval temporal expectations, although the effect did not reach statistical significance.

In general, time-frequency representations for posterior clusters of directed versus neutral spatial expectations (Fig. 2.9) showed also decreases in the beta frequency band which seem to partly overlap with decreases in the alpha frequency range. It is possible that somatosensory and motor preparation (Heideman et al., 2017; van Ede et al., 2011) characterised by a decrease in beta and partly alpha oscillatory power showed an interaction with spatial orienting. In line with this, in a visual spatial attention paradigm, Gould et al. (Gould et al., 2011) contrasted conditions of higher and lower spatial predictability and found a graded decrease in central and posterior

beta power with higher spatial predictability, which could be related to motor processing. Interestingly, with the present paradigm, pronounced higher beta power changes are absent for clusters determined by contrasting left versus right spatial expectations. In addition, clusters obtained for directed versus neutral spatial expectations seem to extend to more anterior regions compared to clusters related to left versus right spatial expectations. More anterior alpha power may therefore need to be interpreted in the context of somatosensory and motor processing. A particularly pronounced left central alpha power decrease may reflect the fact that participants responded with their right hand only.

In order to investigate hemisphere specific effects of combined left and right hemifield orienting, activity relating to left hemifield cues was contrasted with activity for right hemifield cues (Fig. 2.8, i-l). Time-frequency representations of posterior lateralised clusters (Fig. 2.10) confirmed spectral modulation in the alpha frequency range. Modulation extended into low beta frequencies. This has been shown before in a very similar paradigm investigating spatial and temporal expectations (Heideman et al., 2018). The present research showed bilateral posterior modulations for combined short and long, as well as only short temporal interval expectations, although left hemisphere modulation did not reach significance with the latter contrast. With long temporal interval expectations, only the left hemisphere showed a trend toward modulation. Importantly, this pattern of results was confirmed by directly contrasting lateralisation for short versus long temporal interval expectations, indicating that the right but not the left hemisphere showed stronger alpha modulation with short compared to long temporal interval expectations. Overall, it thus seems as if the right hemisphere was specifically sensitive to temporal expectations.

Interestingly, this pattern of right hemisphere sensitivity seemed to be mirrored in perceptual processing as measured by accuracy and d' (Fig. 2.2 b,c). Right hemisphere attentional and visual processing should preferentially relate to the left visual hemifield and vice versa (Heilman & Abell, 1980; Kinsbourne, 1970; Mesulam, 1981). The right hemifield showed only a mild bias of perception with different temporal expectations, which was expressed in the presence of spatial expectations and does not survive correction for multiple comparisons. However, with left but not right hemifield short targets and neutral spatial expectations participants had lower perceptual performance when targets were expected after a long (invalid) compared to short (valid) interval. It may seem surprising that the effect was mirrored behaviourally with neutral as opposed to directed spatial cues. The following explanation is suggested here: Neurally and in the pre-target orienting phase, the spatio-temporal effect only became visible when spatial and temporal expectations were actually employed. Behaviourally and when the target appeared, insufficient preparation might have become particularly obvious in connection with neutral spatial cues where attention still needed to be shifted.

For alpha processing, it is unlikely that lateralisation as calculated by contrasting left versus right spatial expectations was influenced by right-hand responding. With right-hand responses, response-related activity would normally be expected over medial left-lateralised electrodes, as has been found for directed versus neutral spatial expectations. For left versus right spatial expectations, alpha processing was not modulated in this region. Instead, alpha lateralisation could be found more posteriorly.

Posterior alpha power decreases with short versus long temporal expectations have been reported with magnetoencephalography in a very similar paradigm of cued visual spatial and temporal expectations (Heideman et al., 2018). However, contra- and ipsilateral trials were pooled for Heideman et al.'s study, so that an interaction with hemisphere could not be resolved. Interestingly, with another yet purely temporal orienting paradigm featuring centrally presented target stimuli, Zanto and colleagues presented right hemisphere alpha power decreases with predictive short versus neutral cues (Zanto et al., 2011). Unfortunately, they did not show alpha power for the left hemisphere.

How does the present spatio-temporal hemispheric interaction fit more generally into theories of visual attention and hemispheric specialisation? It has been proposed that the right hemisphere has a special role in attentional orienting, where both hemispheres direct attention to the contralateral visual hemifield in a mutually competitive way, but the right hemisphere additionally covers the ipsilateral hemifield to some extent (Heilman & Abell, 1980; Kinsbourne, 1970; Mangun et al., 1994; Mesulam, 1981). It has also been suggested that the right hemisphere is specifically connected to additional aspects of attention like arousal, alerting, vigilance or bottom-up processing (Corbetta & Shulman, 2002; Langner & Eickhoff, 2013; Posner & Petersen, 1990). It could be speculated that temporal expectations like these other biases can specifically well team up with the right hemisphere, generating relatively higher right versus left hemispheric dynamics.

Aging

The present study was conducted in a large population of healthy older participants. Behavioural and neural markers of spatial and temporal orienting were correlated with age in order to investigate potential age-related modulations in behavioural and neural processing.

The size of left ADAN was correlated negatively with age (Fig. 2.12 a). A previous investigation did not find an effect of aging on ADAN (Hong et al., 2015), although averaging across contra- and ipsilateral trials did not allow for the analysis of hemisphere specific processing. It is hard to tell why specifically left ADAN, which did not correlate with behaviour, was connected to aging in the present study. However, Nagamatsu et al. (Nagamatsu et al., 2011) have claimed that older participants exhibit a left visual field deficit. In their study, this deficit seemed to be accompanied neurally, in ADAN related regions, by comparably smaller left versus right hemisphere related potential increases to ipsilateral arrow cues.

The spatio-temporal effect of alpha lateralisation was correlated negatively with aging (Fig. 2.12 b), suggesting that older participants lateralised alpha oscillations less flexibly than younger participants. In line with the fact that alpha oscillations were generally more variable with the right hemisphere, right but not left hemisphere alpha modulation for short interval expectations and short versus long interval expectations correlated negatively with age (Fig. 2.12 c,d). This suggests that right as opposed to left hemisphere alpha oscillations are not only employed more flexibly but are also more sensitive to age related changes. Previous studies investigating spatial attention related alpha lateralisation in aging show conflicting findings. Whereas Heideman et al. and Leenders et al. (Heideman et al., 2018; Leenders et al., 2016) report that alpha

lateralisation can be spared or even increased in older age, Hong et al. and van der Waal et al. (Hong et al., 2015; van der Waal et al., 2017) show that younger but not older participants can lateralise pre-target posterior alpha oscillations. The present results may reconcile both claims: While older people can show alpha related signatures of pre-target spatial orienting, aging seems to have an effect on alpha lateralisation, as long as more flexible, temporal expectation related mechanisms come into play and hemispheres are examined separately. Heideman et al. (Heideman et al., 2018) also examined combined spatial and temporal expectations. However, instead of investigating neural variance across a large group of older participants, lateralisation was only compared between groups of younger and older participants. In addition, Heideman et al. compared spatio-temporal interactions between ipsi- and contralateral topographies, neglecting hemisphere specific contributions.

In line with right hemisphere related decreases in spatio-temporal alpha modulation with age, corresponding left hemifield related temporal reaction time effects decreased with age as well (Fig. 2.13 c). This suggests that age-related changes in alpha processing may have behavioural relevance.

Regarding spatial orienting, despite left ADAN related decreases with age, the spatial effect of d' was correlated positively with age, i.e. older participants had larger spatial effects of perceptual sensitivity (Fig. 2.13 a). Behavioural effects of spatial orienting seem to be largely preserved with aging (Gottlob & Madden, 1998; Nissen & Corkin, 1985; Tales et al., 2002). In fact, larger behavioural benefits and costs with central arrow cues preceding peripheral target discrimination have been reported with aging (Hartley et al., 1990). In this light, the present larger perceptual effect with aging may relate to a larger cueing benefit. Neurally, this may manifest in other measures

than left ADAN, which could not be connected to behaviour. A larger effect of perceptual sensitivity was also observed separately for the left but not right hemifield (Fig. 2.13 b). In line with this, Nagamatsu (Nagamatsu et al., 2011) found that sensory evoked responses to left hemifield stimuli were specifically delayed with older participants when stimuli were unattended, suggesting that left hemifield cues may be especially helpful for older participants.

Conclusion

The present research emphasises the importance of temporal and spatial expectations in guiding pre-target neural activation and facilitating behaviour. Using scalp current density transformation, topographical representations of CNV, ADAN, LDAP and alpha oscillatory lateralisation could be resolved with reasonable spatial resolution. Pre-target markers of spatial and temporal expectations could also be related to behaviour. Importantly, the temporal CNV correlated positively with both response speed and perceptual sensitivity. ADAN and LDAP were sensitive to temporal expectations, supporting their function in flexible top-down modulation. Alpha lateralisation was also sensitive to temporal expectations. Specifically, right but not left hemisphere alpha lateralisation was modulated by temporal expectations. This was mirrored in behaviour, where the left versus right visual field seemed to be more sensitive to temporal expectations. The modulation of alpha lateralisation by temporal expectations was decreased with aging. Effects of aging could also be related specifically to the left visual hemifield. Lateralisation of temporal expectation related effects may suggest that temporal expectations are able to modulate neural

processing and behaviour particularly well in the context of spatial expectations. Future studies should investigate this possibility.

Chapter 3: Temporal expectations and stimulus competition in space

Abstract

Temporal expectations can benefit behavioural performance in many different tasks, and interactions between temporal expectations and other attentional biases have been reported. However, temporal expectations so far have mostly been studied in the context of spatially isolated stimuli. This poses the question of whether and how temporal expectations can act in the context of spatially competing target and distractor stimuli. I conducted two cued spatial and temporal expectation tasks in which participants discriminated the identity of a target stimulus presented either alone or simultaneously together with competing distractors, in either the opposite (Experiment 1) or same (Experiment 2) visual hemifield. I show that, in the presence of interhemifield competition, temporal expectations and competition work in tandem and independently. With intrahemifield competition, however, temporal expectations had a detrimental effect on perceptual measures (accuracy, d'). This context dependency of temporal expectations is discussed from a biased-competition account, suggesting that temporal expectations may have an unspecific effect on target and distractor stimuli being presented in close proximity to each other within the same visual hemifield. In Experiment 1, I also examine the effects of aging on temporal expectations and interhemifield stimulus competition. I show that aging spares participants' ability to use temporal information and deal with competing stimuli. This may suggest retention of cognitive control in aging under certain task demands.

Introduction

A recent body of research clearly indicates the beneficial effects of temporal expectations on perception (Nobre & Rohenkohl, 2014). Multiple types of temporal biases have been proposed. Behavioural benefits in perceptual tasks have been described in tasks manipulating the regularity of ongoing rhythms (Cravo, Rohenkohl, Wyart, & Nobre, 2013; Doherty, Rao, Mesulam, & Nobre, 2005; Jones, 1976; Rohenkohl, Cravo, Wyart, & Nobre, 2012), the temporal conditional probability of events (hazard function) within temporally regular contexts (Correa, Lupiáñez, Milliken, & Tudela, 2004; Ghose & Maunsell, 2002; Rolke & Hofmann, 2007), and informative temporal cues (Correa et al., 2005; Coull & Nobre, 1998; Griffin et al., 2002; Rohenkohl et al., 2014). Correa and colleagues (2005) were the first to show perceptual discrimination benefits with temporal cueing in a rapid serial visual presentation task, where target letters could appear either early or late in the stream. There were benefits in perceptual sensitivity, as measured by d' with validly compared to invalidly cued cue-target intervals.

Interestingly, visual temporal expectations have been shown to interact strongly with spatial expectations. A strong synergy was first noted in a study using event-related potentials within the context of rhythmic temporal expectations (Doherty et al., 2005). Visual potentials elicited by targets were unaffected by isolated temporal expectations, but the effects of spatial expectations were significantly magnified by combined spatiotemporal expectations. Findings from animal-model studies of temporal expectations according to hazard rates also suggest the ability of temporal expectations to enhance processing in visual areas (Ghose & Maunsell, 2002;

Jaramillo & Zador, 2011; Lima, Singer, & Neuenschwander, 2011; Sharma et al., 2014). In order to investigate the consequences of isolated and combined temporal and spatial expectations to perceptual discrimination at the behavioural level, Rohenkohl and colleagues (2014), used orthogonally predictive temporal and spatial cues in a visually demanding task. Complementing the previous neural findings, they showed strong effects of valid temporal cues on perceptual sensitivity only at validly cued spatial locations. One suggestion for such findings is that temporal expectations work through spatial, and perhaps other, receptive field properties to enhance perceptual analysis of anticipated relevant events. Within a biased-competition framework (Desimone & Duncan, 1995), such a mechanism might enable combined spatial and temporal expectations to further enhance discrimination of target stimuli from competing distractors.

Surprisingly, however, most studies on temporal expectations have investigated temporal biases using isolated stimuli. This naturally poses the question of how temporal expectations influence the processing of goal-relevant stimuli in the context of distraction. I therefore designed two experiments, where interhemifield respectively intrahemifield stimulus competition were combined with manipulations of spatial and temporal expectations. Specifically, with Experiment 1, stimulus competition was introduced by a target and a distractor stimulus placed in different visual hemifields (interhemifield competition), where early visual representations were likely separated and competition between stimuli should emerge at later processing stages. With Experiment 2, stimuli were presented in close spatial proximity to each other inside one visual hemifield (intrahemifield competition), so that early visual representations were likely to interact with each other.

A second, parallel line of investigation relates to the use of attention in healthy aging. It has been proposed that older adults exhibit a top-down suppression deficit, which includes impaired filtering of distracting information and is associated with decreased behavioural performance and altered neural activations (Chao, 1997; Gazzaley, 2013). In addition, there is conflicting evidence whether elderly participants can use temporal information to improve performance. In a series of target-detection and discrimination tasks, Zanto et al. (2011) did not observe behavioural benefits with temporal information for elderly participants but decreased post-cue neural modulation. In contrast, a recently published study with a series of speeded detection and rapid serial visual presentation tasks (Chauvin, Gillebert, Rohenkohl, Humphreys, & Nobre, 2016) clearly revealed performance benefits in elderly individuals. In order to help arbitrate between these contrasting reports, Experiment 1 was conducted in both groups of healthy younger and older participants. Given the greater susceptibility of older adults to distraction, it is particularly interesting to investigate whether any preserved temporal-expectation effects in older participants were differentially affected by competing stimulation.

Experiment 1: Temporal expectations and interhemifield competition

Methods

Participants

The study protocol was approved by the Central University Research Ethics Committee (CUREC) of the University of Oxford. Twenty-five younger (23 included, mean age: 23.0 years, SD 3.64 years, 15 females) and 38 older (24 included, mean age: 66 years, SD 8.24 years, 12 females) participants were tested. Participants were excluded if they performed in either condition with reaction time or accuracy above or below 3 standard deviations of the mean. Participants were also excluded, if they had self-reportedly not followed task instructions or suffered from a physical impairment, which could have interfered with performance (brain lesion, impaired visual or motor functions). Physical impairments were assessed independently by a clinically experienced researcher or a neurologist.

Presentation

Stimuli were presented on a 23-inch monitor (refresh rate: 60Hz, spatial resolution: 1920 x 1080) using Psychophysics Toolbox Version 3 for MATLAB (Kleiner et al., 2007). Responses were acquired with a computer keyboard.

The task is shown in figure 3.1. Participants viewed peripheral arrays and had to discriminate the identity of a target letter that was presented in isolation or simultaneously with a distracting stimulus on the opposite visual hemifield.

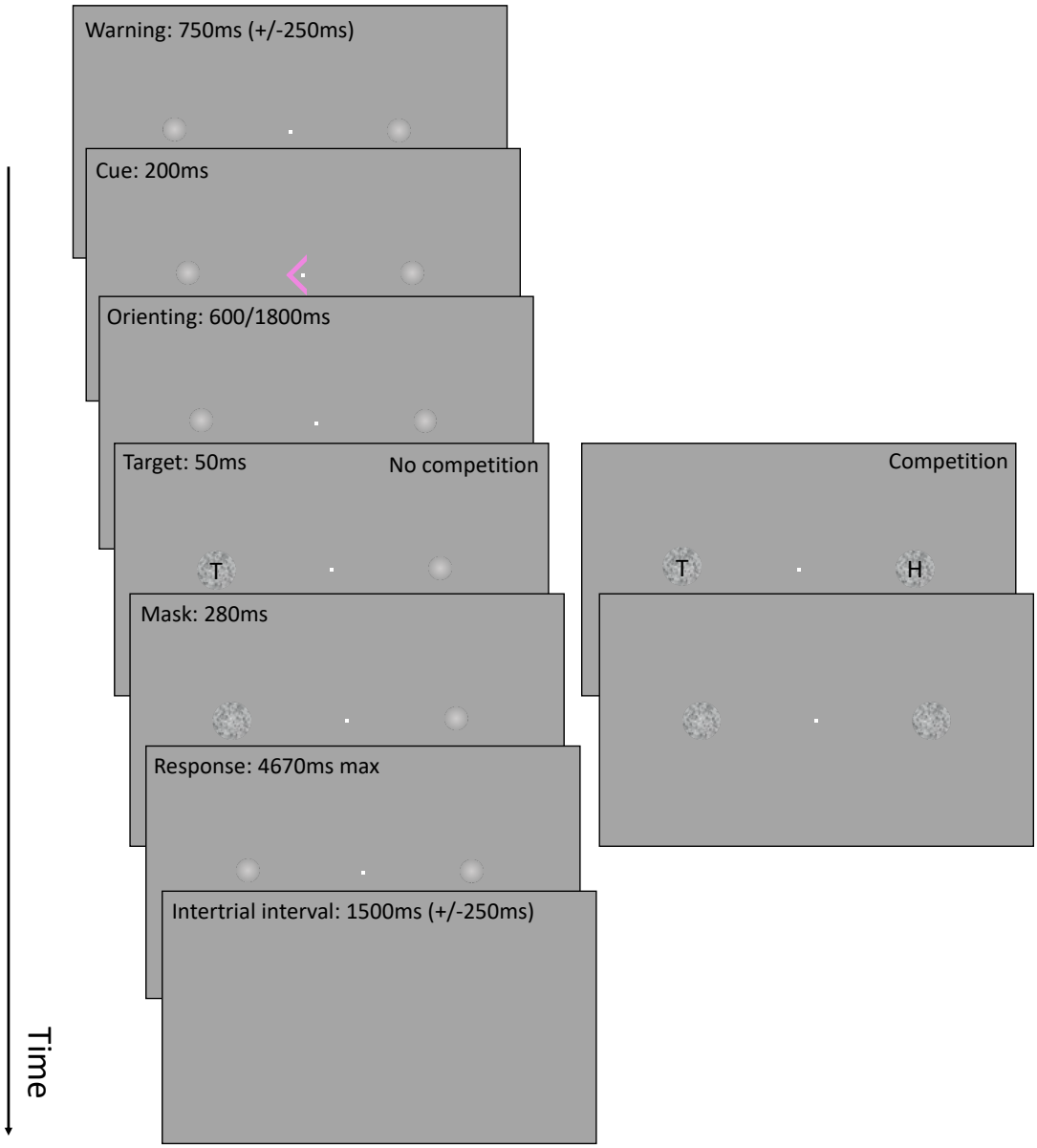


Fig. 3.1. Schematic depiction of an example trial with Experiment 1: Arrows with spatial (direction: target presentation side, 100% validity) and temporal (colour: cue-target interval, 80% validity) information cued target letters (T or L), which are presented together with a distractor (E, F, H, I) in half of the trials (right side depiction). Cue-target inter-stimulus interval duration was either 600 ms (short interval) or 1800 ms (long interval), where letters were either cued for a long or short interval within one block (blocked presentation).

