Attention explores space periodically at the theta frequency

Mehdi Senoussi[1,2] *, James C. Moreland[3], Niko A. Busch[4,5] and Laura Dugué[6,7]

[1] ISAE-Supaéro, Université Fédérale de Toulouse, Toulouse, France
[2] Department of Experimental Psychology, Ghent University, Ghent, Belgium
[3] Department of Psychology, University of Washington, Seattle, USA
[4] Institute of Psychology, Westfälische Wilhelms-Universität, Münster, Germany
[5] Otto Creutzfeldt Center for Cognitive and Behavioral Neuroscience, Westfälische Wilhelms-Universität Münster, Germany
[6] Centre National de la Recherche Scientifique (CNRS), UMR 8242, Paris, France
[7] Université Paris Descartes, Laboratoire Psychologie de la Perception, Paris, France

Corresponding author: Mehdi Senoussi
Current address: Department of Experimental Psychology, Ghent University
H. Dunantlaan 2, 9000 Ghent, Belgium

Email address: mehdi.senoussi@ugent.be

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Abstract

Voluntary attention is at the core of cognitive functions. Attention can be sustained at a location, or reoriented in space to allow processing at other locations, critical in an ever-changing environment. Numerous studies have investigated attentional orienting in time and space but little is known about the spatio-temporal dynamics of attentional reorienting. Here, we explicitly manipulated attentional reorienting using a cueing procedure in a 2-AFC orientation discrimination task. At various delays during the task, we interrogated attentional deployment by flashing two probe stimuli. Then, solving a second-degree equation to estimate the report probability at each probe location, we demonstrated that attention reorients periodically at ~4 Hz (theta) between the two stimulus locations. We further observed that each stimulus location is sampled at ~11 Hz (alpha). Finally, we support our mathematical approach using simulations and show that this method is sufficiently powered making it a valuable tool for studying the spatio-temporal dynamics of attention.

INTRODUCTION

Is visual information continuously processed by our brain, or periodically (rhythmically), as suggested by the last decade of research? Accumulating evidence has shown that information is sampled periodically at low frequencies (theta: 4-7 Hz and alpha: 8-12 Hz). Specifically, the alpha and theta rhythms seem to coexist in the brain and support different functions (Dugué, Beck, Marque, & VanRullen, 2018; Dugué & VanRullen, 2017; Dugué, Xue, & Carrasco, 2017; VanRullen, 2016). If alpha has been related to an ongoing, sensory rhythm, theta appears related to attentional exploration of the visual space. Researchers have used visual search (Dugué, Marque, & VanRullen, 2014; Dugué et al., 2014; Dugué, McLelland, Lajous, & VanRullen, 2015; Dugué, Xue, et al., 2017), priming (Huang, Chen, & Luo, 2015), exogenous (involuntary) (Chen, Wang, Wang, Tang, & Zhang, 2017; Landau & Fries, 2012; Landau, Schreyer, van Pelt, & Fries, 2015) and endogenous (voluntary) (Song, Meng, Chen, Zhou, & Luo, 2014) spatial and feature-based attention (Fiebelkorn, Saalmann, & Kastner, 2013) tasks, and demonstrated that covert attention – selective processing of information in the absence of eye movements (Carrasco, 2011, 2014) – samples visual information periodically over time at the theta frequency. Moreover, recent electrophysiology in macaque monkeys and in humans using ECoG shows that attention-related theta rhythm involves both sensory (V1 and V4; Kienitz et al., 2018; Spyropoulos, Bosman, & Fries, 2018) and frontal (Fiebelkorn, Pinsk, & Kastner, 2018; Helfrich et al., 2018) cortices. This theta rhythmicity could thus emerge from iterative connections between sensory and attentional regions (Dugué, Beck, et al., 2018; Dugué & VanRullen, 2017).

