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Alpha and theta rhythm support perceptual and attentional sampling in vision



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ABSTRACT

The visual system operates rhythmically, through timely coordinated perceptual and attentional processes, involving coexisting patterns in the alpha range (7–13 Hz) at ~10 Hz, and theta (3–6 Hz) range, respectively. Here we aimed to disambiguate whether variations in task requirements, in terms of attentional demand and side of target presentation, might influence the occurrence of either perceptual or attentional components in behavioral visual performance, also uncovering possible differences in the sampling mechanisms of the two cerebral hemispheres. To this aim, visuospatial performance was densely sampled in two versions of a visual detection task where the side of target presentation was fixed (Task 1), with participants monitoring one single hemifield, or randomly varying across trials, with participants monitoring both hemifields simultaneously (Task 2). Performance was analyzed through spectral decomposition, to reveal behavioral oscillatory patterns. For Task 1, when attentional resources were focused on one hemifield only, the results revealed an oscillatory pattern fluctuating at ~10 Hz and ~6–9 Hz, for stimuli presented to the left and the right hemifield, respectively, possibly representing a perceptual sampling mechanism with different efficiency within the left and the right hemispheres. For Task 2, when attentional resources were simultaneously deployed to the two hemifields, a ~5 Hz rhythm emerged both for stimuli presented to the left and the right, reflecting an attentional sampling process, equally supported by the two hemispheres. Overall, the results suggest that distinct perceptual and attentional sampling mechanisms operate at different oscillatory frequencies and their prevalence and hemispheric lateralization depends on task requirements.

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1. Introduction

1.1. The discrete structure of visual perception

In the past two decades, several studies converged in describing an intrinsic rhythmicity in the activity of the visual system, suggesting that visual processing operates through a succession of perceptual cycles that closely rely on the activity of the underlying oscillating networks (VanRullen, 2016; White, 2018). More specifically it has been hypothesized that neural oscillations in the range of alpha (7–13 Hz) play a critical role in sustaining the cyclic structure of visual processing, such that an optimal sampling of visual inputs occurs at favorable phases of the alpha rhythm (Busch et al., 2009; Mathewson et al., 2009; Dugué et al., 2011; Michel et al., 2022). In line with this hypothesis, alpha oscillatory parameters (i.e., phase and power) were consistently shown to be linked to rhythmic fluctuations in the excitability of the posterior cortices and are thought to shape visual perception through a mechanism of pulsed inhibition of the ongoing cortical activity (Busch et al., 2009; Mathewson et al., 2009; Jensen et al., 2012; Van Rullen, 2016). These assumptions were strongly supported by a series of EEG studies revealing a relationship between increased alpha power and decreased target detectability, suggesting that variations in alpha synchronization correspond to fluctuations in behavioral performance and visual awareness (De Graaf et al., 2013; Mathewson et al., 2009; Spaak et al., 2014; Benedetto et al., 2018). In addition, alpha phase at the time of the stimulus onset was also shown to be associated to a diminished target detectability (Mathewson et al., 2009), in favor of the notion that the phase at which the presentation of visual stimuli occurs has an influence on ongoing visual processing (Gho & Varela, 1988; Ronconi et al., 2017). This evidence linking alpha oscillatory activity with periodical visual processing was further supported by several EEG studies demonstrating that the frequency of alpha oscillations is related to the speed and the efficiency of the visual processing (Morillon & Schroeder, 2015; Ronconi et al., 2018; Sadaghiani et al., 2010). Specifically, it has been demonstrated that faster alpha frequencies are predictive of a more accurate flash discrimination in a two-flash fusion task (Samaha & Postle, 2015) or in other similar tasks probing visual temporal segregation/integration (Wutz et al., 2018), suggesting that the frequency of alpha rhythm is strongly related with the temporal resolution of visual perception. In addition, recent findings have shown that modulating prestimulus alpha frequency by rhythmic-TMS affected perceptual accuracy, providing evidence for a link between the speed of alpha oscillations and spatiotemporal sampling resources (Di Gregorio et al., 2022). In line, another EEG investigation showed that the frequency, rather than the power, of alpha oscillations was predictive of objective accuracy in a Posner paradigm, with faster prestimulus alpha frequency accounting for better perceptual performance (Trajkovic et al., 2023), strengthening the notion that alpha oscillatory frequency has a role in shaping objective perceptual performance, whereas alpha power accounts for its subjective readout (Trajkovic et al., 2023). Overall, these observations reinforced the idea that variations in alpha oscillatory activity, and the concurrent

fluctuations in cortical excitability, may be responsible for sustaining the periodical structure of visual perception. Nonetheless, it has been argued that the complex mechanisms underlying the rhythmical sampling of visual information requires a timed coordination of both perceptual and attentional processing across different brain networks, likely involving oscillatory activity at various brain rhythms (Fiebelkorn & Kastner, 2019). In this respect, alpha oscillations have been also posited to reflect an active attentional gating mechanism, which enhances processing of relevant visual stimuli in task-related areas and suppresses irrelevant information (Klimesch et al., 2007). However, in more recent years, several studies have also enlightened the role of other brain rhythms in supporting distinct aspects of periodical visual processing (Fiebelkorn & Kastner, 2019; Gaillard & Ben Hamed, 2022; Keitel et al., 2022). In particular, several studies suggest direct involvement of theta oscillations (3–6 Hz) in spatial attention across multiple cortical regions, with the strongest relationships being measured at frontal and parietal scalp sites (Helfrich et al., 2018). For example, coupling between theta phase and higher-frequency power in frontal and parietal cortices (i.e., the attention network) is predictive of increased hit rates and reaction times (Helfrich et al., 2018) in various cognitive tasks (Canolty et al., 2006; Voytek et al., 2010), suggesting not only that theta-rhythmic sampling might be a fundamental property of the spatial attention network, but also that theta-rhythmic activity cooperates with higher frequency bands, resulting in alternating periods of either enhanced or diminished perceptual sensitivity (Dugué et al., 2015; Fiebelkorn et al., 2013).

1.2. Uncovering the rhythms of visual performance

Direct evidence of rhythmicity in both perceptual and attentional processing can emerge also employing behavioral and psychophysical measures obtained from a methodological approach known as ‘dense-sampling’ (Balestrieri et al., 2022; de Graaf et al., 2013; Drewes et al., 2015; Landau & Fries, 2012; Ronconi et al., 2018; Ronconi & Melcher, 2017). According to this procedure, one sensory stimulus is used to reset neural oscillations and to serve as a temporal reference to probe perceptual accuracy in response to another stimulus at various times after the reset event (de Graaf et al., 2013; Drewes et al., 2015; Landau & Fries, 2012). This dense-sampling procedure requires using a large set of time intervals between the reference and the probe stimuli, in order to sample perception with a relatively high temporal resolution, in a way that the resulting fluctuations in behavioral performance (i.e., behavioral oscillations) can then be analyzed through spectral methods (i.e., Fast Fourier Transform, FFT), that are similarly used for electrophysiological signals (Landau & Fries, 2012), but allow to convert a signal into individual spectral components, providing frequency information about the signal itself. Many of the paradigms (Dugué et al., 2011; McLelland et al., 2016; Van Rullen, 2016) employing this methodology reported the existence of an intrinsic rhythm in behavioral performance fluctuating at approximately 10 Hz. Notably, these studies showed that the 10 Hz rhythm visible in behavioral performance was related to the activity of parieto-occipital scalp sites (Dugué et al., 2011;

McLelland et al., 2016; Van Rullen, 2016). This made possible to assume that this sampling mechanism might be related to the perceptual aspects of the task. Importantly, by manipulating the exogenous attentional resources during visuospatial performance, other investigations uncovered also a slower sampling mechanism in the theta/lower alpha range at around 7 Hz, emerging when participants are requested to attend a single spatial location (Busch & VanRullen, 2010; VanRullen et al., 2007). Other investigations reported a periodical sampling in lower frequency bands at around 3–4 Hz when attentional resources were explicitly or implicitly deployed to two different items or position (Fiebelkorn et al., 2013; Huang et al., 2015; Landau & Fries, 2012; Song et al., 2014), while other studies reported a periodicity in behavioral performance occurring at even lower frequencies (e.g., 2–3 Hz) in presence on multiple items to be attended (Holcombe & Chen, 2013). This decrease in the speed of visual sampling as a function of the number of items to be attended suggests that the intrinsic attentional rhythms measured at any one location at 7 Hz can be split to each possible position or object during alternate cycles (Landau & Fries, 2012).