Cues preceding the array indicated the spatial location and predicted the likely temporal interval at which the target would appear. Stimuli were overlaid on a grey background (RGB 102 102 102, 63 cd/m^2). In each trial, participants kept their eyes on a central white square (0.08° each side), which was continuously present. To reduce spatial uncertainty (Smith & Ratcliff, 2009), a luminance pedestal in which the target or distractor stimuli could appear, was presented to the left and the right of fixation on the horizontal meridian (70 cd/m^2, 5° eccentricity from fixation to the centre of the pedestal. After a random interval of 750 ms (+/- 250 ms), a blue or pink arrow cue (height: 2.1°, width 1°) was presented at the centre of the screen for 200 ms. The direction of the arrow indicated if the target would be presented at the left or right side (100% validity). Arrow colour predicted if the target was more likely to appear after a short (600 ms) or long (1800 ms) interval, after the offset of the cue stimulus (80% validity). Targets consisted of black (RGB: 0 0 0) letters 'T' or 'L', which were presented randomly behind one of eight randomly created translucent circular white-noise patches (size: 1.8°) and on top of pedestals for 50 ms. Targets were presented either alone, or simultaneously with a matched distractor stimulus, which was presented atop the luminance pedestal on the other side of the screen. Distractors could feature letters 'E', 'F', 'I', or 'H'.

After target and distractor stimuli disappeared, circular noise patches remained on the screen for 280 ms. Participants had up to 5 seconds to respond if they had seen a 'T' or 'L' target stimulus. They had to respond by button press with their index or middle finger. Responses were followed immediately by an intertrial interval of 1500 ms (+/- 250 ms), during which participants viewed a uniformly grey screen only.

Cue-target interval duration and temporal cues, presentation side and spatial cues, identity of target and distractor stimuli, and presence of competition were counterbalanced across the experiment. Temporal cues were blocked, while the remaining manipulations were randomised within blocks and unpredictable on a trial-by-trial basis.

Within one block, either blue or pink arrows were presented, indicating a short or long cue-target interval. In a given block, targets appeared at the validly cued interval on 80% of trials. Response mapping and cue-colour cue-target interval assignments were counterbalanced across participants.

Procedures

Participants initially completed a practice session with only valid spatial and temporal cues and no distractor arrays. They were instructed to use spatial and temporal information to anticipate the location and timing of the target stimuli, and to maintain fixation on the central white square, whenever it was present. After that, participants completed a staircasing procedure to adapt the visibility of the targets to participants' perceptual abilities. Presentation was analogous to the practice session. Target visibility as measured by mask contrast was dynamically adjusted every five trials by varying the transparency of the noise patch in steps of 5% of full contrast. If participants responded correctly in less than four of five trials, noise patch contrast was decreased. If they responded correctly with all five trials, noise patch contrast was increased. If four of five trials were completed correctly, noise patch contrast remained constant. Staircasing was complete when contrast levels ceased to fluctuate

and performance levelled at 80% correct responses, which was accomplished after a minimum of 40 trials and approximately 4 minutes.

For the experiment, participants completed 8 blocks of 40 trials, amounting to 320 trials overall. They could rest after each block. There were 64 valid and 16 invalid trials for the short and long condition with and without distraction. All experimental procedures were carried out in approximately 45 minutes.

Analyses

Statistical analyses were conducted using custom-written functions in MATLAB. Staircasing outcomes were compared between older and younger participants using an unpaired two-sample t-test. Reaction times (RT) were log-transformed for outlier exclusion and statistical analysis. Only correct responses within +/- 3 SD of mean individual participants' RT were included. Percent correct (PC) responses were calculated, and two measures derived (Stanislaw & Todorov, 1999): D prime (d', a measure of perceptual sensitivity obtained by subtracting the z score that corresponds to the false alarm rate from the z score corresponding to the hit rate), and a bias measure c (negative average of z scores corresponding to hit and false alarm rate, expressed in standard deviations from the unbiased neutral point).

Repeated-measures analyses of variance (ANOVAs) were used to compare performance measures as a function of the between-subjects factor of age group (Younger or Older), and the within-subjects factors of validity of temporal cue (Valid/Invalid) and presence of stimulus competition (Comp+/Comp-). Measures for

left and right presentation side were collapsed due to low trial numbers with invalid conditions. Statistical tests were two-sided and with a critical alpha level of 0.05.

Because of the well-known asymmetry of temporal expectations effects relative to short versus long intervals (Coull & Nobre, 1998; Griffin et al., 2002), analysis concentrated on targets appearing at the short intervals (short valid, short invalid). Within a trial, when the short interval has passed, the probability of the event occurring at the long interval is 100%, regardless of the cue being presented, making long trials unsuitable to reveal effects of differential temporal expectations.

Results

Comparing sensory thresholds between younger and older participants showed that younger participants finished staircasing with higher individually adjusted mask contrasts than older participants, i.e. had lower sensory thresholds ($t(45)=2.101$, $p=0.041$), Fig. 3.2).

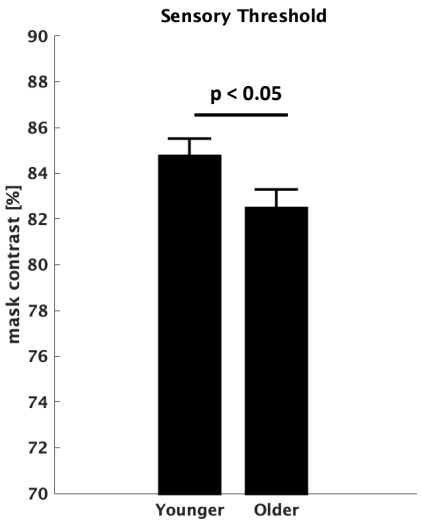


Fig. 3.2. Sensory thresholds for younger and older participants as measured by mask contrast. Whiskers represent SEM.

Analyses of RT (Fig. 3.3) showed main effects of all three factors. Participants were faster in the absence of competition (Log-RT/s, Comp-: -0.170 and Comp+: -0.160; back-transformed RT, Comp-: 689 ms and Comp+: 707 ms) and in the presence of valid temporal expectations (Log-RT/s, Valid: -0.179 and Invalid: -0.152; back-transformed RT, Valid: 677 ms and Invalid: 720 ms). Younger participants were faster (Log-RT/s: -0.198; back-transformed RT: 644 ms) than older participants (Log-RT/s: -0.134; back-transformed RT: 750 ms). No interactions were observed.

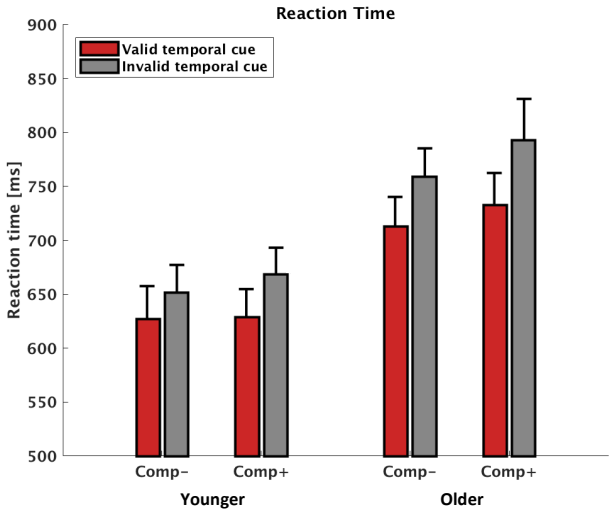


Fig. 3.3. Reaction time for younger and older participants with valid (red bars) and invalid (grey bars) temporal information for competition (Comp+) and no competition (Comp-). Effect of age: p=0.006; effect of temporal validity: p<0.001; effect of competition: p=0.003. Whiskers represent standard error of the mean (SEM). Note: For plotting only, log-RT values were back-transformed to original values. Outlier exclusion and statistics were conducted with log-transformed RT values.

Percent correct (Fig. 3.4) and d' (Fig. 3.5) yielded a similar pattern of results, though the d' measure was more sensitive. Participants were more accurate and perceptually sensitive in the absence of competition (PC, Comp-: 86.9% and Comp+: 83.7%; d', Comp-: 2.39 and Comp+: 2.10) and in the presence of valid temporal expectations (PC, Valid: 86.2% and Invalid: 84.4%; d', Valid: 2.43 and Invalid: 2.06). No effects of age

were observed. There were no interactions. Analysis of response bias, c, yielded no significant effects.

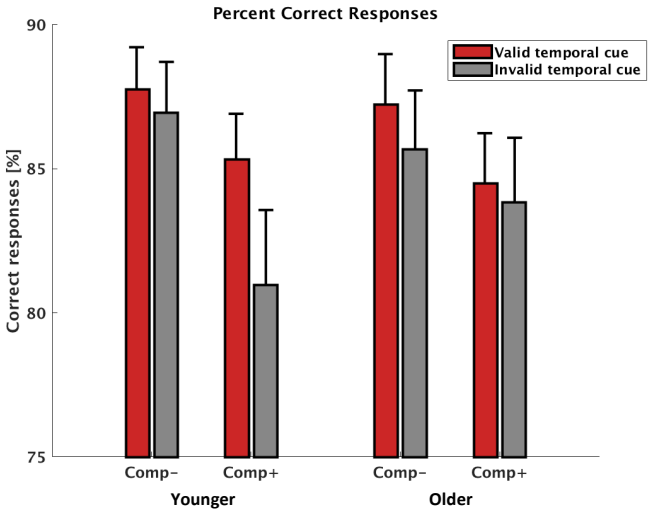


Fig. 3.4. Percent correct responses for younger and older participants with valid (red bars) and invalid (grey bars) temporal information for competition (Comp+) and no competition (Comp-). Effect of temporal validity: p=0.042; effect of competition: p=0.002. Whiskers represent SEM.

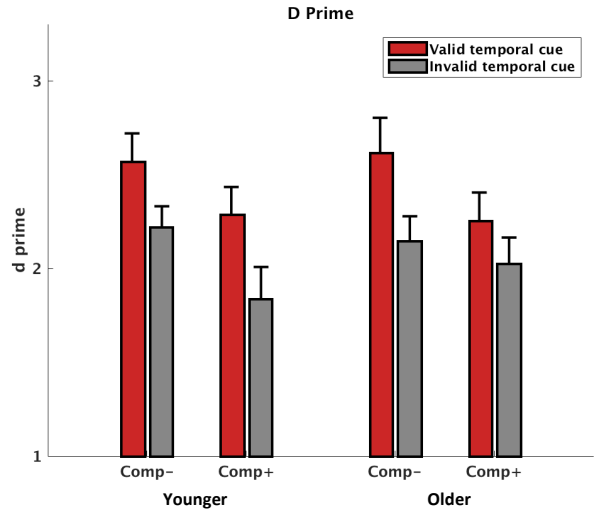


Fig. 3.5. D prime for younger and older participants with valid (red bars) and invalid (grey bars) temporal information for competition (Comp+) and no competition (Comp-). Effect of temporal validity: p<0.001; effect of competition: p<0.001. Whiskers represent SEM.

Log-transformed and back-transformed RT, PC, d' and c and related standard errors of the mean for all conditions with younger and older participants are provided with Table 3.1. Analysis of variance statistics are provided with Table 3.2.

Table 3.1

		Younger		Older	
		Comp-	**Comp+**	**Comp-**	**Comp+**
Log-Reaction Time / s	**Valid**	-0.211 (0.016)	-0.208 (0.016)	-0.154 (0.017)	-0.143 (0.018)
	Invalid	-0.192 (0.015)	-0.180 (0.014)	-0.125 (0.015)	-0.111 (0.020)
Reaction Time [ms]	**Valid**	627 (30)	629 (26)	713 (27)	733 (30)
	Invalid	652 (26)	669 (24)	760 (26)	793 (38)
Percent Correct [%]	**Valid**	87.8 (1.5)	85.3 (1.6)	87.2 (1.7)	84.5 (1.7)
	Invalid	87.0 (1.8)	81.0 (2.6)	85.7 (2.0)	83.9 (2.2)
d'	**Valid**	2.57 (0.15)	2.29 (0.15)	2.62 (0.19)	2.26 (0.15)
	Invalid	2.22 (0.11)	1.84 (0.17)	2.16 (0.13)	2.02 (0.14)
c	**Valid**	0.193 (0.052)	0.056 (0.056)	0.146 (0.073)	0.122 (0.061)
	Invalid	0.051 (0.069)	0.094 (0.053)	0.178 (0.060)	0.138 (0.072)

Table 3.2

	Age	**Temporal Validity**	**Competition**
Log-Reaction Time	F(1,2)=8.17, p=0.006	F(1,46)=35.37, p<0.001	F(1,46)=9.59, p=0.003
Percent Correct	F(1,2)=0, p=0.978	F(1,46)=4.38, p=0.042	F(1,46)=11.45, p=0.002
d'	F(1,2)=0.03, p=0.855	F(1,46)=27.53, p<0.001	F(1,46)=15.77, p<0.001
c	F(1,2)=0.54, p=0.468	F(1,46)=0.18, p=0.676	F(1,46)=1.13, p=0.293

Given the previous reports of deficits in temporal expectations in older participants (Zanto et al., 2011) separate ANOVAs were conducted for each age group in order to confirm whether effects of temporal expectations remained significant in the older group. These subsidiary ANOVAs compared response variables as a function of validity of the temporal cue and the presence of a competing distractor. Temporal expectation benefits were confirmed for both younger (RT: $F(1,22)=16.64$, $p<0.001$; d':

F(1,22)=22.08, p<0.001) and older participants (RT: F(1,23)=19.18, p<0.001; d': F(1,23)=9.51, p=0.005) and no interactions were observed.

Discussion

Both younger and older participants were able to complete the task, and robust effects of combined spatiotemporal expectations were observed in the context of competition. Interestingly, the effects of temporal expectations and stimulus competition seem to be spared by aging, operate in tandem, and in an independent manner.

Perceptual thresholds

Consistent with previous research and theory pointing to impaired sensory function in aging (Madden & Madden, 2007; Monge & Madden, 2016; Park et al., 2004), older participants showed higher perceptual thresholds as indexed by lower mask contrast after staircasing. This emphasises the importance of individually adapting sensory thresholds with tasks investigating top-down processing in the context of perceptually challenging stimuli. With the present experiment, effects of stimulus competition and temporal expectations in younger and older adults should not be confounded by different baseline levels of sensory processing.

Stimulus competition

As predicted by earlier studies investigating the behavioural and neural markers of interhemispheric competition in a perceptually challenging context (Molenberghs, Gillebert, Peeters, & Vandenberghe, 2008; Vandenberghe et al., 2005), participants responded more slowly and less accurately for bilateral compared to unilateral displays.

Although current theories of cognitive aging reject global cognitive decline, selective attention and more generally top down modulation are thought to be sensitive to aging (Drag & Bieliauskas, 2010; Zanto & Gazzaley, 2014). Remarkably, in the present cued-attention study, older participants responded more slowly than younger participants, which was expected (Ratcliff, Thapar, & McKoon, 2001), but were not more impaired by bilateral stimulus presentation than younger participants. This supports findings of an earlier study employing visual search (Ryan, Shen, & Reingold, 2006), in which participants needed to saccade to a target stimulus, which could be presented alone or accompanied by a distractor in the same or different hemifield. The visual hemifield where a target would occur was cued. Although older participants were less accurate in saccading to a target stimulus, they were not more impaired by distraction than younger participants.

Spared distractor suppression with the present study and in the study by Ryan et al. (2006), as compared to previous studies showing suppression-specific attentional deficits in aging (Chao, 1997; Gazzaley, Cooney, Rissman, & D'Esposito, 2005), might be explained by different task demands and stimulation parameters. Chao (1997) and Gazzaley (2005) presented target and distracting stimuli subsequently and not simultaneously, and their tasks featured an additional working-memory component.

Preserved cognitive performance may also relate to independent sensory processing. Age-related visual cognitive deficits have previously been linked to bottom-up sensory processes (Madden & Madden, 2007). Gazzaley presented stimuli at the same visual location, whereas target and distracting stimuli with the present paradigm were separated into different hemifields and sensory representations presumably did not overlap (Kastner et al., 2001).

Temporal expectations

Behavioural benefits of temporal expectations can arise from effects at multiple levels of processing (Nobre & Rohenkohl, 2014). Response times have been shown to decrease in tasks using predictive temporal cues (Coull & Nobre, 1998) as well as predictable temporal contexts in which no cues are presented (Niemi & Näätänen, 1981). Similarly, benefits at the perceptual level have also been reported in tasks with temporal expectations signalled by the ongoing context (Jepma, Wagenmakers, & Nieuwenhuis, 2012; Vangkilde, Coull, & Bundesen, 2012) or cues (Correa et al. 2005). Correa et al. (2005) were the first to show perceptual benefits with cued temporal expectations. The present task manipulated temporal expectations using both context (blocked) and cues to indicate the probable cue-target interval, and produced results supporting previous evidence. Valid temporal information in connection with a difficult perceptual discrimination task was linked to more correct responses, an increase in perceptual sensitivity, and shorter reaction times. It has been suggested that decision-related processes are rather unaffected by temporal expectations (Jepma et al., 2012).

The present results are in line with these findings, featuring no changes in response bias.