Together, these findings suggest that the periodic modulation of attentional processing in time is related to the periodic sampling of visual information in space. However, attentional reorienting was not directly manipulated in these studies. It is thus unclear if attention operates at a single location at a time, sampling sequentially across locations, or if attention samples multiple locations simultaneously (VanRullen, 2013). Recently, Dugué and colleagues (2016) used Transcranial Magnetic Stimulation (TMS) to directly address the question of the interplay between temporal periodicity and spatial, sequential exploration. They investigated the dynamics of endogenous (voluntary), spatial attention. Using a cueing procedure, they explicitly manipulated attentional orienting and reorienting, which encouraged processing at other, previously unattended, locations (Corbetta, Patel, & Shulman, 2008; Dugué, Merriam, Heeger, & Carrasco, 2017). By applying TMS at various delays over the occipital pole (V1/V2), they demonstrated that performance in a 2-AFC orientation discrimination task was modulated by occipital TMS periodically at the theta frequency (~5 Hz) only when attention had to be reallocated from a distractor to a target location. However, due to the use of TMS, the frequency resolution was not optimal to allow the precise characterization of the peak frequency of attentional reorienting, i.e. 2.5 Hz resolution (eight stimulation delays on a 400-ms window).

Here, we investigated the spatial and temporal dynamics of attentional sampling by explicitly manipulating attentional reorienting. In a psychophysical task, we probed the state of attentional allocation during the course of the trial with high temporal resolution. Two probes were flashed at various delays after a 2-AFC orientation discrimination task in which voluntary attentional orienting and reorienting was manipulated using a central cue. We then solved a second-degree equation to estimate the amount of attention allocated to the different stimulus locations over time. This approach, first introduced by Dubois and colleagues (Dubois, Hamker, & VanRullen, 2009) and then successfully applied to investigate the spatio-temporal deployment of attention during visual search (Dugué et al., 2015; Dugué, Xue, et al., 2017), allowed us to demonstrate that attentional deployment was periodically modulated over time at the theta frequency (~4 Hz), only when attention had to be reoriented. By explicitly manipulating the reorienting of endogenous attention, and using a fine-tuned psychophysical and analytical approach, these results suggest that the periodicity in task performance was due to the sequential reorienting of attention from one stimulus location to another, and not the independent sampling of either location. Moreover, we showed that each stimulus location was processed periodically at the alpha frequency (~11 Hz), suggesting a functional dissociation between the alpha and theta rhythms.

MATERIALS & METHODS

Observers

Thirteen human observers were recruited for this experiment (similar number of participants used in prior studies using the same mathematical approach (Dugué et al., 2015; Dugué, Xue, et al., 2017); the decision to stop recruiting new observers was not based on preliminary analyses of the data). We selected a study design in which each participant underwent a large number of trials (1,872 trials total). Note that the power analysis presented in **Fig5** confirms that our approach is sufficiently powered to detect the reported effect. Due to technical issues during data recording, two observers were excluded from the analysis (M ± SD = 20.9 ± 0.8 years old, range: 20-22 years old; 9 females). All observers had normal or corrected-to-normal vision. They provided written informed consent and received monetary compensation for their participation. All procedures were approved by the CERES (Conseil d'Évaluation Éthique pour les Recherches En Santé) ethics committee of Paris Descartes University. All research was performed in accordance with the relevant guidelines and regulations from the committee.

Apparatus

Observers sat in a dark room, 57.5 cm from a calibrated and linearized CRT monitor (refresh rate: 85 Hz; resolution: 1280 × 1024 pixels). A chinrest was used to stabilize head position and distance from the screen. Visual stimuli were generated and presented using MATLAB (The MathWorks, Natick, MA) and the MGL toolbox (http://gru.stanford.edu/doku.php/mgl/overview).

Procedure

Data collection took part in five sessions conducted on five consecutive days. Note that the collected data sets are available through the Open Science Framework repository (https://osf.io/2d9sc/). The first session was used to familiarize observers with the experimental protocol. In the four remaining 1-hour sessions, observers performed the main task.

