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Introduction

To manage the information processing constraints of the brain, selective attention biases neural processing towards information that is relevant for the current behavior (Bruckmaier et al., 2020; Desimone & Duncan, 1995; Wolfe, 1994). Traditional theories proposed a continuous 'spotlight of attention' that shifts from one spatial location to another, facilitating stimulus processing at the presently attended location (Posner, 1980). However, more recent evidence has shown that attention samples information rhythmically along with underlying neuronal theta-band (3–8 Hz) oscillations in the frontoparietal network (Busch et al., 2009; Busch & VanRullen, 2010; Fiebelkorn et al., 2013, 2018, 2019; Helfrich et al., 2018; Landau & Fries, 2012; VanRullen et al., 2007; VanRullen, 2016). For instance, electroencephalography (EEG) recordings have revealed that the detection of an attended threshold stimulus depends on the prestimulus phase of frontocentral theta oscillations at approximately 7 Hz (Busch et al., 2009; Busch & VanRullen, 2010). Such phase-dependent rhythmic sampling is believed to provide discrete temporal windows to either process information at the attended location (i.e., 'optimal' phase) or to shift attention to other potentially relevant locations (i.e., 'less optimal' phase), resolving the fundamental tradeoff between exploration and exploitation (Fiebelkorn & Kastner, 2019; VanRullen, 2013, 2016).

Other recent studies have reported rhythmic behavioral fluctuations by measuring performance at variable time intervals between a reset event (e.g., spatial cue) and target (e.g., Fiebelkorn et al., 2013; Landau & Fries, 2012; Re et al., 2019; Song et al., 2014). In an initial study, participants monitored two spatial locations for an upcoming target. After attention was cued towards one location, target detection fluctuated rhythmically at a theta frequency (~4 Hz) at each location, and in antiphase between the two locations (Landau & Fries, 2012). Further studies have observed antiphasic theta-rhythmic sampling between two non-spatial features (Re et al., 2019) and objects (Fiebelkorn et al., 2013; Helfrich et al., 2018) at approximately 4 Hz. Together, these findings indicate that attention alternates theta-rhythmically between several relevant options (e.g., locations), selecting one option at a given time (Busch et al., 2009; Fries, 2023; VanRullen, 2016).

Similarly, recent work has demonstrated that internal representations in visual working memory (VWM) are prioritized at lower theta frequencies between 3.5 and 6 Hz, resembling rhythmic sampling patterns of external information (Abdalaziz et al., 2023; Chota et al., 2022; Peters et al., 2021; Pomper & Ansorge, 2021; Roux & Uhlhaas, 2014; Schmid et al., 2022). For instance, Pomper and Ansorge (2021) observed that two features in

VWM are attended rhythmically at approximately 6 Hz, and that both features are prioritized at opposite phases of the theta rhythm. Therefore, it has been theorized that theta rhythms may, in general, coordinate competing internal and external information in time (Abdalaziz et al., 2023; Fries, 2023). Particularly, rhythmic sampling of internal information in VWM may prevent interference between several representations that activate overlapping neuronal populations in the prefrontal cortex (Abdalaziz et al., 2023; Panichello & Buschman, 2021; Roux & Uhlhaas, 2014; Warden & Miller, 2007).

However, little is known about the interplay between external (i.e., attention directed towards external events) and internal rhythmic sampling (i.e., attention directed towards internal cognitive representations, e.g., VWM representations; Chun et al., 2011; Miller & Cohen, 2001; Rowe et al., 2000) during attentional selection (e.g., Balestrieri et al., 2022). To locate a known object in a highly cluttered scene, attention is guided by an internal VWM representation of the target object, commonly termed *attentional template* (Bundesen et al., 2005; Carlisle et al., 2011; Desimone & Duncan, 1995; Olivers & Eimer, 2011). In the present study, we tested whether such template-guided attentional selection during visual search is orchestrated by theta-rhythmic sampling. We propose that several attentional templates are activated rhythmically at a theta rhythm, whereby one template is prioritized over the other at a given time. Particularly, this might prevent interference between several templates when searching for more than one feature, maximizing the precision and, in turn, search efficiency of each template (Abdalaziz et al., 2023; Panichello & Buschman, 2021; Roux & Uhlhaas, 2014; Warden & Miller, 2007). Critically, this would imply that attentional guidance is somewhat restricted to one active template at a given time, which partially contradicts previous work advocating simultaneous guidance by multiple templates (Bahle et al., 2018; Beck et al., 2012; Beck & Hollingworth, 2017).

Simultaneous guidance of attention by more than one template remains strictly debated (Frătescu et al., 2019), although a VWM capacity of approximately three to four items is largely undisputed (Cowan, 2001; Vogel et al., 2001). The prevailing single template account assumes that attentional guidance is limited to one template at a given time (Olivers et al., 2011). This theory is supported by memory-driven attentional capture effects in dual-task experiments (Olivers et al., 2006; Soto et al., 2006). In one study, participants maintained a feature in VWM (e.g., color) and subsequently searched for an unrelated target object (e.g., diamond shape) among distractors. One of the distractors had either the same feature as the remembered item, an unrelated feature, or none. Distractors that matched the

remembered feature slowed down visual search compared to unrelated distractors, indicating that memory-matching distractors automatically captured attention (Olivers et al., 2006). However, such memory-driven interference disappeared when participants maintained more than one feature (e.g., two different colors) in VWM (Olivers et al., 2006; van Moorselaar et al., 2014). Therefore, Olivers and colleagues (2011) assumed that VWM representations automatically interact with attentional selection, but that this interaction is limited to one item. However, when participants maintain more than one feature in VWM, interference should be only reduced, but not entirely eliminated, as one feature should still act as the attentional template (Hollingworth & Beck, 2016). Therefore, it has been proposed that multiple representations in VWM compete for limited resources that allow them to switch into the active template state. The VWM representation that wins the competition will interact with attentional selection, while the remaining representations stay in a passive, accessory state (Olivers et al., 2011; van Moorselaar et al., 2014). With increased competition, none of the representations will become active, eliminating any memory-driven capture effects (van Moorselaar et al., 2014). Nonetheless, it remains unclear how this competition is resolved and why it does not follow a 'winner-takes-all' principle, analogously to the biased competition between external visual information (Desimone & Duncan, 1995).

Other studies provided evidence in favor of a multiple template account assuming simultaneous guidance by multiple attentional templates (Bahle et al., 2018; Beck et al., 2012; Beck & Hollingworth, 2017). For instance, Hollingworth and Beck (2016) reported stronger memory-driven interference by two different colors when participants were presented with two instead of one distractor matching the two colors in VWM, indicating that both colors guided attentional selection (but see also Fan et al., 2022). However, dual tasks only assess whether multiple items in VWM interfere with attentional selection, but do not differentiate whether these items are strategically used for visual search (Beck & Hollingworth, 2017). In classical contingent capture experiments, participants strategically search for two feature-defined targets (e.g., two different colors) in a search array. Prior to the target, participants are presented with a cue either matching or mismatching one of the target features. In typical spatial cueing tasks, target detection is improved when cues indicate the target location (valid cues) compared to cues that indicate a different location (invalid cues; Posner, 1980). According to the contingent capture theory, only cues matching the template-features elicit such validity effects (Folk et al., 1992). Critically, validity effects

have been shown for cues matching one of two color-defined targets, but not for unrelated color cues, providing further support for the simultaneous guidance of attention by multiple templates (Irons et al., 2012). Altogether, these findings suggest that multiple templates can indeed guide attentional selection, albeit often accompanied by performance costs (e.g., slower response times; Barrett & Zobay, 2014; Biderman et al., 2017; Houtkamp & Roelfsema, 2009; Ort et al., 2017). However, it remains unclear why different paradigms lead to robust yet opposite conclusions (e.g., Frătescu et al., 2019).