Deficits in interval timing, which may relate to attentional decline in aging, have been reviewed before (Balci, Meck, Moore, & Brunner, 2009). Zanto et al. (2011) extended these findings to the domain of cued temporal expectations. In both, target detection and perceptually more challenging target discrimination tasks, elderly participants consistently showed behavioural and neural deficits with the usage of temporal information. With the present study, despite an expected increase in response times, ageing did not affect participants' ability to use temporal information in the context of distraction. This remained valid even when separate ANOVAs for each age group were performed. It is conceivable, that elderly participants in the present experiment experienced less fatigue than those in the study by Zanto and colleagues (2011), and could thus use temporal cues more effectively. In addition to collecting behavioural data, Zanto and colleagues acquired EEG recordings and had participants perform in 6 blocks of roughly 10 minutes duration. In contrast, the present study was purely behavioural, lasted only around 45 minutes including breaks, and featured block lengths of approximately 4 minutes. More importantly, the present study compared valid against invalid temporal expectation conditions, which may yield stronger effects than comparing valid and neutral conditions, as in Zanto et al. (2011). Furthermore, in addition to using temporal cues, the present study also manipulated cue-target interval distributions across blocks, which may provide a stronger source of temporal expectations than predictive cues. Overall, the results are well in line with a recent study that showed speeded-response and perceptual-discrimination benefits in both blocked and trial-by-trial temporal cueing contexts (neutral/valid and valid/invalid

cues) with both younger and older participants (Chauvin et al., 2016). The present investigations extend these findings by showing that such benefits can still be retained in a competitive stimulus context.

Independent effects of stimulus competition and temporal expectations

Previous studies using non-competing stimuli have shown synergies between temporal and spatial expectation (Doherty et al., 2005) or motor output (Kornysheva, Sierk, & Diedrichsen, 2013; O'Reilly, McCarthy, Capizzi, & Nobre, 2008) representations. Because of the present task design, using 100% spatially valid cues, it was not possible to test whether effects of combined spatiotemporal biases were stronger than effects of isolated temporal or spatial biases. Nevertheless, strong and consistent effects of temporal expectations were observed, which were present in the context of spatial cueing effects.

Experiment 1 did not reveal an interaction between the effects of stimulus competition and temporal expectations. If temporal expectations work through spatial biases to enhance processing, this might be expected to lead to perceptual enhancements specifically at the spatially cued location and relatively better suppression of effects of competing stimuli in other locations (Desimone & Ducan, 1995). Centres of target and distractor stimuli in Experiment 1 were 9° apart from each other, so that stimulus representations at low or early levels of visual analysis did not overlap (Kastner et al., 2001). Immediate effects of temporal expectations acting on those representations would then be comparably restricted to individual stimuli, preventing an interaction between temporal expectations and competition.

Competition between visual stimuli in opposite hemifields can principally also exert influences on occipital cortex more indirectly via intraparietal sulcus (Geng et al., 2006). However, the lack of an interaction between temporal expectations and stimulus competition suggests that temporal information was also not specifically beneficial for rather higher order attentional selection mechanisms.

In a second experiment, I further explored the effects of temporal expectations on more low-level sensory competition.

Experiment 2: Temporal expectations and intrahemifield competition

Methods

Participants

The study protocol was approved by the Central University Research Ethics Committee (CUREC). There were 23 younger participants included in the study (mean age: 24.5 years, SD: 4 years, 13 females). Three participants were excluded, according to the same exclusion criteria used in Experiment 1.

Presentation

If not stated otherwise, presentation parameters, including timings, were identical to Experiment 1. Participants viewed peripheral arrays of Gabor gratings and had to discriminate the direction of the tilt of a target grating that was presented in isolation or simultaneously with surrounding gratings (Fig. 3.6). Cues preceding the array provided predictions about the spatial location and the temporal interval at which the target would appear.

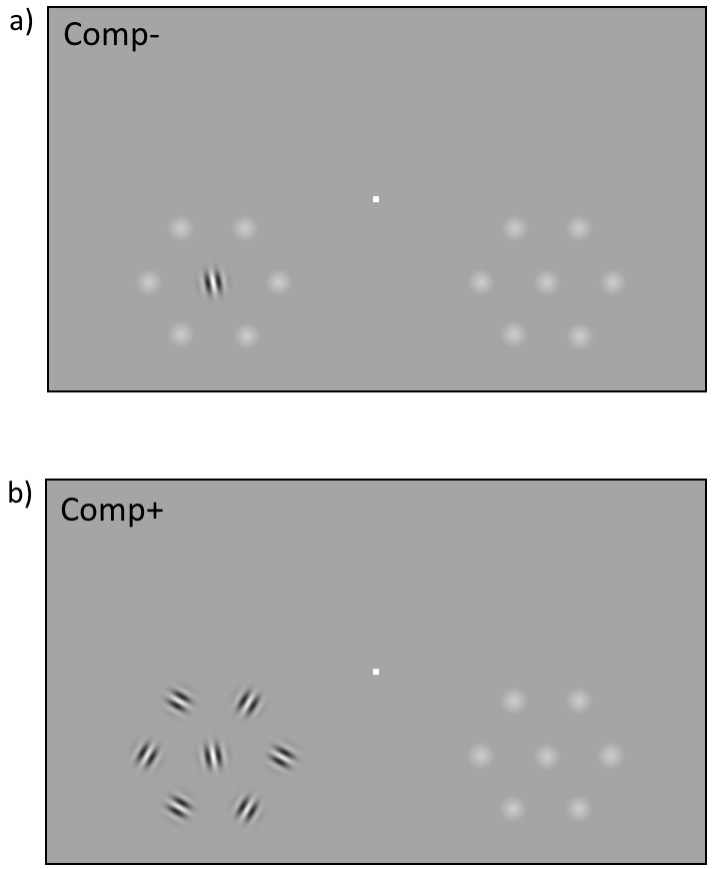


Fig. 3.6. Schematic depiction of target and distractor stimuli with Experiment 2. Target stimuli consisted of slightly left- or rightward tilted Gabor gratings presented to the left or right visual hemifield. With half of the trials, there was no competition (Comp-) and targets were presented in isolation (a). With the other half of the trials, representing competition trials (Comp+), target stimuli were surrounded by six other Gabor gratings (b).

In each trial, a central white fixation square was presented together with several luminance pedestals. One pedestal was presented to the lower left and one pedestal to the lower right of fixation (70 cd/m^2, horizontal distance: 5°, vertical distance 2.4°, size: 0.8°), where target stimuli could appear. These pedestals were each surrounded by six other pedestals of the same size, where distractor stimuli could appear. The surrounding pedestals were positioned in the corners of an imaginary hexagon around their central pedestal (distance to central pedestal: 2.2°). Cue presentation was identical to the interhemispheric competition study.

Targets consisted of circular grayscale Gabor patches (size: 1.2°, 3 cycles / degree visual angle), which were presented on top of the central pedestals. They had an orientation of +/- 2° from the vertical axis. In half of the trials, six grayscale distracting stimuli of matched size and spatial frequency were presented simultaneously with the target atop the surrounding pedestals. Distractors could be oriented 0, 90, 60 or 150 degrees from the vertical axis. Adjacent distractors were always oriented perpendicularly to each other, so that there were four different distractor arrays. Distractor stimuli featured 25% less contrast than target stimuli. Target and distractor stimuli were unmasked, in order to reduce task difficulty. This was done in order to keep stimulus exposure duration matched with the interhemifield competition study. After target presentation, participants were given a maximum of 3 seconds to indicate if the target was tilted slightly to the left or right from the vertical axis. They had to respond by button press with their index or middle finger. Responses were immediately followed by an intertrial interval, which was identical to the one used with the interhemifield competition experiment.

Cue-target interval duration and temporal cues, presentation side and spatial cues, identity of target and distractor stimuli, and presence of competition were counterbalanced and randomised and unpredictable on a trial by trial basis. Temporal cues were valid in 80% of trials, spatial cues were always valid. Response mapping and cue-colour cue-target interval assignment were counterbalanced across participants.

Procedures and analyses

Procedures were analogous to the interhemifield competition experiment, with practice and stimulus adjustment blocks preceding the experimental session. For stimulus adjustment, target contrast was initially set to 10%. Only spatially and temporally valid cues were presented. The target contrast level was adjusted every five trials. Target contrast was increased by 1% if less than four of five trials were correct; decreased by 1% if all five trials were correct; or held constant if four of five trials were correct. Analogous to Experiment 1, there were a minimum of 40 trials. Staircasing was complete after approximately 4 minutes, when contrast levels ceased to fluctuate with 80% correct responses.

For the experiment, participants completed 20 blocks of 32 trials. They could have a rest after each block. There were 128 valid and 32 invalid trials for the short-interval and long-interval condition with and without distraction, amounting to 640 trials overall. All experimental procedures were carried out in slightly more than an hour.

Data pre-processing and statistical analyses were identical to Experiment 1. Analyses of variance considered the experimental factors of temporal validity (Valid/Invalid) and stimulus competition (Comp-/Comp+). T-tests were applied for post-hoc comparisons. After post-hoc comparisons, if two conditions differed between each other with PC or d', the difference between conditions was calculated for each participant. With RT, differences between the same conditions were calculated for each participant. In order to examine potential speed-accuracy trade-offs, perceptual and response related differences were correlated across participants.

Results

Analysis of RT (Fig. 3.7) yielded similar results as with the interhemifield competition experiment. There were strong effects of both experimental factors. Participants were faster with valid temporal cues (Log-RT/s, Valid: -0.151 and Invalid: -0.139; back-transformed RT, Valid: 724 ms and Invalid: 748 ms) and in the absence of competing distractors (Log-RT/s, Comp-: -0.157 and Comp+: -0.133; back-transformed RT, Comp-: 714 ms and Comp+: 759 ms). No interaction was observed.

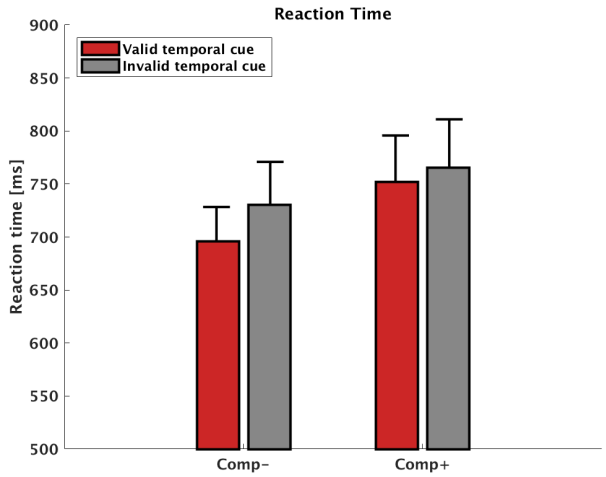


Fig. 3.7. Reaction time with valid (red bars) and invalid (grey bars) temporal information for competition (Comp+) and no competition (Comp-). Effect of temporal validity: p=0.003; effect of competition: p=0.003. Whiskers represent SEM. Note: For plotting only, log-RT values were back-transformed to original values. Outlier exclusion and statistics were conducted with log-transformed RT values.

Analysis of percent-correct responses (Fig 3.8) and d' (Fig 3.9) lead to comparable results. There was a main effect of competition, indicating overall higher accuracy (Comp-: 75.8%, Comp+: 72.3%) and perceptual sensitivity d' (Comp-: 1.55, Comp+: 1.30) without competition. Crucially, competition interacted with temporal validity. Post-hoc comparisons for both measures indicated that there was a difference

between valid and invalid temporal expectations in the presence of competition (PC: t(22)=2.172, p=0.041; d': t(22)=2.323, p=0.030): participants were more accurate and perceptually sensitive with invalid temporal information. Importantly, differences between valid and invalid temporal expectations in the presence of competition did not correlate with matching RT differences across participants (PC: r=0.047, p=0.831; d': r=0.062, p=0.780). Therefore, a trade-off between perceptual and response related measures could not be shown. There was no difference between temporal expectation conditions in the absence of competition (PC: t(22)=1.421, p=0.169; d': t(22)=1.029, p=0.315). Post-hoc statistics were not corrected for multiple comparisons. No significant effects of response bias c were obtained.

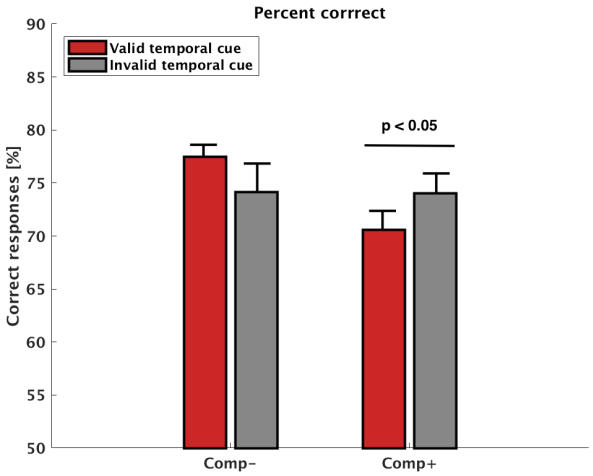


Fig. 3.8. Percent correct responses with valid (red bars) and invalid (grey bars) temporal information for competition (Comp+) and no competition (Comp-). Effect of competition: p=0.020; effect of temporal validity x competition: p=0.032. Whiskers represent SEM.

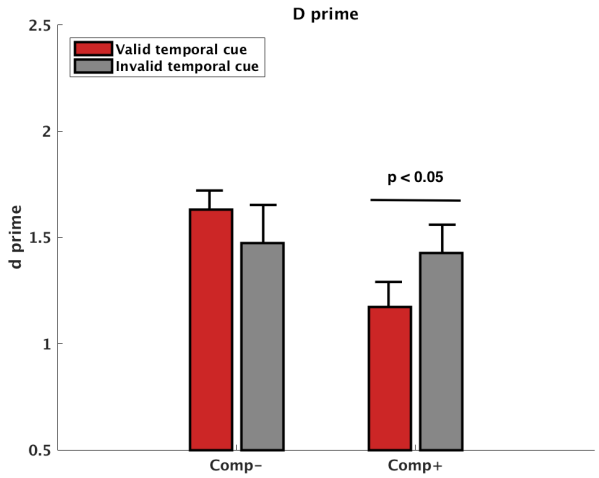


Fig. 3.9. D prime with valid (red bars) and invalid (grey bars) temporal information for competition (Comp+) and no competition (Comp-). Effect of competition: p=0.016; effect of temporal validity x competition: p=0.040. Whiskers represent SEM.

Log-transformed and back-transformed RT, PC, d' and c for all conditions are provided with Table 3.3. Analysis of variance statistics are provided with Table 3.4.

Table 3.3

		Comp-	Comp+
Log-Reaction Time / s	**Valid**	-0.166 (0.018)	-0.137 (0.022)
	Invalid	-0.148 (0.020)	-0.130 (0.023)
Reaction Time [ms]	**Valid**	696 (32)	752 (43)
	Invalid	731 (40)	766 (46)
Percent Correct [%]	**Valid**	77.5 (1.1)	70.6 (1.8)
	Invalid	74.2 (2.7)	74.1 (1.9)
d'	**Valid**	1.63 (0.09)	1.17 (0.12)
	Invalid	1.47 (0.18)	1.43 (0.13)
c	**Valid**	0.183 (0.065)	0.030 (0.062)
	Invalid	0.074 (0.066)	0.095 (0.075)

Table 3.4

	Temporal Validity	Competition	Temporal Validity X Competition
Log-Reaction Time	F(1,22)=10.87, p=0.003	F(1,22)=11.07, p=0.003	F(1,22)=1.92, p=0.180
Percent Correct	F(1,22)=0, p=0.950	F(1,22)=6.33, p=0.020	F(1,22)=5.24, p=0.032
d'	F(1,22)=0.26, p=0.616	F(1,22)=6.83, p=0.016	F(1,22)=4.79, p=0.040
c	F(1,22)=0.22, p=0.641	F(1,22)=1.39, p=0.251	F(1,22)=3.42, p=0.078

Discussion

Reaction time

For RTs, there were benefits with valid temporal expectations and costs with stimulus competition, where both factors seem to work independently. This is in line with Experiment 1 and conforms with findings that temporal expectations enhance response preparation (Coull & Nobre, 1998; Miniussi, Wilding, Coull, & Nobre, 1999; Nobre, 2001).

Results from the present experiments furthermore suggest that such a temporal RT benefit can even be achieved in the context of stimulus competition. This beneficial effect on RT is in agreement with a study by (Los, 2004), investigating the relationship between inhibition of return (IOR) and temporal biases relating to the sequential presentation of different cue-target intervals. A target stimulus consisted of a small square, appearing after a certain cue-target interval and participants needed to indicate if the target appeared in the left or right visual hemifield. The exogenous cue was presented in either hemifield prior to target onset and was spatially non-predictive. The cue facilitated response speed at short cue-target intervals and relatively impaired it at longer ones. This IOR effect was independent of the temporal effect, which was linked to longer reaction times when the cue-target interval of a preceding trial was longer compared to the one of a current trial. Los' study is different to the present studies in certain respects. He investigated a different and rather implicit temporal bias in connection with stimulus information competing over different time points within a perceptually non-challenging task. Nevertheless, as in

the present paradigms, temporal biases worked independently of spatial inhibitory control mechanisms.

Accuracy and perceptual sensitivity

Accuracy and perceptual sensitivity, as measured by d', were generally lower in the presence of stimulus competition. Interestingly, in contrast to Experiment 1, stimulus competition interacted with temporal expectations.

Valid temporal expectations did not significantly improve perceptual measures in the absence of competition. This may be explained by the fact that Experiment 2 did not feature visual masking of target stimuli in order to reduce task difficulty. Backward masking is probably a very good predictor for the presence of attentional effects with signal detection tasks (see Smith 2009 for a review). In addition, temporal information was conveyed by explicit temporal cues only and not in combination with blocked cue-target intervals, as it was the case with Experiment 1. This may have led to an overall weaker effect of temporal expectations.

Most importantly, valid temporal expectations had a deteriorating effect on perceptual sensitivity in the context of spatially distracting information. This is in contrast to Experiment 1, where temporal expectations did not alter the effects of distraction. Perceptual effects of temporal expectations have been shown in numerous tasks (Nobre & Rohenkohl, 2014), and it has been suggested that these are conveyed by a speed-up of perceptual processing and improved stimulus encoding (Jepma et al., 2012; Seibold & Rolke, 2014b; Vangkilde et al., 2012). However, the effects of time can only be apprehended in relation to other, e.g. spatial task dimensions.

Temporal expectations and visual stimulus competition

Drawing on evidence from Experiment 1 and 2, I suggest that the perceptual effects of temporal expectations on stimulus competition depend on spatial receptive field stimulus context. In the presence of interhemifield competition, temporal expectations and competition worked in tandem and independently, which can plausibly be explained by a lack of sensory interactions between competing stimuli (see above). With intrahemifield competition, where sensory interactions likely occur, temporal expectations increased competitive stimulus conflict. As spatial attention was always directed toward the target, it cannot be determined if spatial attention reduced competitive stimulus conflict, as could be predicted by the theory of biased competition (Desimone & Ducan, 1995). However, I suggest that target location did not benefit selectively from temporal expectations. On the contrary, on a biased competition account, target and distractor representations could have been facilitated indiscriminately. As there were 6 distractors and only one central target, distractor representations should in sum have gained comparably more competitive strength than the single target representation, which was thus weakened. As a result, perceptual sensitivity declined. An alternative interpretation of the results of Experiment 2, namely that temporal information altered the selective read-out of already further processed target representations (Pestilli, Carrasco, Heeger, & Gardner, 2011), is unlikely in light of Experiment 1, as temporal expectations did not interact with interhemifield competition.