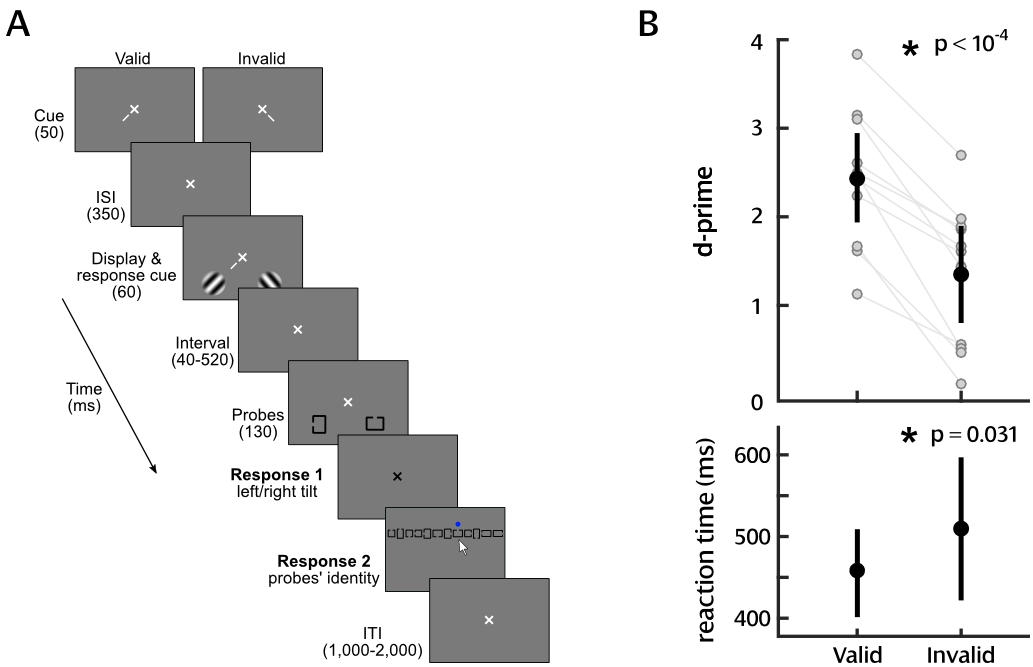

Figure 1. Experimental protocol. *(A) Trial sequence: each trial consists of (1) cueing, (2) a 2-AFC orientation discrimination task, and (3) a probe identification task. (B) Performance in the 2-AFC orientation discrimination task. Top panel: d-prime as a function of validity condition (valid and invalid). Each gray dot represents an individual observer. Black dots represent the average across observers. Error bars reflect 95% confidence intervals. D-prime are significantly higher in the valid than invalid condition (t(10)=7.57, p<0.0001, Cohen's d = 1.368). Bottom panel: median reaction time across observers. Error bars reflect 95% confidence intervals. Reaction times are significantly*

faster in the valid than invalid condition (t(10)=-2.54, p=0.031, Cohen's d = 0.479). Results confirm that attention was successfully manipulated, with no speed-accuracy trade-off.

Observers performed a 2-AFC orientation discrimination task as depicted in **Fig1A**. A central endogenous cue presented for 50 ms instructed observers to deploy their attention toward the left or right bottom quadrant. The cue was followed by a 350 ms inter-stimulus interval (ISI, necessary time to deploy voluntary attention (Busse, Katzner, & Treue, 2008; Carrasco, 2011; Cheal & Lyon, 1991; Dugué, Merriam, et al., 2017; Liu, Stevens, & Carrasco, 2007; Müller & Rabbitt, 1989; K. Nakayama & Mackeben, 1989; Pestilli, Ling, & Carrasco, 2009)). Two stimuli were then presented for 60 ms: sinusoidal gratings windowed by a raised cosine (15% contrast, 3 cycles per degree, at 4° eccentricity, on a gray background). They were tilted randomly clockwise or counter-clockwise relative to the vertical. The tilt angle was chosen for each individual using a staircase procedure, performed during the first session, so that all observers started at ~75% accuracy (averaged tilt angle, M ± S.D = 7.02 ± 4.02 degrees). The target grating, i.e. stimulus for which observers had to report the orientation, was indicated by a central endogenous response cue pointing either toward the left or the right bottom quadrant. Two gratings were always presented, one on each quadrant (in each quadrant the location was randomly selected from one of five possible locations). A trial was valid when the location of the target grating matched the previously cued location (75% of the trials). A trial was invalid when the target appeared at the uncued location (25% of the trials), requiring reorienting endogenously attention to the opposite location. For each participant there were a total of 1404 valid and 468 invalid trials.