1.3. Is it possible to reveal distinct rhythms in visual performance, depending on task demands and side of target presentation?

Overall, the existing literature suggests the presence of an intrinsic rhythmicity in visual perception and visuospatial attention, strengthening the evidence that both perceptual and attentional systems operate periodically, possibly at different frequencies. At the same time, specific characteristics of the experimental paradigms employed in the different studies, as well as the basic features of visual stimuli, may have a significant influence on the main visual sampling frequency, as some initial evidence suggest (Benedetto et al., 2016, p. 2017; Chen et al., 2017). Another central aspect that still needs to be understood is whether differences in periodical perceptual and attentional sampling could depend on the side of stimulus presentation, and consequently on the hemisphere that preferentially processes the incoming sensory input. Indeed, in accordance with the current view of perceptual cycles, it is possible to assume that the different rhythms of visual perception and visuospatial attention may depend not only on task characteristics or stimulus properties, but also on the brain circuits supporting these periodical mechanisms (Van Rullen, 2016). Nevertheless, the behavioral paradigms investigating perceptual and attentional rhythms were either based on a central stimulus presentation (Mathewson et al., 2012), or in case of lateralized visual stimulus presentation (Landau & Fries, 2012; Michel et al., 2022; Senoussi et al., 2019; Song et al., 2014; Chen et al., 2017), evidence for differences between a left-side versus heric asymmetries in oscillatory patterns (i.e., alpha rhythm, theta rhythm) have been reported in healthy participants during spatial attention (Gallotto et al., 2020) and patients with posterior brain lesions and visual field defects at rest (Pietrelli et al., 2019; Gallina et al., 2022a,b). As a consequence, if both perceptual and attentional cycles supposedly mirror the oscillatory activity of the underlying neural populations, the left and the right brain hemispheres may show substantial differences in their sampling frequency.

To test this hypothesis and to uncover possible distinct rhythms in visuospatial performance, behavioral oscillations in response to the presentation of visual stimuli were assessed in two versions of a visual detection task, in a large group of 48 healthy participants where the endogenous attentional requirements were manipulated. A simple visual detection task, was used to differentiate possible perceptual and attentional rhythms, depending on the endogenous attentional demands, but restraining possible effects of task execution and basic visual stimulus properties. Indeed, most of the previous studies describing the co-occurrence of various frequencies in visual sampling often employed tasks requiring more subtle perceptual abilities (e.g., discrimination and visual search; Landau & Fries, 2012; Dugué et al., 2015; Michel et al., 2022), without the possibility to disambiguate whether each of these behavioral rhythms would represent either the perceptual or the attentional aspects of the visuospatial performance. In the first version of this task a Gabor patch at the contrast threshold was presented exclusively to the left or to the right hemifield, with participants being instructed to monitor one hemifield only within the same experimental block (Task 1), whereas in the second version of this task, the same visual target could appear randomly to the left or to the right hemifield, without any spatial cue, with participants monitoring both hemifields within the same experimental block (Task 2). In this way, participants' endogenous attentional resources were directed selectively to one single spatial location or split between two different spatial locations simultaneously. Similarly to what was previously done in other studies measuring perceptual oscillations (Drewes et al., 2015; Ronconi & Melcher, 2017), participants' perceptual performance, in terms of percentage of detection accuracy, was then analyzed through a spectral decomposition as a function of the time interval occurring between reference stimuli and the probe stimuli, following the logic of the dense-sampling method described above. Finally, the resulting spectral components were statistically tested by performing a permutation analysis, in order to characterize the main behavioral oscillatory components emerging in the task in response to stimulus presentation to the left and to the right hemifield. Importantly, all the analysis will be performed separately on participants exhibiting or not exhibiting a reliable performance to isolate genuine oscillations in the visuospatial performance, ruling out possible background noise caused by inconsistent task execution.

2. Material and methods

2.1. Participants

Forty-eight neurologically healthy volunteers (28 females, 20 males) males aged 18–45 took part in the study. In the following method sections, we report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. Sample size was estimated with an a priori power analysis (G*Power version 3.1.9.7; Faul et al., 2007), set with a medium effect size (Cohen's $d = .20$), significance criterion

$\alpha = .05$, power = .90, one group and 4 measurements (Task 1 and 2, Left hemifield vs Right hemifield), resulting in a sample size of 46. Inclusion and exclusion criteria were established prior to the study and data analysis: all participants showed normal or corrected-to-normal visual acuity and did not report history of neurological disorders or epilepsy. Participants were informed about the procedure and the purpose of the study and gave written informed consent. The study was designed and performed in accordance with the ethical principles of the Declaration of Helsinki and was approved by the ethical committee of the Department of Psychology “Renzo Canestrari” of the University of Bologna (Prot. 42483).

No part of the study, including experimental procedures and analyses, was pre-registered in a time-stamped, institutional registry prior to research conduction.

2.2. Apparatus and stimuli

Participants seated in a sound-proof room, positioned on a chin-rest at a viewing distance of 57 cm, in front of a 24-inch LED monitor at 1080×980 pixels of spatial resolution with a vertical refresh rate of 144 Hz (32-bit depth; gamma value was set to +1). Throughout the experimental procedure eye-movements were monitored and recorded with a Pan/Tilt optic eye-tracker (ASL 6000), with a sampling rate of 60 Hz. All visual stimuli were delivered on a middle gray background and consisted of vertically oriented Gabor patches ($.5 \times .5^\circ$), appearing at 15° at the right or the left to a black central fixation cross ($.5 \times .5^\circ$), on the midline. To ensure that stimuli were presented at threshold (contrast detection threshold was set at 75% of accuracy; [Drewes et al., 2015](#); [Lesmes et al., 2015](#)), the contrast of the Gabor patches was adjusted individually before the experiment, through a Bayesian QUEST procedure ([Watson & Pelli, 1983](#), for a detailed description of the QUEST procedure, see 2.4 and 2.5). The experiment was developed in MATLAB (R2018a; The Mathworks Inc., USA) using customized routines implemented with the PsychToolbox ([Brainard & Vision, 1997](#)).

2.3. Experimental procedure

All participants were asked to complete two versions of a visual detection task that differ based on the type of target presentation, with respect to a central fixation cross. Prior to task execution, participants were informed about the type of target presentation. Participants were instructed to respond whether they saw the Gabor or not, by pressing two different buttons on a keyboard (i.e., 25 participants responded using the left hand, 23 participants responded using the right hand) and to keep their gaze on the central fixation cross, for the entire duration of the experimental session.

In Task 1, the Gabor could appear only to the left or to right of the central fixation cross, in separate experimental blocks. Therefore, participants, in each block, had to attend a single hemifield at time, directing their endogenous attentional resources to one location only, in absence of an exogenous spatial cue. In Task 2, the Gabor could appear randomly in either the left or the right hemifield, with equal probability, during the same experimental block. As a consequence, participants had to monitor both the left and the right hemifield,

simultaneously, splitting their endogenous attentional resources to two locations at the same time, in the absence of an exogenous spatial cue. Each participant completed all the experimental blocks for Task 1 and Task 2 separately and the order of execution of Task 1 and 2 was counterbalanced across participants. All the stimuli and the apparatus were identical for Task 1 and Task 2.