A subset of studies did not replicate the above mentioned findings using similar paradigms but variable targets (e.g., Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006; Olivers, 2009; Woodman & Luck, 2007). For example, all studies that observed memory-driven interference had participants search for the same target throughout the experiment (i.e., fixed targets). With practice, fixed targets might be transferred from VWM to long-term memory (Carlisle et al., 2011; Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006; Kerzel & Witzel, 2019), leaving only the accessory item to be stored in VWM. When the target changes from trial to trial (i.e., variable targets), target and accessory item both compete for representation in VWM and only the target receives sufficient resources to interact with perception (Kerzel & Witzel, 2019; Olivers, 2009).

Therefore, it has recently been proposed that the flexible allocation of limited VWM resources may account for the observed differences between paradigms (Cong & Kerzel, 2021, 2022; Kerzel & Witzel, 2019). Resource theories postulate that VWM capacity is limited by cognitive resources (e.g., Bays & Husain, 2008). The available resources can be flexibly distributed across VWM representations (e.g., depending on their task-relevance; Bays & Husain, 2008; Cong & Kerzel, 2021, 2022; Ma et al., 2014) to strategically enhance the precision of relevant items (Cong & Kerzel, 2021, 2022; Kerzel & Witzel, 2019). In contingent capture tasks, two templates are equally relevant for search and therefore receive equal amounts of resources to become simultaneously active, while resources are shifted away from the accessory item to the template during visual search in dual tasks (with variable targets), eliminating memory-driven interference (Cong & Kerzel, 2021; Kerzel & Witzel, 2019).

To test the resource hypothesis, Kerzel and Witzel (2019) had participants search for one or two color-defined targets that changed from trial to trial (i.e., variable targets; Experiment 1). The target colors were presented at the beginning of each trial. Note that participants were always presented with two colors to provide equivalent sensory stimulation

across search conditions. Hence, a central letter indicated the target color in single-target search. Prior to the target, participants were shown a cue that either matched or mismatched the target color(s). Contrary to previous work (e.g., Barrett & Zobay, 2014; Houtkamp & Roelfsema, 2009; Ort et al., 2017), they observed equal-sized cueing effects for target-matching cues irrespective of the number of target colors. The authors concluded that at least two templates can guide target selection if they are equally relevant to the task at hand (Kerzel & Witzel, 2019). However, this is unexpected under the assumption that limited resources are distributed across the two templates: Distributed resources should reduce the precision of each template representation, leading to weaker cueing effects in dual- relative to single-target search (Cong & Kerzel, 2021, 2022). Critically, Kerzel and Witzel (2019) introduced two colors on each trial, irrespective of the search condition (i.e., one target color and one non-target color in single-target search). In single-target search, the non-target color determined the distractor in 50% of all trials. Therefore, it is possible that participants established an additional rejection template for the non-target color (e.g., Arita et al., 2012; Carlisle et al., 2011; Reeder et al., 2017), which might have led to dual-target search unintentionally (cf. Cong & Kerzel, 2022).

In the present study, we tested whether template-guided attention during visual search is orchestrated by rhythmic sampling in the theta-band (3–8 Hz). To test this, we adapted the visual search task of Kerzel and Witzel (2019) using behavioral dense sampling (Fig. 1). We measured attentional search performance (i.e., hit rate) at variable template-to-target intervals (250–1,250 ms), while participants searched for one (i.e., single-target search) or two (i.e., dual-target search) color-defined targets. On each trial, two search templates (template A and template B) were presented successively. Participants searched for either one (i.e., single-target search) or both (i.e., dual-target search) of the two templates and reported the orientation of a template-matching target. A central letter, presented at center of template B, indicated the search template in single-target search. Consistent with previous work, we hypothesized that one attentional template (i.e., single-target search) induces rhythmic oscillations of search performance at around 8–10 Hz. Further, we expected two active attentional templates (i.e., dual-target search) to be activated sequentially and at opposite phase of a theta cycle, resulting in rhythmic oscillations of search performance at around 4–5 Hz per template.

Our results revealed theta-rhythmic oscillations in attentional search performance at 5 Hz, irrespective of the search condition. Contrary to our expectations, search performance

fluctuated at 5 Hz when participants searched for one target (i.e., single-target search). An exploratory analysis further revealed two distinct rhythms at 5 Hz and 9 Hz for the second template that did not determine the search template. This pattern raises the intriguing possibility that 1) participants might have established a second search template for the non-target color (i.e., negative search template), or 2) that the non-target color induced rhythmic perceptual priming. Crucially, when participants searched for two templates, only one template was activated rhythmically at 5 Hz. Although the relative strength between the two templates (i.e., the difference) oscillated at 5 Hz, the two templates were not prioritized at opposite phases of the theta rhythm. Therefore, our findings challenge a strictly sequential prioritization of attentional templates.

Methods

Participants

Thirty psychology students from the University of Vienna performed the experiment in exchange for course credits. The sample size was estimated based on previous dense sampling studies, which commonly included 15 to 25 participants (see Fiebelkorn et al., 2013; Landau & Fries, 2012; Michel et al., 2022; Pomper & Ansorge, 2021; Re et al., 2019; Schmid et al., 2022). Four participants were excluded from further analyses due to technical issues during data collection (n = 1), timeouts on more than 15% of trials (n = 1), or because they withdrew from participation after the first experimental session (n = 2). The remaining 26 participants (19 females; M_{age} = 20.7 years, SD_{age} = 2.5 years, range = 18 to 31 years) reported normal or corrected-to-normal vision, were naïve to the experimental procedure, and gave written informed consent prior to data collection. After completing the experiment, all participants received verbal and written debriefing. The study adheres to the standards of the Declaration of Helsinki and national ethical standards (Austrian Universities Act of 2002).

Apparatus and Stimuli

The visual stimuli were presented on a 24.5'' G2590PX AOC Gaming LCD monitor (1,920 x 1,080 pixel resolution, refresh rate of 100 Hz, automatic gamma correction) at a viewing distance of 57 cm. Participants were placed in front of the computer screen in a soundproof, dimly lit room, while their head position was stabilized by a chin and forehead rest to ensure a constant viewing distance throughout the experiment. The experiment was

executed in OpenSesame (Version 3.3.10; Mathôt et al., 2012) running on Windows 7. All stimuli were presented on a black background (0.0 cd/m2). Participants were instructed to fixate on a light grey fixation cross (0.6° x 0.6°; HSL value: [0;0;77]) throughout each trial.