Two Landolt C's, squares or rectangles with an aperture on one of the sides (12 possible probes: four squares, four horizontal rectangles and four vertical rectangles), were presented after one of 13 possible delays after search display onset (ISI: 40-520 ms, in 40 ms increments; 144 trials per delay). These probes, presented for 130 ms, were used to measure attentional deployment. To ensure that identification of each probe is independent (i.e. the choice of the second probe does not depend on the choice of the first one), the two probes could be identical (observers were aware of this possibility). The rationale behind the probe manipulation is that performance to identify two probes presented at different locations shortly after the gratings informs us on how attention was differentially distributed in the visual field (see **Probability estimates** section). Was attention more at a given location relative to another one? This manipulation allows interrogating the attentional modulation of the Gabor stimulus' internal representation, i.e. stimulus processing by the visual hierarchy continues after it disappears from the screen (Dugué, Merriam, Heeger, & Carrasco, 2018) and attention can still selectively enhance processing at that location in visual space –at the specific retinotopic location.

There were three conditions of probes presentation. They were presented either one in each quadrant (randomly located in one of the 5 possible locations), or both in the same quadrant as the target (congruent side) or distractor (opposite, incongruent side). Our main analysis was on the trials in which one probe was presented in each quadrant to investigate attentional sampling during attentional reorienting. All analyses were performed on trials in which observers correctly responded in the 2-AFC task (grating's orientation) to ensure that they followed the primary task's instructions (i.e. successful attentional manipulation). Crucially, these Landolt C's were used to probe the state of attentional deployment at multiple delays during a single trial (see next section for further explanation). Note that our approach allowed us to determine whether both probes received the same amount of attention, or whether one received more than the other one on average across all trials. Yet, we remain agnostic of the exact location of the attentional focus on a trial-by-trial basis.

Upon offset of the probes, the fixation-cross turned black to indicate the beginning of the response window during which observers had to report the tilt orientation of the target (clockwise or counter-clockwise to vertical). Auditory, positive (high tone) or negative (low tone), feedback was provided to the observers. We measured accuracy as our main dependent variable as per d-prime. To rule out any speed-accuracy trade-offs, we also report reaction time (RT) from the onset of the response window as secondary dependent variable. The fixation-cross disappeared after the observers responded and a horizontally aligned array of the 12 possible probes appeared. The order of the probes in the array was randomized between trials. Observers used the computer mouse to report probes' identity by clicking on each of the two probes they perceived (see **Fig1A**). When observers clicked on a given probe in the array a blue dot appeared for 500 ms above the

probe to indicate that it was selected. If two identical probes were shown during the trial, observers had to click twice on the same probe. There was no feedback for performance on the probe task in order to ensure that observers prioritized the first task. For each trial, we collected whether the observer reported none, one, or both probes correctly. We then used these probe report probabilities to estimate the probability that attention was deployed at a certain location.

Probability estimates

We aimed to investigate the spatio-temporal behavior of attentional deployment during a task in which we explicitly manipulated the orienting and reorienting of endogenous attention. We asked whether attention is sampling both probe locations equally at each time point, or whether there is greater attentional resources allocated to one probe location at a time, suggesting that attention alternates between probe locations over time. To examine this question, we used the method previously introduced by Dubois et al. (2009) and then successfully applied in visual search tasks by Dugué and colleagues (Dugué et al., 2015; Dugué, Xue, et al., 2017) to characterize attentional deployment. The probabilities of attending to each of the probed locations, called P1 (probability of reporting the probe at the most attended location) and P2 (probability of reporting the probe at the least attended location), were determined using the probabilities of reporting both probes correctly (Pboth) and none of the probes correctly (Pnone).