2.3.1. Visual detection task with fixed-hemifield target presentation (Task 1)

Each trial started with the presentation of a full-sized black screen (duration: 21 ms), which served to induce a phase reset of the ongoing functionally relevant oscillations within (i.e., from visual stimuli to visual areas; [Landau & Fries, 2012](#)) sensory modalities. This allows to measure fluctuations in behavior over time aligned to a putative reset point ([Fiebelkorn et al., 2011](#); [Landau & Fries, 2012](#)). At the offset of the black screen, target stimuli (i.e., Gabor patches; see 2.2) appeared for 42 ms at different stimulus onset asynchrony (SOA), exclusively in the left or the right hemifield. Specifically, in order to sample rhythmic perceptual activity, the SOAs randomly varied among 17 possible time points, ranging from 56 to 292 ms in regular steps of 14 ms, following the logic of the dense sampling procedure ([Fiebelkorn et al., 2011](#); [Landau & Fries, 2012](#)). At the Gabor offset, when a black central question mark sized $.5 \times .5$ cm replaced the central fixation cross, participants had to provide their response (no response time limit). After the participants' response, the central fixation cross appeared again at a randomly varying duration (Intertrial Interval, ITI), ranging from .5 to 1.5 s, before the subsequent trial (see [Fig. 1](#)). Each experimental block comprised 6 trials for each SOA where the target was present (for a total of 102 trials), and 17 catch trials in which the target was absent, for a total of 119 trials per block. All participants completed 3 experimental blocks for each hemifield, for a total number of 357 trials per hemifield. Prior to the task execution, the contrast of the Gabor was adjusted individually with a QUEST procedure, performed separately for the left and for the right hemifield. The QUEST procedure consists in an adaptive psychometric method that places each trial at the current most probable Bayesian estimate of threshold. The QUEST procedure takes advantage of the common finding that the human psychometric function is invariant in form when expressed as a function of log intensity ([Watson & Pelli, 1983](#)). The experimental set-up, method and procedure employed for the QUEST had the same characteristics of the visual detection used in the task. However, in the QUEST procedure no catch trials were presented. In particular, the QUEST consisted of 4 target presentations for each SOA, for a total of 68 trials per hemifield. The resulting contrast threshold values for the left and the right hemifield were .26 and .27, respectively, in a range comprised between 0 and 1. In order to exclude that possible differences in the subsequent detection performance may depend on differences in the contrast threshold between the left and the right hemifield, a paired t-test on the individual contrast values was performed. No statistical difference was found between the mean contrast value of the left hemifield and the right hemifield ($t(96) = -.611$, $p = .338$).

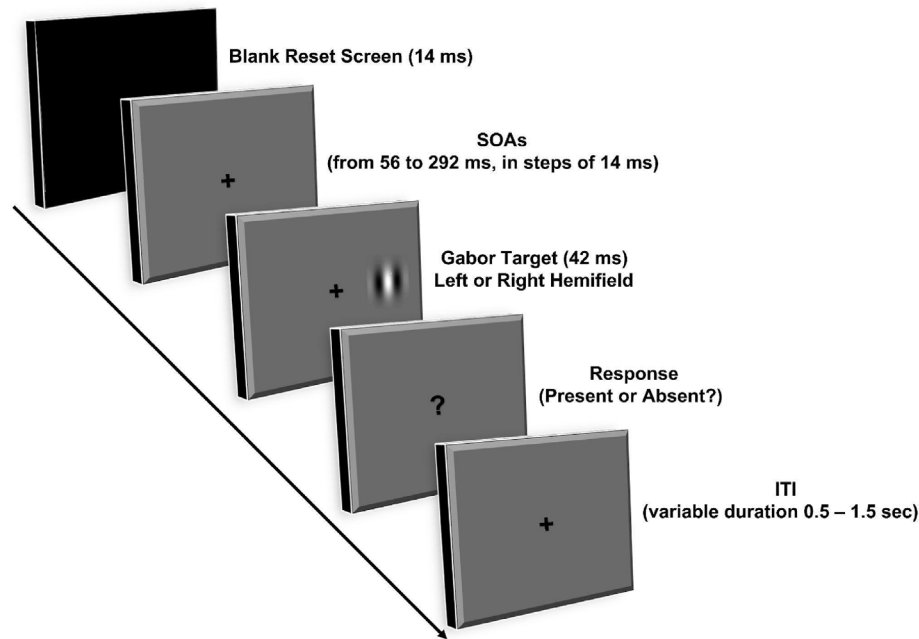


Fig. 1 – Schematic representation of the experimental paradigm. A) Each trial began with the presentation of a blank reset screen (14 ms), to induce a phase reset of the ongoing perceptual oscillations. To reveal potential oscillatory components in the detection performance, perpetual performance was densely sampled over time, using different stimulus onset asynchronies (SOAs; from 56 to 292 ms, in steps of 14 ms) preceding the appearance of lateralized Gabor target stimuli (42 ms) presented at the participants' contrast threshold. Target stimuli were delivered to the right or left hemifield in separate experimental blocks (Task 1), or randomly presented to the left or right hemifield within the same experimental block (Task 2). At the Gabor target offset, participants had to report whether the target stimulus was perceived as present or absent. After the participants' response, the central fixation cross appeared again at a randomly varying duration (Intertrial Interval, ITI; ranging from .5 to 1.5 s) before the subsequent trial.

2.3.2. Visual detection task with alternate hemifield target presentation (Task 2)

The experimental procedure in Task 2 was identical to that of Task 1, with the exception that in this task stimuli were randomly presented in the left and right hemifield within each experimental block. Each experimental block consisted in 3 target presentations per hemifield, with the Gabor patch randomly appearing in either the left or the right hemifield (i.e., 51 trials per hemifield), and in 17 catch trials in which the target was absent, for a total of 119 trials per block. All participants completed 6 experimental blocks, for a total number of 357 trials for each hemifield. Similarly to Task 1, prior to task execution the contrast of the Gabor was adjusted individually with a QUEST, where Gabor patches were randomly appearing at either the left or the right hemifield, within the same block and no catch trials were presented. The QUEST consisted of 4 target presentations for each SOA per hemifield, for a total number of 68 trials for each hemifield. The resulting contrast threshold values for the left and the right hemifield were .30 and .31, respectively, in a range comprised between 0 and 1. Similarly to Task 1, to rule out that possible differences in the subsequent detection performance may depend on differences in the contrast threshold between the left and the right hemifield, a paired *t*-test on the individual contrast values was performed. No statistical difference was found

between the mean contrast value of the left hemifield and the right hemifield ($t(96) = -.269, p = .655$).

2.4. Data processing and analysis

All data processing and analysis were identical for Task 1 and Task 2. Eye-movements recordings from all participants (with the exception of 9 participants, whose recordings were not available due to technical issues) were offline processed. Trials in which participants' gaze was diverted from the central fixation cross were excluded from further analysis. In particular, in Task 1, 3% of the total number of trials were discarded for the left hemifield and 3.5% of trials for the right hemifield; in Task 2, 3% of trials were discarded for the left hemifield and 3% of trials for the right hemifield. The analyses on the remaining trials were performed separately for the left and for the right hemifield, for each participant. Importantly, to perform the subsequent analysis following the dense sampling method a large number of trials is required and this, in a basic visual detection performance, is likely to induce fluctuations in the participants' perceptual sensitivity and in the decision criterion, that possibly lead to inconsistent and unreliable performance. Moreover, response variability during detection tasks might also occur when individual contrast threshold is computed with standard titration procedures

(such as the QUEST procedure used in the present study) where catch trials are not included (Tarasi et al., 2022). Therefore, in order to isolate possible confounding due to variability in the perceptual sensitivity across subjects, possibly caused by the specific characteristics of the visual detection task and the titration procedure, observed participants' perceptual sensitivity in terms of d' was calculated (Macmillan & Creelman, 2004; Statilite software Version 1.05 developed by Chris Rorden) for each hemifield in each task. Then, each d' value was statistically compared to the d' value reflecting the chance level of performance, by computing the confidence interval (95%) and the relative p -values associated to the difference between the 2 d' values (Macmillan & Creelman, 2004; variance for the d' was calculated for two-alternative forced-choice paradigm, as suggested by Bi et al. (1997) and Gourevitch and Galanter (1967). Based on that, participants were split in two groups: one group of 25 subjects that we will refer to as Good Performers (13 participants responded using the left hand, 12 participants using the right hand), whose d' was found to be significantly above the chance level in both the left and right hemifield, for both Task 1 (all p -values $<.045$) and Task 2 (all p -values $<.037$; Task 1: Mean d' left hemifield: $M = 1.86$, $SD = .68$; Mean d' right hemifield: $M = 1.81$, $SD = .78$; Task 2: Mean d' left hemifield: $M = 1.86$, $SD = .80$; Mean d' right hemifield: $M = 1.81$, $SD = .80$); another group of 23 subjects that we will refer to as Bad Performers (12 participants responded using the left hand, 11 participants using the right hand), whose d' was not significantly different from the chance level in at least one hemifield (all p -values $>.072$; Task 1: Mean d' left hemifield: $M = .83$, $SD = .66$; Mean d' right hemifield: $M = .85$, $SD = .73$; Task 2: Mean d' left hemifield: $M = 1.53$, $SD = 1.11$; Mean d' right hemifield: $M = .94$, $SD = .86$). Importantly, the d' values calculated for each task and hemifield were used only to assign participant to either the group of the Good or the Bad Performers. For all the subsequent analysis, performed separately for the group of Good Performers and Bad Performers, we considered the detection accuracy rate, as a function of the SOA, separately for Task 1 (see Fig. 2) and Task 2 (see Fig. 3). Initially, all trials were sorted by the SOA.