Detrimental effects of temporal expectations have been reported previously. Correa et al. (Correa, Cappucci, Nobre, & Lupiáñez, 2010) manipulated temporal expectations in two tasks featuring response conflict. With a flanker task (see also

Weinbach, 2013 for comparable results) and a Simon task, which introduced response conflict by presenting left- and rightward pointing arrows in the right respectively left visual hemifield, larger conflict effects with valid compared to invalid temporal cueing were found. Similarly to the current interpretation, Correa et al. argued that the two competing response representations would have been equally activated. This would then in fact have led to unspecific activation above a certain threshold, ultimately interfering with controlled response selection (Botvinick, Braver, Barch, Carter, & Cohen, 2001).

In the perceptual domain, Seibold et al. (Seibold & Rolke, 2014a) designed a series of visual perceptual discrimination tasks with blocked short or long cue-target intervals. There were visual search and cued spatial expectation conditions in the context of distraction. A distractor item was presented either further away from or closer to the target, where sensory competition was presumably possible. They showed independent effects of competition and temporal expectations. Better performance was associated with a larger distance between target and distractor stimuli and with blocked short as opposed to blocked long cue-target intervals, an expected outcome in constant foreperiod paradigms (Mueller-Gethmann, Ulrich, & Rinkenauer, 2003). The lack of an interaction effect in that study may stem from various reasons, including insufficient perceptual challenge (stimuli remained on the screen until a response was given) and stimulus competition (only one blue distractor was presented together with a salient red target on a dark background).

It has been suggested that temporal expectations map onto spatial expectation related receptive field modulations (Ghose & Maunsell, 2002; Rohenkohl et al., 2014). Such a mechanism would be compatible with the present results. When stimulus

representations are in separate hemifields so that they cannot interact, spatial expectations and temporal expectations mapping onto these expectations should not help in the resolution of competitive conflict. Such a scenario could explain results of Experiment 1. To the contrary, temporal expectations may boost target and distractor representations similarly when their underlying neuronal assemblies are overlapping and are not accessed selectively by spatial expectations. Experiment 2 could be compatible with such a scenario. However, spatial expectations were not orthogonal to stimulus competition in the present experiment. Effects of spatial expectations on the resolution of competitive stimulus conflict could therefore not be determined. Likewise, the effect of temporal expectations on stimulus competition could not be determined independently of spatial expectations. In order to better characterise a spatio-temporal receptive field bias, future experiments should orthogonalise spatial and temporal expectations and parametrically vary the distance between target and distractor stimuli.

Conclusion

The present findings shed light on the relatively unexplored field of temporal expectations in the context of stimulus competition. The set of experiments demonstrates that the effects of temporal expectations on visual stimulus competition are context dependent. With interhemifield competitive stimulus conflict, temporal expectations acted independently of competition and improved behavioural performance. In contrast, in the context of proximal, intrahemifield competition,

temporal expectations impaired perceptual measures of task performance, suggesting an unspecific action on target and distractor stimuli.

Furthermore, Experiment 1 showed that, interestingly, aging spared both participants' ability to deal with interhemifield distraction and their employment of temporal information in such a context, suggesting retention of cognitive control with aging under certain task demands.

Chapter 4: Temporal expectations and stimulus competition in time

Abstract

Expecting a relevant event in time can improve behavioural performance and facilitate neural processing related to that event. However, little is known about the processing of temporally competing task-irrelevant distractors in the presence of a temporal bias toward the task-relevant target. Using a combination of event-related potential (ERP) and decoding analyses, I investigated the processing of task-irrelevant distractors presented after a warning stimulus and in rapid temporal succession during the pre-target interval with different levels of temporal expectation for the onset of the target stimulus. Target identity could be discriminated faster with valid versus invalid temporal expectations for the target. ERPs after the onset of the warning stimulus and before the onset of the target stimulus featured 3 negative clusters for expecting the target after a short versus long temporal interval. A contingent negative variation (CNV)-like negativity emerged 150 ms after the warning stimulus and remained throughout early time points of distractor presentation. Decreased potentials were also observed during extended periods of distractor presentation. Topography and timing of a late frontal negativity from 150 ms before and up to the onset of the target stimulus suggest anticipatory function similar to a CNV. In addition, distractor information was decreased temporarily with expecting a target after a short versus long interval. Although behavioural performance could not be related to neural measures of distractor processing, decreased distractor-related potentials and decoding suggest reduced distractor processing for conditions of high versus low levels of target expectation. Future investigations employing further stimulus configurations and analyses techniques would be necessary to clarify the extent of distractor modulation by temporal expectations, including its relevance for target processing.

Introduction

Chapter 2 investigated cued spatio-temporal expectations toward individual stimuli, adding to a growing body of literature emphasising the beneficial effects of temporal expectations on perceptual and response-related performance measures, and their corresponding neural processing (Nobre & Rohenkohl, 2014; Nobre & Van Ede, 2018). However, in more natural settings, stimuli are not perceived in isolation on a uniform background. Instead, selection occurs in the context of temporally as well as spatially proximal distractors. Chapter 3 and previous research (Correa, Cappucci, Nobre, & Lupiáñez, 2010; Seibold & Rolke, 2014; Weinbach & Henik, 2013) could not show evidence for specific effects of temporal expectation in overcoming spatial distraction either across hemifields or within a hemifield. To the contrary, when stimuli are presented in close spatial proximity to one another, findings from Chapter 3 rather suggest that temporal expectation increases competitive stimulus conflict. As described before, this may point to a spatially relatively unspecific upregulation of neural processing by temporal expectations, which similarly benefits target and distractor stimuli. (As distractors usually outnumber targets, a net decrease in performance is observed.)

If temporal expectations do not benefit stimulus selectivity in the spatial domain, there is still the possibility that they are beneficial when stimuli compete in the temporal domain. In fact, processing limitations over time have been reported long ago (Broadbent & Broadbent, 1987; Reeves & Sperling, 1986; Weichselgartner & Sperling, 1987). Weichselgartner and Sperling (Weichselgartner & Sperling, 1987) conducted a series of experiments in which participants reported the identity of a

target number stimulus and three successive number stimuli, which were presented centrally and in rapid succession. Further number stimuli preceded and occurred after the relevant stimuli. All stimuli were presented at a rate of 10 Hz. Weichselgartner found a bimodal response distribution, reflecting a deficit in reporting the identity of stimuli occurring 200 ms after target presentation. In addition, the two peaks matched participants' subjective experience. Stimuli perceived as "perceptually attached to the target" constituted the first peak. It occurred within 200 ms of target presentation. A second peak occurred after 200 ms, connected to stimuli perceived as perceptually separate from the target. As the first peak was found to be relatively insensitive to experimental manipulations, it was suggested that the underlying process was rather fast and automatic. The second peak was sensitive to practice, expectancy level and target signal-to-noise ratio, so that a more controlled and effortful process was inferred. However, the study does not show where in the processing stream limitations should be located. For instance, it is not clear if the deficit was related only to stimulus identification or more basic stimulus detection. As four stimuli needed to be memorised and retrieved, there was also considerable load on memory mechanisms.

Broadbent and Broadbent (Broadbent & Broadbent, 1987) also presented stimuli in rapid temporal succession. However, only two targets needed to be identified. They found that identification of a second target was impaired for time points of more than half a second after the first target. Although even unidentified first targets impaired detection of the second target stimulus under certain conditions, Broadbent and Broadbent argued that identification of the first target interfered with subsequent target processing.

A few years later, Raymond and colleagues (Raymond et al., 1992) emphasised the attentional nature of the post-target processing limitation arising with rapid serial visual presentation (RSVP) tasks. Processing deficits were observed in the range of 180 - 450 ms after a pop-out stimulus. However, this occurred only if the pop-out stimulus served as a task-relevant first target. Furthermore, the post-target processing deficit was even observed for simple probe detection, yet was contingent on a distractor stimulus following the first target in close temporal proximity. A "shut-and-lock model" was proposed, where the processing of the first distractor after the first target would fall into one attentional episode with the processing of the first target. This would lead to an increased risk of interference between target and distractor processing. In fact, the study showed that there was a relatively high proportion of post-target distractors being reported as targets. In order to prevent further interference proactively, processing channels would be locked and could only be accessed again a few hundred milliseconds later. During this period, attention would "blink". Stimuli could not be detected during this attentional blink (AB). The same authors later proposed a different model, rather emphasising a late-selection account, in which target, post-target and probe stimuli would compete for representation in visual short-term memory (Shapiro et al., 1994).

Later research has challenged and refined original assumptions of the nature and mechanisms of post-target processing deficits (Dux & Marois, 2009; Martens & Wyble, 2010). As a minimum requirement, a stimulus which is sufficiently hard to detect needs to be preceded by another (consciously detected) stimulus (Nieuwenstein, Van der Burg, Theeuwes, Wyble, & Potter, 2009).

Interestingly, temporal expectations can ameliorate the attentional blink (Badcock, Badcock, Fletcher, & Hogben, 2013; Hilkenmeier & Scharlau, 2010; Martens & Johnson, 2005; Visser, Tang, Badcock, & Enns, 2014). Martens and colleagues (Martens & Johnson, 2005) presented participants with a classical attentional blink paradigm, featuring two target stimuli embedded in an RSVP sequence. In addition, the second target could appear early, i.e. at 300 ms post-target, where an attentional blink is usually expected, or late, at 800 ms post-target. Temporal cueing of the second target benefitted the identification of that target specifically with short intervals, i.e. it helped to overcome the attentional blink. Behavioural performance related to the first target remained unchanged. The results were explained by representational competition in visual short-term memory, compatible with Shapiro's AB model (Shapiro et al., 1994). According to this account, temporal cues benefitted the attentional weighting of second target stimuli. As performance for the first targets was unchanged, it was concluded that distractor stimuli should have experienced relative decreases in their attentional weights. In another study, Visser et al. (Visser et al., 2014) showed that temporal cueing of the second target in an AB paradigm was specifically beneficial for target identification when distractor and target stimuli were highly similar.

If attentional weights can be changed across time when stimuli are anticipated in time, it seems reasonable that processing of stimuli preceding a target stimulus can be changed. In fact, Denison and colleagues (Denison et al., 2017) recently developed a series of tasks in which perceptual processing over time was investigated in the presence of temporal cueing. They presented two or three Gabor stimuli successively at the same spatial location in the lower right visual field. In different conditions,

different Gabor patches were temporally cued by an auditory stimulus preceding the first Gabor stimulus by 1 s. Temporally informative cues were 75% valid. As a control condition, a temporally uninformative auditory cue was presented. After stimulus presentation, participants were cued to report the orientation of one of the stimuli. Denison and colleagues showed that temporal cueing improved perceptual processing at validly cued locations. At the same time, there were perceptual processing costs for stimuli occurring before and after the cued stimulus. This finding was extended by a positive correlation between perceptual benefits for cued stimuli and perceptual costs for corresponding non-cued stimuli. Therefore, the authors concluded that attention can be traded off flexibly across time. While the results provide interesting first insights into flexible modulation of attention across time, they still remain rather indirect. As responses are only taken after the presentation of all stimuli, prompted by a post-cue, it is unclear to which extent memory mechanisms, as opposed to mechanisms linked to immediate sensory attention, contributed to their findings. Furthermore, stimuli in their tasks were never truly irrelevant, as any of the stimuli could be probed in a given trial. Different selection mechanisms, therefore, could be involved compared to those involved in overcoming temporally proximal distractors. Finally, it would be interesting to investigate attentional selection mechanisms across a sequence of more than two or three stimuli.

Recent methodological developments in multivariate decoding techniques for magneto- and electro-encephalography (M/EEG) data have enabled the tracking of visual information with high temporal resolution (Garcia, Srinivasan, & Serences, 2013; King & Dehaene, 2014; Myers et al., 2015; Ramkumar, Jas, Pannasch, Hari, & Parkkonen, 2013; Stokes, Wolff, & Spaak, 2015). Marti and Dehaene (Marti &

Dehaene, 2017) studied the dynamics of attentional selection in a variant of an RSVP task featuring two targets among 13 distractor stimuli. The first target was always presented in the beginning. The second target was presented at various inter-target lags. Analysis concentrated on the second target and surrounding distractors. Multivariate decoding of MEG data enabled them to track information processing of target and distractor stimuli despite low stimulus-onset asynchronies of 116 ms, indicating that stimuli must have been processed partly in parallel at least during early processing stages. Furthermore, decoding for early time points cross-generalised to later time points, but only with the target stimulus and the two target-preceding distractors. This was taken as a sign of later, gradual stimulus selection. Decoding of late time points cross-generalised to even later time points, but only with the target stimulus. This was interpreted as a late, discrete selection mechanism.

Using multivariate orientation decoding, van Ede et al. (Van Ede, Chekroud, Stokes, & Nobre, 2018) showed that a simple, temporally informative warning stimulus can enhance the quality of the representation of a visual target as well as decrease and delay interference of that representation by a temporally proximal succeeding visual distractor. The authors suggested that stimulus anticipation may have established a protective temporal window for target processing.

The present study built on these previous experimental demonstrations to investigate the role of cued temporal expectations in modulating the processing of distractors within a stream of temporally competing stimuli. The effect of temporal expectations on distractor stimulus representations was investigated in the context of rapid serial visual presentation, employing multivariate EEG decoding with high temporal resolution to measure the quality of processing of distractor orientation-

grating stimuli. Focussing on pre-target attentional deployment, the study concentrated on pre-target distractor stimuli. Two potential outcomes were envisaged. In one scenario, stimulus representations would gradually be amplified the closer they occur with respect to the expected onset of the target. In this case, distractor representations would benefit from close temporal proximity to the target. The other scenario relates to the idea that attention can trade off capacities over time and modulate temporal windows for stimulus analysis. In this case, distractor representations could be suppressed with temporal expectations toward target onset, resolving stimulus competition over time. In order to evaluate the functional significance of distractor processing, the relation between distractor decoding fidelity according to different temporal expectations and behavioural performance was tested. Decoding analyses were complemented by matched analyses of the broadband EEG signal, relating the present study to event-related potential (ERP) research.

Methods

Participants

The protocol of the study was approved by the Central University Research Ethics Committee (CUREC) of the University of Oxford. Twenty-seven healthy participants were enrolled. Two participants dropped out after the first session and one participant performed at chance level in more than half of the blocks. These participants were excluded, leaving 24 participants (mean age: 27.08, SD: 5.2, 10 females) for the analysis.

Presentation

Visual stimuli were presented via a 27-inch monitor with a 1920 x 1080-pixel spatial resolution and at a refresh rate of 100 Hz. Participants used a standard UK layout computer keyboard for responding. Psychophysics Toolbox Version 3 (Kleiner et al., 2007) for MATLAB (The MathWorks) enabled visual stimulus presentation and response collection.

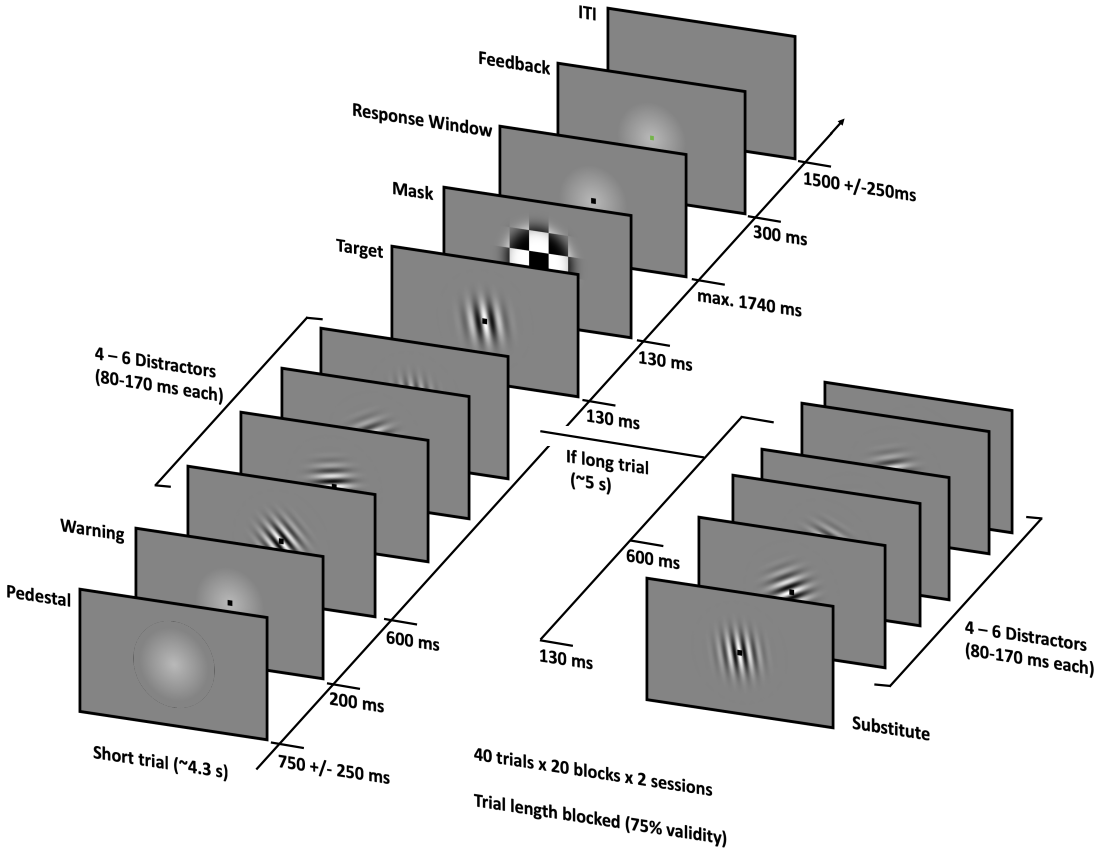


Fig. 4.1. Schematic layout of the experimental task. In short trials, after a warning stimulus, four to six distractor Gabor stimuli were presented in rapid temporal succession. Participants indicated the orientation (clockwise or counter-clockwise) of a succeeding target Gabor stimulus, specified by comparably lower spatial frequency. In long trials, the target was in addition preceded by a target substitute stimulus and a further four to six distractor stimuli. Long and short trials were blocked (75% validity), and participants were informed about the block type, so that the onset of the target could be anticipated.

The task is schematically laid out in figure 4.1. Participants were instructed to discriminate the orientation of a centrally presented target Gabor patch, which was temporally preceded by a succession of rapidly presented distractor Gabor stimuli. The likely temporal interval of target presentation after a warning stimulus was blocked and indicated to participants at the beginning of each block.

