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Microsaccadic Contributions to Rhythmic Attentional Sampling

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## 1. Introduction

Imagine you are at an arcade playing a round of *Whac-A-Mole*. As the game's name suggests, your task is to monitor multiple holes in a tabletop for moles that randomly pop out to hit them with a hammer. The goal is to earn as many points as possible by successfully hitting the moles within a specified time limit. To achieve this, multiple cognitive processes are involved. First, you need to be able to block out all surrounding sensory signals, such as background noise or flashy lights, that are not goal-relevant and focus your attention to the task. Then, you need to be able to dynamically shift your attention back and forth between the holes. As we will discuss in the subsequent section, this attentional sampling process has been shown to occur in a theta-rhythmic manner (e.g., Fiebelkorn et al., 2013; Landau & Fries, 2012; Re et al., 2019; VanRullen, 2016, 2018; VanRullen et al., 2007). Furthermore, your visual attention will allocate both in an overt manner (i.e., in the direction of eye movements) and in a covert manner (i.e., without eye movements) in order to examine the visual environment (e.g., Busch et al., 2009; Busch & VanRullen, 2010; Fiebelkorn et al., 2018; Helfrich et al., 2018; Landau et al., 2015; Mathewson et al., 2009; Otero-Millan et al., 2008). During covert attentional shifts, your eyes will exhibit miniature fixational eye movements, so-called microsaccades, that are indicative of attentional allocations (e.g., Engbert & Kliegl, 2003; Hafed & Clark, 2002). The goal of this current study is to understand the role of microsaccades in rhythmic attentional sampling.

To this end, we designed a study in which participants had to complete a target detection task similar to the game of *Whac-A-Mole* described above with regard to attention allocation. In our experimental protocol, participants were instructed to monitor two locations for the appearance of contrast decrements. Importantly, this was done while gaze position was fixated on a central dot. This way, we were able to measure fixational microsaccades and examine whether their rate and direction correlated with oscillations in target detection.

## 2. Theoretical Background

To understand how microsaccades could contribute to rhythmic attentional sampling, it is important to first clarify basic theoretical constructs on attention. To this end, theories on selective attention will be discussed as well as previous findings on oscillatory attentional sampling. Subsequently, findings on the role of microsaccades in covert attention will be examined. The evaluation of the current state of research will finally lead to the research question of this current thesis.

## 2.1. Selective Attention

In every moment of our lives our senses are concurrently flooded with an overwhelming amount of information. Due to limited cognitive capacities a selection mechanism is necessary to distinguish relevant from irrelevant stimuli (Wolfe, 2021). While you are reading this sentence your mobile phone's display might light up or a loud motorcycle might drive by your window. Nevertheless, you somehow manage to block out these sensory signals and focus on what is important for your behavioral goal in this moment: reading. This psychological and neural mechanism that allows perceptual selectivity is called attention (Yantis, 2000). Selective attention is described as a cognitive mechanism that induces the prioritization and enhanced processing of behaviorally relevant objects or locations, while simultaneously inhibiting the processing of irrelevant ones (Fiebelkorn et al., 2019). But how exactly does attention decide which sensory signals to select and which to ignore?

Over the past decades researchers have debated this topic excessively (Luck et al., 2021; Wolfe, 2021). Early theoretical frameworks on visual attention such as the *feature integration theory* (FIT) proposed by Treisman and Gelade (1980) suggest that there are two distinctive stages. In an early *preattentive* stage basic features such as color or orientation (i.e., angle or direction of the visual stimulus) are processed in a parallel and automatic manner. In a later stage selective attention is required for perceptual grouping or segregation of these basic features. Thus, selective attention is suggested to operate like a filter that helps overcome processing limits. One notion that is strongly represented in the scientific literature is that selective attention is directed in a *top-down* or goal-directed way (e.g., Folk et al., 1992). According to the *contingent capture hypothesis* by Folk and colleagues (1992), attention will only be allocated to a given stimulus if it matches an attentional set (i.e., if the stimulus shares a feature property that is goal-relevant). On the contrary, attention can also be directed in a *bottom-up* or stimulus-driven manner (e.g., Theeuwes, 1992). According to the *stimulus-driven selection hypothesis* proposed by Theeuwes (1992), some kinds of stimuli (e.g., abrupt onsets, color singletons) can automatically capture attention solely due to their high saliency even though they are completely goal-irrelevant (Egeth & Yantis, 1997; Theeuwes, 1992).

More recent empirical evidence suggests that an interaction of both top-down and bottom-up processes directs attention (Luck et al., 2021; Wolfe, 2021; Yantis, 2000). According to *Guided Search 6.0* (GS6), attention is guided by a *priority map* which derives information from five different sources: “(1) top-down and (2) bottom-up feature guidance,

(3) prior history (e.g., priming), (4) reward, and (5) scene syntax and semantics” (Wolfe, 2021, p. 1060). Similarly, Luck and colleagues (2021) present a framework for models of attentional control according to which a priority map allows both for proactive goal-directed control as well as reactive stimulus-driven control.

One of the most widely used experimental methods to study visual attention is visual spatial orienting as developed by Posner (1980). In a typical Posner-cueing task, participants are instructed to detect a target at one of two possible locations. First, they are presented with a cue that can either be valid (i.e., pointing at the direction of the target), invalid (i.e., pointing at the opposite direction of the target) or neutral (i.e., non-informative regarding the target’s location). Shortly thereafter, the target stimulus is presented. Studies using the Posner-cueing protocol have consistently demonstrated that valid cues lead to improved behavioral outcomes such as faster reaction times (RTs) and more accurate target detection compared to invalid or neutral cues (e.g., Posner, 1980; Posner & Cohen, 1984). Thus, Posner (1980) concluded that attention operates like a spotlight, which can be attracted by salient cues, and which facilitates the detection of stimuli under its beam. However, subsequent research (e.g., Klein, 2000, Michel & Busch, 2023; Posner & Cohen, 1984) revealed that the facilitatory effects for cued locations only occur when cue-target intervals are short (i.e.,  $< 225$  ms). For cue-target intervals between 225 ms and 3 s, reversed patterns have been observed, showing that behavioral performance is typically worse in valid conditions compared to invalid conditions (Klein, 2000; Michel & Busch, 2023; Posner & Cohen 1984). This inhibitory effect is commonly referred to as inhibition of return (IOR). Traditional theories on IOR describe this phenomenon as a foraging facilitator encouraging orienting towards novel items and, thus, enhancing the efficiency of environmental exploration (e.g., Klein, 2000; Posner & Cohen, 1984).

## **2.2. Attentional Sampling**

When it comes to our subjective experience of the outside world, our sensory perception seems to evolve in a continuous way. However, a highly influential paper by VanRullen and Koch (2003) called this idea into question. Instead, a discrete account for perceptual processes was postulated in which perception as well as attention are suggested to operate in rhythmic cycles. Since then, numerous studies reporting behavioral fluctuations in visual attention (for reviews, see VanRullen, 2016, 2018) have further challenged the notion that attention is a continuous cognitive process.

Instead of a sustained spotlight of attention, VanRullen and colleagues (2007) proposed that attention operates like a *blinking spotlight* that takes discrete samples of the environment (e.g., locations or objects) about seven times per second. Landau and Fries (2012) were among the first to examine how visual attention samples from more than one location. In their study, a target detection task with two simultaneously presented stimuli (drifting gratings) on the left and right side of the screen was applied. Participants were instructed to monitor for the appearance of a visual target (contrast change in one of the gratings) after a spatial cue was presented. This is a common experimental design in attentional sampling research as the first stimulus (e.g., predictive or unpredictable cue) resets perceptual cycles and serves as a temporal reference, while the second stimulus (e.g., target) can be used to assess the state of attentional oscillations by measuring target detection accuracy. To allow for a continuous assessment of performance, the target could appear following one of 105 possible inter-stimulus intervals (ISIs), from 750 ms before to 1,000 ms after the cue in steps of 11.7 ms. This approach is commonly referred to as *dense sampling*, as all possible ISIs are closely spaced to achieve fine temporal resolution of the investigated effect. Their results indicate that visual stimuli are sampled in rhythmic patterns between 4 Hz and 10 Hz. Moreover, after cueing attention to one location, Landau and Fries (2012) found theta-rhythmic performance fluctuations for spatially valid (i.e., same position as cue) and spatially invalid targets (i.e., different position than the cue) to be in anti-phase. Based on their observation, the authors concluded that when spatial attention is divided between two locations, the general attentional sampling rhythm of about 8 Hz manifests as an alternating 4 Hz rhythm for both locations. In other words, if two or more spatial locations need to be covertly monitored, our attention rhythmically switches back and forth between them, at a rate of about 4-8 Hz. This implies that human perception operates rhythmically, with alternating periods that are more favorable for target detection (i.e., the *good* phase) and periods that are less favorable (i.e., the *bad* phase). Several subsequent studies were able to report similar findings on the temporal structure of visual attention as well as the anti-phasic relationship between detection accuracy at distinct locations (e.g., Fiebelkorn et al., 2013; Huang et al., 2015; Re et al., 2019; Senoussi et al., 2019; Song et al., 2014).

The notion that attention is a rhythmic process finds support in studies that utilize neurophysiological methods (e.g., Busch et al., 2009; Busch & VanRullen, 2010; Fiebelkorn et al., 2018; Helfrich et al., 2018; Kienitz et al., 2018; Landau et al., 2015) such as electroencephalography (EEG) or magnetoencephalography (MEG). Previous findings on rhythmic brain signals led to the idea that neural oscillations might constitute the



neurophysiological basis of behavioral fluctuations (for review, see Buzsáki & Draguhn, 2004). Studies that examine the connection between neural oscillations and perception typically apply an experimental protocol in which perceptual outcomes are compared based on pre-stimulus EEG oscillatory phase in otherwise identical trials (VanRullen, 2016). Using this technique, early studies reported a strong link between pre-stimulus phase of EEG alpha (8-12 Hz) and theta (4-8 Hz) oscillations and target detection probability (Busch et al., 2009; Busch & VanRullen, 2010; Mathewson et al., 2009). Thus, whether a stimulus is perceived or not does not only depend on its properties such as luminance or contrast, but also on the time it appears relative to the phase of ongoing neural oscillations. In a MEG study, Landau and colleagues (2015) found that when participants monitored two locations for the appearance of a target, the power of laterized gamma-band activity (30-90 Hz) over the occipital and parietal cortex in the contralateral hemisphere was predictive of accuracy in target detection. Moreover, this gamma-band activity as well as attention-related enhancements in target detection alternated between hemispheres at about 4 Hz. More recent studies using electrocorticography (ECoG) revealed that theta-rhythmic modulations of the cortical excitability in frontal and parietal cortices were associated with behavioral oscillations during attention tasks in both humans (Helfrich et al., 2018) and monkeys (Fiebelkorn et al., 2018). Interestingly, Fiebelkorn and colleagues (2018) found theta-activity to serve as a clocking mechanism throughout the frontal eye fields (FEF) and lateral intraparietal area (LIP) with distinct neural correlates for the two rhythmically alternating states. More precisely, the first stage in which behavioral performance is enhanced was associated with FEF-dominated as well as LIP-dominated gamma-band activity. The second stage, in which behavioral performance is diminished was associated with LIP-specific alpha-band activity.