To remove linear trends from the raw data due to background noise, pointing to a general decrease of the detection accuracy rates as the SOA increases (see Figs. 2 and 3), a linear detrend was applied. Then, a moving average (window size: 2) and a zero padding (frequency resolution with zero padding: .6 Hz) were applied to the resulting time series, to further smooth out random background fluctuations and to increase the frequency resolution, respectively.

Then a Fast Fourier Transform (FFT) was computed for the individual time series, similarly to what was done in previous studies measuring behavioral oscillations in perception (Balestrieri et al., 2022; Drewes et al., 2015; Ronconi et al., 2018; Ronconi & Melcher, 2017). All individual FFT spectra were subsequently averaged across participants to characterize the perceptual oscillations in response to stimulus presentation, in terms of the main oscillatory components. The statistical significance of the resulting FFT spectrum was tested by performing a permutation test. In particular, for each individual dataset, 2500 permutations were calculated from the real data by randomizing the SOA labels. Permuted data were analyzed

with the same procedure described for real data (i.e., linear detrend, moving average and zero padding) before undergoing the FFT. The amplitude values, averaged across participants, of the 2500 permuted FFT spectra represented the null distribution that was used to set the statistical significance for the frequency bins constituting the real observed Fourier spectra. Specifically, after calculating the 95th percentile (corresponding to an $\alpha = .05$) for the permuted data to set the cut-off of statistical significance, and considering the frequency bins of the real FFT spectra whose magnitude resulted significantly above the cut-off, we could conclude that there were one or more sampling rhythms for detecting stimuli presented in the left or in the right hemifield, in line with previous studies investigating perceptual oscillations (Balestrieri et al., 2022; Benedetto et al., 2016; Drewes et al., 2015; Ronconi et al., 2018; Ronconi & Melcher, 2017).

Along with the spectral decomposition and permutation analysis on the aggregated data, we performed also and additional analysis on the participants' individual frequency peaks in Task 1 and Task 2, separately for the group of Good performers and Bad performers. To this aim, participants' individual spectra were preprocessed with the same routine described for the aggregated data (i.e., linear detrend, moving average and zero padding) and visually inspected. The participants' individual frequency peak was identified as the main component exhibiting the highest magnitude. Then, to confirm the presence of possible differences in the frequency of the spectral components, across groups, tasks and hemifields, we performed an ANOVA having Group (Good performers, Bad performers), Task (Task 1, Task 2) and Hemifield (Left, Right), as factors. Significant main effects and interactions were subsequently explored with post-hoc analysis using Tukey HSD test.

3. Results

3.1. Visual detection task with fixed-hemifield target presentation (Task 1)

When participants had to direct their attentional resources to one single hemifield within the same experimental block, for the group of Good Performers, the permutation analyses revealed the presence of an oscillatory component in the upper alpha range peaking at 10.5 Hz ($p = .045$; see Fig. 4A) for stimuli presented to the left hemifield. Furthermore, for stimuli presented in the right hemifield a wide significant peak was observed in the lower alpha range of the FFT spectra, spanning frequencies between 6 Hz ($p = .031$) and 9 Hz ($p = .034$, see Fig. 4A). To exclude that these differences in oscillatory components could be due to differences in accuracy, perceptual sensitivity and bias between the two hemifields, we statistically compared left and right hemifield performance (i.e., detection rates, d' and criterion). No significant difference in terms of detection rate (Task 1 left: $M = 66\%$, $SD = .16$; Task 1 right: $M = 67\%$, $SD = .17$; $t(48) = -.241$, $p = .778$), d' (Task 1 left: $M = 1.86$, $SD = .68$; Task 1 right: $M = 1.91$, $SD = .78$; $t(48) = -.012$, $p = .899$) and criterion (c ; Task 1 left: $M = .48$, $SD = .37$; Task 1 right: $M = .44$, $SD = .49$; $t(48) = -.402$, $p = .633$) between left and right hemifield

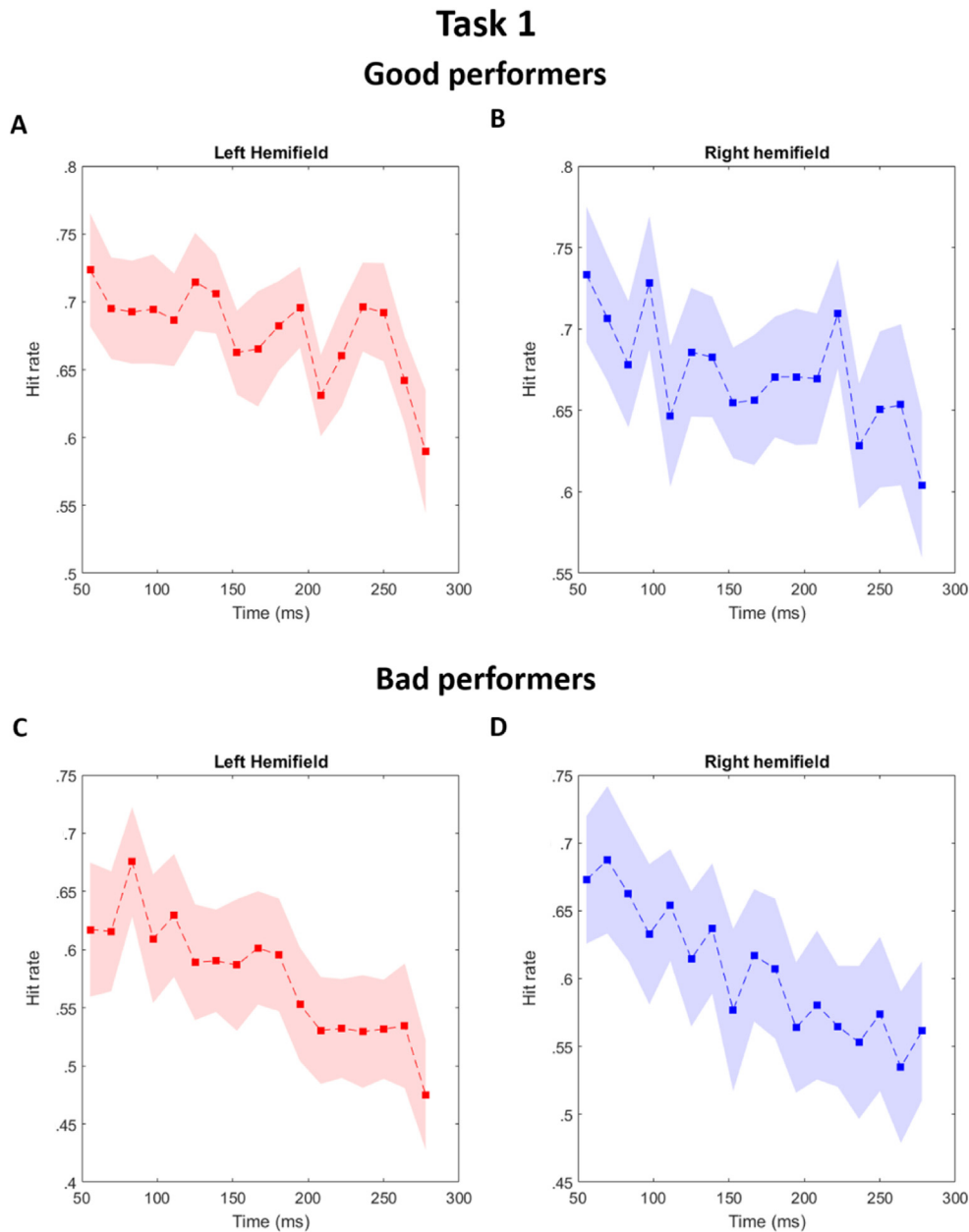


Fig. 2 – Average raw hit rates over the different SOAs for the group of Good Performers (A,B) and the group of Bad Performers (C,D), relative to the left (red line) and the right (blue line) hemifield performance in Task 1.

performance was found, confirming that perceptual sensitivity and bias cannot account for the observed differences in terms of oscillatory behavioral patterns.