All stimuli were presented on a grey background (RGB: 102 102 102). With every trial, a circular light grey central pedestal was presented (size: 13.69°, max. contrast: 10%). After 750 ms +/-250 ms (uniform distribution sampling), a small black square occurred at the centre of the pedestal (size: 0.08° each side). Participants were asked to keep their eyes fixed on the square throughout the trial. The fixation square also served as a warning stimulus. After 200 ms, a series of four to six greyscale circular distractor Gabor stimuli (size: 13.69°, cycles / degree visual angle: 3.22, max. contrast: 90%) occurred. Distractor stimuli occurred centrally in rapid temporal succession and were overlaid by the fixation square. In order to specify distractor identity, four to six Gabor patch orientations were sampled randomly with replacement from a pool of 16 unique orientations (11.25°-180° in steps of 11.25°) with the restriction that two same orientations could not be sampled for two successive stimuli. Durations of individual distractors varied randomly in order to discourage the use of distractor onsets for temporal orienting. Specifically, distractor durations were randomly sampled without replacement from a pool of four (130 ms, 140 ms, 160 ms, 170 ms), five (100 ms, 110 ms, 120 ms, 130 ms, 140 ms) or six durations (80 ms, 90 ms, 100 ms, 100 ms, 110 ms, 120 ms) relating to the presentation of four, five or six distractors. Individual distractor durations were chosen so that a series of distractors was always presented for 600 ms. There were short- and long-interval trials. With ‘short’ trials, distractor presentation

was followed by a greyscale target Gabor stimulus featuring lower spatial frequency than distractor stimuli (size: 13.69°, cycles / degree visual angle: 0.86, max. contrast staircased average across participants: 59%). The target patch was presented for 130 ms and randomly tilted by 5 ° either to the left or right of the vertical axis. In 'long' trials, target presentation was preceded by a target substitute stimulus (size: 13.69°, cycles / degree visual angle: 3.22, max. contrast: 90%, orientation: +/- 5° relative to vertical axis) and a further series of four to six distractors. The target was followed by a checkerboard mask stimulus of matched size, spatial frequency and duration (size: 13.69°, cycles / degree visual angle: 0.86, duration: 130 ms, max. contrast: 100%), whereupon only the pedestal and fixation square were presented. Participants were required to indicate by button press if the target stimulus was tilted clockwise or counter-clockwise. Their left index finger was mapped to letter 'c', their right index finger was mapped to letter 'm' on the keyboard. Target stimulus identity response mapping was counterbalanced across participants. Participants were given a maximum of 2 seconds response time from target onset. A response was immediately followed by a feedback stimulus, lasting for 300 ms and consisting of a colour change of the fixation square. A green square was related to correct responses, a red square to incorrect responses. When no response was given, a red square was presented. A blank grey screen was presented for 1500 ms +/- 250 ms during the inter-trial interval.

Procedures

Participants took part in two sessions on two separate days. Each session lasted around 3 hours, including EEG-setup, practice, staircasing and experimental

procedures. During each session, participants sat in front of the computer screen at a viewing distance of circa 100 cm with their chin comfortably positioned on a chin rest.

For practice, participants completed 40 short and long trials, in which target-stimulus contrast was set at 90%. Participants were instructed to indicate the orientation of the target stimulus, which featured lower spatial frequency than distractor stimuli and could appear after a short or long interval. If accuracy did not clearly exceed chance performance, further practice trials were presented.

After that, participants completed a staircasing procedure to adjust target visibility individually. Target contrast was initially set at 60% and was dynamically adjusted every four trials. If all four targets were identified correctly, stimulus contrast was decreased by 2%. If half or less of the targets were identified correctly, stimulus contrast was increased by 2%. Target contrast did not change if participants identified three of four targets correctly. If performance levels did not cease to fluctuate and level at 75% correct responses after 40 trials, further trials were presented. Practice and staircasing was completed after approximately 15 minutes.

For the experiment, there were 20 blocks of 40 trials, amounting to 800 trials. Participants had self-timed rest breaks between the blocks. Two block types were presented in alternating order. Short-interval blocks contained randomly intermixed 75% short and 25% long trials. Long-interval blocks featured a reverse distribution, with 75% long and 25% short trials. At the beginning of each block, and depending on block type, participants were instructed to expect the target predominantly after a short or long temporal interval. Target interval and validity were therefore manipulated orthogonally in a factorial design. The target could occur validly or invalidly after a short or long interval. The actual experiment took around 80 minutes.

In total, 1600 trials were performed over two sessions. Temporal expectations were valid in 600 trials and invalid in 200 trials for each of the short and long intervals.

Behavioural analyses

Behavioural data analysis was conducted with custom written Matlab code. Trials in which participants did not respond, trials in which participants performed outside a range of three standard deviations (SD) of their mean reaction time (RT), and trials within blocks where participants performed at or below chance level ($\leq$ 20 correct responses) were excluded from the analysis. Trials excluded through the electroencephalogram (EEG) artefact-rejection procedures (see below) were also excluded for behavioural analysis. Clean data from both sessions were then concatenated. For RT analysis, only correct trials were used and averaged.

For a first set of analyses, RTs were averaged and perceptual sensitivity (d') determined by subtracting z-transformed false alarm rates from hit rates. Both measures were calculated at the participant level for the two factors of temporal expectation (Validity: Valid / Invalid) and interval length (Interval: Short Interval / Long Interval), and then subjected to two-way repeated-measures analyses of variance (ANOVAs) with a critical alpha level of 0.05 (two-sided).

In order to more explicitly examine the influence of distractor processing on target processing, target processing was also investigated as a function of the similarity of the target stimulus and last distractor stimulus according to different temporal expectations. The reasoning was that more similar distractor stimuli might more potently interfere with target processing, and that temporal expectations might

interact with distractor-target interference. A subset of trials was selected in which the orientation of the last distractor stimulus was specifically similar (distractor orientations with left tilted target stimuli: 11.25°, 157.5°, 168.75°, 180°; distractor orientations with right tilted target stimuli: 11.25°, 22.5°, 168.75°, 180°) or dissimilar (distractor orientations with left tilted target stimuli: 67.5°, 78.75°, 90°, 101.25°; distractor orientations with right tilted target stimuli: 78.75°, 90°, 101.25°, 112.5°) to the orientation of the target stimulus. Averaged RTs and d' were computed for each participant for the two factors of temporal expectation (Validity: Valid / Invalid) and similarity (Similarity: Similar / Dissimilar). Two-way repeated-measures ANOVAs with a critical alpha level of 0.05 (two-sided) were conducted.

EEG acquisition

EEG acquisition was identical to Chapter 2. Brain potentials were sampled from the following electrodes: FP(z,1,2), AF(z,3,4,7,8), F(z,1-8), FC(z,1-6), FT(7,8), C(z,1-6), T(7,8), CP(z,1-6), TP(7,8), P(z,1-8), PO(z,3,4,7,8), O(z,1,2).

EEG processing

EEG data were processed in Matlab with custom written functions and FieldTrip (Oostenveld et al., 2011). Data for each session were initially bandpass-filtered between 0.1 and 90 Hz and epoched around the onset of the warning signal (-1000 ms to +1000 ms). Signals from electrodes with poor contact were interpolated by averaging neighbouring electrodes. Epochs were then screened for excessive noise

between – 300 ms and 1000 ms. Trials were first rejected according to their relative variance across all channels, and then on the basis of vertical and horizontal EEG traces. Trials excluded for behavioural analyses were also rejected. Clean data of the first and second session were then concatenated.

To derive event-related potentials (ERP), epochs were baseline-corrected by subtracting for each electrode the mean potential within a range of 100 ms prior to warning signal onset from the whole epoch. The main effect of expectation was assessed by comparing time courses elicited by trials in which a target was expected after a short vs. long temporal interval.

For multivariate analyses, only posterior electrodes P(z,1-8), PO(z,3,4,7,8) and O(z,1,2) were used. Epochs were subdivided into smaller epochs around each pre-target distractor (-100 ms to 370 ms relative to distractor onset) and individually baselined (-100 ms to 0 ms). Distractors were then grouped according to presentation position (1^{st}, 2^{nd}, 3^{rd}, 4^{th}, 5^{th} or 6^{th} position). For each presentation position and condition, orientation decoding was carried out using a leave-one-out procedure. Specifically, with each iteration, one distractor served as a test sample and all other distractors as training samples. Each distractor was a test sample once. Training samples similar and dissimilar to the test sample were selected and separated. Training samples were determined to be similar if they featured the same or the next smaller (-11.25°) or larger (+11.25°) orientation as the test sample. Training samples were determined to be dissimilar if they featured the maximally different orientation (+90° for angles smaller or equal to 90°, -90° for angles larger than 90°) or the next smaller or larger orientation than this maximally different orientation. As distractor Gabor stimuli spanned the full circle, the next larger orientation from 180°, i.e.

191.25°, equalled 11.25°. For co-variance matrix estimation only, similar (dissimilar) train samples were de-meaned by subtracting the similar (dissimilar) train sample average over trials. The co-variance matrix was estimated with all train samples on all 17 electrodes used, averaged across time points. This matrix was used to calculate Mahalanobis distances between the test sample and the averaged similar and dissimilar train samples for each time point. Subtracting dissimilar from similar Mahalanobis distance time courses averaged across iterations served as a measure of orientation decoding quality for each single participant and condition (Short / Long).

Pre-target distractor decoding was compared for each distractor position separately between trials in which a target was expected after a short or long interval. In addition, distractor decoding was assessed by averaging distractor decoding time courses time point-wise across positions relative to warning signal onset. In this way, decoding performance at a given time point could relate to several distractors at different stages of processing, where the temporal distance to the onset of the target was matched between distractors. As the time points of distractor occurrence varied between trials, averaging over trials resulted in a smooth and continuous decoding time course which was evaluated according to different temporal expectations (Short / Long).

Statistical procedures were similar to those in Chapter 2, and relied on cluster-based permutation tests (Maris & Oostenveld, 2007). A more detailed description of the cluster-based permutation method can be found there. For ERP analysis, statistical comparisons were conducted across electrodes and time points, where time points were restricted from warning signal onset (0 ms) to the time point when a target stimulus could first occur (800 ms). In the multivariate analysis of distractor-position

resolved decoding, time points were restricted from individual distractor onset to the end of the epoch (0 ms to 370 ms, relative to distractor onset). For position averaged decoding statistics, time points were restricted from the onset of the first distractor to the time point when a target stimulus could first occur (200 ms to 800ms, relative to warning stimulus onset). For ERPs and position averaged decoding, in order to investigate potential interactions with behaviour, the difference between time courses relating to trials in which participants identified targets correctly or incorrectly (Correct / Incorrect) and time courses relating to trials in which participants responded fast or slowly (Fast / Slow; median split) after the occurrence of a target at a short interval were compared according to temporal expectations (Short / Long).

Results

Behaviour

For reaction time (Fig. 4.2 a), analysing the effects of temporal expectations on target processing according to cue-target interval length revealed main effects of Interval ($F(1,23)=5.205$, $p=0.032$) and Validity ($F(1,23)=13.635$, $p=0.001$), as well as an interaction between these two factors ($F(1,23)=18.021$, $p < 0.001$). Participants were generally faster with valid temporal expectations and at short intervals. Post-hoc t-tests indicated that participants responded more quickly with Valid Short Interval compared to all other conditions (Valid Short Interval < Invalid Short Interval: $t(23)= -6.871$, $p < 0.001$; Valid Short Interval < Valid Long Interval: $t(23)= -4.334$, $p < 0.001$; Valid Short Interval < Invalid Long Interval: $t(23)= -4.073$, $p < 0.001$). No effects were

observed for perceptual sensitivity d' (Fig. 4.2 b; Interval: F(1,23)=0.148, p=0.704; Validity: F(1,23)=1.534, p=0.228; Interval x Validity: F(1,23)=1.088, p=0.308).

Post-hoc statistics were not adjusted for multiple comparisons. All significant effects are still significant after Bonferroni correction if an adjusted alpha level of $p < 0.008$ (0.05 / 6 possible comparisons per hemifield) is assumed.

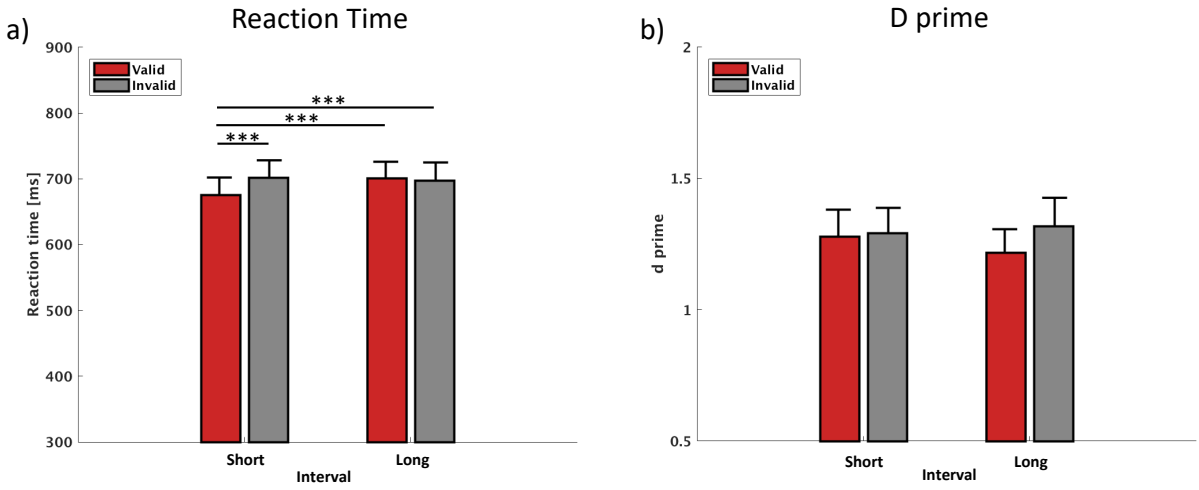


Fig. 4.2. Reaction time (a) and perceptual sensitivity d prime (b) with valid (red) and invalid (grey) temporal expectations for targets occurring at the short and long interval. a) Effect of Interval: p=0.032; effect of Validity: p=0.001; effect of Interval x Validity: $p < 0.001$; ***: $p < 0.001$. b) No effects were observed. Whiskers represent SEM.

Analysing the effects of temporal expectations and target-distractor similarity on target processing showed a main effect of Validity ($F(1,23)=35.865$, $p < 0.001$) with RT (Fig. 4.3 a) and a main effect of Similarity ($F(1,23)=29.529$, $p < 0.001$) with d' (Fig. 4.3 b). Participants responded generally faster with valid temporal expectations and were perceptually more sensitive for dissimilar distractor-target orientations. No other effects were observed, neither for RT (Similarity: F(1,23)=1.4, p=0.250; Similarity x Validity: F(1,23)=2.861, p=0.104) nor with d' (Validity: F(1,23)=0.418, p=0.524; Similarity x Validity: F(1,23)=0.161, p=0.692).

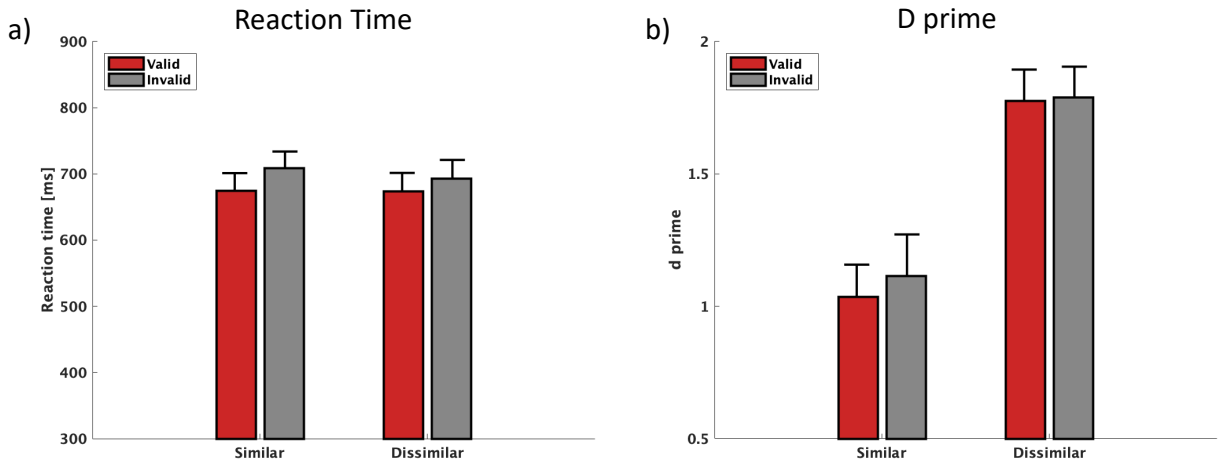


Fig. 4.3. Reaction time (a) and perceptual sensitivity d prime (b) with valid (red) and invalid (grey) temporal expectations for targets occurring at the short interval after distractors featuring similar or dissimilar orientations. a) Effect of Validity: $p < 0.001$. b) Effect of Similarity: $p < 0.001$. Whiskers represent SEM.

Event related potentials

Trials in which participants could expect a target after a short interval (Short) were contrasted with trials where they could expect a target after a long interval (Long). Three electrode-time clusters were determined, in which potentials related to Short were always more negative compared to Long. The first cluster (Cluster 1, p=0.019) was identified between 144 ms and 238 ms (Fig. 4.4) relative to warning-signal onset. Specifically, a negativity started in medial frontal regions around 50 ms before distractor onset and then spread to more medial central regions, and across all channels just before and after distractor onset. At the end of the cluster, several frontal as well as right-sided medial / posterior electrodes showed differences between conditions.

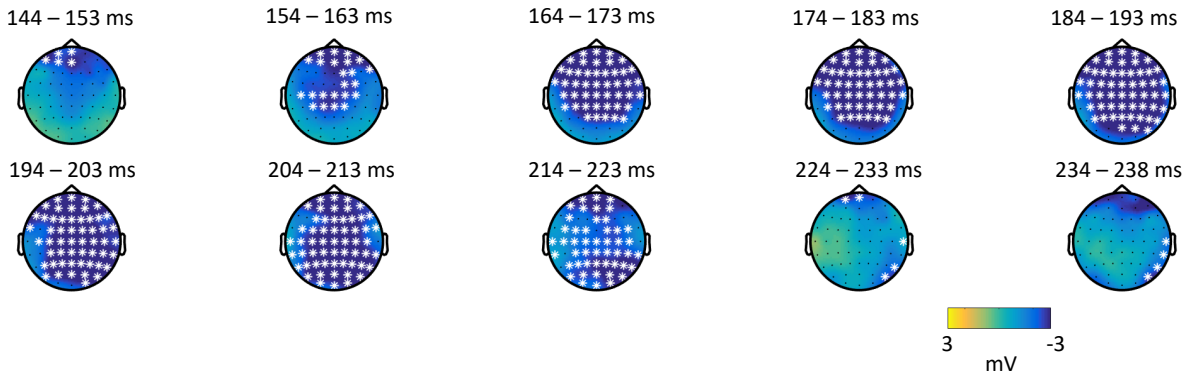


Fig. 4.4. Topographical representation of Short vs. Long, Cluster 1 (144 ms – 238 ms, p=0.019). Dark colours indicate lower potentials for Short vs. Long, bright colours indicate an opposite relationship. White stars mark electrodes where significant differences occurred. Note: statistics were conducted with a temporal step size of 1 ms. For illustrative purposes, potentials were averaged every 10 ms and all significant electrodes were marked.