Each trial sequence started with two colored search templates (a central disk with an outer radius of 0.6° and a peripheral ring with an outer radius of 1.2°), which were presented sequentially at the center of the screen. In the single-target search condition, an additional letter ('C' for central color or 'P' for peripheral color; letter height 0.31°; HSL value: [0;0;0]) was presented at center of the central disk to indicate the search color. The search templates were followed by a variable fixation period, in which participants fixated on a light grey fixation cross (0.6° x 0.6°; HSL value: [0;0;77]). The target display included four outline rings (inner radius 1.1°, outer radius 1.4°) shown left, right, above, and below the fixation cross at a center-to-center distance of 3°. On each trial, two rings were shown in light grey (HSL value: [0;0;77]), while the remaining two rings (here: target and distractor) were filled with a color (see below). Each ring contained a light grey T-shaped stimulus (horizontal length 1°, vertical length 1°; bar width 0.3°; HSL value: [0;0;77])), which was randomly oriented to the left, right, upwards, or downwards. The outline rings slowly faded out 100 ms after target onset. The T-shaped stimuli remained in the target display until a response was delivered or the time limit of 2,000 ms was exceeded.

Stimulus colors were defined in HSL (hue, saturation, luminance) color space, which represents colors on three axes: Hue (base color), saturation (color intensity), and luminance (perceived brightness). In contrast to CIELAB color space used by Kerzel and Witzel (2019), HSL separates the color information into three distinct dimensions. Therefore, we were better able to adjust the colors in the target display using an adaptive staircase procedure (see Experimental Design and Procedure) while preserving the hue of the target color. On each trial, three colors (template A, template B, distractor) were sampled randomly from a hue circle with a saturation of 90% and a luminance of 77%. This way, attentional templates (here: template colors) changed from trial to trial (i.e., variable targets, see Kerzel & Witzel, 2019) and were not transferred to long-term memory (Carlisle et al., 2011; Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006; Kerzel & Witzel, 2019). All three colors had a discriminable hue difference of 120° to prevent attentional biases arising from color similarity (Ansorge & Becker, 2014; Kerzel & Witzel, 2019; Witzel & Gegenfurtner, 2015).

Experimental Design and Procedure

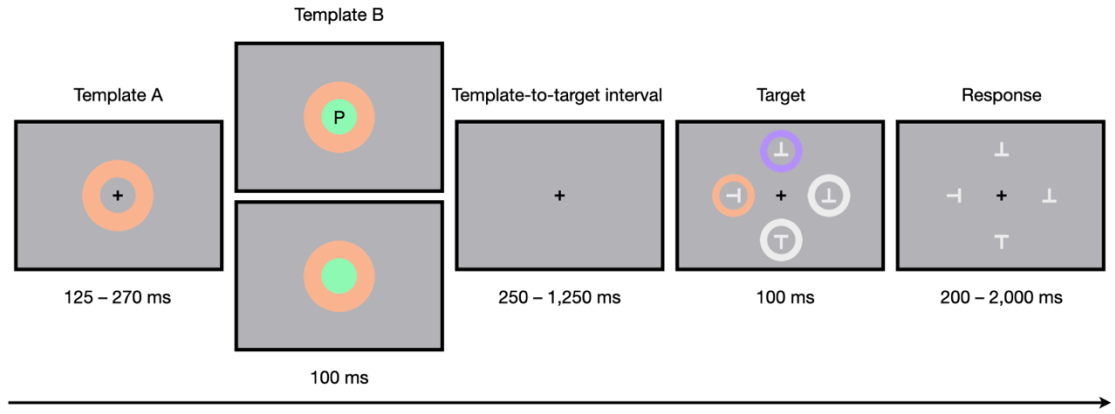
Figure 1 illustrates the experimental task. Participants were instructed to search for either one (single-target search) or two (dual-target search) template colors. Each trial began with the sequential presentation of two visual search templates. The first template (template A; 50 ms) consisted either of a colored central disk or a peripheral ring (50% of trials each), followed by the second template (template B; 100 ms), consisting of the respective other. Critically, we randomly jittered the time delay between template A and template B (75–220 ms) to prevent any artificial behavioral rhythms resulting from temporal predictability (Pomper & Ansorge, 2021; Re et al., 2019; Schmid et al., 2022). Due to its unpredictable onset, template B further acted as an attentional reset event, resetting the phase of ongoing perceptual and attentional oscillations (Landau & Fries, 2012). In the single-target search condition, an additional letter ('C' for central color or 'P' for peripheral color), presented at the center of template B, indicated the search color of the respective trial. The target appeared after a variable time delay (250–1,250 ms; in steps of 10 ms), in which participants maintained fixation. Template A and template B determined the target in 50% of the trials, respectively. Target positions were counterbalanced across trials. In the single-target search condition, the additional distractor in the target display had either the primed (i.e., second template color that did not determine the target) or an unprimed color (50% of trials each). In the dual-target search condition, only one of the template colors could appear in the target display to prevent response conflicts. Participants reported the target orientation as quickly and accurately as possible by pressing the corresponding arrow key. Hit rates were titrated to 75% to ensure a variable range of performance, avoiding floor and ceiling effects (for similar procedures see Fiebelkorn et al., 2013; Helfrich et al., 2018; Landau & Fries, 2012; Pomper & Ansorge, 2021; Re et al., 2019; Schmid et al., 2022). To achieve this, we adaptively increased or decreased the saturation of the target and distractor colors in the target display on each trial. Responses had to be delivered within 2,000 ms after target offset. At the end of each trial, participants received visual feedback on the correctness of their response.

All participants completed three experimental sessions on separate days with a maximum of 7 days between each session. The two search conditions were accomplished on different days. The order of both conditions was counterbalanced across participants (n = 14 participants started with single-target search). Each session started with a short training phase (30 trials), followed by the main experiment (1,600 trials split into 20 blocks of 80 trials each). Participants performed 1,600 trials for dual-target and 3,200 trials for single-

target search (given the additional factor of the primed vs. unprimed distractor). After each block, participants had a self-paced break, in which they received visual feedback on their overall accuracy. The entire experiment lasted approximately six hours (2 hours per session).

Figure 1

Schematic Task Design



Note. Not drawn to scale. Participants searched for either one (single-target search) or two (dual-target search) color-defined targets. Two colored templates, namely template A and template B, were presented sequentially at the center of the screen. An additional letter ('C' for central color or 'P' for peripheral color), presented at center of template B, indicated the search color in the single-target search condition. The target appeared after a variable fixation period (250–1,250 ms) following template B. Participants reported the target orientation as quickly and accurately as possible by pressing the corresponding arrow key.

Data Analysis

Analyses were executed in MATLAB (Version 2021; The MathWorks, Natick, MA) using custom-written code and the CircStat toolbox (Version 1.21; Berens, 2009). Response times were only analyzed for correct trials. Outlier trials with response times shorter than 200 ms and longer than 2,000 ms were excluded for each subject and condition. In a traditional analysis, we compared group average hit rates (percentage of correct trials) and response times for the two search conditions, distractors with primed and unprimed colors (single-target search), and for targets matching template A and template B (dual-target search) using paired-samples t tests.

Data Processing

To evaluate the time course of search performance for each condition and template, we analyzed hit rates as a function of template-to-target interval (TTI). The TTI was measured relative to the onset of template B, which acted as the attentional reset event. Using a moving-window procedure, we first sorted all trials by their TTI and computed the average hit rate within 50-ms windows of five subsequent TTIs. We first calculated the average hit rate for trials with a TTI between 250 and 300 ms. Then, we shifted the time window by 10 ms and re-calculated the average hit rate for trials with a TTI between 260 and 310 ms. We repeated this procedure until we reached the maximum TTI duration (1,250 ms).