In contrast, in the group of Bad Performers, no significant component was found (all p -values $>.149$, see Fig. 4B). These latter results, where rhythmic sampling of visual information over time was studied as a function of differences in perceptual sensitivity, suggest that when attentional resources are allocated exclusively to one spatial location at time, participants' perceptual sensitivity has an influence in determining the perceptual fluctuations measured in the visual detection tasks. At the same time, these perceptual oscillations are present at slightly different rhythms, with a slower rhythmic

sampling evident in the right as compared to the left hemifield.

3.2. Visual detection task with alternate hemifield target presentation (Task 2)

When participants had to monitor both the left and the right hemifield within the same experimental block, the group of Good Performers showed the presence of significant oscillatory components that were comparable across hemifields. Specifically, a peak in the theta range at 5.5 Hz was observed in the FFT spectra for stimuli presented both in the left ($p = .014$, see Fig. 5A) and in the right hemifield ($p = .019$, see Fig. 5A), in a

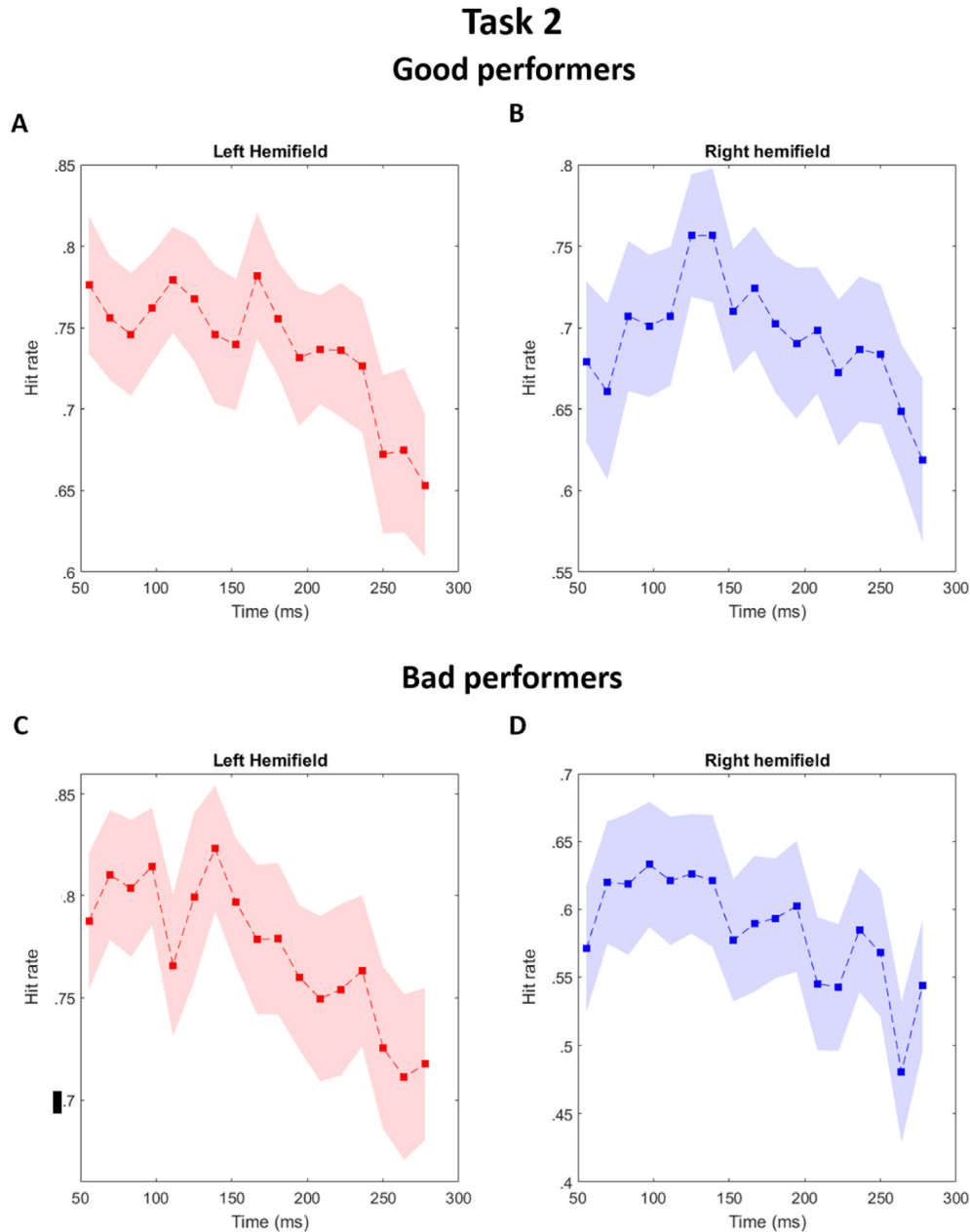


Fig. 3 – Average raw hit rates over the different SOAs for the group of Good Performers (A,B) and the group of Bad Performers (C,D), relative to the left (red line) and the right (blue line) hemifield performance in Task 2.

frequency range comprised between 5 and 6 Hz. We also statistically compared left and right hemifield's accuracy, perceptual sensitivity and bias (i.e., detection rate, d' and criterion) and no significant difference in terms of detection rate (Task 2 left: $M = 74\%$, $SD = .17$; Task 2 right: $M = 68\%$, $SD = .18$; $t(48) = 1.258$, $p = .264$) d' (Task 2 left: $M = 1.95$, $SD = .80$; Task 2 right: $M = 1.85$, $SD = .80$; $t(48) = -.511$, $p = .615$) and criterion (c) (Task 2 left: $M = .23$, $SD = .46$; Task 2 right: $M = .34$, $SD = .47$; $t(48) = .425$, $p = .222$) was found.

In contrast, for the group of Bad Performers, no significant component was found in response to stimuli presented to the left, nor to the right hemifield (all p -values $> .351$ see Fig. 5B).

Overall, these latter results suggest that when attentional resources are deployed to two spatial locations simultaneously, visual stimuli were sampled uniformly across the visual field at a theta rhythm and that perceptual sensitivity has an impact on rhythmic sampling of multiple locations in a visual detection task. When comparing results between the two tasks, it is relevant to note that while in Task 1, where one single location at a time was monitored, Good Performers showed a differentiation in their perceptual oscillations between the left and the right hemifield (i.e. the right hemifield was sampled at a lower frequency as compared to the left hemifield), this differentiation did not emerge when two