Taking all this empirical evidence together, the existence of a continuous attentional process seems more and more unlikely. Instead, the above presented studies provide robust empirical support for the idea that attention is a dynamic cognitive process that operates in a rhythmic way. Supporting evidence stems both from behavioral (e.g., Fiebelkorn et al., 2013; Huang et al., 2015; Landau & Fries, 2012; Re et al., 2019; Senoussi et al., 2019; Song et al., 2014; VanRullen et al., 2007) and neurophysiological research (e.g., Busch et al., 2009; Busch & VanRullen, 2010; Fiebelkorn et al., 2018; Helfrich et al., 2018; Landau et al., 2015; Mathewson et al., 2009) and suggests attentional rhythms at theta frequencies of about 4-8 Hz as well as anti-phasic relationships between several simultaneously attended locations or objects.

### 2.3. Microsaccades in Covert Attention

Microsaccades are miniature, fast, involuntary eye movements that continuously arise during sustained visual fixation (Martinez-Conde et al., 2004). These small eye movements with amplitudes below  $1^\circ$  of visual angle typically occur at a rate of around 1-2 Hz (Engbert & Kliegl, 2003; Hafed & Clark, 2002). Several possible functions have been attributed to microsaccades in the past, such as the maintenance of fixation position, the prevention of visual fading, the synchronization of visual transients, the maintenance of visual acuity, the exploration of fine spatial detail and resolving visual ambiguity (for review, see Rolfs, 2009). In the last decades, microsaccades have repeatedly been linked to *covert attention* (e.g., Engbert & Kliegl, 2003; Hafed & Clark, 2002; Laubrock et al., 2005, 2007, 2010; Liu et al., 2022; Lowet et al., 2018; Lv et al., 2022), a term used for cases in which the orientation of attention differs from the orientation of eye position (Posner, 1980).

Using a spatial cueing task, Hafed and Clark (2002) found that after the presentation of a spatial cue, microsaccades are biased towards that attended location. Thus, the authors concluded that directions of microsaccades directly reflect directions of covert attentional shifts. Several subsequent studies were able to replicate findings on the post-cue microsaccadic directional bias towards attended locations (e.g., Engbert & Kliegl 2003; Laubrock et al., 2005; Lowet et al., 2018; Xue et al., 2020). Furthermore, subsequent studies (e.g., Engbert & Kliegl, 2003; Laubrock et al., 2005, 2007, 2010; Lv et al., 2022) reported that microsaccade rates were modulated by shifts of visual attention, a phenomenon that is commonly referred to as the *microsaccadic rate signature* (Hafed & Ignashchenkova, 2013). More precisely, the microsaccade rate was found to drop to about 20% of the baseline rate about 100-150 ms after stimulus onset and then increase to about twice the baseline rate about 300-350 ms after cue onset. Eventually, microsaccade rate returned to baseline level at about 500 ms after cue onset. Interestingly, microsaccade direction was biased towards the cued location in the inhibitory phase and largely biased towards the uncued location in the rebound phase when peripheral cues (i.e., sensory-driven and involuntary) were applied (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Laubrock et al., 2005; Rolfs et al., 2004). This temporal modulation resembles a classic IOR effect (Galfano et al., 2004; Klein et al., 2000), in the sense that attention is facilitated towards a cued location shortly after cue presentation, followed by an inhibition of the cued location. On the contrary, when endogenous cues (i.e., goal-driven and voluntary) were applied, microsaccade rate was biased towards the cued location in the rebound phase (Engbert & Kliegl, 2003; Laubrock et al., 2010). Other studies reported that spontaneous microsaccade direction reflected the location of spontaneous

attentional shifts when no spatial cue was presented (Xue et al., 2020; Yuval-Greenberg et al., 2014). In light of the empirical evidence presented above, the existence of a strong link between microsaccades and spatial attention seems compelling. But what exactly does this link look like?

Lowet and colleagues (2018) argue for a critical and causal relationship between microsaccades and covert spatial attention. The authors found that neural processing in the area V4 and the inferior temporal cortex (IT) was only enhanced when microsaccades towards the attended stimulus occurred. Similarly, Chen et al. (2015) observed neural response enhancements in the superior colliculus (SC) and FEF for stimuli that appeared prior to the onset of microsaccades. Importantly, this pre-microsaccadic enhancement was most pronounced for directionally congruent stimuli (i.e., stimuli that were presented on the same hemifield as the microsaccade). On the contrary, other studies reported, that while the direction and timing of microsaccades is correlated with attention-related modulations of neural alpha activity (Liu et al., 2022) and firing rates in the SC (Yu et al., 2022), they are not necessary for such modulations to occur. Thus, the link between microsaccades and neural modulations might be a functional, rather than an obligatory one. Moreover, Liu and colleagues (2023) suggested, that while attentional shifts bias the direction of ongoing microsaccades they do not generate new ones, further challenging the notion of an obligatory relationship. With the intention to clarify these partially inconsistent findings, Srinivasan et al. (2023) re-analyzed the dataset of their original study (Lowet et al., 2018). Again, their results showed that attentional processes were strongly modulated when the first microsaccade was directed towards the cued location, while microsaccades away from the cued location had little or no effect. In addition to the first microsaccade that occurred after stimulus or cue onset, the authors investigated the effect of subsequent microsaccades. Interestingly, they found that subsequent microsaccades towards both directions enhanced attentional responses. Nevertheless, subsequent microsaccades towards the cued location still had the largest effects. Given these results, Srinivasan et al. (2023) suggest that when the first microsaccade is directed away from the cued location, attentional processes are delayed until a subsequent microsaccade (towards the cued location) occurs. Moreover, they suggest that once attention is deployed, the effect persists even if a later microsaccade is directed away from the attenuated stimulus. This conclusion is in line with previously reported findings on attentional effects for microsaccades directed both towards and away from the attended stimulus (Liu et al., 2022; Yu et al., 2022). Thus, Srinivasan et al. (2023) conclude that microsaccades are in fact not only markers, but also a cause for attentional effects. While this might constitute an

explanation for studies that did not report an obligatory link between attentional shifts and microsaccades (Liu et al., 2022; Yu et al., 2022), more research is necessary to really clarify the matter. Although the current state of research implies that microsaccades and spatial attention are strongly connected, the precise nature of this connection remains to be fully understood.

## **2.4. The Potential Link between Microsaccades and Attentional Sampling**

In the sections above, empirical evidence on the link between theta oscillations and attentional sampling as well as microsaccades and covert attention has been presented. Now, the possible link between rhythmic attentional sampling and microsaccades will be evaluated.

Previous research has found microsaccade direction to be biased towards the cued location in an inhibitory phase, towards the uncued location in the rebound phase and then towards the cued location again when microsaccade rate returned to baseline levels (e.g., Engbert & Kliegl, 2003; Hafed & Clark, 2002; Laubrock et al., 2005, 2007). This temporal dynamic of sequential shifting between two locations is in line with the notion that attention samples objects and locations in a rhythmic manner (e.g., Fiebelkorn et al., 2013; Huang et al., 2015; Landau & Fries, 2012; Re et al., 2019; Senoussi et al., 2019; Song et al., 2014; VanRullen et al., 2007). In other words, both microsaccades and attention switch back and forth between locations that are being monitored. As stated above, the microsaccade rate in previous research was commonly found to be at about 1-2 Hz (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Kienitz et al., 2018). However, other studies (Bosman et al., 2009; Lowet et al., 2016) found that at least under some experimental circumstances microsaccades can occur at a rate of about 3-4 Hz, a frequency similar to the theta rhythms of attentional sampling. Studies on rhythmic attentional sampling typically use cues to reset perceptual cycles (e.g., Landau & Fries, 2012). Similarly, cues were found to reset rhythms in ongoing microsaccadic oscillations (Hafed & Ignashchenkova, 2013; Tian et al., 2016). Given that microsaccades have been observed to reset neural oscillations (Gaarder et al., 1966), and since these oscillations play a role in rhythmic attentional sampling (e.g., Fiebelkorn et al., 2018; Landau et al., 2015), it is reasonable to expect synchrony between these two processes. Indeed, Bosman et al. (2009) show that ongoing oscillations in areas V1 and V4 predict microsaccades. Moreover, in their study microsaccades induced a modulation of gamma-band synchronization and behavioral responses (i.e., RTs). These observations suggest that microsaccadic rhythms are linked to the phase of ongoing brain oscillations as well as the process of sampling and exploring the visual environment.

Studies that argue for an obligatory link between microsaccades and visual attention (Lowet et al., 2018; Srinivasan et al., 2023) ultimately refer to the significant overlap between brain areas that are responsible for controlling (microsaccadic) eye movements and attentional processes, such as the SC (Chen et al., 2015; Krauzlis et al., 2013), the LIP (Bisley & Goldberg, 2010), the FEF (Chen et al., 2015; Squire et al., 2013) and the pulvinar nucleus of the thalamus (Halassa & Kastner, 2017; Saalman & Kastner, 2011). However, the idea that eye movements and attention are closely related is not novel. According to the *premotor theory of attention* (Rizzolatti et al., 1987) the same neural circuits that are responsible for planning and executing movements are also in charge of attention allocation. Thus, covert spatial attention is suggested to arise from weaker activation of the same neural circuits that prepare and initiate eye movements. Although the original form of the premotor theory of attention has largely been disproven (Smith & Schenk, 2012), current empirical evidence demonstrates that sensory and motor processes are tightly linked. For instance, Srinivasan and colleagues (2023) propose that the relationship between microsaccades and covert attention might resemble the relationship between larger saccades and feature attention, being typically controlled by the same neural circuit while becoming disconnected under certain conditions. In what way overlapping brain regions coordinate both rhythmic attentional sampling and exploratory (microsaccadic) eye movements remains to be fully understood through future research.

In their *rhythmic theory of attention* Fiebelkorn and Kastner (2019) propose that facilitatory attentional effects and exploratory (microsaccadic) eye movements might be associated with opposite phases of the same theta rhythms. Thus, they predict that microsaccades might be more likely to occur during periods of attentional disengagement (i.e., the *bad* period of the attentional fluctuation). Furthermore, the authors suggest that the direction of microsaccadic eye movements might be indicative of the state of attentional oscillations. For instance, microsaccades away from the cue might occur during attentional shifts, while microsaccades towards the cue might occur during another round of attentional sampling. This proposed relationship is perfectly in line with studies suggesting that microsaccades are an index of covert spatial attention (e.g., Engbert & Kliegl, 2003; Hafed & Clark, 2002; Laubrock et al., 2005, 2007, 2010). A few studies on attentional sampling have collected and analyzed eye movement data (e.g., Fiebelkorn et al., 2018; Landau et al., 2015; Spyropoulos et al., 2018). In doing so, they demonstrated that attention-related theta rhythms in behavioral and neural data remain present even when microsaccades are being controlled

for. However, the potential association between microsaccades and rhythmic attentional sampling has not yet been addressed as the main research question in a dedicated study.