To obtain frequency and phase values for each participant, we linearly detrended the averaged time courses with a second-order polynomial and extracted spectral components using the Fast Fourier Transform (FFT). So far, attentional rhythms have been found predominantly in the lower-alpha and theta band, ranging from 4 to 12 Hz (e.g., Fiebelkorn et al., 2013; Landau & Fries, 2012; Pomper & Ansorge, 2021; Re et al., 2019). Therefore, we only considered frequencies between 2 and 12 Hz in our analysis, reducing the number of statistical tests performed on the data.

Statistical Analysis

To determine whether the observed power values were statistically significant, we performed a non-parametric randomization procedure. The null hypothesis claims the absence of any temporal structure in search performance. First, we created a null distribution of power values by randomly shuffling hits and misses across TTIs 1,000 times within each participant (separately for each template and condition). We then performed the data processing procedure as described above on the time-shuffled data, resulting in a surrogate distribution of 1,000 power values for each frequency bin (2–12 Hz, bin size: 1 Hz). *P* values represent the proportion of time-shuffled power values at each frequency bin that are greater than or equal to the observed power spectrum. Next, we applied a false discovery rate (FDR) procedure to correct for multiple comparisons across frequency bins (Benjamini & Hochberg, 1995). After FDR correction, *p* values less than .05 were considered significant.

For significant peaks in the power spectrum, we further assessed the phase coherence across participants and conditions (i.e., templates and distractors). Different from the spectral analysis, we obtained phase values by applying an FFT on the participants' individual time

courses (Michel et al., 2022). We computed individual phase differences (between templates and distractor conditions) based on the complex FFT outputs for their respective frequencies. To determine whether phase differences were uniformly distributed around the circle, we then performed a Rayleigh-test (Berens, 2009). As before, we applied this procedure to the observed and 1,000 time-shuffled data and adjusted *p* values using an FDR correction (Benjamini & Hochberg, 1995). Again, *p* values less than .05 were considered significant.

Results

Search Performance

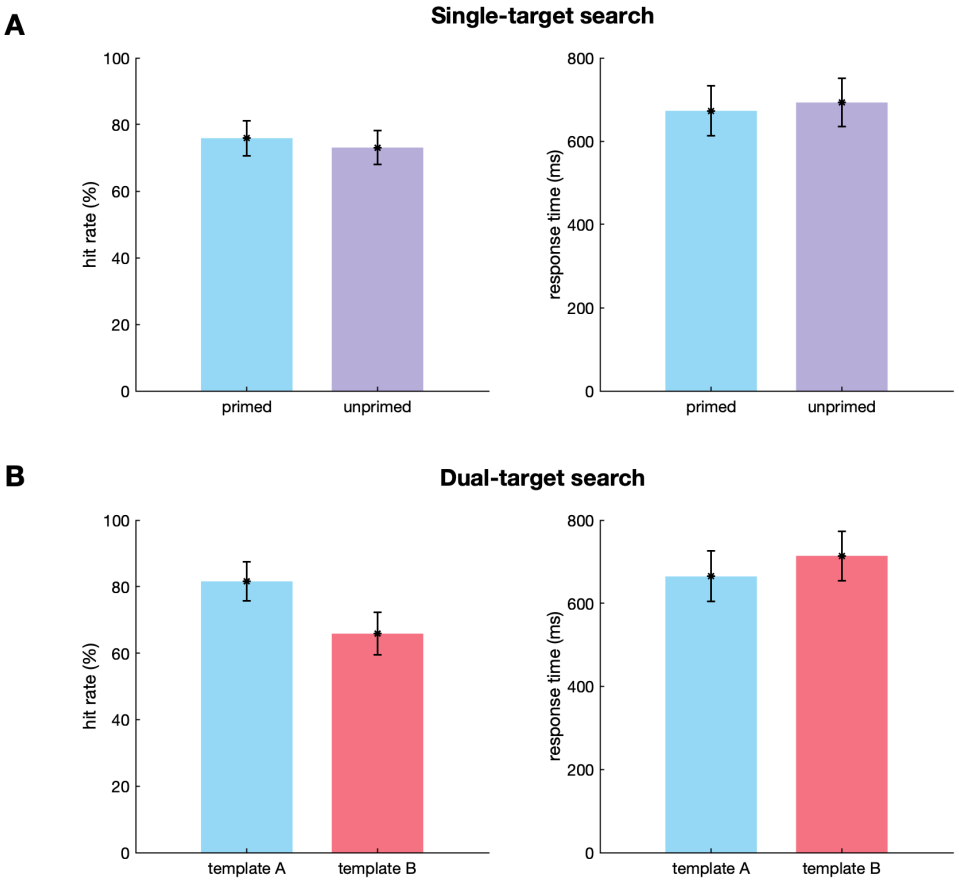
Figure 2 shows the average hit rates and response times for single- and dual-target search. Searching for two target colors did not incur performance costs relative to a single target color. Precisely, response times were not significantly different between single-target (M = 682.6 ms, SD = 58.4 ms) and dual-target (M = 685.7 ms, SD = 57.2 ms) search, $t(25) = -0.38$, $p = .709$, $d = 0.05$. Furthermore, hit rates did not differ significantly between single-target (M = 74.5%, SD = 4.5%) and dual-target (M = 73.7%, SD = 3.8%) search, $t(25) = 0.68$, $p = .504$, $d = 0.18$.

When participants searched for a single target color, response times were significantly faster when the distractor in the search array had a primed color (i.e., second to-be-ignored template color; M = 672.9 ms, SD = 59.9 ms) as compared to an unprimed color (M = 692.9 ms, SD = 58.0 ms), $t(25) = -6.21$, $p < .001$, $d = 0.34$ (Fig. 2A, right). Similarly, participants were more accurate when the distractor color was primed (M = 75.9%, SD = 5.2%) compared to when it was unprimed (M = 73.1%, SD = 5.0%), $t(25) = 2.92$, $p = .007$, $d = 0.55$ (Fig. 2A, left).

When searching for two possible target colors, participants responded significantly faster to targets that matched template A (M = 664.7 ms, SD = 60.8 ms) than to those that matched template B (M = 714.1 ms, SD = 59.4 ms), $t(25) = -6.63$, $p < .001$, $d = 0.82$ (Fig. 2B, right). Likewise, hit rates were significantly higher for targets matching template A (M = 81.6%, SD = 5.8%) compared to those matching template B (M = 65.9%, SD = 6.4%), $t(25) = 8.49$, $p < .001$, $d = 2.58$ (Fig. 2B, left).

Figure 2

Average Hit Rates and Response Times for Single- and Dual-Target Search



(A) Average hit rates (left) and response times (right) for primed and unprimed distractor trials in single-target search. Error bars represent standard errors of the mean.

(B) Average hit rates (left) and response times (right) for targets matching template A and template B in dual-target search. Error bars represent standard errors of the mean.