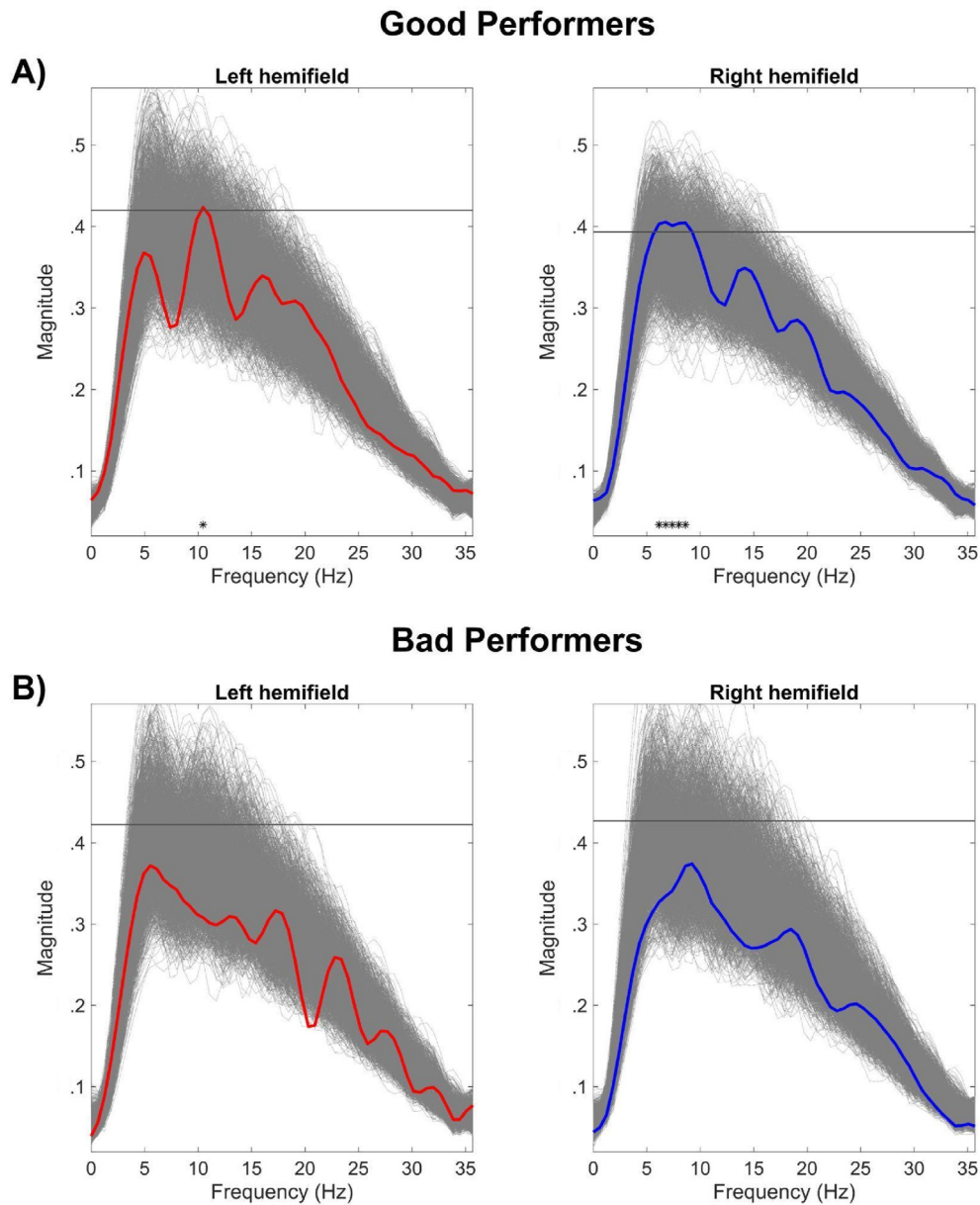


Fig. 4 – Power spectrum of perceptual oscillations in Task 1, where target stimuli appeared exclusively in the left or the right hemifield. A) Power spectrum (Magnitude) observed in Good Performers participants in response to target stimuli presented to the left hemifield (left panel; red solid line) and to the right hemifield (right panel; blue solid line). B) Power spectrum (Magnitude) observed in Bad Performers participants in response to target stimuli presented to the left hemifield (left panel; red solid line) and to the right hemifield (right panel; blue solid line). Gray lines indicate power spectra obtained from permuted data. The black horizontal lines represent the significance cut-off. * = $p < .05$. Black asterisks indicate the frequency bins in the observed spectrum that are significantly different compared to the spectra obtained from the permutation test.

different locations had to be monitored at the same time, and theta became the unique sampling rhythm involved.

3.3. Individual frequency peaks for visual detection task with fixed-hemifield (Task 1) and alternate hemifield (Task 2) target presentation

The ANOVA on the participants' individual frequency peaks revealed a significant main effect of Hemifield ($F_{1,46} = 6.417$, $p < .001$), with a higher mean peak for stimuli presented to the

left ($M = 8.4$ Hz), than to the right hemifield ($M = 7.7$ Hz, $p = .013$) and a significant main effect of Task ($F_{1,46} = 45.91$, $p < .001$). Post-hoc analysis on this latter main effect revealed a higher frequency for Task 1 ($M = 9.4$ Hz), than for Task 2 ($M = 7.4$ Hz, $p = .001$), suggesting that the frequency of behavioral oscillations is faster when participants attentional resources are focused on a single spatial location, rather than split between two locations simultaneously. In addition, the ANOVA revealed a significant Group $\times$ Task ($F_{1,46} = 13.78$, $p < .001$) and Group $\times$ Task $\times$ Hemifield ($F_{1,46} = 4.44$, $p = .040$)

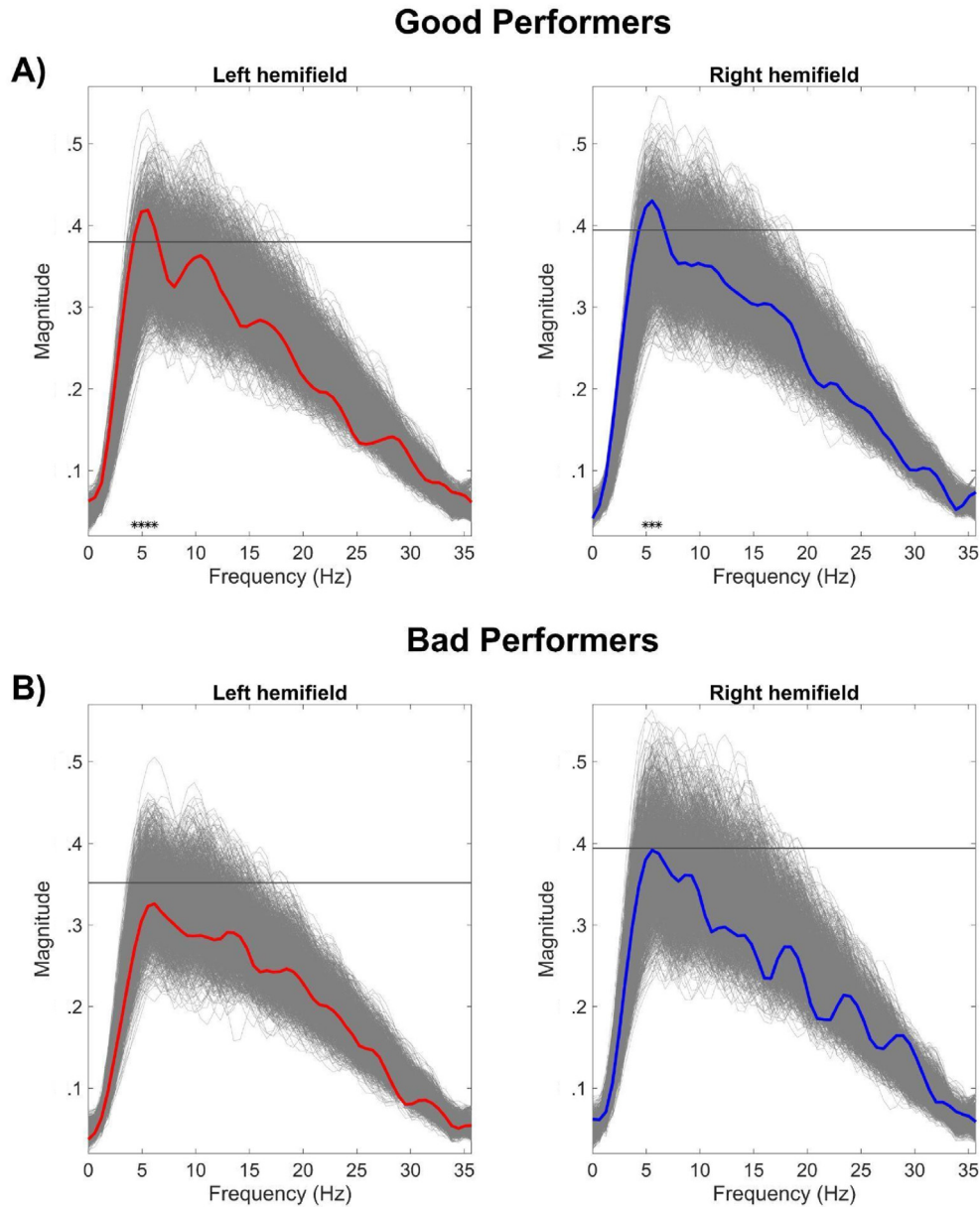


Fig. 5 – Power spectrum of perceptual oscillations in Task 2, where target stimuli were randomly presented in the left and right hemifield. A) Power spectrum (Magnitude) observed in Good Performers participants in response to target stimuli presented to the left hemifield (left panel; red solid line) and to the right hemifield (right panel; blue solid line). B) Power spectrum (Magnitude) observed in Bad Performers participants in response to target stimuli presented to the left hemifield (left panel; red solid line) and to the right hemifield (right panel; blue solid line). Gray lines indicate power spectra obtained from permuted data. The black horizontal lines represent the significance cut-off. $* = p < .05$. Black asterisks indicate the frequency bins in the observed spectrum that are significantly different compared to the spectra obtained from the permutation test.