## 2.5. Research Questions and Hypotheses

After reviewing the current state of research, we sensed a strong demand for a study dedicated to the potential relationship between microsaccades and attentional sampling as the main research question. The goal of this current study is to examine whether the rhythmic alternation between monitored locations is solely based on changes in cortical activity, or instead is at least in part already reflected peripherally in microsaccadic eye movements. To investigate this, we conducted a densely sampled covert spatial attention protocol, while measuring eye movements. Based on the empirical evidence presented above, we formulated the following hypotheses:

H1: The time course of target detection performance (i.e., hit rates, RTs and perceptual sensitivity at the various cue-target intervals) fluctuates rhythmically. Based on previous evidence, we suspect these fluctuations to be in the range of 4-12 Hz.

H2: For spatially valid and invalid trials, the rhythmic fluctuations in performance time courses are not in parallel, but in anti-phase with each other, suggesting that spatial attention samples distinct stimuli in alternation.

H3: Trials with successful target detection are associated with microsaccadic eye movements towards the target location, while trials with unsuccessful target detection are associated with microsaccadic eye movements away from the target location.

H4: The rhythmic spatial attentional sampling (alternating between left and right target locations), as hypothesized in H1 and H2, correlates with microsaccadic horizontal eye movements.

## 3. Methods

### 3.1. Participants

Twenty-seven participants (sixteen female;  $M_{age} = 24.5$  years,  $SD_{age} = 5.5$  years, range = 19 to 45 years) were recruited in exchange for either course credit or monetary compensation. Sample size was determined based on previous studies investigating rhythmic attentional sampling, commonly using a sample size of 15 to 25 participants (e.g., Fiebelkorn et al., 2013; Landau et al., 2015; Pomper & Ansorge, 2021; Re et al., 2019). All participants had normal or corrected-to-normal visual acuity as well as full color vision and had no history

of neurological or psychiatric diseases. All were naïve to the purpose of the experiment and gave written informed consent prior to data collection.

### 3.2. Apparatus and Stimuli

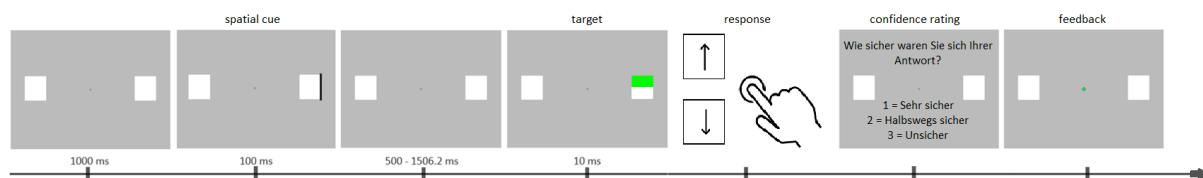
Participants were seated in a silent room wearing noise-cancelling earmuffs with their head positioned on a chin- and forehead rest 64 cm in front of the computer screen. Eye movement data were recorded via an Eyelink 1000 system (SR Research, Osgoode, Ontario, Canada) with a sampling rate of 1,000 Hz and a spatial resolution of less than  $0.005^\circ$ . The eyetracker was calibrated with a standard 5-point calibration procedure at the beginning of each experimental block. The experiment was presented via OpenSesame (Mathôt et al., 2012) on a 19-inch CRT monitor with a resolution of  $1,024 \times 768$  pixels (px) and a refresh rate of 85 Hz. Responses were delivered via a standard QWERTZ keyboard.

Visual stimuli were presented against a grey background. A central fixation dot (radius: 4 px) as well as two rectangular placeholders (160x160 px) placed on either side of the fixation dot were presented throughout the experiment. Note that both the fixation dot and the rectangular placeholders were positioned about 75 px below screen center (see Fig. 6). The cue stimulus consisted of a black vertical bar (10x160 px) briefly presented at the outer edge of either of the two placeholders. The target stimulus consisted of a contrast decrement (140x60 px) in the upper or lower half of one of the two placeholders.

### 3.3. Procedure

Figure 1 illustrates the experimental protocol. Each trial started with a presentation of the fixational screen (1 s) consisting of a central fixation dot and two placeholders on either side of it. Then, the unpredictable spatial cue was presented for 100 ms. After the cue, a variable ISI ranging from 500 to 1506.2 ms followed. ISI duration varied in steps of 11.7 ms, a consequence of the 85 Hz monitor refresh rate, resulting in 87 possible intervals. This manipulation allowed for a continuous assessment of target detection performance. After the varying ISIs, the target was randomly and with equal likelihood presented on either the same side (*valid condition*) as or the opposite side (*invalid condition*) of the cue for 10 ms. The luminance of the target was determined individually prior to the experiment using an adaptive staircase procedure to keep performance accuracy at around 66.7%. During the experiment, the luminance was further continuously adjusted every nine trials. Participants were instructed to press the down arrow of a keyboard when the stimulus appeared in the lower half of a placeholder and the up arrow when the stimulus appeared in the upper half of a placeholder, using their right hand. When the target was not perceived, participants were instructed to

guess. After the keyboard response, participants gave a confidence rating by either pressing Key 1 when they were very certain, Key 2 when they were fairly certain or Key 3 when they had guessed the response, using their left hand. At the end of each trial, participants were given visual feedback on their performance, with the central fixation dot turning green when target localization was successful or turning red when target localization was not successful. Each participant completed one practice block of 41 trials as well as two experimental sessions on separate days. Each experimental session consisted of 696 trials, split into 10 blocks with sufficient breaks in between. This resulted in a total of eight trials per ISI and condition (valid and invalid). After each block participants received additional feedback on their average RTs and target detection accuracy.



**Figure 1.** The experimental procedure. After an unpredictable spatial cue and a varying ISI, participants were presented with the target. Their task was to detect the target's location and give a confidence rating. After each trial participants were given visual feedback.

### 3.4. Statistical Analysis

All analyses were performed using MATLAB (Version 2021; The MathWorks, Natick, MA) and the CircStat toolbox (Version 1.21; Berens, 2009).

#### 3.4.1. Behavioral Data

We assessed target detection performance by computing average hit rates (percentage of correct responses), average RTs (for trials with correct responses) and d-prime ( $d'$ ). As a first step, we checked whether spatial cues generated the expected cueing effect by computing  $t$ -tests with the variables cue validity (valid vs. invalid cues) and average hit rates as well as average RTs. To ensure that correct responses truly reflected target detection, we excluded guess trials for following steps of our analysis. Moreover, trials with responses prior to target presentation have been excluded. All subsequent analyses on target detection performance were done separately for valid and invalid conditions as well as for pooled conditions (i.e., performance in the valid and invalid conditions combined). Moreover, a  $t$ -test was conducted



to compare the luminance of the targets in valid and invalid conditions, ensuring their proximity to the perceptual threshold across all trials.

Next, we computed the time course of target detection performance (i.e., mean hit rates, mean RTs and  $d'$ ) as a function of cue-target interval, separately for each participant. To this end, we first sorted all trials according to the duration of the cue-target interval. Then, we applied a moving-window approach with a step size of 11.7 ms to compute target detection performance within five bins of consecutive cue-target intervals (i.e., within 58.5 ms). Thus, we first computed performance for trials with ISIs between 500 and 558.5 ms before shifting the bin by 11.7 ms and computing performance for trials with ISIs between 511.7 and 570.2 ms. This procedure was repeated until all possible ISIs were covered.

To reveal the rhythmic nature of target detection performance (H1), we detrended and normalized the time courses of mean hit rates, mean RTs and  $d'$  by subtracting the second order polynomial fit. To measure periodicity in target detection, we used fast Fourier transform (FFT) to convert time-series into the frequency domain. This resulted in power and phase values within 11 frequency bins from 1 to 23 Hz. Since previous studies on attentional sampling reported fluctuations of behavioral performance to be in the theta and low-alpha range (e.g., Fiebelkorn et al., 2013; Landau & Fries, 2012; Re et al., 2019), our frequencies of interest were set to around 4 Hz to 12 Hz. Finally, the power spectra were averaged across participants.

Presence of statistically significant peaks as well as statistically significant phase relationships in the resulting power spectrum was assessed through permutation statistics ( $p = .05$ ). Actual cue-target intervals were randomly shuffled within participants before repeating the analysis steps described above. This reshuffling procedure was repeated 1,000 times to create a distribution of spectral peaks and phase values under the null hypothesis (i.e., no temporal pattern in the target detection performance time courses). When this distribution was compared to the actual empirical data, empirical spectral peaks exceeding the 95<sup>th</sup> percentile of peaks in the surrogate data after correcting for multiple comparisons for all tested frequencies were considered significant. The correction for multiple comparisons was performed using the false-discovery rate (FDR) correction, as outlined by Benjamini and Hochberg (1995).

For each significant spectral peak, the distribution of phase angles was tested for non-uniformity of circular data using Rayleigh tests (Berens, 2009). Furthermore, to test for the anti-phasic relationship between valid and invalid conditions (H2), William-Watson tests were

carried out (Berens, 2009). Again, these tests were conducted both on empirical data and on 1,000 surrogate data sets. If empirical  $p$ -values exceeded the 95<sup>th</sup> percentile of surrogate  $p$ -values, we considered the findings to be statistically significant.

### **3.4.2. Eyetracking Data**

Due to noisy eyetracking data, one participant had to be excluded from eye movement analysis. Eye movements were detected using an adapted version of the velocity-based algorithm developed by Engbert and Kliegl (2003). After translating vertical and horizontal eye positions into a two-dimensional velocity space a threshold of 4 standard deviations was used to detect (micro-)saccades. Moreover, for eye movements to be classified as microsaccades amplitudes up to 1° of visual angle, a minimum duration of 6 ms and temporal overlap of the two eyes were required. Eye movements with an amplitude above 1° of visual angle were classified as saccades. For our study only horizontal (micro-)saccades were of interest. Eye movements that were directed towards the cue were referred to as congruent, those that were directed away from the cue were referred to as incongruent.

To investigate the relationship between (micro-)saccades and target detection performance (H3), two-way repeated-measures analyses of variance (ANOVAs) were conducted using the independent variables saccade type (congruent microsaccade, incongruent microsaccade, congruent saccade, incongruent saccade or no saccade) and cue validity (valid cue or invalid cue) and the dependent variables hit rate and RT.

If previous spectral and phase analyses had validated the predicted rhythmic oscillations in target detection performance as well as the anti-phasic relationship between valid and invalid conditions, we would have proceeded to examine the correlation between rhythmic spatial attentional sampling and microsaccade direction (H4). More precisely, time courses as well as spectral outcomes of the relative number of (micro-)saccades would have been examined both for congruent and incongruent (micro-)saccades. We expected that the likelihood of (micro-)saccade occurrence fluctuates rhythmically and in anti-phase for congruent and incongruent (micro-)saccades, at the same frequency as target detection performance. However, as will be outlined in the next section, not all expected behavioral effects were found. Moreover, the number of (micro-)saccades in our study was not sufficient to perform spectral analysis. Consequently, H4 could not directly be tested.