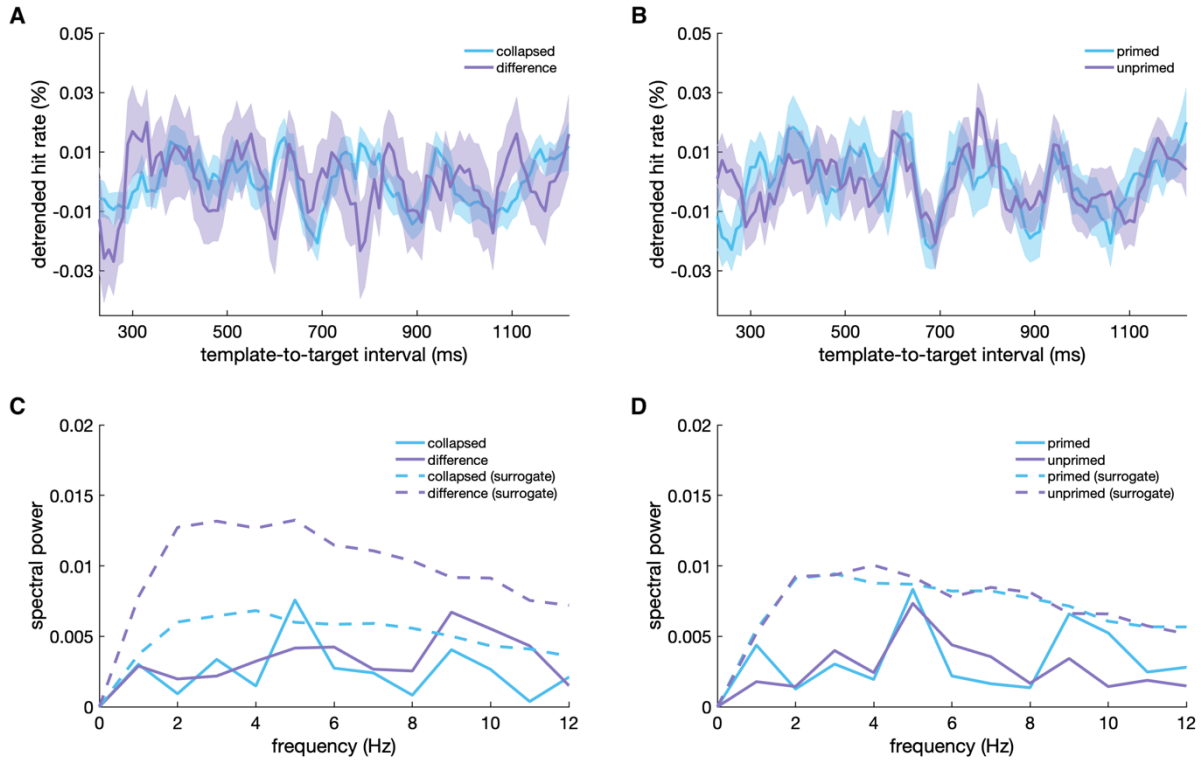
Spectral Analysis of Single-Target Search Performance

The spectral analysis of the single-target search performance (collapsed across distractor conditions) revealed a significant peak in the power spectrum at 5 Hz (Fig. 3C, solid blue line; $p < .001$, FDR corrected). We further found significant peaks at 5 Hz ($p = .045$, FDR corrected) and 9 Hz ($p = .045$, FDR corrected) in primed distractor trials (Fig. 3D, solid blue line), but no significant peaks in unprimed distractor trials (Fig. 3D, solid violet line). Oscillatory phases of the performance time course (collapsed across distractor

conditions) at 5 Hz were not uniformly distributed (Rayleigh test, $\overline{R} = 5.4$, $p = .006$), indicating a consistent phase concentration across participants (Fig. 4).

Figure 3

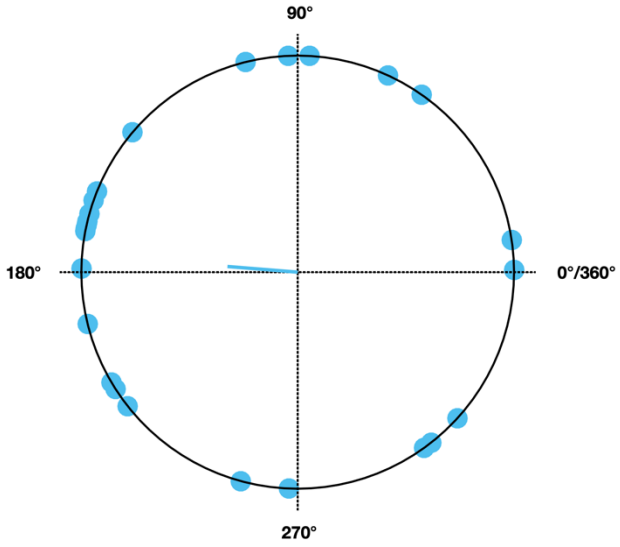
Spectral Analysis Results of Single-Target Search Performance



Note. (A and B) Detrended hit rate as a function of template-to-target interval. Shaded regions represent standard errors of the mean. (A) Blue (violet) line: Search performance collapsed across distractor conditions (difference between distractor conditions). (B) Blue (violet) line: Search performance in primed (unprimed) distractor trials.
(C and D) Power spectra for performance time courses depicted in (A) and (B). Solid (dashed) lines represent observed (time-shuffled surrogate) data.

Figure 4

Oscillatory Phases of Single-Target Search Performance (Collapsed Across Distractor Conditions) at 5 Hz (p = .006)



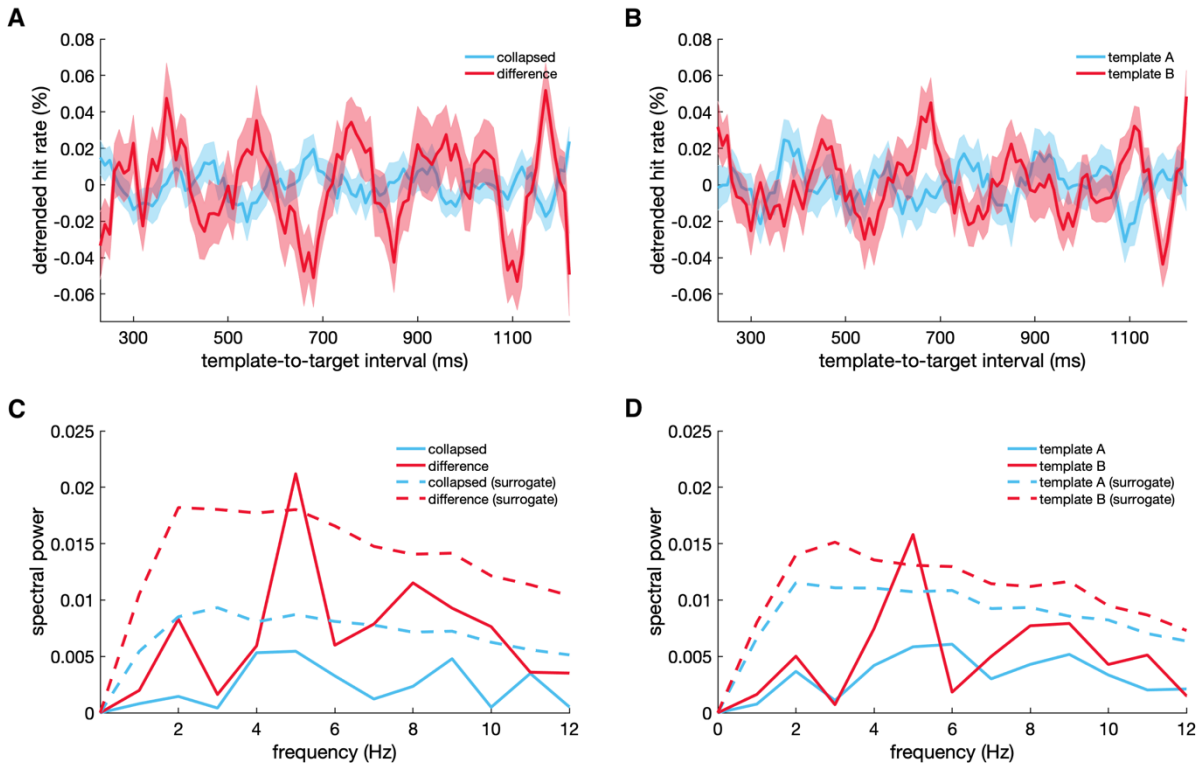
Note. Individual participants' phase angles at 5 Hz (collapsed across primed and unprimed distractor trials) are plotted on the circle. The vector represents the group-average phase angle.