interaction, that was further explored by performing two separate ANOVAs on Task 1 and Task 2, having Group (Good performers, Bad performers) and Hemifield (Left, Right), as factors. The ANOVA on Task 1 revealed a significant main effect of Group ($F_{1,46} = 11.31, p = .002$), with a overall higher frequency for the Good performers ($M = 10.4$ Hz), compared to the Bad performers ($M = 8.3$ Hz, $p = .002$), a significant main effect of Hemifield ($F_{1,46} = 6.68, p < .012$), with a higher frequency for the Left ($M = 10$ Hz), versus Right hemifield

($M = 8$ Hz, $p = .001$) and a significant Group $\times$ Hemifield ($F_{1,46} = 4.15, p < .047$) interaction (see Fig. 6). Post-hoc analysis on this latter interaction revealed a higher frequency for stimuli presented to the Left ($M = 11.3$ Hz, see Fig. 6A), than to the Right hemifield ($M = 9.4$ Hz, $p = .008$, see Fig. 6A), only for the Good performers, but not for the Bad performers (Left, $M = 8.4$ Hz vs Right, $M = 8.2$ Hz; $P = .649$, see Fig. 6B).

On the contrary, for Task 2, the ANOVA did not show any significant main effect or interaction (all $ps > .112$, see Fig. 6B).

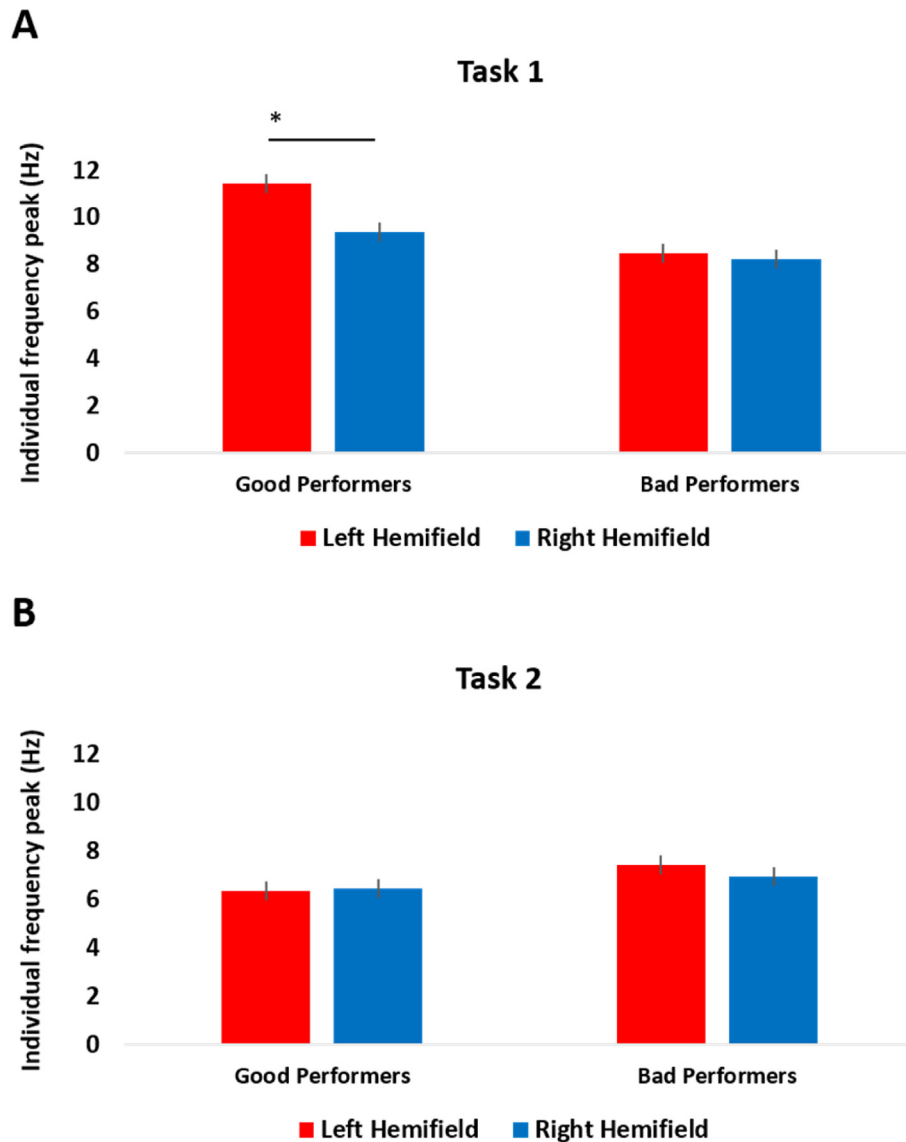


Fig. 6 – Bar histograms show the average participants' individual frequency peaks in the Good performers and Bad performers, for the left and the right hemifield, in Task 1 (panel A) and Task 2 (panel B). Error bars represent standard error; asterisks indicate the significant comparisons.

Overall, these results confirm that stimuli presented to the left hemifield undergo a faster sampling mechanism, compared to stimuli presented to the right, when one single spatial location is attended (Task 1), whereas no differences in the speed of the sampling mechanism emerge when attentional resources are deployed between two spatial locations (Task 2), in line with the results of the FFT and permutation analysis performed on the aggregated data for Task 1 and Task 2 (see, 3.1 and 3.2).

4. Discussion

The results of the present study revealed the existence of distinct oscillatory patterns in visual detection performance,

in response to a lateralized visual target that differed based on the attentional requirements of the task, and on the side of the target presentation. Importantly, in the present study, participants were assigned to two distinct groups (i.e., Good Performers and Bad Performers) according to the reliability of their detection performance. This step was crucial to enlighten reliable components from the spectral analysis, and to assure that they resulted from the specific attentional demands of the task and not from the background noise due to the presence of high interindividual variability in task execution. Indeed, participants may show changes in perceptual sensitivity and decision criteria or variations in their response bias over time during basic visual detection tasks at threshold, especially when catch trials are not employed during the titration procedure (Tarasi et al., 2022),

leading to highly variable responses (Schwiedrzik et al., 2009), that might result in performance at chance level.

Noteworthy, the group of Good Performers included participants whose detection performance resulted to be above chance level in both the left and the right hemifield, whereas participants classified as Bad Performers could either perform at the chance level in one single hemifield or both. As a result, reliable oscillations in the detection performance can be observed only in the group of the Good Performers, but not in the group of Bad Performers. Looking at the results of Task 1, when the side of target presentation was stable across trials and participants were instructed to monitor one single hemifield at time, the group of Good Performers showed a significant component peaking at ~10 Hz in response to stimuli presented to the left hemifield. When visual stimuli were presented to the right hemifield, detection performance significantly fluctuated in a broader and slower frequency within the range ~6–9 Hz. In contrast, for the group of Bad Performers, no significant oscillatory component was evident for stimuli presented to the left nor to the right hemifield. These results were further supported by the analysis performed on the participants' individual frequency peaks, that confirmed the presence for the Good performers, of a faster rhythm for stimuli presented to the left hemifield (11.4 Hz), whereas a slower rhythm (9.3 Hz) emerged for stimuli presented to the right.

Overall, these findings are in line with previous studies showing the existence of a rhythmicity in visual processing at 10–12 Hz (Van Rullen et al., 2007; Busch & VanRullen, 2010; Michel et al., 2022), which often involves the activity of posterior brain areas, related to perceptual aspects of visuospatial performance (Dugué et al., 2011; McLelland et al., 2016; Van Rullen, 2016) and are in line with recent findings, strongly suggesting that the frequency of alpha oscillations has a direct role in shaping objective perceptual performance (Di Gregorio et al., 2022; Trajkovich et al., 2023). In addition, alpha rhythm is also thought to reflect an attentional gating mechanism, which inhibits task irrelevant cortical areas and facilitates information processing in task relevant cortical networks, thus confirming previous claims that neural oscillations in this frequency band may orchestrate a complex interplay between sensory and attentional processing, shaping visual perception (Jensen & Mazaheri, 2010; Palva & Palva, 2007). Crucially, in most of the previous studies, the reset of the ongoing oscillatory processes was usually achieved by either employing a rhythmic stimulation, which imposes an external frequency on the subsequent neural and behavioral oscillation (i.e., rhythmic entrainment; Thut et al., 2011; Mathewson et al., 2012; Spaak et al., 2014; Ronconi et al., 2018), or by manipulating the attentional resources through single lateralized exogenous flash events (Landau & Fries, 2012). In contrast, in the present study, a single resetting event that did not entail any rhythmic pattern and did not represent an exogenous spatial cue was used. Therefore, these oscillatory patterns reflect an intrinsic perceptual rhythm in response to the presentation of simple visual stimuli, occurring in the absence of a trial-by-trial exogenous manipulation of the attentional resources.