The second cluster (Cluster 2, p=0.034) was identified between 267 ms and 508 ms (Fig. 4.5). The cluster began with a mainly medial frontal negativity for around 50 ms, which also spread to more right-sided posterior regions. Thereafter, while medial regions showed a non-significant inversion of polarity, a posterior negativity remained until the end of the cluster, being more right-sided toward the end.

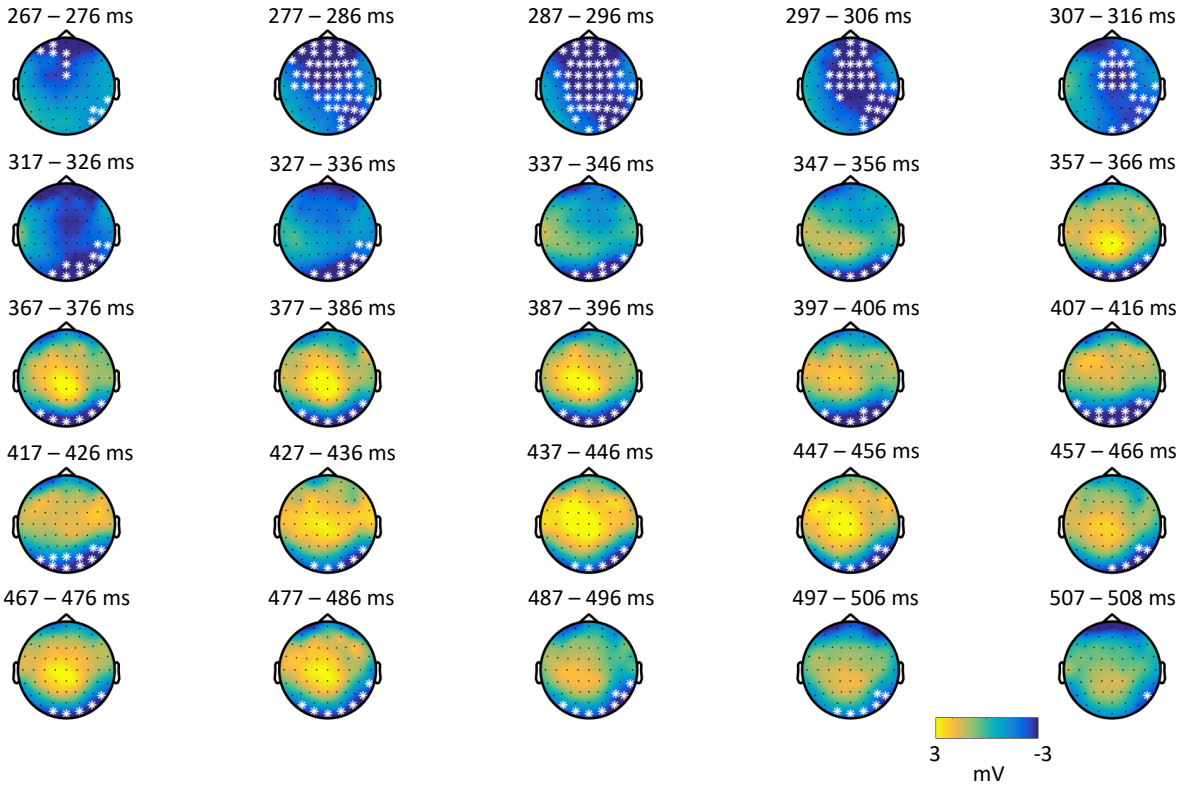


Fig. 4.5. Topographical representation of Short vs. Long, Cluster 2 (267 ms – 508 ms, p=0.034). Dark colours indicate lower potentials for Short vs. Long, bright colours indicate an opposite relationship. White stars mark electrodes where significant differences occurred. Note: statistics were conducted with a temporal step size of 1 ms. For illustrative purposes, potentials were averaged every 10 ms and all significant electrodes were marked.

The third cluster (Cluster 3, p=0.038) was observed from 646 ms to 800 ms (Fig. 4.6), marking the end of pre-target statistical testing and target onset. There was a frontal negativity which spread to more lateral, predominantly right-sided posterior regions from around 40 ms until the end of the cluster, sparing medial and left posterior regions.

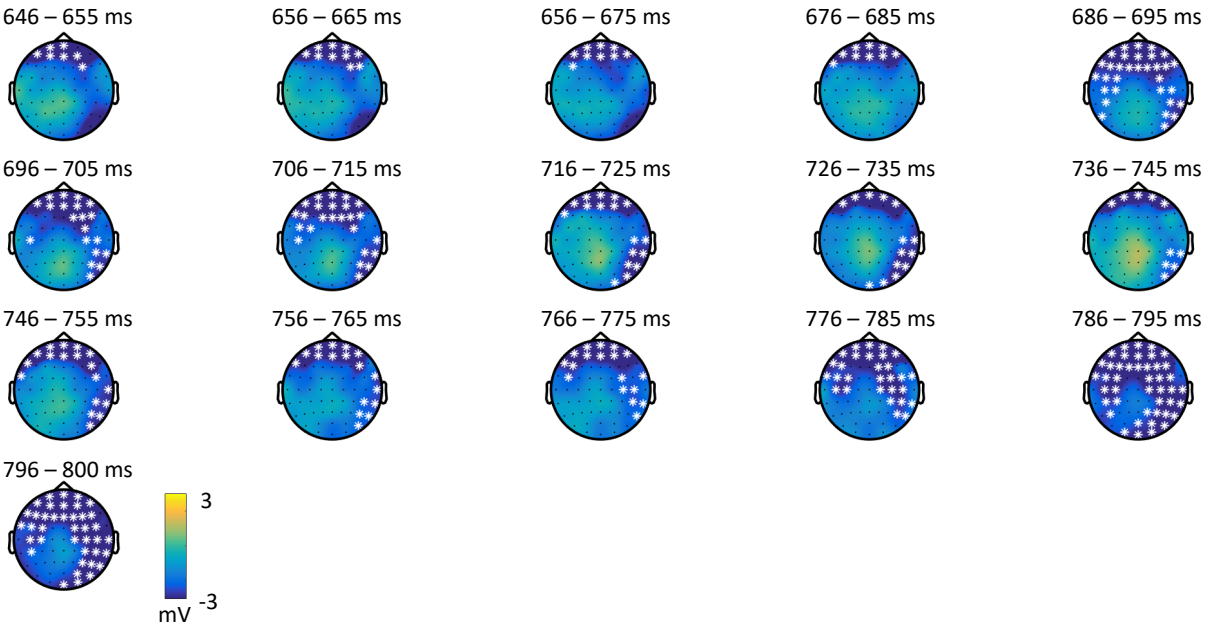


Fig. 4.6. Topographical representation of Short vs. Long, Cluster 3 (646 ms – 800 ms, p=0.038). Dark colours indicate lower potentials for Short vs. Long, bright colours indicate an opposite relationship. White stars mark electrodes where significant differences occurred. Note: statistics were conducted with a temporal step size of 1 ms. For illustrative purposes, potentials were averaged every 10 ms and all significant electrodes were marked.

Figure 4.7 illustrates high-resolution time courses for the Short vs. Long contrast with a set of 12 representative medial and lateral electrodes (F5, Fz, F6, C5, Cz, C6, P5, Pz, P6, PO7, Oz, PO8). Significant differences obtained with electrode-time clusters one, two and three are marked.

Comparisons between potentials averaged across behavioural outcomes (Correct / Incorrect, Fast / Slow) and temporal expectations (Short / Long) did not show interactions.

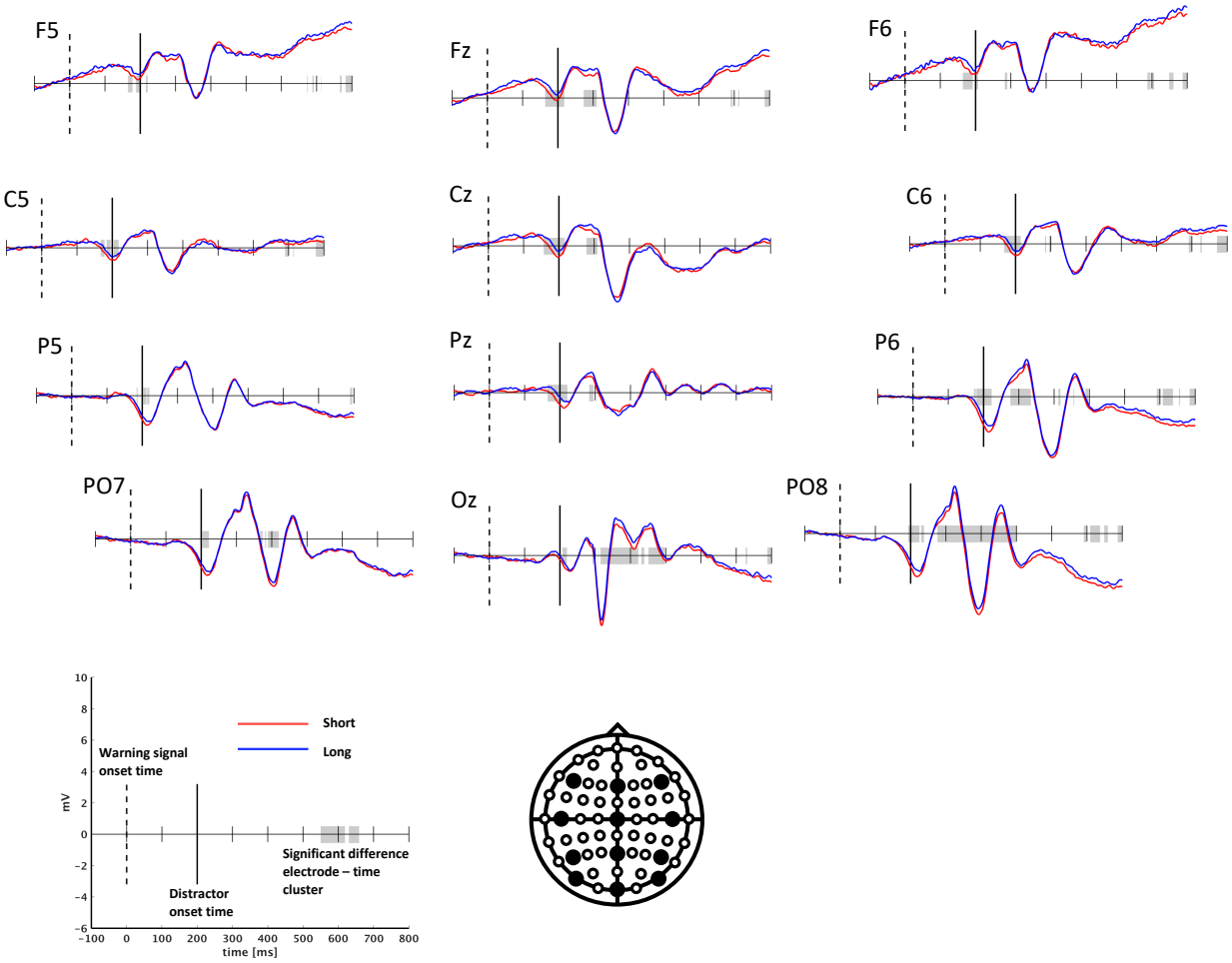


Fig 4.7. Time courses for Short (red) vs. Long (blue) across a set of representative electrodes. Dashed vertical lines represent warning signal onset, vertical solid lines distractor onset. Significant differences ($p < 0.05$) between conditions as obtained from electrode-time clusters 1, 2 and 3 are marked with grey bars on the x-axes. The target stimulus occurs at 800 ms. The lower right figure represents a topographical outline of the selected electrodes (filled circles).

Multivariate analyses

Mahalanobis-distance decoding of distractor orientations averaged across pre-target distractor positions showed a difference between Short and Long ($p=0.004$, Fig. 4.8) from 488 ms to 514 ms. Expecting a target after a short compared to long interval lead to comparably lower distractor decoding. Analysis of decoding for individual distractor positions revealed that this difference can most likely be attributed to the first

distractor. Only with the first distractor, a difference between conditions was observed. In addition, this difference matched the decoding analysis across distractors with regard to the level of significance (Short < Long: p=0.005) and temporal distribution (488 ms to 513 ms).

In line with the ERP analysis, comparisons between time courses averaged across behavioural outcomes (Correct / Incorrect, Fast / Slow) and temporal expectations (Short / Long) did not show interactions.

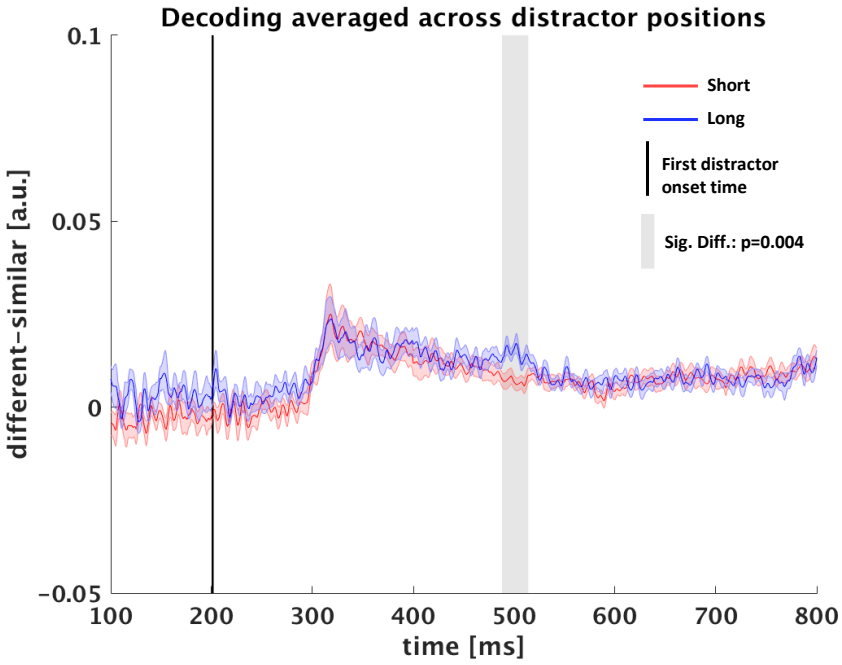


Fig. 4.8. Mahalanobis-distance decoding of distractor orientations averaged across pre-target distractors. Expecting a target after a short (red) vs. long (blue) interval showed comparably lower decoding around 300 ms after distractor onset. The onset of the first distractor occurs at 200 ms (black vertical line), the target occurs at 800 ms. The significant difference between conditions (p=0.004) is marked with grey shading. Blue and red shading of time courses indicates SEM.

Discussion

Temporal expectations are known to benefit individual target processing, both behaviourally and neurally (Nobre & Rohenkohl, 2014). However, in more natural situations, behaviourally relevant stimuli are rarely presented in isolation. Instead, they are temporally surrounded by other, often task-irrelevant and distracting stimuli. The fate of these distracting stimuli in the context of temporal expectations is largely unknown. The aim of the present research was to evaluate the extent to which temporal expectations can modulate stimulus processing across time, focussing on task-irrelevant pre-target input.

In order to replicate the beneficial effects of temporal expectations on task-relevant stimuli, reaction times and perceptual sensitivity d' to target stimuli were compared between conditions of valid and invalid temporal expectations across short and long intervals. Temporal expectations speeded up reaction times, where this effect was specifically related to the short interval. The finding accords well with previous studies investigating temporal expectations with two possible temporal intervals of target occurrence (Griffin et al., 2002; Miniussi et al., 1999). Reaction-time benefits were only reported for the first and shorter of two intervals. It was argued that this effect could be explained by participants' ability to re-focus their attention dynamically: If a target must occur at a short or long interval, when the target has not occurred after the short interval, the target necessarily needs to occur at the long interval, rendering prior temporal expectations for the long interval rather ineffective. This argumentation most likely also applies to the present finding. As expected, faster

responses for validly cued targets at the short interval were also observed across similar and dissimilar distractor-target orientations.

The present paradigm was perceptually very challenging. It is therefore not surprising that more similar distractor-target orientations had a larger detrimental effect on target processing as measured by d'. For conditions of rapidly succeeding distractor and target stimuli it has been known that greater target-distractor similarity can cause larger stimulus interference leading to weaker stimulus representations (Dux & Marois, 2009). Temporal expectations did not modulate perceptual sensitivity, and there were no interactions with cue-target interval length and distractor-target similarity. This contrasts with previous research (Chauvin et al., 2016; Correa et al., 2005; Rohenkohl et al., 2014) showing beneficial effects of temporal expectations on behavioural perceptual measures. It is also in opposition to findings in Chapter two and three using perceptual discrimination tasks in the context of temporal expectations. However, perceptual tasks do not necessarily lead to improved d' or accuracy measures with temporal expectations. For target detection, Doherty et al. (Doherty et al., 2005) showed neural perceptual processing benefits (P1 amplitude) with spatio-temporal expectations, which did not translate into accuracy measures. It may therefore be possible that potential perceptual modulations of target processing by temporal expectations could have been observed more easily in neural responses. Unfortunately, target stimuli were not optimised for EEG investigation, as they featured comparably low contrast, and were immediately followed and preceded by high contrast stimuli. A target substitute stimulus with higher contrast was included in the paradigm to facilitate stimulus decoding at the position where a target could occur. However, target substitute orientation could not be decoded. Target and target

substitute stimuli featured only two and relatively similar orientations, which may have impaired decoding.

ERP analyses showed more negative pre-target potentials when a target was expected after a short versus long interval. Interestingly, with the earliest cluster, a negativity emerged shortly after the warning signal and before the onset of the distractor stimuli. It featured an early frontal medial topography (Fig. 4.4) spreading across the whole scalp just before and up to shortly after distractor stimulus onset. There was also a negative drift regardless of condition and just up to distractor stimulus onset (Fig. 4.7, fronto-medial electrodes). Cluster 1 could therefore represent a very fast manifestation of a contingent negative variation (CNV; Walter, Cooper, Aldridge, McCallum, & Winter, 1964) modulated by temporal expectations (Miniussi et al., 1999) in anticipation of the distractor stimuli. The CNV is a well-known marker of stimulus anticipation and response preparation after a warning signal, which develops up to the onset of a second relevant stimulus. The present task does not require a motor response after the onset of the distractors. However, it could still be task-relevant to anticipate the onset of distracting information. As reviewed in Chapter 2, composition, functional significance and timing of CNVs can vary according to task context, expressing only rapid, non-motor related processes of anticipation under certain conditions.