As an alternative approach, two additional spectral analyses identical to the one outlined above were conducted to investigate how (microsaccadic) eye movements might have contributed to the rhythmic pattern of target detection performance. One analysis was

solely based on trials without (micro-)saccades, while the other was solely based on trials containing (micro-)saccades. By comparing results of the two spectral analyses to each other as well as to spectral analysis results based on the complete behavioral data set, we aimed to reveal the contributions of (micro-)saccades to rhythmic oscillations in behavioral performance.

### **3.4.3. Exploratory Eye Position Analysis**

In addition to analysis of (micro-)saccadic eye movements, we conducted an exploratory analysis on non-saccadic shifts in eye position. More precisely, the time course of vertical and horizontal eye positions was analyzed during two time intervals of interest: one set around cue onset (i.e., 100 ms before to 500 ms after cue presentation) and the other set around target onset (i.e., 500 ms before to 190 ms after target presentation). Importantly, to differentiate this analysis from the analysis of (micro-)saccades detailed above, this step only included trials with no (micro-)saccades. Within the time interval around cue onset, average eye positions were compared based on cue location (i.e., left or right) and target detection performance (i.e., hit or miss). Within the time interval around target onset, average eye positions were compared based on cue location (i.e., left or right), target location (i.e., left or right), cue validity (i.e., valid or invalid) and target detection performance (i.e., hit or miss). Moreover, for each sample, significance of the differences in eye position was tested via *t*-test (i.e., running *t*-tests over time, uncorrected).

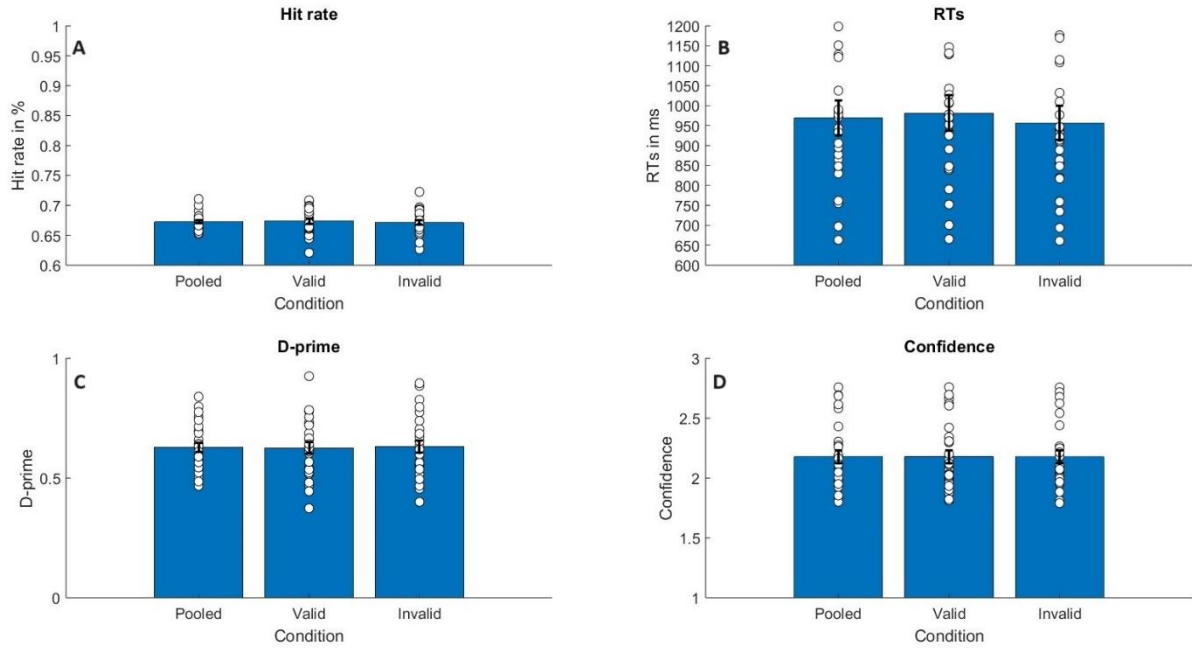
## **4. Results**

### **4.1. Behavioral Data**

#### **4.1.1. Descriptive Statistics**

The average target detection accuracy did not significantly differ between valid (hit rate:  $M = 0.7$ ,  $SD = 0.02$ ) and invalid trials (hit rate:  $M = 0.7$ ,  $SD = 0.02$ ,  $t(26) = 0.42$ ,  $p = .675$ ,  $d = 0.08$ ). Participants were significantly faster in invalid trials (RT:  $M = 956.8$ ,  $SD = 221.8$ ) compared to valid trials (RT:  $M = 981.1$ ,  $SD = 231.7$ ,  $t(26) = 2.92$ ,  $p = .007$ ,  $d = 0.56$ ), resembling a classic IOR effect. Moreover, sensitivity did not significantly differ between valid ( $d'$ :  $M = 0.6$ ,  $SD = 0.1$ ) and invalid conditions ( $d'$ :  $M = 0.6$ ,  $SD = 0.1$ ,  $t(26) = -0.19$ ,  $p = .848$ ,  $d = -0.04$ ). Likewise, average confidence did not significantly differ between valid ( $M = 2.2$ ,  $SD = 0.3$ ) and invalid trials ( $M = 2.2$ ,  $SD = 0.3$ ,  $t(26) = 0.21$ ,  $p = .833$ ,  $d = 0.04$ ).

Importantly, a considerable portion of trials, about 44.9% ( $M = 612.1$ ,  $SD = 235.4$ ), consisted of guess trials. This resulted in a substantial reduction in trial count for subsequent analysis steps. The targets' mean luminance did not significantly differ between valid ( $M = 252.3$ ,  $SD = 0.6$ ) and invalid trials ( $M = 252.3$ ,  $SD = 0.6$ ,  $t(26) = -1.96$ ,  $p = .061$ ,  $d = -0.38$ ). This ensures that comparisons can be made between valid and invalid conditions.

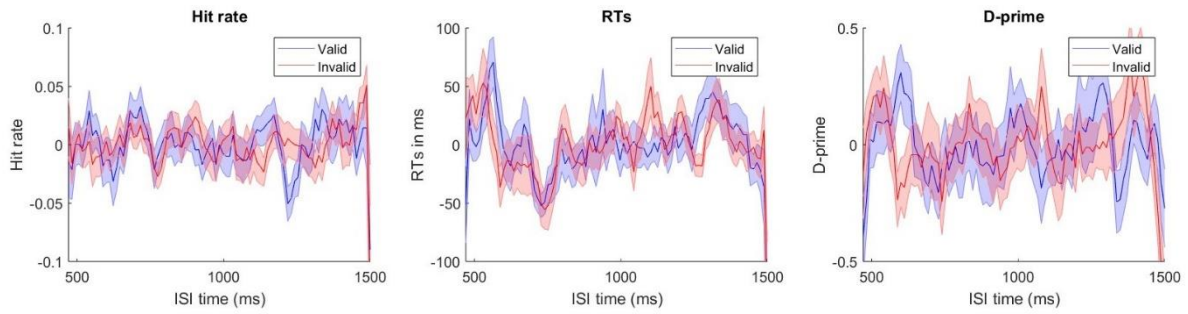


**Figure 2.** Overall behavioral results for pooled (left bars), valid (middle bars) and invalid (right bars) conditions. **A:** Average hit rate in percentages. **B:** Average RTs in ms. **C:** Average  $d'$ . **D:** Average confidence ratings. Error bars represent the standard error of the mean. White dots represent individual participants.

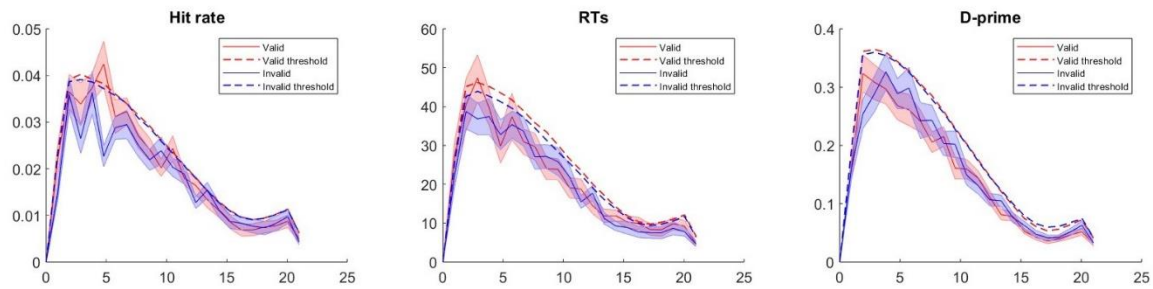
#### 4.1.2. Spectral Analysis

Figure 3 displays the grand-average time courses of hit rates, RTs and  $d'$  as a function of cue-target interval. Based on the time courses, target detection performance appeared to fluctuate rhythmically, especially in valid conditions.

In Figure 4, spectral analysis results of target detection performance (H1) are illustrated. For hit rates, the spectral analysis revealed a significant peak at  $\sim 5$  Hz ( $p = .026$  for 4.8 Hz) for valid conditions. For hit rates in invalid conditions, two smaller spectral peaks were observed at around 2 Hz ( $p = .652$  for 1.9 Hz) and around 4 Hz ( $p = .652$  for 3.8 Hz) that did not reach significance. A  $\sim 3$  Hz peak was present for RTs in valid conditions, which did not reach significance after correcting for multiple testing ( $p = .389$  for 2.9 Hz). Moreover, none of the observed spectral peaks of  $d'$  exceeded the significance threshold.

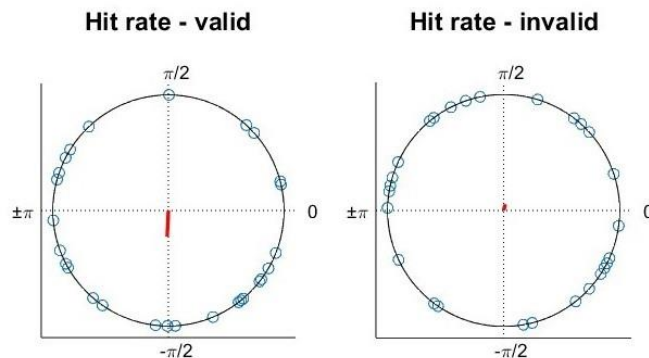


**Figure 3.** Time courses of target detection performance. Grand-average hit rates (left), RTs (middle) and  $d'$  (right) are shown for valid (blue) and invalid (red) conditions. Shaded areas represent the standard error of the mean.



**Figure 4.** Spectral power plots of target detection performance. Spectral power for hit rates (left), RTs (middle) and  $d'$  (right) is illustrated for valid (red) and invalid (blue) conditions. Solid lines represent empirical data, dashed lines represent resampled surrogate data. Shaded areas represent the standard error of the mean.