Spectral Analysis of Dual-Target Search Performance

The spectral analysis of the dual-target search performance revealed a significant peak in the difference between template A and template B at 5 Hz (Fig. 5C, solid red line; p = .01, FDR corrected). We further observed a significant peak in the power spectrum at 5 Hz (p = .01, FDR corrected) for template B-matching targets (Fig. 5D, solid red line), but not for template A-matching targets (Fig. 5D, solid blue line). In two comparable studies, spectral peaks in the average power spectrum also did not reach significance in one of two conditions. However, subsequent analyses of participant's individual phase differences indicated a temporal relationship between the two conditions (Chota et al., 2022; Pomper & Ansorge, 2021). We therefore examined whether template A and B exhibited an antiphase relationship, even though we could not find significant peaks in the average power spectrum for template A-matching targets. However, oscillatory phase differences between template A and B at 5 Hz were uniformly distributed (Fig. 6, Rayleigh test, $\overline{R}$ = 0.1, p = .381), indicating no antiphase relationship between the two templates (Fig. 7).

Figure 5

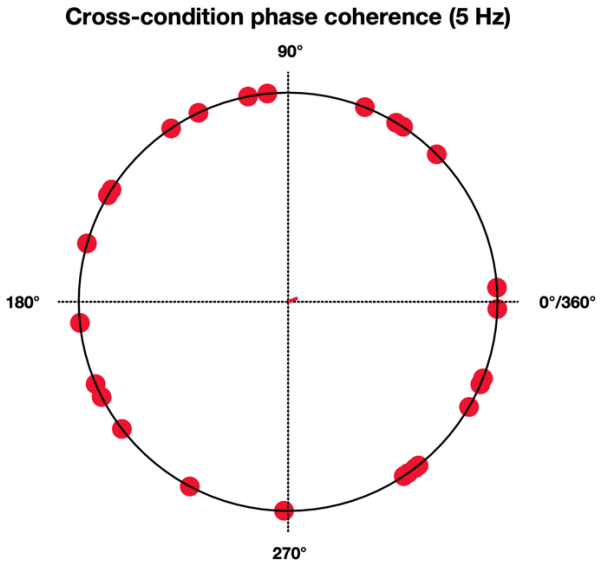
Spectral Analysis Results of Dual-Target Search Performance



Note. (A and B) Detrended hit rate as a function of template-to-target interval. Shaded regions represent standard errors of the mean. (A) Blue (red) line: Search performance collapsed across templates (difference between templates). (B) Blue (red) line: Search performance for targets matching template A (targets matching template B).
(C and D) Power spectra for performance time courses depicted in (A) and (B). Solid (dashed) lines represent the observed (time-shuffled) data.

Figure 6

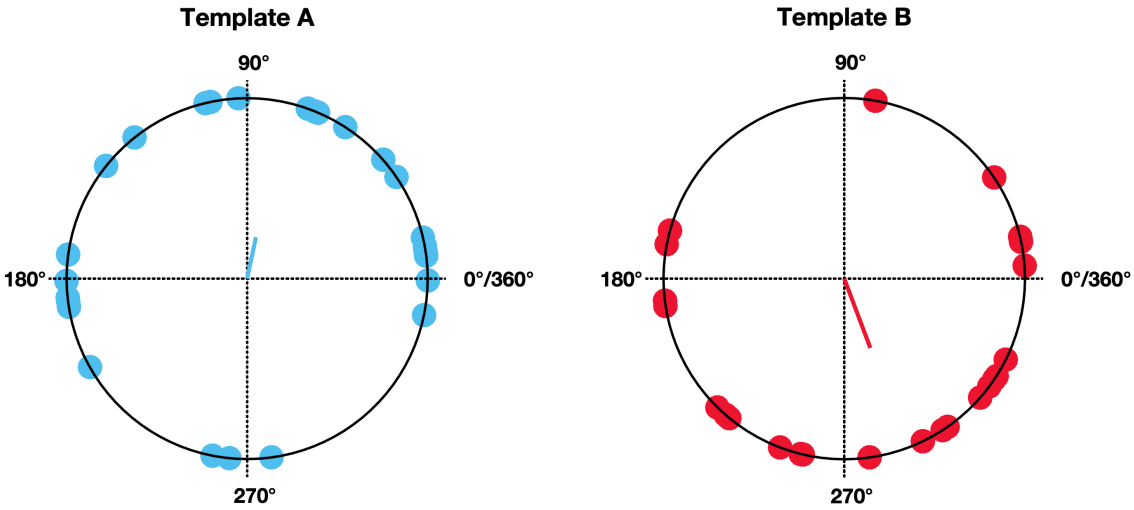
Cross-Condition Phase Coherence at 5 Hz (p = .381) between Template A- and Template B-Matching Targets



Note. Individual participants' phase differences at 5 Hz between template A- and template B-matching targets are plotted on the circle. The vector represents the group-average phase difference.

Figure 7

Oscillatory Phases of Dual-Target Search Performance for Template A- and Template B-Matching Targets at 5 Hz



Note. Individual participants' phase angles at 5 Hz for template A- (blue) and template B-matching (red) targets are plotted on the circle. Vectors depict group-average phase angles.

Discussion

In the present study, we tested whether template-guided attentional selection during visual search is orchestrated by theta-band (3–8 Hz) oscillations. To this end, we measured attentional search performance at variable template-to-target intervals, while participants searched for one (i.e., single-target search) or two (i.e., dual-target search) color-defined targets. Our results revealed theta-rhythmic oscillations in search performance at 5 Hz, irrespective of the number of to-be-searched-for targets. Crucially, when participants searched for two targets, only one template was activated rhythmically at 5 Hz. Although the relative strength between the two templates (i.e., the difference) oscillated at 5 Hz, the two templates were not prioritized at opposite phases of the theta rhythm. Our findings challenge a strictly sequential prioritization of attentional templates.