The second cluster (Fig. 4.5) starting around 70 ms after distractor onset showed a short-lived frontal medial negativity with Short vs. Long expectations for around 50 ms. After that, there was a longer mainly posterior occipital negativity for around 200 ms. Broadband amplitude reductions in posterior occipital regions during rhythmic continuous visual stimulation (steady-state visual evoked potentials) have

been associated with reduced spatial attentional deployment (Müller, Malinowski, Gruber, & Hillyard, 2003; Müller et al., 1998). Keil and Heim (2009) acquired EEG data during a typical attentional-blink paradigm and compared amplitudes of steady state visual evoked potentials after the presentation of the first target for trials where the second target was identified correctly or incorrectly. When second targets were identified correctly, visual evoked potentials after the first target and over parietal occipital electrodes were comparably lower. Results were interpreted in terms of biased stimulus competition over time. Lower attentional investment in the first target, as measured by smaller evoked potentials, would lead to a comparatively increased ability to engage with the second target. As a result, identification of the second target would improve. The present study did not find interactions between behavioural outcomes and pre-target distractor processing. However, reduced posterior distractor-related evoked potentials when a target was expected after a short versus long interval may still serve a similar function. Pre-target stimulus processing could have been reduced in order to facilitate attentional engagement with the target.

The last cluster (Fig. 4.6) of significant differences between Short and Long expectations commenced around 150 ms before target onset with a frontal negativity that spread laterally and posteriorly by the end of the pre-target interval. The effect developed over a longer period and just up to target presentation. The frontal negativity could therefore represent a marker of target anticipation. As stated before, the CNV featuring frontal and medial amplitude decreases is a well-known marker of stimulus anticipation. It is described for stimulus-free intervals between the offset of the warning stimulus and the onset of a second relevant stimulus. The present results

suggest that temporally modulated signals of anticipation could still develop in the context of continuous, unpredictable and rapid distraction.

It is worth noting that in general and across all three clusters, more negative posterior potentials during distractor presentation featured a mild right hemispheric bias. This is in accordance with Chapter 2, where the right hemisphere was more sensitive to pre-target temporal orienting as indexed by larger alpha oscillatory power modulation.

Going beyond ERP analyses, time courses of multivariate distractor-orientation decoding averaged across distractor positions should have provided a continuous measure of overall distractor information with regard to the expected onset of the target. Decoding was comparably lower when the target was expected after a short versus long interval (Fig. 4.8). This effect was relatively short-lived (~ 25 ms) and could mainly be related to the processing of the first distractor. The original hypotheses of enhanced or suppressed distractor decoding with increasing temporal proximity to the target could therefore not be confirmed. Relating the difference between conditions around 300 ms before target onset to immediate competitive distractor-target interactions is not warranted given the short duration of the effect. Nevertheless, the direction of the effect matched related ERP results. There was reduced distractor stimulus amplitude and information. Previous behavioural research has investigated the effect of temporal expectations on stimulus processing across time (Denison et al., 2017; Martens & Johnson, 2005). It was argued that temporal biases toward a target can come at the expense of temporally competing distractor stimuli. Although the present study did not show an immediate attentional trade-off between target and distractor stimuli as indexed by a lack of interactions between behavioural outcomes

and pre-target distractor processing, reduced pre-target distractor processing may still have facilitated engagement with the target.

In another recent study (van Ede et al., 2018), a distractor Gabor stimulus was presented shortly after a target Gabor stimulus. The detrimental influence of the distractor on target decoding was observed to be delayed by an anticipatory cue predicting the time for target onset. The authors argued that the cue might have established a protective temporal window for target processing. With the present study, temporal expectations could modulate the processing of distractor information preceding the onset of a target, suggesting that temporal expectations may still work more proactively across time.

In the current study, temporal expectation showed only a moderate effect on stimulus decoding. It is possible that different stimulus-presentation parameters could have allowed for more pronounced effects. The effect was mainly related to late time points of decoding of the first distractor. In fact, distractor decoding was only differentiated 300 ms after distractor onset and when a subsequent distractor was already on the screen. Unlike for all other distractors, stimulus onset for the first distractor was temporally predictable. Longer distractor durations with more predictable stimulus onsets might therefore have led to larger differences between conditions. However, in order to benefit general decoding relatively short distractor durations were chosen, so that stimulus energy could be reinstated with every distractor onset. Unpredictable distractor onsets with the present paradigm should discourage participants from using stimulus onsets as temporal cues. Changing potentially promising presentation parameters could thus generate other methodological or more principal temporal expectation-related shortcomings.

There is still a chance that the current analysis did not track crucial stages of stimulus selection. Marti and Dehaene (2017) acquired MEG data in an attentional-blink paradigm using real-world images. Multivariate decoding performance varied across different complementary analyses. Stimulus decoding across matched time points of train and test sample activity enabled decoding of the target and all distractor stimuli. Temporal cross-generalisation analyses additionally differentiated target and surrounding distractor stimuli, respectively only the reported stimulus from all other stimuli, suggesting different levels of temporal selection. Specifically, for the target and stimuli surrounding the target, train trial information at 170 ms could be used to decode test trial information after 170 ms. Moreover, for reported targets, train trial information at 370 ms could be used to decode test trial information at later time points. Marti et al. used complex, real-world stimuli and acquired data points with comparably high spatial sampling. Nevertheless, a similar analysis approach could be used with the present study, where a temporal bias might lead to differences in sustained brain responses for different distractors. These differences might be modulated by the temporal proximity of the distractors to the target.

Conclusion

Chapter 4 investigated the effects of temporal expectations on neural processing during task-irrelevant pre-target distractor stimulation. Temporal expectation to the target showed a CNV-like negativity to the onset of the distractors after the warning stimulus. In addition, a late frontal negativity during distractor presentation and until target onset was observed. Topography and timing suggest that this effect may have

anticipatory function similar to a CNV. First insights could be gained studying distractor broadband neural representations and information. Both ERP and multivariate analyses showed reduced pre-target distractor processing with temporal expectation for the target. However, effects were short-lived and moderate, and could not be related to measures of behavioural performance. Further investigations employing different stimulus configurations and analyses techniques would be required to clarify the extent of pre-target distractor modulation by temporal expectations.

Chapter 5: General discussion

With this thesis, I investigated temporal expectations in the context of spatial expectations and stimulus competition. In addition, I examined the effects of aging on these functions. This last chapter summarises the major findings from the 3 experimental chapters, deriving commonalities and differences across the studies. Starting from the discussion of findings relating to the presentation of one target stimulus, I proceed to experimental contexts where target and distractor stimuli compete in space or time. After that, I discuss lateralised effects with different measures characterised by interactions. Subsequently, I discuss effects of aging. Finally, I chart future questions and research directions relating to the main topics of the thesis.

Improved behavioural performance and facilitated neural processing with temporal expectations in the context of a single target stimulus

Temporal expectations consistently improved behavioural performance across Chapters 2 and 3 when only one target stimulus was presented, i.e. in the absence of competition. Response speed was strongly facilitated for valid versus invalid temporal expectations. The results match previous findings showing response-time benefits when valid temporal predictions are available for the target stimulus (Coull & Nobre, 1998; Cravo et al., 2011; Niemi & Näätänen, 1981). Importantly, perceptual processing, as measured by d', was also improved for valid versus invalid temporal expectations in

Chapter 2 and in Experiment 1 of Chapter 3. In Experiment 2 of Chapter 3, there was only a qualitative improvement, which may relate to insufficient perceptual challenge due to a lack of backward masking (Smith & Ratcliff, 2009). Overall, findings conform to the previous literature reporting perceptual benefits with temporal expectations (Correa et al., 2005; Rolke & Hofmann, 2007).

As in previous studies, the behavioural benefits of temporal cues were accompanied by temporal modulation of neural activity related to the target anticipated during the pre-target period – the CNV potential (Miniussi et al., 1999; Walter et al., 1964) (Chapter 2). In addition, a novel earlier frontal negativity was also observed, which warrants further investigation (Chapter 2). Using scalp current density transformation, the temporal CNV could be characterised with reasonable spatial resolution. Crucially, it could be shown for the first time that a temporal CNV effect can correlate positively with both response speed and the quality of perceptual processing, emphasising its behavioural relevance.

Differential effects of temporal expectations in the context of competing stimuli

Temporal expectations can have differential effects in the context of target and distractor stimulus competition. When one target was presented together with a distractor in the opposite visual hemifield (Chapter 3, Experiment 1), stimulus competition and temporal expectation worked independently. Both response speed and perceptual processing were improved with temporal expectations. Intra-hemifield competition between one target and six surrounding distractor stimuli (Chapter 3, Experiment 2) spared the beneficial effects of temporal expectations on response

speed. However, stimulus competition interacted with temporal expectations for perceptual measures. Temporal expectations negatively affected perceptual processing of the target stimulus. Opposing findings in the perceptual domain for the two experiments of Chapter 3 were explained according to the theory of biased competition (Desimone & Ducan, 1995). This theory poses that mutual competition between stimuli at the level of the receptive field is a precondition for selective processing. Top-down signals like spatial or temporal expectations can bias the competitive strength of individual receptive field representations, indirectly aiding with the resolution of competitive stimulus conflict. In Chapter 3 it was argued that spatial representations of inter-hemifield arrays would not overlap (Kastner et al., 2001), preventing stimulus competition at the level of the receptive field. Temporal expectations acting onto these spatial representations (Ghose & Maunsell, 2002; Rohenkohl et al., 2014) would be ineffective. However, when stimuli are presented in close spatial proximity, as was the case with intra-hemifield competition, stimulus representations should overlap, and temporal expectations should therefore be able to influence stimulus competition. It was proposed that temporal expectations boosted stimuli indiscriminately. Six distractors would have gained overall more competitive strength than one target stimulus, so that the target stimulus representation would have been weakened, and related perceptual discrimination ability decreased.

Stimulus competition can also happen across different time points. Although backward masking in Chapters 2 and 3 also represents a form of temporal stimulus competition, stimulus competition across different time points was specifically examined in Chapter 4. Target stimuli were embedded in a stream of temporally

proximal high-contrast distractor stimuli. In line with all other experiments of the thesis, response times were faster in the presence of valid versus invalid temporal expectations. Previous research has shown that temporal expectations can improve d' measures for targets embedded into a stream of distractors (Correa et al., 2005). With the present paradigm, however, effects of d' were not observed. The task was perceptually highly challenging, and it has been shown that spatio-temporal expectations can act perceptually at the neural level without translating into accuracy measures (Doherty et al., 2005). Therefore, perceptual benefits of temporal expectations with the present task might rather have been observed neurally.

Whereas many studies have investigated how temporal expectations influence target processing (Nobre & Rohenkohl, 2014), the fate of temporally proximal non-target stimuli is very scarcely investigated (Denison et al., 2017; Martens & Johnson, 2005). In particular, the processing of pre-target distractors potentially interfering with proactive pre-target orienting processes has only recently been investigated behaviourally (Denison et al., 2017). In Chapter 4, related neural processes were explored. Results from ERP and decoding analyses point to decreased distractor processing when temporal expectations are directed toward the target. Future research will need to better characterise this processing decrement and examine its behavioural relevance.

Temporal expectations and lateralised effects

It has been proposed that, on the perceptual level, temporal expectations might primarily work through other, e.g. spatial biases (Ghose & Maunsell, 2002; Rohenkohl

et al., 2014). Results of Chapter 2 may support this proposition both behaviourally and neurally, if a third factor hemifield or hemisphere is included.

Decreased alpha power processing has been connected to enhanced cortical excitability (Jensen et al., 2012; Klimesch et al., 2007). Lateralised posterior alpha power is a well-established marker of directed spatial expectations, presumably facilitating sensory processing (Kelly et al., 2009; Sauseng et al., 2005; Thut, 2006; Worden et al., 2000). Chapter 2 showed a clear contralateral alpha-power decrease over posterior regions after spatial cueing. Interestingly, spatial alpha-power modulation (Thut, 2006) was only susceptible to temporal orienting over the right hemisphere. The control of spatial attention is thought to rely on lateralised brain functions that show a right-hemisphere dominance (Heilman & Abell, 1980; Kinsbourne, 1970; Mesulam, 1981; Vallar & Bolognini, 2014), resulting in a generally slightly larger left versus right hemifield attentional bias (Bowers & Heilman, 1980; Jewell & McCourt, 2000; McCourt & Jewell, 1999). Relating to the present findings, temporal expectations may thus have teamed up with this right-dominant attention system, so that the right versus left hemisphere may generally experience larger dynamics. The neural effects furthermore showed a link to behavioural measures of perceptual processing. Behavioural results showed a complex 3-way interaction of Spatial Cue x Temporal Validity x Hemifield with perceptual measure d'. Overall, perceptual sensitivity in the left visual hemifield was more strongly influenced by temporal expectation than that in the right visual hemifield. Similarly, in both experiments of Chapter 3, hemifield-resolved perceptual modulation by temporal expectations seemed to mainly relate to the left visual field. These results are shown in the appendix (Appendix: A2). Due to very low trial numbers, these results are only

described qualitatively. Hemispheric asymmetries have not been described in the context of performance or neural-modulation measures of visual temporal expectation. In most studies, the results are simply amalgamated across visual fields. The set of results in this thesis calls out for replication in future studies and suggests that it may be fruitful to consider the implications of systematic lateralisation of effects.

Stimuli in Chapter 4 were presented centrally, so that a lateralised perceptual effect should not be expected. Posterior broadband processing when a target was expected after a short versus long interval and during distractor presentation was generally reduced and may have featured a mild bias to the right hemisphere, especially before target onset. Unlike in the experiment of Chapter 2, it was not straightforward to use scalp current density transformation, since the continuous presentation of distractor stimuli complicated signals and topographies.

In the experiment of Chapter 2, temporal expectations also interacted with neural markers of spatial expectation – ADAN (Hopf & Mangun, 2000; Nobre et al., 2000) and LDAP (Harter et al., 1989; Hopf & Mangun, 2000). This is the first report showing that both ADAN and LDAP can be increased with temporal expectations. However, contrary to modulations of alpha and of behaviour in the same experiment, ERP modulations were stronger in the left hemisphere. It may be possible that ADAN and LDAP represent qualitatively different aspects of attentional processing. Imaging studies have revealed a left-dominant network of parietal and frontal areas involved in the control of temporal orienting (Coull & Nobre, 1998, 2008). Thus, the ADAN and LDAP may have reflected activity in this left-dominant network or its interaction with the modulatory sites. In contrast, modulation of the posterior alpha power and

behavioural performance may reflect right-lateralised spatial attention processes that were affected by temporal expectation. Overall, the pattern of lateralisation during the control of temporal expectations and its modulatory effect over visual cortices remains to be investigated much more thoroughly. Future research is required to clarify the specific roles of alpha power, ADAN and LDAP in spatio-temporal processing.

Temporal and spatial expectations and stimulus competition in aging

Cognitive aging is a complex process. It has become clear that behavioural performance and brain function and structure do not simply decline with age. Behavioural performance may be largely maintained in certain tasks, and brain function may be spared or experience complex and gradual re-organisation (Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Campbell, 2008). The prefrontal cortex is thought to be particularly important in cognitive aging, with its proposed role of guiding proactive and flexible cognitive control, including its involvement in the generation of task relevant expectations and the selection of relevant over irrelevant information (Braver et al., 2001; Gazzaley, 2013; West & Schwarb, 2006). The present thesis investigated combined temporal and spatial expectations in the presence or absence of stimulus competition. These functions have so far mostly been studied separately in aging. As aging may also affect sensory function (Monge & Madden, 2016; Park et al., 2004), perceptual challenge was individually adapted by staircasing procedures across all experiments.

Experiment 1 of Chapter 3 examined the effects of aging on temporal expectations and stimulus competition. As expected, older participants responded

more slowly than younger participants (Ratcliff, Thapar, & McKoon, 2001). However, older participants were not more impaired by stimulus competition. Previous research has found stimulus suppression deficits in aging (Chao, 1997; Gazzaley et al., 2005). However, these studies rather targeted stimulus competition across time and in combination with memory mechanisms. Experiment 1 of Chapter 3 showed that aging can spare participants' ability to suppress task irrelevant information when simultaneously presented visual stimuli compete for representation. Temporal expectations did not interact with inter-hemifield competition. Stimulus representations presumably did not overlap at early processing stages. Importantly, the experiment also challenged research pointing to a general timing deficit in older age (Balci, Meck, Moore, & Brunner, 2009; Zanto et al., 2011). Instead, the findings support more recent research (Chauvin et al., 2016; Heideman et al., 2018) showing similar effects of temporal expectations in older and younger participants, suggesting that aging does not necessarily compromise the ability to generate temporal expectations.

In the experiment of Chapter 2, a large group of older participants was tested. Effects of aging were investigated by examining behavioural and neural variability relating to common pre-target markers of spatial and temporal expectations. The CNV (Miniussi et al., 1999; Walter et al., 1964) was clearly modulated by temporal expectations and could in addition be related to behaviour. However, the CNV was not sensitive to aging within the cohort tested. This may support findings from Chapter 3, in which the use of temporal information in older age was unimpaired. The ADAN effect, connected to the control of spatial shifts (Eimer, 2004), correlated negatively with age in the left hemisphere. Although spatial expectations are thought to be

relatively spared by aging, a smaller modulation of left versus right ADAN in older participants has been reported before (Nagamatsu et al., 2011). Lateralisation of posterior alpha power to spatial expectation (Kelly et al., 2009; Sauseng et al., 2005; Thut, 2006; Worden et al., 2000) was also investigated. Alpha oscillations are a marker of flexible modulation of sensory cortical excitability (Jensen et al., 2012; Sauseng et al., 2005). There are conflicting findings as to whether older participants can engage in pre-target alpha lateralisation (Heideman et al., 2018; Hong et al., 2015; Leenders et al., 2016; van der Waal et al., 2017). Results from Chapter 2 may reconcile these conflicting findings. Alpha lateralisation modulated by spatial expectations was not sensitive to aging. However, younger participants showed stronger alpha lateralisation modulation across different levels of temporal expectancy. Hence, effects of aging may only become apparent when two different domains of cognitive flexibility are investigated in parallel and resolved by hemisphere. In addition, alpha modulation showed rather more variability in the right compared to the left hemisphere. Furthermore, behavioural variability for stimuli occurring in the left visual hemifield also seemed to be more susceptible to aging than for stimuli in the right visual field. It was speculated that temporal expectations might preferentially work via the right-dominant network for controlling spatial attention. If this were true, effects of aging may become particularly apparent in the right hemisphere and left visual hemifield. There is indeed some evidence that left visual-field processing might be altered in older adults (Nagamatsu et al., 2011). Studying lateralised expectation biases in the context of temporal expectations may therefore be a fruitful subject for future aging research.