The probability of getting both probes correct is,

$$P(both) = P_1 * P_2 \quad \rightarrow \quad P_1 = \frac{P(both)}{P_2} \quad (1)$$

and the probability of getting neither correct is,

$$P(none) = (1 - P_1)(1 - P_2) \quad \rightarrow \quad P(none) = 1 - P_1 - P_2 + P_1 * P_2 \quad (2)$$

Substituting (1) into (2) and moving all to one side of the equation,

$$0 = 1 - P(none) - \frac{P(both)}{P_2} - P_2 + \frac{P_2 * P(both)}{P_2} \quad (4)$$

Multiplying all by -P_2 and rearranging:

$$0 = {P_2}^2 - P_2 - P(none) * P_2 - \frac{{P_2}^2 * P(both)}{P_2} + P(both) \quad (5)$$

$$0 = {P_2}^2 - P_2 * (1 - P(none) + P(both)) + P(both) \quad (6)$$

$$0 = {P_2}^2 - P_2 * \Sigma + \Pi \quad (7)$$

With:

$$\Pi = P(both)$$

$$\Sigma = P_1 - P(none) + P(both)$$

Equation 6 is now quadratic and can be solved using the quadratic formula for P_2. Because P_1 and P_2 are symmetric in the equations above, the two solutions of (7) are P_1 and P_2.

To solve this Equation, we first need to calculate its discriminant (Δ):

$$\Delta = \Sigma^2 - 4 * \Pi \quad (8)$$

And the solutions of equation (7) are:

$$\mathrm{P1} = \frac{\Sigma + \ \mathrm{sign}(\Delta) * \sqrt{|\Delta|}}{2}$$

$$\mathrm{P2} = \frac{\Sigma - \mathrm{sign}(\Delta) * \sqrt{|\Delta|}}{2}$$

Note that due to noise in responses and performance, and a relatively low number of trials per condition, negative values of Δ were sometimes obtained, which can produce non-real solutions. To address this problem, we followed the same approach than Dugué and colleagues (2015; 2017) and used |Δ| and $\mathrm{sign}(\Delta)$ thus allowing P1 and P2 values to be negative.

Evaluating the mathematical approach to calculate attentional deployment

For comparison purposes with the results of the previous studies, we present the results as a function of P1 and P2 using the absolute value and the sign of the discriminant (see previous section). As developed in the previous studies, this is a more conservative solution than assigning a zero value to Δ or taking its absolute, which would artificially lead to larger differences between P1 and P2. This approach has also the advantage of giving a straightforward, intuitive interpretation, i.e. if P1 equal P2 then both probe locations received the same amount of attention; however, if P1 greater than P2, then one location received more attention than the other one.

Yet, to further test our mathematical approach we also performed the analysis of the discriminant. As shown below, the discriminant is the square of the difference between P_1 and P_2 in the case where coefficient a = 1, and is an unbiased estimate.

Beginning with the quadratic formula,

$$(P_1,\ P_2) = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

We can subtract the negative solution from the positive to describe $P_1 - P_2$,

$$P_1 - P_2 = \frac{-b + \sqrt{b^2 - 4ac}}{2a} - \frac{-b - \sqrt{b^2 - 4ac}}{2a}$$

Which reduces to,

$$P_1 - P_2 = \frac{2\sqrt{b^2 - 4ac}}{2a}$$

$$P_1 - P_2 = \frac{\sqrt{b^2 - 4ac}}{a}$$

Then, because ${P_2}^2$ in (5) has a coefficient of 1, $a = 1$, and we can simplify this further,

$$(P_1 - P_2)^2 = \ b^2 - 4c, \qquad when\ a = 1$$

This means that the discriminant as it was used in the analyses of the previous papers is equal to $(P_1 - P_2)^2$ before the absolute value was taken. Then, if there is no difference between the probability of reporting either probe, then $P_1 - P_2 = 0$, and so will the discriminant, $(P_1 - P_2)^2 = 0$. If performance on one probe depends on the other, and correctly reporting one makes reporting the other correctly less likely, then the discriminant will scale (non-linearly) with the size of this difference.

Spectral analysis

To analyze the temporal dynamics of attentional deployment in valid and invalid conditions, we computed a Fast Fourier Transform (FFT) for each observer on the difference between P1 and P2, and then averaged the resulting amplitude spectra across observers. The data of each observer was average-padded, i.e. padded to the average of the P1-P2 difference across delays,

to increase the frequency resolution. The 13 time points, spanning 480 ms, were padded to get a 2000 ms segment, thus adding 18 data points before the first data point and 19 data points after the last one.