Finally, the phase relationships between valid and invalid hit rate time courses at  $\sim 5$  Hz were investigated (H2). Note that this analysis step was conducted although oscillations in invalid conditions lacked significance. In Figure 5, phase angles of hit rates at  $\sim 5$  Hz are displayed for valid and invalid conditions. The results of Rayleigh tests for non-uniformity revealed that the phases were not significantly different from a uniform distribution for both valid ( $p = .392$ ) and invalid ( $p = .383$ ) conditions. Furthermore, we found no significant phase relationship between valid and invalid conditions using the Watson-Williams ( $p = .476$ ).



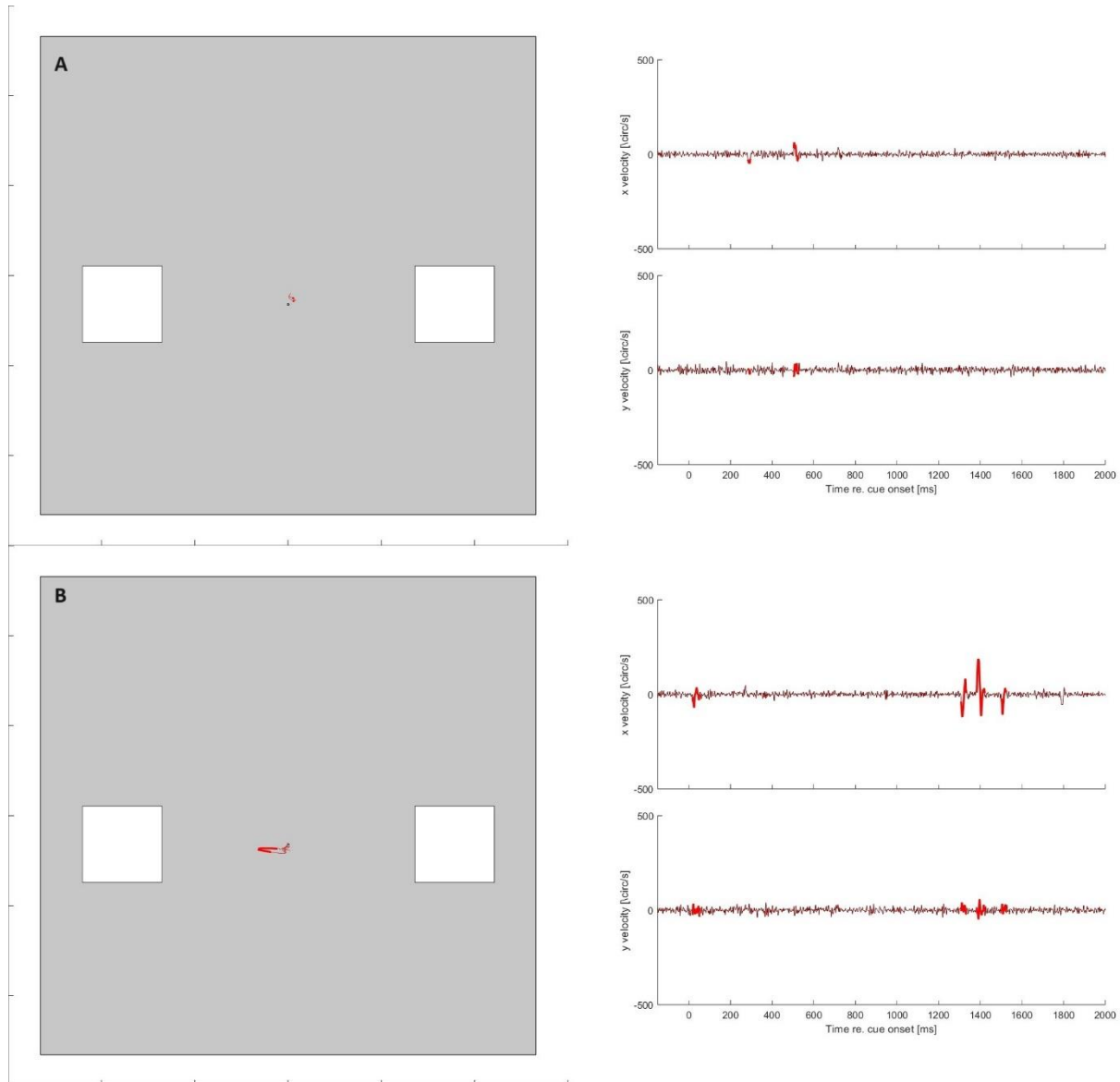
**Figure 5.** Phase angles of hit rate for valid (left) and invalid (right) conditions at ~5 Hz. Blue circles represent individual participants' phase angles. Red vectors represent the mean phase across participants.

## 4.2. Eyetracking Data

### 4.2.1. (Micro-)Saccade Characteristics

Figure 6 illustrates examples of a microsaccade (Panel A) and a saccade (Panel B). Over the course of the experiment, at least one (micro-)saccade was generated in a mean of 565.1 trials ( $SD = 217.1$ ). In a mean of 250.9 trials ( $SD = 144.8$ ), more than one eye movement took place. Given that every participant completed a total of 1,392 trials, this implies that (micro-)saccadic eye movements only occurred in less than half of all trials. On average, participants exhibited 755.6 microsaccades ( $SD = 411.5$ ) and 190.2 larger saccades ( $SD = 191.2$ ) during the whole experiment. Of these, about 64.5% of microsaccades ( $M = 487.2$ ,  $SD = 265.7$ ) occurred during hit trials, while about 35.5% ( $M = 268.4$ ,  $SD = 146.9$ ) occurred during miss trials. Moreover, about 61.5% of larger saccades ( $M = 118.8$ ,  $SD = 116.0$ ) occurred during hit trials, while about 38.5% ( $M = 71.4$ ,  $SD = 76.0$ ) occurred during miss trials. Having a look at the direction of microsaccadic eye movements, an average of 48.4% of microsaccades ( $M = 368.8$ ,  $SD = 193.3$ ) landed on the same hemifield as the cue, whereas about 51.6% ( $M = 386.9$ ,  $SD = 219.3$ ) landed on the opposite hemifield of the cue. Furthermore, it was observed that microsaccades were significantly more likely to be directed away from the cued location than towards the cued location ( $t(25) = -2.32$ ,  $p = .029$ ,  $d = 0.45$ ). Relative to the location of the target, a mean of 50.4% of microsaccades ( $M = 381.3$ ,  $SD = 207.3$ ) landed on the same hemifield, while about 49.6% ( $M = 374.4$ ,  $SD = 204.7$ ) landed on the opposite hemifield. This difference, however, was not significant ( $t(26) = 1.64$ ,  $p = .113$ ,  $d = 0.32$ ). When it comes to the direction of larger saccades, about 52.1% of saccades ( $M = 98.3$ ,  $SD = 100.9$ ) landed on the same hemifield as the cue, whereas about 47.9% ( $M = 92.0$ ,  $SD = 91.6$ ) landed on the opposite hemifield. This difference, however, also did not reach

significance ( $t(25) = 1.30, p = .206, d = 0.25$ ). Furthermore, an average of 49.2% of saccades ( $M = 93.5, SD = 94.1$ ) were directed to the same hemifield as the target, while about 50.8% ( $M = 96.7, SD = 97.37$ ) were directed to the opposite hemifield. Again, this difference did not yield significance ( $t(25) = -1.56, p = .131, d = 0.31$ ).



**Figure 6.** Example of a microsaccade (A) and a saccade (B). On the left side the display between cue and target onset is illustrated. Red lines represent shifts in eye position, bold lines represent (micro-)saccades. On the right side horizontal and vertical velocities are plotted against time relative to cue onset. Bold lines represent velocities during (micro-)saccades.

#### 4.2.4. Two-Way ANOVAs

As a next step, we investigated the relationship between (micro-)saccade direction and target detection performance (H3). Results of the two-way ANOVA with saccade type (congruent microsaccade, incongruent microsaccade, congruent saccade, incongruent saccade or no saccade) and cue validity (valid cue or invalid cue) as independent variables and hit rate as the dependent variable revealed that saccade type ( $F(4,100) = 1.01, p = .408, \eta_p^2 = 0.02$ ) as well as cue congruency ( $F(1,25) = 0.04, p = .845, \eta_p^2 < 0.01$ ) had no significant main effect. Moreover, no significant interaction between saccade type and cue congruency was observed ( $F(4,100) = 0.58, p = .677, \eta_p^2 < 0.01$ ). Similarly, results of the two-way ANOVA with the same independent variables as before but with RT as the dependent variable revealed no significant main effect for saccade type ( $F(4,100) = 1.93, p = .111, \eta_p^2 = 0.01$ ) and cue congruency ( $F(1,25) < 0.01, p = .981, \eta_p^2 < 0.01$ ). Furthermore, interaction between saccade type and cue congruency did not reach significance ( $F(4,100) = 0.88, p = .481, \eta_p^2 < 0.01$ ).

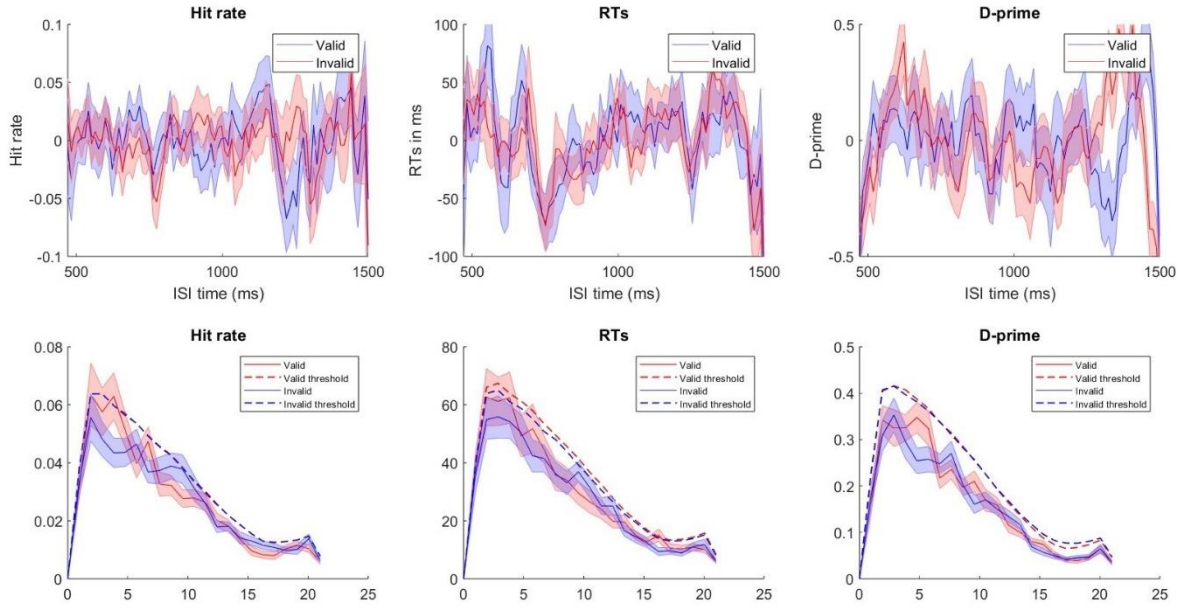
#### 4.2.2. Spectral Analysis without (Micro-)Saccades

Finally, we report the results of our analysis investigating how (micro-)saccades contribute to oscillations in target detection. We performed the same spectral analyses as in the previous section but split our sample into trials that contained (micro-)saccades and those that did not. In Figure 7, time courses as well as spectral power plots of target detection performance for trials without (micro-)saccadic eye movements are displayed. For hit rates in valid conditions, a spectral peak at ~4 Hz was observed. However, after correcting for multiple testing the significance threshold was not met ( $p = .195$  for 3.8 Hz).