The findings of this thesis confirm that aging is not associated with general functional and structural decline (Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Campbell, 2008; Zanto & Gazzaley, 2014). However, when behaviour and neural activity are resolved by a combination of top-down biases and lateralisation is respected, age-related deficits may become apparent.

Future questions and directions

The findings of the thesis open the doors for several interesting further questions and research directions. Chapter 3 and 4 focussed on temporal and spatial expectations in the context of competition. Many important questions about the ability of spatiotemporal expectations to overcome stimulus-related competition still need to be explored. For example, experiments similar to the ones in Chapter 3, could investigate the influence of target-distractor similarity on spatiotemporal competition. In Chapter 4, target-distractor similarity did not interact with temporal expectations in the context of competition across time. However, only target-related effects of behaviour were studied. Neural effects of target and distractor processing should still be investigated. It would also be interesting to explore whether and how temporal expectations combine with other types of non-spatial biases to guide target processing and resolution of competition. There are studies pointing to interactions of temporal expectations with response conflict (Correa et al., 2010) and spectral features of competing auditory streams (Lakatos et al., 2013).

Spatial receptive-field interactions should be mapped more systematically in the context of temporal expectations. Chapter 3 shows additive and detrimental

effects of temporal expectations in combination with stimulus competition. Parametrically varying the distance between target and distractor stimuli may clarify whether temporal expectations map onto a "spatial beam" of attention (Ghose & Maunsell, 2002; Rohenkohl et al., 2014), work independently from spatial expectations, or even modulate spatial receptive-field properties (Ghose & Bearl, 2010). This could contribute to the interesting question of how temporal expectations are encoded in the brain (Goel & Buonomano, 2016; Mauk & Buonomano, 2004). Single-cell or E/MEG recordings would be particularly useful to study the fate of task irrelevant distractors, which may e.g. experience decreased response rates or increased oscillatory synchrony in the alpha band (Jensen et al., 2012).

Future research on lateralised effects of temporal expectations could contribute to a better understanding of hemispheric differences in spatial expectation function. As already discussed, spatial expectation is generally lateralised to the right hemisphere and temporal expectation may be particularly effective there. Future combined fMRI-EEG studies could provide further regional evidence of potential spatio-temporal synergies taking hemispheric lateralisation into account. Causal involvement of particular brain regions in spatio-temporal expectations could be studied by testing patients with specified lesions. In some cases, brain damage can lead to clinical symptoms of hemispatial neglect or extinction (Vallar & Bolognini, 2014). The core symptom of visual hemispatial neglect is the patient's inability to report sensory events occurring contralaterally to the lesioned hemisphere. Extinction may be regarded as a milder form of neglect where contralesional stimuli are only neglected if they compete with a simultaneously presented stimulus in the opposite hemifield. Interestingly, symptoms with these conditions are generally larger with

right-sided hemispheric lesions. In addition, case studies in neglect and extinction have shown spatio-temporal processing deficits for the contralesional (left) hemifield (Di Pellegrino, Basso, & Frassinetti, 1997, 1998; Hillstrom, Husain, Shapiro, & Rorden, 2004). Applying spatio-temporal expectation paradigms to stroke survivors suffering from neglect or extinction may therefore help to further clarify in how far neglect and extinction stem from impaired combined action of spatial and temporal expectations. Such an approach would also be helpful for the development of more dynamic, and more refined, models of top-down processing. Indeed, the experimental tasks in the experiments of Chapters 2 and 3 were designed to allow investigation in stroke survivors. Although not included in the thesis, the approach was shown to be effective for testing individual stroke survivors. The patterns of results in experiments of Chapters 2 and 3, for which volunteers were carefully screened for brain damage, thus contribute to normative, control data against which deficits resulting from different brain lesions can be explored.

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Appendix

A1. Chapter 2, target-related ERPs

ERPs related to the target stimulus were pre-processed using the same analysis pipeline that was also used for cue-related ERP pre-processing. However, data were epoched (-1300 ms to 1600 ms), cleaned (-500 ms to 1200 ms) and baselined (-50 ms to 50 ms) around target onset. The effect of spatial expectation allocation was assessed by contrasting target ERPs after directed (Left/Right) and Neutral (Neutral) spatial expectations. Temporal expectation allocation was investigated by contrasting target ERPs after short valid (Valid) and long invalid (Invalid) temporal expectations. All ERPs were related to targets occurring after the short interval. The interaction between spatial and temporal expectation allocation could not be assessed due low trial numbers for conditions where the target occurred invalidly after a short interval. Furthermore, as a consequence of excessively noisy data three additional subjects needed to be excluded, resulting in the inclusion of 38 subjects for target analyses. Statistical comparisons where conducted using the same analysis pipeline that was also used for cue-related analysis. In particular, electrode-time clusters were determined for a time-window of 800 milliseconds from target onset.

Figure A1.1 depicts the posterior contralateral negative cluster for Left versus Neutral. Figure A1.2 shows the earlier negative cluster for Right versus Neutral, which is located ipsi- and contralaterally. Figure A1.3 displays the later posterior contralateral negative cluster for Right versus Neutral. Figure A1.4 shows the central positive cluster obtained by contrasting Valid versus Invalid.

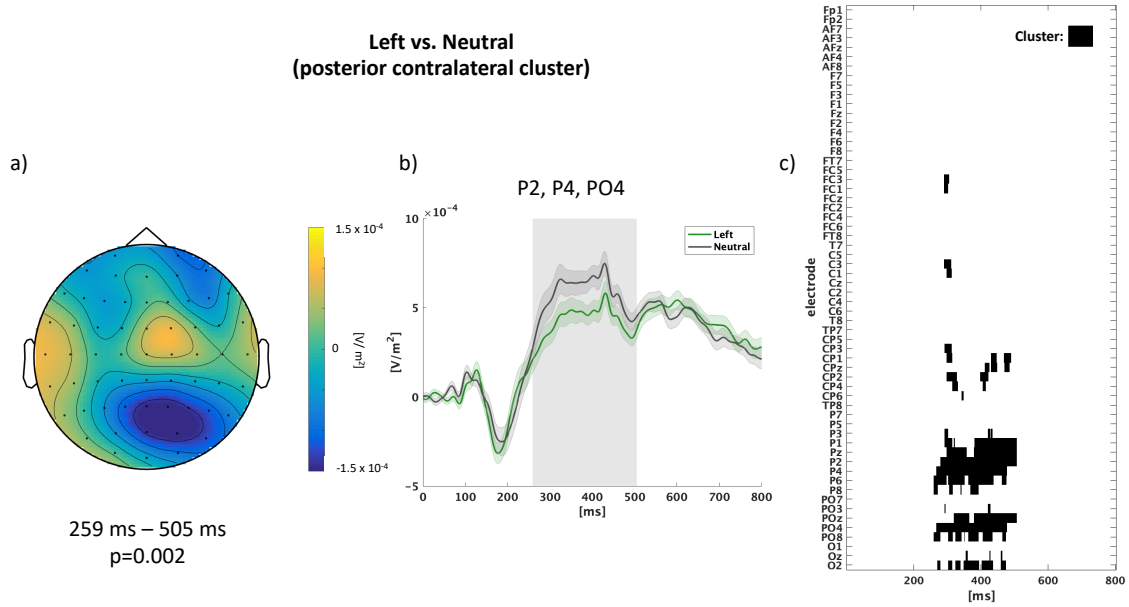


Fig. A1.1. Topography (a), time courses (b) and electrodes (c) for the posterior contralateral negative cluster obtained when contrasting target-related ERPs for Left vs. Neutral. Time courses were plotted for electrodes which are part of the cluster in more than 80% of cluster time points. Grey shading indicates cluster time points. Green and grey shading of time courses indicates SEM.

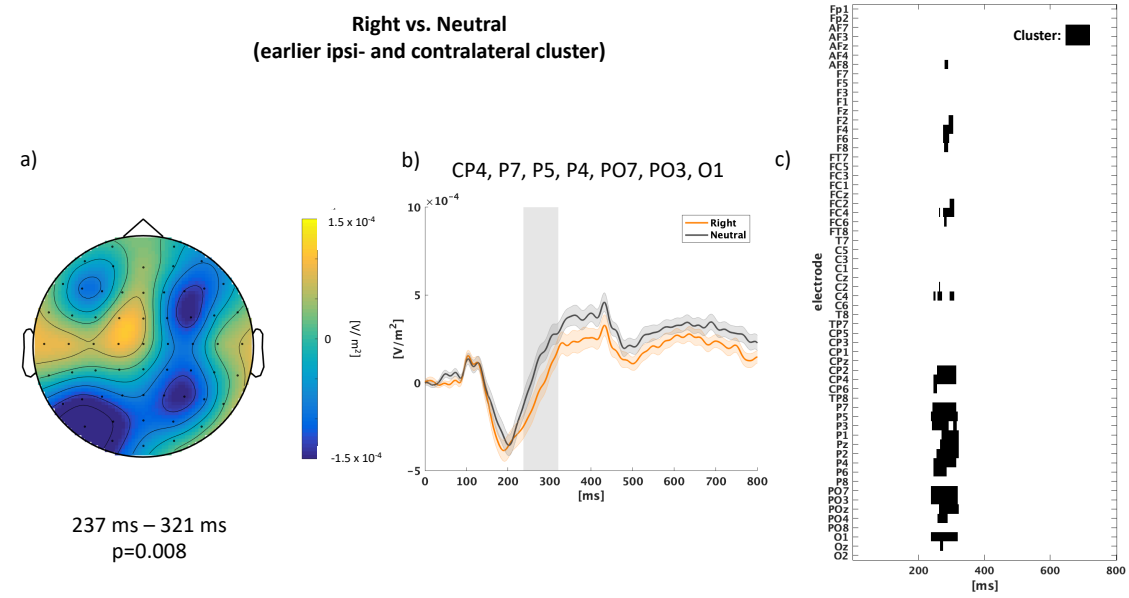


Fig. A1.2. Topography (a), time courses (b) and electrodes (c) for the earlier ipsi- and contralaterally located negative cluster obtained when contrasting target-related ERPs for Right vs. Neutral. Time courses were plotted for electrodes which are part of the cluster in more than 80% of cluster time points. Grey shading indicates cluster time points. Orange and grey shading of time courses indicates SEM.

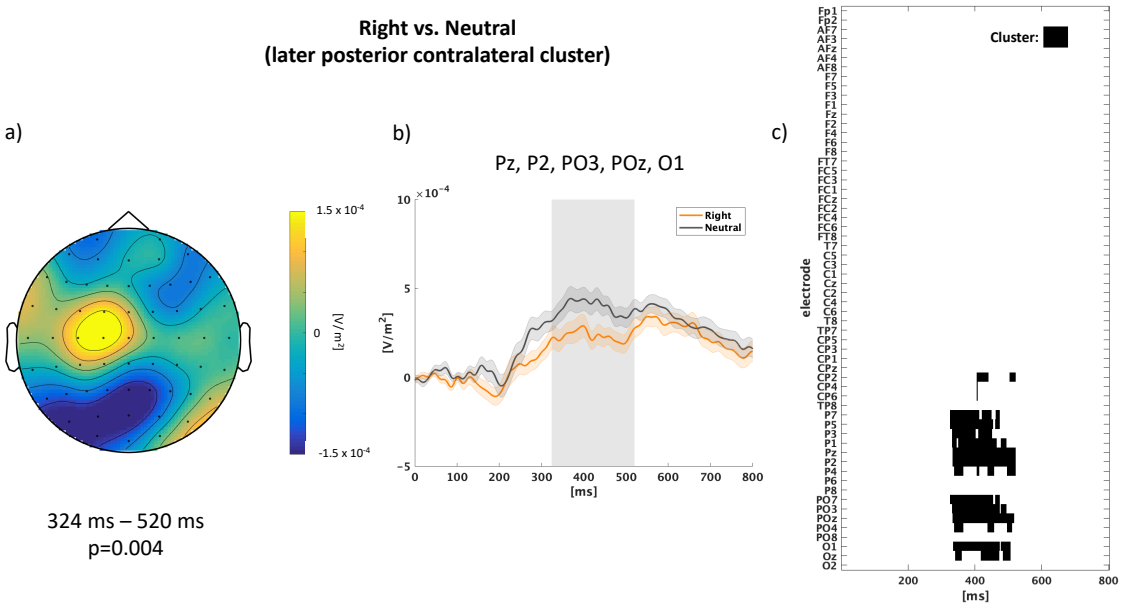


Fig. A1.3. Topography (a), time courses (b) and electrodes (c) for the later posterior contralateral negative cluster obtained when contrasting target-related ERPs for Right vs. Neutral. Time courses were plotted for electrodes which are part of the cluster in more than 80% of cluster time points. Grey shading indicates cluster time points. Orange and grey shading of time courses indicates SEM.

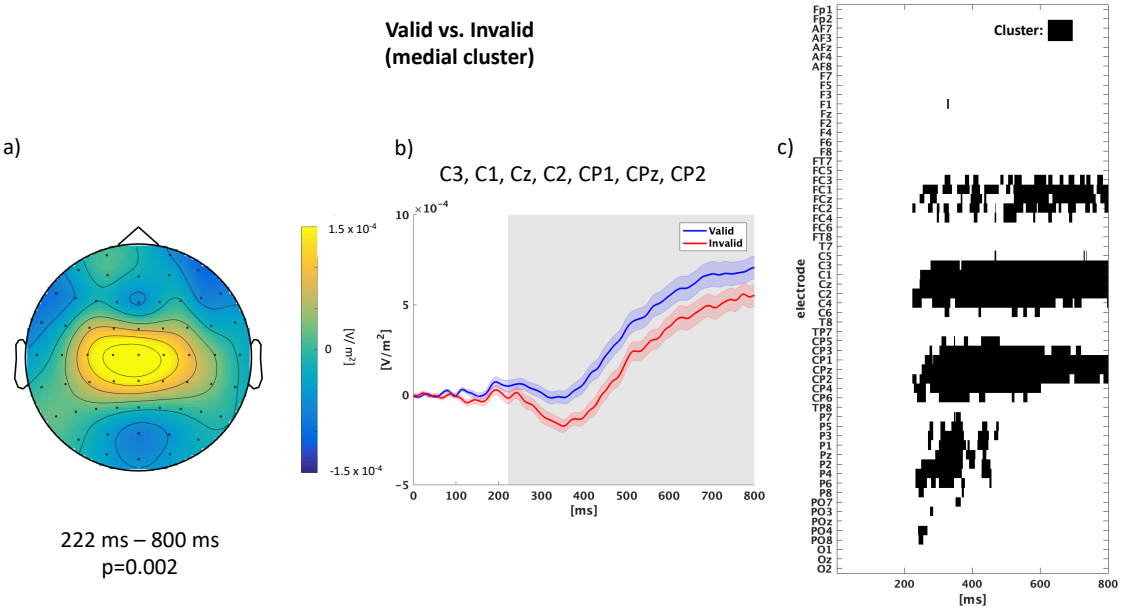


Fig. A1.4. Topography (a), time courses (b) and electrodes (c) for the medial positive cluster obtained when contrasting target-related ERPs for Valid vs. Invalid. Time courses were plotted for electrodes which are part of the cluster in more than 80% of cluster time points. Grey shading indicates cluster time points. Blue and red shading of time courses indicates SEM.

A2. Chapter 3, Hemifield resolved perceptual effects of temporal expectations

Results of Chapter 2 showed that temporal expectations can influence behavioural and neural processing in a lateralised pattern. Specifically, for perceptual processing related measures, the right hemisphere and the left hemifield seemed to be more susceptible to temporal expectation related modulation. To further test this hypothesis, behavioural results of Chapter 3 were resolved by hemifield. Due to very low trial numbers, hemifield resolved results are only presented qualitatively (Fig. A2). In line with findings of Chapter 2, temporal expectations seemed to have a larger effect in the left versus right visual hemifield.

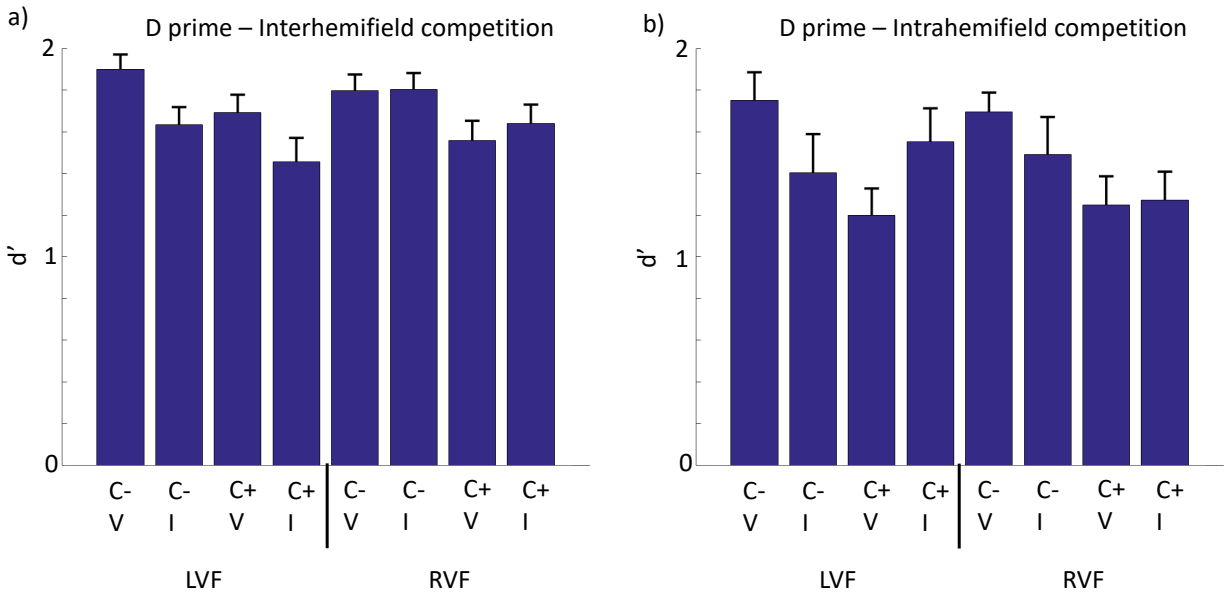


Fig. A2. Hemifield resolved results from Experiment 1 (a) and 2 (b) of Chapter 3. Perceptual sensitivity d' is plotted as a function of conditions resolved by left (LVF) and right (RVF) visual field. C-: no competition, C+: competition, V: valid temporal expectations, I: invalid temporal expectations. Whiskers represent SEM.