To calculate the level of significance, we used permutation tests (100,000 surrogates of the index for each participant), under the null hypothesis of a random temporal structure of the P1-P2 difference. We shuffled the delays, padded the data as described above, and computed the FFT over each surrogate. The amplitude of the surrogate FFT results was then sorted in ascending order. We used a statistical threshold at $p < 0.05$, corrected for multiple comparisons (6 frequency components corresponding to the true frequency resolution of the P1-P2 difference) using Bonferroni correction (833rd highest value, in other words $p < 0.00833$).

RESULTS

Grating task

We first evaluated the performance in the 2-AFC orientation discrimination task (**Fig1B**) in order to ensure that observers correctly performed the task and that attention was successfully manipulated. We computed d-prime for reporting the tilt orientation of the target grating in the valid and invalid conditions and observed significantly higher sensitivities for the valid than invalid condition (two-tailed, paired-sample t-test, $t(10) = 7.57$, $p < 10^{-4}$, 95%-CI, confidence interval = [0.76 1.4], Cohen's d = 1.368). There was also a significant difference in median reaction times between valid and invalid condition, i.e. observers responded faster in the valid condition ($t(10) = -2.54$, $p = 0.031$, 95%-CI = [-0.10 -0.006], Cohen's d = 0.479). Both variables reflected an attentional facilitation in the 2-AFC orientation discrimination task demonstrating that attention was successfully manipulated, with no speed-accuracy trade-offs.

Probe task

We recorded accuracy in reporting both probes (Pboth) and neither of the probes (Pnone) correctly. We then first used Pboth and Pnone (see Methods section) to estimate the probe report probabilities for the condition in which one probe was presented in each quadrant. We observed that P1 and P2 were marginally significantly different in the valid condition (two-way repeated-measures ANOVA: $F(1,10) = 4.405$, $p = 0.062$, $\eta^2 = 0.30$; **Fig2A**, left panel). This difference was significant in the invalid condition ($F(1,10) = 22.976$, $p = 0.0007$, $\eta^2 = 0.69$; **Fig2A**, right panel), indicating that attention was non-uniformly distributed across stimulus locations. Both were well above chance (0.083). We argue that attentional deployment in the probe task was non-uniformly distributed across the two stimulus locations.

To assess the temporal dynamics of attentional deployment, we calculated the difference between P1 and P2 (**Fig2B**), separately for valid and invalid trials, and analyzed the amplitude spectra of the P1-P2 difference (**Fig2C**). In the valid condition, there was no significant peak frequency. In the invalid condition, there was a significant peak at 3.5 and 4 Hz ($p < 0.05$, Bonferroni corrected) suggesting that the P1-P2 difference of each observer was modulated periodically at the theta frequency.