Theta-Rhythmic Sampling of Attentional Templates in Visual Search

Previous studies have shown that attention alternates sequentially between two relevant options (e.g., features), sampling each at around 4 Hz (Busch et al., 2009; Chota et al., 2022; Fiebelkorn et al., 2013; Fries, 2023; Helfrich et al., 2018; Landau & Fries, 2012; Peters et al., 2021; Pomper & Ansorge, 2021; Re et al., 2019; VanRullen, 2016). Contrary to our expectations, we observed theta-rhythmic oscillations in search performance at 5 Hz, irrespective of the number of to-be-searched-for targets. That is, we found no proportional decrease in sampling frequency when participants searched for two targets relative to one.

This might be due to three reasons: Firstly, our experimental task might have not been suitable to distinguish between single- and dual-target search scenarios because participants might have established an additional negative template for the non-target color during single-target search (Arita et al., 2012; Carlisle, 2023; Carlisle et al., 2011; Reeder et al., 2017); as discussed below.

Secondly, the non-target color might have induced rhythmic perceptual priming effects. The search history (e.g., intertrial priming of target features) has been shown to influence attentional guidance in pop-out search scenarios, speeding up response times and increasing detection accuracy (Brascamp et al., 2011; Chetverikov & Kristjansson, 2015; Maljkovic & Nakayama, 1994; Shurygina et al., 2019; Theeuwes, 2019). In this study, the non-target color might have directed attention towards the primed distractor, leading to a faster and more accurate distractor suppression (i.e., reflected by faster response times and higher accuracy in primed compared to unprimed distractor trials; Geng, 2014). Furthermore,

one study has reported antiphasic behavioral fluctuations in the time course of perceptual priming at 4 Hz for congruent and incongruent trials, respectively (Huang et al., 2015). Therefore, the oscillations in search performance during single-target search might have been influenced by rhythmicity in perceptual priming. However, based on our experimental task, we cannot differentiate between perceptual priming effects and the potential existence of a negative template. Further research is warranted to isolate theta-rhythmic sampling during single-target search from possible confounds.

Thirdly, internal representations might not affect the sampling frequency proportionally until the capacity of VWM is exceeded (cf. Chota et al., 2022; Peters et al., 2021; Pomper & Ansorge, 2021; Schmid et al., 2022). A recent study has reported that the sampling frequency during visual search decreases with increasing memory load, but that this interaction is disproportional. Specifically, search performance oscillated at around 7.5 Hz when the VWM load was low (i.e., zero or two), only decreasing to 5 Hz when the load exceeded the VWM capacity (i.e., four; Balestrieri et al., 2022). However, in our study, this interpretation seems implausible since searching for two targets (i.e., memory load of two) already affected the sampling frequency, contradicting the findings of Balestrieri and colleagues (2022).

When participants searched for two targets (i.e., dual-target search), only one of the two templates (i.e., template B) induced a theta-rhythmic attentional bias at 5 Hz. Further, the two templates exhibited no antiphasic relationship, although the relative strength of the two templates (i.e., difference between template A and template B) oscillated at 5 Hz. Together, our findings suggest an overall prioritization of the second template over the first, which paradoxically led to poorer behavioral performance for targets that matched the second template compared to the first. These performance benefits for template A may reflect the extended duration available for search preparation compared to template B (Wolfe et al., 2004). However, the prioritization of one internal representation over the other has been frequently observed in previous dense sampling experiments and might be an inherent characteristic of internal sampling (Chota et al., 2022; Peters et al., 2021; Pomper & Ansorge, 2021).

Interestingly, Pomper and Ansorge (2021) used a comparable experimental task to ours, in which participants maintained two sequentially presented templates in VWM that were equally relevant for the current task. Consistent with our findings, they observed a prioritization of the second template, however, accompanied by an overall better behavioral

performance for targets that matched the second template compared to the first. The authors interpreted this finding as a recency effect (Vergauwe et al., 2016). In our study, it remains unclear why both the rhythmic prioritization and the overall search performance associated with the second template diverge fundamentally.

Consistent with our findings, previous studies reported internal sampling frequencies between 3.5 and 6 Hz (Chota et al., 2022; Pomper & Ansorge, 2021; Schmid et al., 2022). This variance might be attributed to variable stimulus complexities across studies (Chota et al., 2022). Studies reporting frequencies between 3.5 and 4.4 Hz required participants to remember two features from different feature dimensions (Schmid et al., 2022) or multi-feature objects (Chota et al., 2022), whereas Pomper and Ansorge (2021), similar to our study, observed behavioral oscillations at 6 Hz for two features from the same feature dimension. Electrophysiological evidence from humans and rodents suggests that multiple VWM representations are maintained in separate gamma cycles (30–80 Hz) nested within one theta cycle (Jensen & Lisman, 2005; Lisman & Idiart, 1995). With increasing stimulus complexity, a greater number of theta-nested gamma cycles might be required for the maintenance of stored features, increasing the length of each theta cycle, and reducing the overall sampling frequency. Interestingly, one study investigating the influence of task complexity (e.g., number of distractors in a search array) on external rhythmic sampling found a strikingly opposite pattern, suggesting that more theta cycles are required to perform more complex tasks (Merholz et al., 2022). Further research will be needed to elucidate this functional difference between internal and external rhythmic sampling.

Single-Target Search: Negative Attentional Template for the Non-Target Color?

Contrary to our expectations, we observed no proportional decrease in sampling frequency when participants searched for two targets relative to one. Further, an exploratory analysis revealed two distinct behavioral rhythms at 5 and 9 Hz in primed distractor trials during single-target search, suggesting that participants might have established a negative attentional template (i.e., rejection template) for the non-target color to direct attention away from the known distractor color (Arita et al., 2012; Carlisle, 2023; Carlisle et al., 2011; Reeder et al., 2017). To provide equivalent sensory stimulation across conditions, Kerzel and Witzel (2019) introduced two colors on each trial, regardless of the search condition (i.e., one target color and one non-target color in single-target search). Crucially, the non-target color determined the distractor in 50% of all trials and might have been, therefore,

considered behaviorally relevant. Hence, the activation of a negative template for the non-target color might have been advantageous to inhibit the known distractor information in advance. Consistent with this idea, we observed search benefits in primed distractor trials relative to unprimed distractor trials (Arita et al., 2012; Carlisle et al., 2011; Reeder et al., 2017). Altogether, our findings suggest that the experimental task used by Kerzel and Witzel (2019) might have not been suitable to distinguish between single- and dual-target search scenarios, leading to inaccurate conclusions about the simultaneous attentional guidance by multiple templates.

Relatedly, there is an ongoing debate whether positive and negative templates share a common mechanism, whereby positive templates enhance processing of target features and negative templates inhibit processing of distractor features (Carlisle, 2019, 2023; Reeder et al., 2017), or whether target enhancement and distractor suppression rely on distinct mechanisms (Geng & Witkowski, 2019; Navalpakkam & Itti, 2007; Noonan et al., 2016). Our findings raise the intriguing possibility that both types of attentional modulation might be coordinated by theta-band oscillations, thus sharing a common underlying mechanism. Further studies will be needed to systematically compare the behavioral oscillations associated with positive and negative templates.