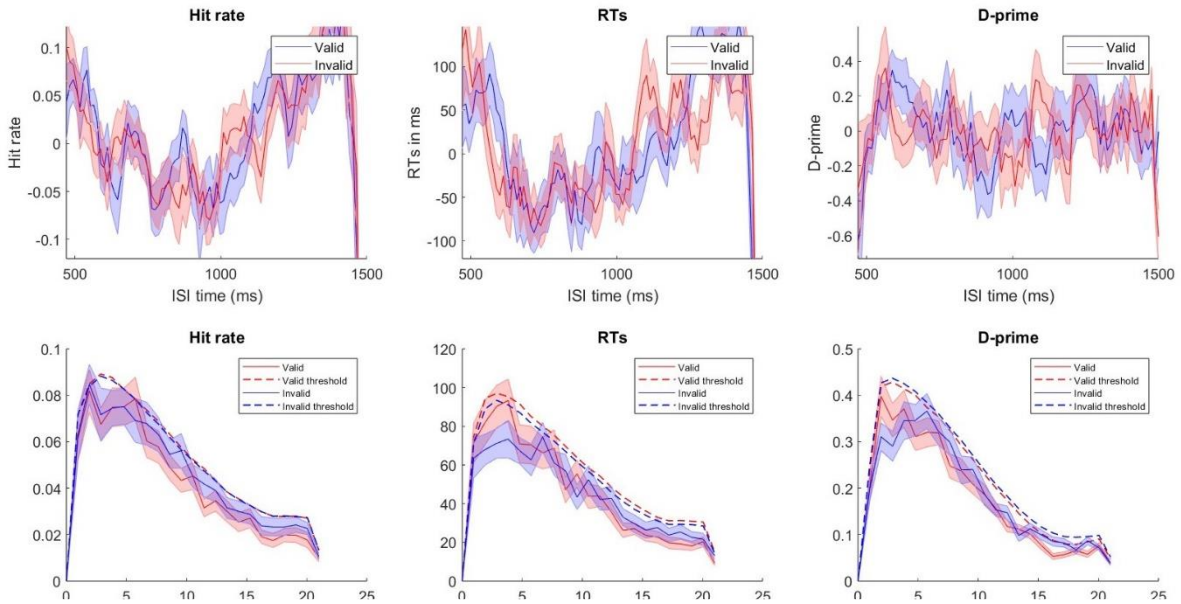
#### 4.2.3. Spectral Analysis with (Micro-)Saccades

In addition to spectral analysis without (micro-)saccades, fluctuations in target detection performance have been investigated solely based on trials with (micro-)saccades. Figure 8 illustrates the resulting time courses as well as spectral power plots of target detection performance. In this spectral analysis, no significant spectral peaks were observed.





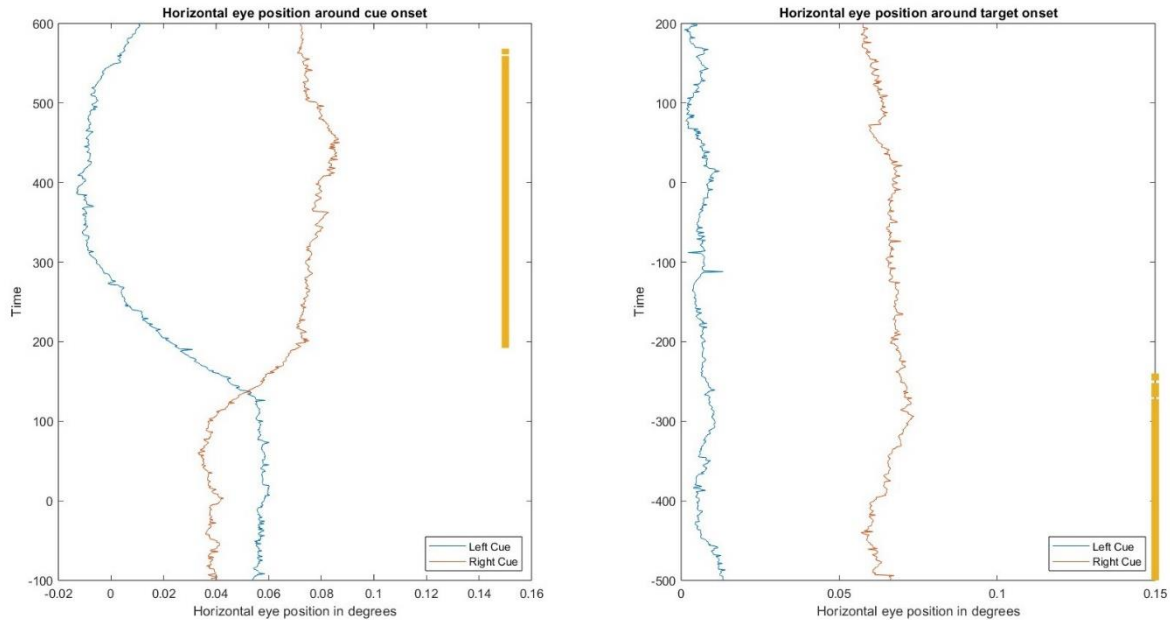
**Figure 7.** First row: time courses of target detection performance for trials without (micro-)saccades. Grand-average hit rates (left), RTs (middle) and  $d'$  (right) are shown for valid (blue) and invalid (red) conditions. Shaded areas represent the standard error of the mean. Second row: spectral power plots of target detection performance for trials without (micro-)saccades. Spectral power for hit rates (left), RTs (middle) and  $d'$  (right) is illustrated for valid (red) and invalid (blue) conditions. Solid lines represent empirical data, dashed lines represent resampled surrogate data. Shaded areas represent the standard error of the mean.



**Figure 8.** First row: time courses of target detection performance for trials with (micro-)saccades. Grand-average hit rates (left), RTs (middle) and  $d'$  (right) are shown for valid (blue) and invalid (red) conditions. Shaded areas represent the standard error of the mean. Second row: spectral power plots of target detection performance for trials with (micro-)saccades. Spectral power for hit rates (left), RTs (middle) and  $d'$  (right) is illustrated for valid (red) and invalid (blue) conditions. Solid lines represent empirical data, dashed lines represent resampled surrogate data. Shaded areas represent the standard error of the mean.

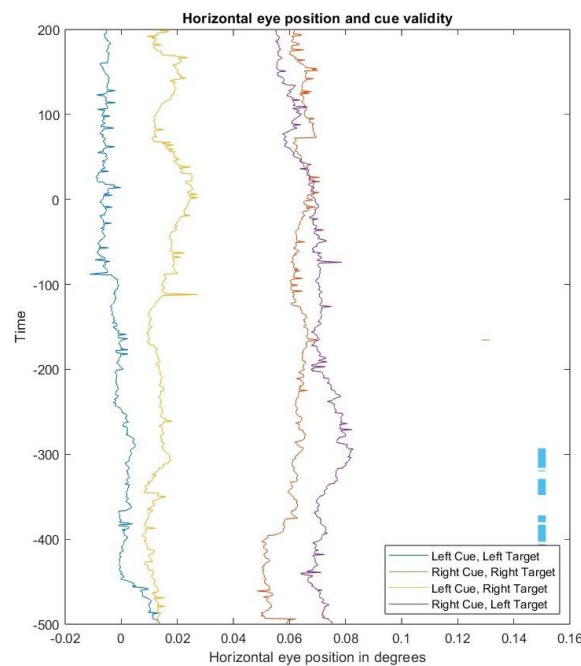
#### 4.2.5. Eye Position Time Courses

As an exploratory analysis, the time courses of vertical and horizontal eye positions around cue and target presentation were investigated across participants. Note that there was a consistent, slight deviation in both vertical and horizontal eye positions from the central fixation point. We suspect this deviation to be of random nature. No systematic shifts were observed in vertical eye positions (see Appendix). Figure 9 illustrates horizontal eye positions locked to cue and target onset based on cue location (i.e., left or right). Analysis of horizontal eye positions around cue onset indicated that gaze position shifted towards the location of the cue. When the cue was presented on the left hemifield horizontal, eye positions were biased to the left and vice versa. Moreover, running  $t$ -tests revealed that this systematic difference in horizontal eye positions was significant ( $p < .05$ ) throughout the time interval of about 200 to 550 ms after cue presentation. Similarly, a shift in gaze position towards the direction of the cue was found around target onset. Moreover, running  $t$ -tests indicated that this systematic difference was significant ( $p < .05$ ) throughout the time interval of 500 to 250 ms prior to target presentation.



**Figure 9.** Horizontal eye positions in degrees of visual angle against time around cue onset (left) and target onset (right) when cue was presented on the left hemifield (blue) vs. right hemifield (red). Yellow bars represent timepoints in which the difference in eye position between left and right cues was significant ( $p < .05$ ).

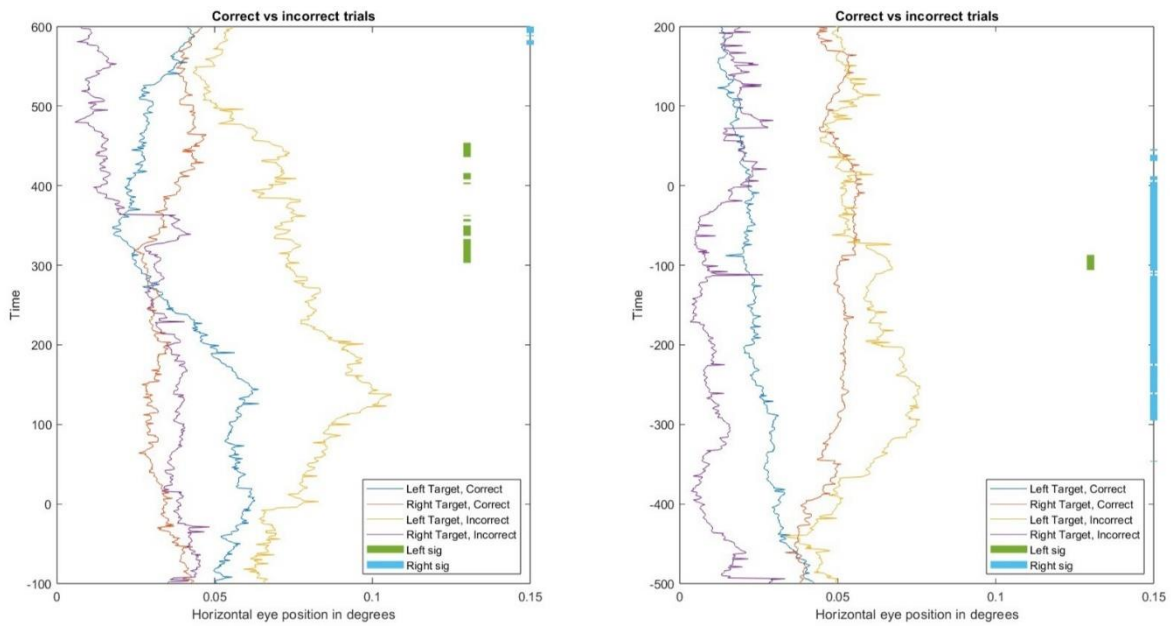
As a next step, shifts of horizontal eye positions were investigated based on cue validity. Figure 10 displays gaze positions around target onset when cues were valid versus when cues were invalid. In conditions with both valid and invalid cues, horizontal eye positions were found to be biased towards the cued location. When targets were presented on the right hemifield, the difference in eye positions for valid and invalid conditions was significant ( $p < .05$ ) around 435 to 300 ms prior to target onset. For left targets, differences in eye position did not reach significance.