When looking at the results of Task 2, where the side of target presentation was randomized across trials and

participants had to deploy their attentional resources to both hemifields simultaneously, the group of Good Performers revealed the presence of a significant component peaking at ~5 Hz both for stimuli presented to the left and to the right hemifield. In contrast, for the group of Bad Performers, no significant component emerged in response to visual stimuli presented to the left or to the right hemifield. In line, the analysis performed on the participants' individual frequency peaks, confirmed the presence of a rhythm fluctuating at a similar frequency (~6 Hz), for both hemifields. The findings observed in Good Performers are consistent with previous studies revealing the existence of an attentional sampling mechanism in the theta range (Busch et al., 2009; Dugué et al., 2015; Van Rullen, 2015; Ronconi et al., 2018), usually related to the activity of fronto-parietal scalp sites (Busch et al., 2009; Dugué et al., 2015; Voloh et al., 2015; Van Rullen, 2016; Ronconi et al., 2018). In particular, it has been demonstrated that psychophysical performance fluctuates at approximately 2–6 Hz when the features of the experimental task lead to a division of the attentional resources among two or more objects or spatial locations (Landau & Fries, 2012; Fiebelkorn et al., 2013; Song et al., 2014; Huang et al., 2015; Van Rullen, 2016). Overall, these findings have important implications and suggest that the attentional system is able to operate with useful and effective functional flexibility, rapidly scanning multiple objects or positions, simultaneously, making possible to disengage from one attended spatial position and shift to another location efficiently (Van Rullen, 2016). Furthermore, according to more recent evidence, it has been also proposed that theta periodic sampling may be related to rhythmic attenuations in visual processing at the presently attended location that prevents from being overly focused on any given position or object and promotes a more active sampling of the visual environment (Fiebelkorn and Kastner, 2019). Nonetheless, as discussed above for Task 1, in the previous studies the attentional resources were usually manipulated using exogenous and lateralized spatial cues (Landau & Fries, 2012; Song et al., 2014; Senoussi et al., 2019). In contrast, a crucial aspect of the current study is that we induced a deployment of the covert endogenous spatial attention during the detection performance, in absence of exogenous spatial cues.

Altogether, the results of Task 1 and Task 2 are in line with previous research on behavioral oscillations and suggest that oscillatory patterns in various frequency bands orchestrate different visuo-spatial processes (Helfrich et al., 2017; Klimesch, 2018). However, the current findings add knowledge to previous literature and help shed light on the perceptual and the attentional mechanisms that may be involved in the rhythmical sampling of simple and lateralized visual stimuli, depending on the specific task characteristics. Another relevant aspect emerging from our results is that the speed of such rhythmic mechanisms may also depend on the visual hemifield where the target stimuli appear. In particular, we observed a faster rhythm (i.e., ~10 Hz) in response to visual stimuli presented to the left hemifield, compared to a slower rhythm (i.e., ~6–9 Hz) observed in response to stimuli presented to the right hemifield. This different sampling rhythm between the left and the right visual hemifield emerged only in Task 1, where attentional resources were sustained on a

single spatial location over time. This evidence suggests that the right and the left brain hemispheres had a differential efficiency in supporting the rhythmical sampling processes, as they sampled visual information at different speeds. On the contrary, when the task required to split endogenous attentional resources between two different spatial locations, a condition where the left and the right brain hemispheres may equally contribute to support the alternate sampling of the visual stimuli at each location, visual stimuli were sampled at the same rhythm in the two hemifields. These observations may be interpreted in light of well-known models of the attentional control that put forward the hypothesis of a fronto-parietal dorsal attention network (DAN), encompassing the frontal eye fields, intraparietal sulcus and superior parietal lobe, in the orienting of endogenous spatial attention (Vernet et al., 2014). Importantly, the DAN was shown to be preactivated by the expectation of seeing an object at a specific location (Corbetta et al., 2000; Hopfinger et al., 2000; Kastner et al., 1999; Shulman et al., 1999) and to drive the selection of visual stimuli based on internal goals or predictions (Corbetta et al., 2008). Consistent with that, the DAN was shown to contain topographic maps encoding the attentional priority of items of the visual field, depending on their behavioral relevance (Bisley & Goldberg, 2010; Silver & Kastner, 2009) and to drive the process of selective attention by modifying stimulus representations in the visual cortex, based on their respective priority in the topographic map (Corbetta & Shulman, 2002). These findings are supported by additional evidence demonstrating the presence of white matter connections between subregions of the DAN and visual areas (Greenberg et al., 2012), suggesting that the DAN might control the gateways to visual processing in the visual cortex (Bressler et al., 2008; Vernet, 2014). Based on this evidence, we can speculate that when visual stimuli are expected at a particular position (i.e., Task 1), the faster rhythm in response to a left-sided target presentation (i.e., ~10 Hz), compared to the slower rhythm following a right-sided target presentation (i.e., ~6–9 Hz), may be due to a more efficient gating mechanisms mediated by right DAN areas, which may translate into a more efficient perceptual processing for stimuli presented to the left hemifield. This interpretation is in line with the longstanding theories about the dominance of the right hemisphere in visuospatial processing (Heilman & Valenstein, 1979; Heilman & Van Den Abell, 1980; Kinsbourne, 1977; Shulman et al., 2010) and is further supported by a large number of investigations in healthy participants in paradigms investigating the neural basis of spatial representation (Bowers & Heilman, 1980; Jewell & McCourt, 2000; McCourt & Olafson, 1997; Nicholls et al., 1999) and perceptual processing of simple visual features (Corballis et al., 2002; Nicholls et al., 2017) as well as in clinical populations suffering from spatial hemineglect (Bisiach & Luzzatti, 1978; Heilman et al., 1984; Heilman & Valenstein, 1979). Importantly, EEG studies have also described a central role of the right hemisphere in orchestrating the activity of alpha oscillations in visuospatial processing. For instance, an EEG study on healthy participants revealed a greater involvement of the right hemisphere in modulating alpha oscillations to tune visual abilities during

spatial orienting tasks (Gallotto et al., 2020). Together with these converging findings, the current results provide new insight on possible differences between the left and the right brain hemisphere in supporting rhythmic perceptual sampling mechanisms, and stimulate further deeper investigations into these potential hemispherical differences.

Overall, these findings strongly suggest that attentional and perceptual sampling mechanisms operate at different frequencies, depending on the requirements of the experimental paradigm. In addition, the efficiency of these rhythms may depend not only on task characteristics, but also on the different brain networks, within the left and the right hemisphere, which support these periodical mechanisms.

Finally, we hope that these results, suggesting a strong interaction between temporal and spatial mechanisms in regulating visual processes, can honor the memory of Prof. Francesca Frassinetti, to whom this Special Issue is dedicated and whose outstanding scientific contribution about the brain mechanisms underlying time and space representation (Anelli et al., 2018; Anelli & Frassinetti, 2019; Anelli & Frassinetti, 2019; Candini et al., 2022; Cantarella et al., 2023; Magnani et al., 2021) inspired our work.

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Open practices section

The study in this article has earned Open Data and Open Materials badges for transparent practices. The data and materials studies are available at: <https://osf.io/hpgnc/>.

CRediT authorship contribution statement

Jessica Gallina: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Luca Ronconi:** Methodology, Supervision, Writing – original draft, Writing – review & editing, Formal analysis, Conceptualization, Data curation. **Gianluca Marsicano:** Writing – original draft, Data curation, Methodology. **Caterina Bertini:** Project administration, Supervision, Writing – original draft, Writing – review & editing, Conceptualization, Funding acquisition, Methodology.

Declaration of competing interest

None.

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