Additionally, we observed a behavioral alpha rhythm at 9 Hz in primed distractor trials. Alpha rhythms (8–12 Hz) have been often found in behavioral sampling studies and have been discussed as an oscillatory signature of visual information processing (Chota et al., 2022; Pomper & Ansorge, 2021; VanRullen, 2016). In electrophysiological studies, the power of posterior alpha-band oscillations has been shown to increase contralateral to distracting information (Wöstmann et al., 2019) and might be, therefore, a potential mechanism for distractor inhibition (Bonnefond & Jensen, 2013; cf. Foster & Awh, 2019; Jensen & Mazaheri, 2010). In our study, we only observed a behavioral alpha rhythm in primed distractor trials, which might potentially reflect a template-guided rhythmic inhibition of distractors. However, this remains speculative because the behavioral sampling approach used in our study is not suited to disentangle inhibitory oscillatory dynamics. Future studies using electrophysiological methods (e.g., magnetoencephalography) will be needed to explore the potential role of alpha oscillations in template-guided distractor inhibition.

Rhythmic Sampling as a Framework for Template-Guided Visual Search

Based on our preliminary findings, we propose that theta-band (3–8 Hz) oscillations orchestrate template-guided attentional selection during visual search. We argue that attentional templates are activated rhythmically, characterized by alternating phases of enhanced or diminished template precision (Abdalaziz et al., 2023; Michel et al., 2022). Our findings suggest an overall prioritization of one template over the other, causing only the prioritized template to induce an observable rhythmic attentional bias on behavior. Importantly, this prioritization might be characterized by alternating phases, in which the two templates are prioritized in rhythmic alternation, and phases, in which the two templates are prioritized equally (Chota et al., 2022; Fiebelkorn et al., 2013; Peters et al., 2021; Pomper & Ansorge, 2021). This way, attentional selection might be dominated by one template, but the second template might be occasionally activated to allow for exploration of a different search strategy. In other words, the guidance efficiency of each template might be periodically reassessed in phases of exploration, analogously to the alternating states of sampling and exploration during external rhythmic attention (Fiebelkorn & Kastner, 2019). Note, however, that this functional interpretation remains speculative and needs further scrutiny.

The rhythmic prioritization of attentional templates, as described above, has important implications for template-guided visual search, fueling the ongoing debate on the simultaneous guidance by multiple attentional templates (Beck et al., 2012; Frătescu et al., 2019; Hollingworth & Beck, 2016; Kerzel & Witzel, 2019; Olivers et al., 2011; van Moorselaar et al., 2014). Consistent with previous findings, attentional guidance might be characterized by alternating phases, in which only one active template drives attentional selection, and phases, in which two templates drive selection simultaneously (Chota et al., 2022; Fiebelkorn et al., 2013; Peters et al., 2021; Pomper & Ansorge, 2021). Therefore, rhythmic sampling of attentional templates may provide a unifying framework for template-guided attentional selection, bridging the gap between existing theories.

Whereas the two templates in our study were equally relevant for the current task (similar to Pomper & Ansorge, 2021), attentional templates can vary in their behavioral relevance (e.g., when one target feature is less frequently observed). Recently, it has been shown that the frequency of attentional sampling can be modulated by the relevance of a given option. Precisely, options (e.g., spatial locations) with higher relevance for the current behavior were sampled more frequently than options with lower relevance (van der Werf et

al., 2023). Consequently, highly relevant templates may be sampled with higher frequencies, aligning with the central assumption of the resource hypothesis of visual search (Cong & Kerzel, 2021, 2022; Kerzel & Witzel, 2019).

Interestingly, such (re-)weighting of internal rhythmic sampling could also explain how different states in VWM (i.e., template state and accessory state) are achieved; an open question under the premise of the single template account (Olivers et al., 2011). The different states may be characterized by their relative difference in sampling frequency, whereby the template state is associated with a relatively higher sampling frequency than the accessory state. Depending on the situation (i.e., task-relevance), the distribution of the common sampler over two items can be reweighted, causing the most frequently sampled item to switch into the template state (Kerzel & Witzel, 2019; Olivers, 2009).

Conclusion

Our findings provide novel evidence that template-guided attentional selection during visual search is orchestrated by theta-band (3–8 Hz) oscillations. Our results revealed theta-rhythmic oscillations in search performance at 5 Hz, irrespective of the number of to-be-searched-for targets. When participants searched for two targets, only one template was activated rhythmically at 5 Hz, and both templates were not prioritized in antiphase. Therefore, our findings challenge a strictly sequential prioritization of attentional templates. However, the present study only provided correlational evidence for the theta-rhythmic coordination of attentional templates during visual search. Further research will be needed to investigate the neuronal sources of rhythmic internal sampling (Fiebelkorn et al., 2018, 2019; Fiebelkorn & Kastner, 2019; Helfrich et al., 2018; Raposo et al., 2023).

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List of Abbreviations

EEG	Electroencephalography
FDR	False Discovery Rate
FFT	Fast Fourier Transform
TTI	Template-to-target interval
VWM	Visual working memory

Appendix

Abstract

To localize a target object among several distractors, visual attention can be guided by an internal representation of the target object stored in working memory, commonly termed attentional template. To date, however, it remains unclear how many attentional templates can drive visual search simultaneously. In the present study, we tested whether attentional templates are activated theta-rhythmically (3–8 Hz), prioritizing multiple templates in alternation. To this end, we measured attentional search performance at variable template-to-target intervals, while participants searched for one (single-target search; e.g., green) or two (dual-target search; e.g., green and orange) color-defined targets. Our results revealed theta-rhythmic oscillations in search performance at 5 Hz, irrespective of the number of to-be-searched-for targets. In contrast to previous studies, we found no anti-phasic prioritization of two attentional templates. Our findings challenge a strict sequential prioritization of attentional templates, having important implications for template-guided visual search.

Keywords

behavioral oscillations; rhythmic sampling; dense sampling; theta; template; visual attention

Zusammenfassung

Visuelle Aufmerksamkeit kann zur Lokalisation eines Zielobjekts durch eine interne Repräsentation des Zielobjekts im Arbeitsgedächtnis („Aufmerksamkeitsschablone“) gesteuert werden. Bislang ist jedoch unklar, wie viele Aufmerksamkeitsschablonen die visuelle Suche gleichzeitig beeinflussen können. In der vorliegenden Studie haben wir untersucht, ob Aufmerksamkeitsschablonen während der visuellen Suche theta-rhythmisch (3–8 Hz) aktiviert und anti-phasisch priorisiert werden. Dazu haben wir ein Experiment durchgeführt, bei dem die Versuchspersonen entweder nach einer (einfache Farbsuche; z.B. „grün“) oder nach zwei (zweifache Farbsuche; z.B. „grün und orange“) Zielreizfarben suchten. Die Suchleistung wurde dabei in dichten Zeitintervallen gemessen, um den zeitlichen Verlauf der Suchleistung zu ermitteln. Unsere Ergebnisse legen nahe, dass die Suchleistung unabhängig von der Anzahl der zu suchenden Farben theta-rhythmisch mit 5 Hertz oszilliert. Im Gegensatz zu vorherigen Studien, konnten wir keine anti-phasische Priorisierung von zwei Suchschablonen feststellen. Unsere Ergebnisse stellen damit eine strikte sequenzielle Priorisierung von Suchschablonen in Frage und haben somit wichtige Implikationen für unser Verständnis der schablonengelenkten visuellen Suche.

Schlüsselbegriffe

Verhaltensoszillationen; rhythmische Aufmerksamkeit; dichte Verhaltensmessung; Theta; Aufmerksamkeitsschablone; visuelle Aufmerksamkeit