**Figure 10.** Horizontal eye positions in degrees of visual angle against time around target onset. Average eye positions are displayed for left and right targets when the cue was valid (blue line for left target, red line for right target) and invalid (purple line for left target, yellow line for right target). The blue bar represents timepoints in which the difference in eye position between valid and invalid conditions when target was right was significant ( $p < .05$ ).

Finally, we investigated whether shifts in gaze position had an impact on task performance. In Figure 11, horizontal eye positions locked to cue and target onset are displayed both for correct (i.e., hit) and incorrect (i.e., miss) trials. When left targets were successfully detected, horizontal eye position was biased more to the left hemifield compared to when left targets were not successfully detected. Likewise, when right targets were successfully detected, horizontal eye position was shifted more to the right than when right targets were not successfully detected. These systematic differences in gaze position around cue onset based on target detection performance were significant around 300 to 450 ms after

cue onset for left targets ( $p < .05$ ) and around 580 to 600 ms after cue onset for right targets ( $p < .05$ ). Moreover, we found eye positions to be shifted more to the right prior to target onset when right targets were successfully detected compared to when right targets were missed. Similarly, for left targets, successful target detection was associated with a more left eye position compared to when left targets were missed. Running  $t$ -tests revealed that these systematic differences in gaze position were significant around 100 to 70 ms prior to target onset for left targets ( $p < .05$ ) and around 300 ms before to 50 ms after target onset for right targets ( $p < .05$ ).



**Figure 11.** Horizontal eye positions in degrees of visual angle against time around cue onset (left) and target onset (right) when target was successfully detected (blue line for left targets, red line for right targets) vs not successfully detected (yellow line for left targets, purple line for right targets). Green bars represent time points in which the difference in eye position between correct and incorrect trials was significant when target was left ( $p < .05$ ), blue bars represent time points in which the difference in eye position between correct and incorrect trials was significant when target was right ( $p < .05$ ).

## 5. Discussion

The present study is the first to address the potential link between microsaccades and attentional sampling as its main research question. Previous research found that microsaccades directly reflect shifts in covert spatial attention (e.g., Engbert & Kliegl 2003; Hafed & Clark, 2002; Laubrock et al., 2005; Lowet et al., 2018; Xue et al., 2020; Yuval-Greenberg et al., 2014). Furthermore, the temporal dynamic of the *microsaccadic rate*

*signature* (Hafed & Ignashchenkova, 2013) is in line with the notion that attention samples several locations or objects in a theta-rhythmic manner (e.g., Busch et al., 2009; Fiebelkorn et al., 2013; Helfrich et al., 2018; Landau & Fries, 2012; Landau et al., 2015; Re et al., 2019; VanRullen, 2016, 2018). Based on these observations, Fiebelkorn and Kastner (2019) proposed the *rhythmic theory of attention* in which they predicted facilitatory attentional effects and microsaccadic eye movements to occur during opposite periods of the same theta rhythms. According to their theory, microsaccades occur more frequently during so-called *bad* phases of attentional fluctuation. The goal of our study was to investigate whether rhythmic attentional sampling is at least partly reflected peripherally in microsaccadic eye movements. To examine this, we conducted a densely sampled Posner-cueing protocol with targets near the perception threshold while measuring participants' eye movements.

### 5.1. Replicating Theta-Rhythmic Oscillations in Behavioral Performance

Spectral analysis revealed significant ~5 Hz fluctuations of target detection performance in valid trials. For invalid trials, non-significant behavioral oscillations were observed at around 2 Hz and 4 Hz. Moreover, analysis of phase coherence did not reveal non-uniform phase distribution or an anti-phasic relationship of the two rhythms. Note, however, that results of the phase analysis need to be taken with a grain of salt as rhythmic oscillations in invalid trials did not reach significance. Taken together, the hypothesized 4-12 Hz rhythmic oscillations of target detection performance (H1) could only partially be confirmed, namely solely for the valid condition. While we suspect that behavioral fluctuations occurred around 4 Hz in invalid conditions, we were not able to confirm statistical significance. Furthermore, we did not find evidence for the expected anti-phasic relationship of time courses for valid and invalid trials (H2).

The fact that previous findings on rhythmic attentional sampling (e.g., Busch et al., 2009; Fiebelkorn et al., 2013; Helfrich et al., 2018; Landau & Fries, 2012; Landau et al., 2015; Re et al., 2019; VanRullen, 2016, 2018) could only partially be replicated in this study might be attributed to different reasons. One contributing factor to the limited replication of previous findings might be the low trial count, resulting from exclusion of guess trials. Importantly, to our knowledge this study was the first to implement confidence ratings into an attentional sampling protocol. This allowed us to exclude non-informative trials in which participants did not perceive the target (i.e., guess trials) and only investigate trials in which the target was near perception threshold, but responses were not guessed. However, this exclusion procedure reduced our trial count by about 44.9%, thus almost dividing our

behavioral data set in half. This low trial count decreased the signal-to-noise ratio in our data, likely contributing to the non-significance of behavioral oscillations in invalid conditions as well as the anti-phasic relationship. It is important to note that in light of the reduction in trial count, our findings regarding the ~5 Hz fluctuations in valid trials are even more convincing.

Another factor that might have impeded the replication of previous results might be our chosen experimental task. Although our experimental design largely resembles those of previous studies (i.e., densely sampled Posner-cueing protocol with targets near perception threshold), our experiment consisted of a discrimination task, while most previous attentional sampling protocols (e.g., Busch et al., 2009; Helfrich et al., 2018; Fiebelkorn et al., 2018, Landau & Fries, 2012, Re et al., 2019) employed more simple detection tasks. This way, we were able to assess false alarm rates through incorrect responses instead of catch trials. However, combining target detection and localization likely resulted in the engagement of more complex cognitive and neural processes, potentially involving more internal noise and variance.

## **5.2. (Micro-)Saccadic Contributions to Rhythmic Attentional Sampling**

Given that not all expected results on rhythmic fluctuations in behavioral performance could be observed, the specific role of (micro-)saccades in attentional sampling is difficult to assess. When eye movements occurred, they mirrored the overall (i.e., not time-resolved) results of RTs in the sense that microsaccades were significantly more likely to be directed away from the cued location than towards the cued location, resembling a classic IOR effect (Klein, 2000; Michel & Busch, 2023; Posner & Cohen, 1984). This is in line with previous observations, suggesting that microsaccades reflect the orientation of covert attention (e.g., Engbert & Kliegl 2003; Hafed & Clark, 2002; Laubrock et al., 2005; Lowet et al., 2018; Xue et al., 2020; Yuval-Greenberg et al., 2014). However, contrary to our expectations (micro-)saccades were only observed in less than half of our trials. In contrast to that, previous studies reported microsaccade rates of 1-2 Hz (Engbert & Kliegl, 2003; Hafed & Clark, 2002) and under certain experimental circumstances even of 3-4 Hz (Bosman et al., 2009; Lowet et al., 2016). Considering the analysis time window of about 1 s on each trial as well as the high spatial resolution ( $< 0.005^\circ$ ) and high sampling rate (1,000 Hz) of our eyetracking system, we would have expected a larger microsaccade count.

As a next step, we investigated the impact of (micro-)saccadic eye movements on target detection performance (H3). To do this, we conducted two two-way repeated-measures ANOVAs with saccade type and cue congruency as independent variables and hit rate and RT

as dependent variables. Neither of the ANOVAs revealed significant main effects for saccade type and cue congruency on behavioral performance. Furthermore, interactions between the two independent variables did not yield significance. While this general analysis lacks the temporal specificity of the spectral approach, these results challenge the notion that microsaccades influenced the present behavioral performance.

As outlined before, directly examining the correlation between rhythmic attentional sampling and microsaccade direction (H4) was not possible due to the limited significance of behavioral effects as well as the limited number of (micro-)saccades. Thus, we chose an alternative approach to investigate contributions of (micro-)saccadic eye movements to rhythmic attentional sampling. This led us to conduct two additional spectral analyses: one solely based on trials with (micro-)saccades, and one solely based on trials without (micro-)saccades. Through comparison of these two spectral outcomes with each other, as well as with the spectral outcomes obtained from the complete behavioral data set, we aimed to examine the influence of (micro-)saccades on rhythmic fluctuations in target detection performance. However, neither of the two additional spectral analyses revealed significant outcomes. Again, we speculate that the lack of significance could be attributed to the limited number of available trials. Separation of trials based on (micro-)saccade occurrence, on top of the exclusion of guess trials, led to a substantial reduction in the number of available trials, thus reducing the likelihood of observing significant behavioral effects in either case.

### **5.3. Exploratory Findings on Systematic Shifts in Horizontal Eye Position**

Based on the inconclusive results on the role of microsaccades in rhythmic attentional sampling, we decided to have a closer look at the time courses of vertical and horizontal eye positions around cue and target onset, for trials in which we did not detect any (micro-)saccades. Note that this analysis was purely exploratory and thus needs to be interpreted with caution.

For average vertical eye positions no systematic shifts have been observed.

Time courses of horizontal eye positions, however, revealed several noteworthy findings. Both around cue and target onset, we found horizontal eye positions to be systematically shifted towards the cued location. Moreover, these systematic shifts yielded significance throughout large portions of the analyzed time intervals (i.e., about 200-550 ms after cue presentation and about 500-250 ms prior to target presentation). Thus, while (micro-)saccades were more likely to be directed away from the cued location, average eye

positions in trials without microsaccades were more likely to be directed towards the cued location.

We also found that when targets were presented on the right hemifield, right (i.e., valid) cues compared to left (i.e., invalid) cues caused significantly distinct eye positions prior to target presentation (i.e., 435-300 ms before the target). For left targets, this systematic difference did not reach significance.

Finally and most interestingly, we found small changes in horizontal eye positions to have a significant impact on target detection performance. More precisely, when targets were successfully detected eye positions were biased more towards the targets' location compared to when targets were not successfully detected. This systematic difference reached significance throughout prolonged time intervals both around cue onset (i.e., about 300-450 ms after cue onset) and around target onset (i.e., about 300 ms before to 50 ms after target onset). Thus, targets were more likely to be successfully detected when horizontal eye positions were shifted towards their direction. Based on these observations, we speculate that even in absence of (micro-)saccades, small changes in eye position can influence behavioral performance. To clarify whether the observed effects were merely a result of noise in our data or, instead, whether these small eye position shifts are a part of an exploratory behavior, such as attentional sampling, further research is necessary.

#### **5.4. Conclusion**

The present study examined whether rhythmic attentional sampling is a process solely driven by changes in cortical activity or at least partly reflected in microsaccadic eye movements. However, we were not able to provide conclusive results on microsaccadic contributions to rhythmic attentional sampling. This is likely due to the limited replication of previously observed theta-rhythmic fluctuations in behavioral performance and the insufficient number of trials containing microsaccades. To assess the specific role of microsaccadic eye movements, future research should increase the number of trials to ensure sufficient microsaccade count. Nevertheless, this study presents novel and highly interesting findings on small non-saccadic shifts in horizontal eye position and their potential impact on target detection performance. Future research needs to take a closer look at these systematic changes in eye position to determine whether they constitute a component of an exploratory behavior, such as rhythmic attentional sampling.



## 6. References

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## 7. Appendix

### 7.1. Abstract

Current research suggests that spatial attention samples from distinct objects and locations in alternating phases of a theta rhythm (3-8 Hz). Moreover, microsaccades have frequently been described as a potential index of covert spatial attention, leading us to the question what role microsaccadic eye movements might play in rhythmic attentional sampling. To this end, we assessed target detection performance in a Posner-cueing task at different inter-stimulus intervals (ISIs), while measuring participants' eye movements. The experimental task used in our study only partly elicited the expected theta-rhythmic oscillations in behavioral performance. While we found that behavioral performance in validly cued trials fluctuated at ~5 Hz, no significant behavioral oscillations were observed in invalid trials. Due to the limited replication of behavioral effects of attentional sampling as well as the low microsaccade count in our study, assessing the degree of microsaccadic contributions to attentional sampling was difficult. Nevertheless, our study provides novel and interesting findings on small non-saccadic shifts in eye position and their potential impact on target detection performance and should thus be of high value for future research in the field.

#### ***Keywords***

attentional sampling, behavioral oscillations, theta, microsaccades, visual attention, spatial attention, eye position

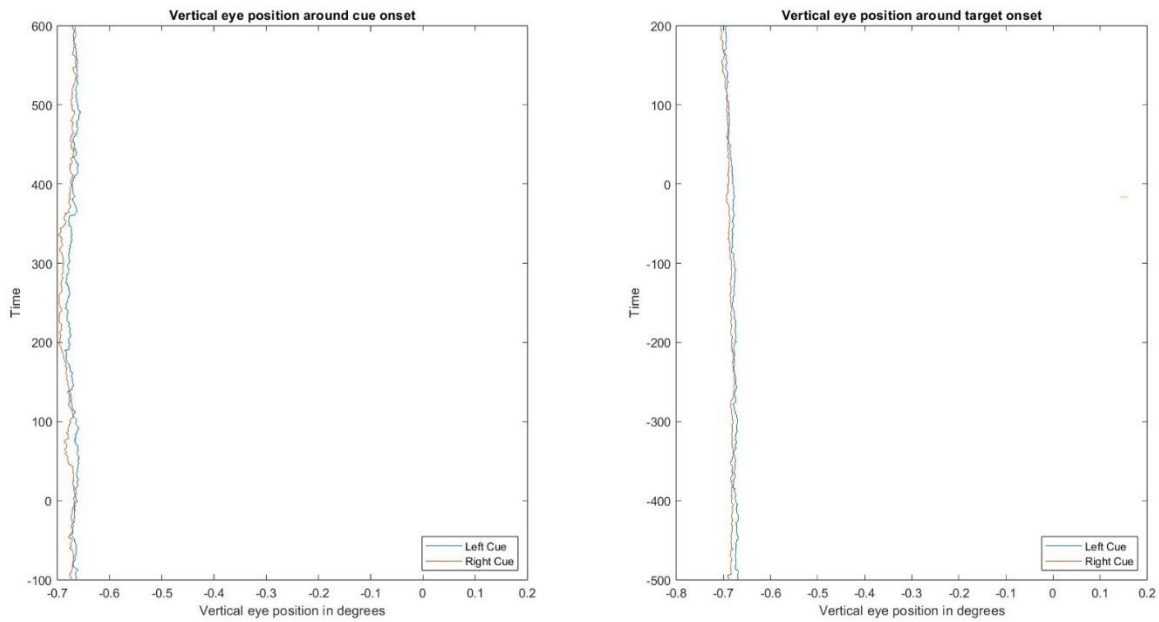
## 7.2. Zusammenfassung

Aktuelle Forschungsergebnisse deuten darauf hin, dass räumliche Aufmerksamkeit verschiedene Objekte und Orte in abwechselnden Phasen eines Theta-Rhythmus (3-8 Hz) abtastet. Zudem wurden Mikrosakkaden in früheren Studien vermehrt als potenzieller Index verdeckter Aufmerksamkeit bezeichnet, was uns zu der Frage führte welche Rolle mikrosakkadischen Augenbewegungen in rhythmischer Aufmerksamkeitsabtastung (engl. *rhythmic attentional sampling*) zugeschrieben werden kann. Um dies zu untersuchen, wurde bei einer Posner-Cueing Aufgabe die Leistung der Zielreizerfassung in verschiedenen Zeitintervallen erhoben. Gleichzeitig wurden Augenbewegungen der Versuchspersonen gemessen. Die von uns verwendete experimentelle Aufgabe konnte die erwarteten theta-rhythmischen Oszillationen der Verhaltensleistung nur teilweise hervorrufen. Während die Verhaltensleistung in validen Durchgängen mit ~5 Hz fluktuierte, konnten in nicht-validen Durchgängen keine signifikanten Verhaltensoszillationen nachgewiesen werden. Aufgrund der begrenzten Replikation erwarteter Verhaltenseffekte sowie der geringen Anzahl an Mikrosakkaden in unserer Studie, konnten die Effekte mikrosakkadischer Augenbewegungen auf die Aufmerksamkeitsabtastung nicht klar bestimmt werden. Nichtsdestotrotz liefert unsere Studie neue und interessante Erkenntnisse über kleine nicht-sakkadische Verschiebungen der Augenpositionen und deren mögliche Auswirkung auf die Verhaltensleistung, weshalb sie für zukünftige Forschung einen wichtigen Beitrag leistet.

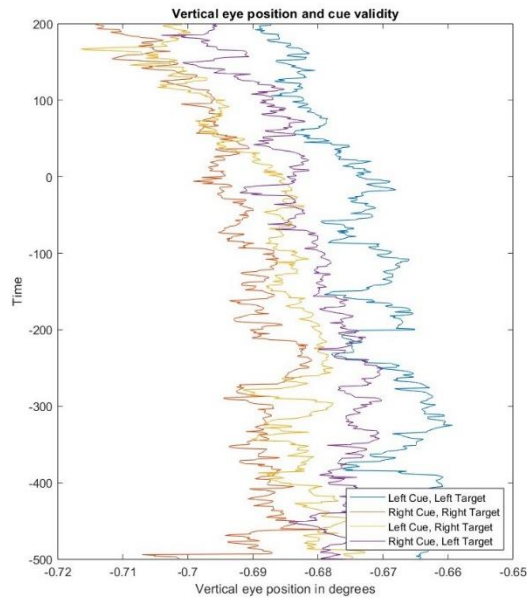
### ***Schlagwörter:***

Aufmerksamkeitsabtastung, behaviorale Oszillationen, Theta, Mikrosakkaden, visuelle Aufmerksamkeit, räumliche Aufmerksamkeit, Augenposition

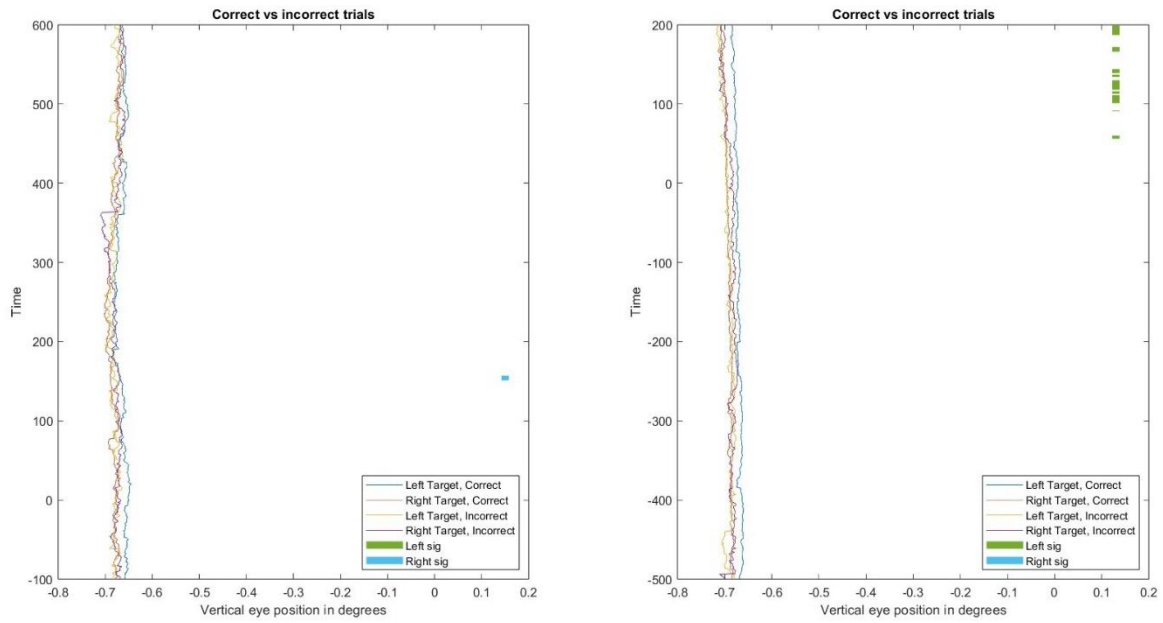
### 7.3. Vertical Eye Position Plots



**Figure 12.** Vertical eye positions in degrees of visual angle against time around cue onset (left) and target onset (right) when cue was presented on the left hemifield (blue) vs. right hemifield (red).



**Figure 13.** Vertical eye positions in degrees of visual angle against time around target onset. Average eye positions are displayed for left and right targets when the cue was valid (blue line for left target, red line for right target) and invalid (purple line for left target, yellow line for right target).



**Figure 14.** Vertical eye positions in degrees of visual angle against time around cue onset (left) and target onset (right) when target was successfully detected (blue line for left targets, red line for right targets) vs not successfully detected (yellow line for left targets, purple line for right targets).