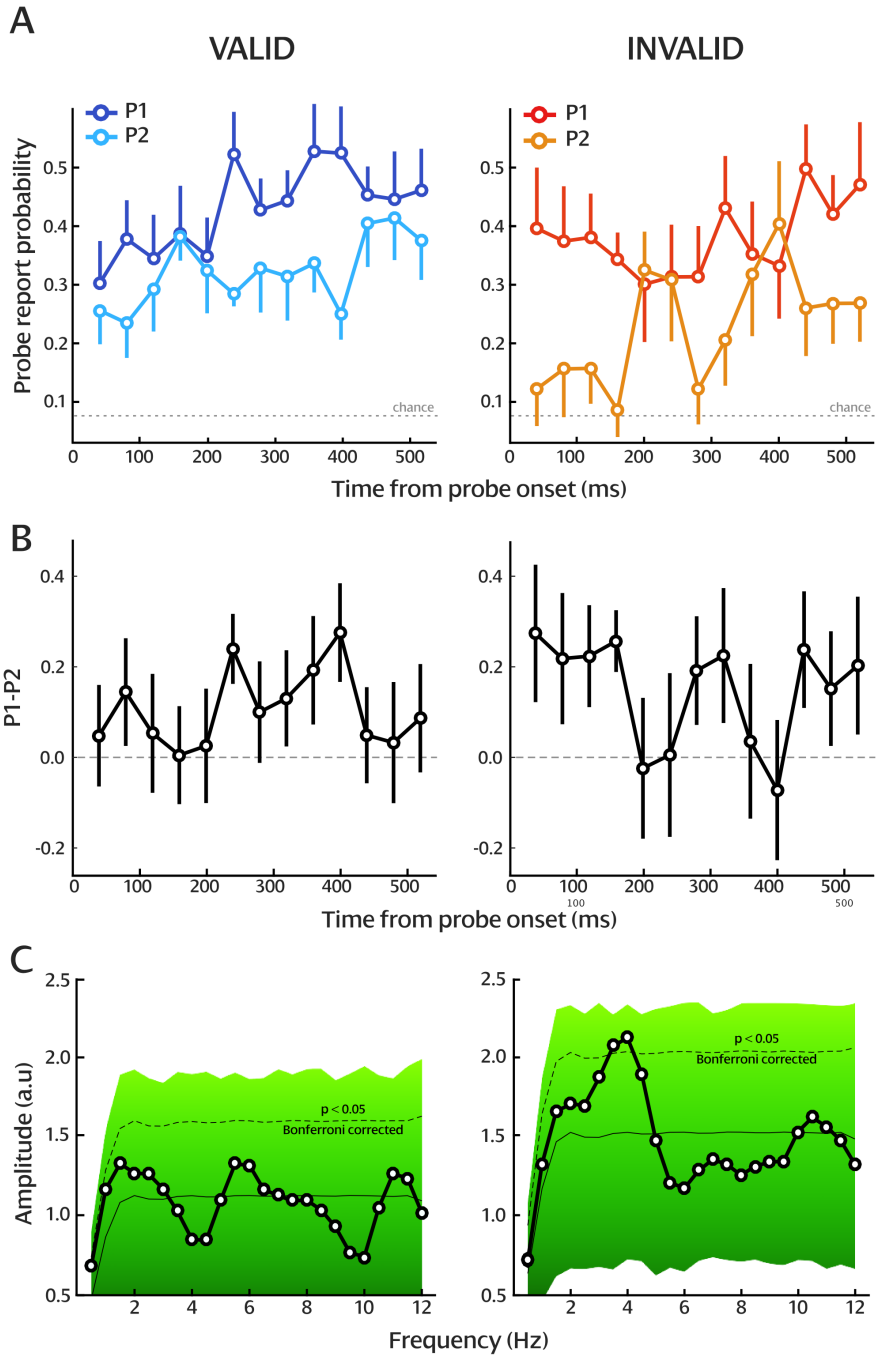

Figure 2. Dynamics of attentional orienting and reorienting. *(A) P1 and P2 by delays for valid (left column) and invalid (right column) conditions (probability estimation from the probe task). The dotted line represents the probability of reporting the correct probe by chance (0.083). Error bars reflect ±1 standard error of the mean (S.E.M) Only one half of the error bars is shown to reduce visual clutter. (B) P1 minus P2 difference. The dashed line represents a zero difference. Error bars reflect ±1 SEM. (C) Power spectrum of P1-P2 difference and results of the 100,000 surrogate analysis for valid and invalid conditions. The solid line represents the average of the surrogate analysis. The black-to-green background represents the distribution of surrogate values, i.e. the level of significance of each frequency component. The dashed line represents the p < 0.05 limit (Bonferroni corrected).*

To further validate our analysis method, we compared valid and invalid conditions (**Fig3A**) for the P1-P2 difference and replicated it on the discriminant (see Methods section). For the P1-P2 difference, the amplitude of the 4 Hz component for each observer was significantly higher in the invalid than valid condition (one-tailed, paired-sample t-test, t(10) = 3.86, p = 0.001, 95%-CI =

[0.5296 1.977], Cohen's d = 1.647), coherent with the results of **Fig2C**. For the discriminant, the amplitude of the 4 Hz component was also significantly higher for the invalid than the valid condition (**Fig3B**; one-tailed, paired-sample t-test, $t(10) = 3.36$, $p = 0.004$, 95%-CI = [0.2691 1.3298], Cohen's d = 1.383). This result confirms the validity of our method.

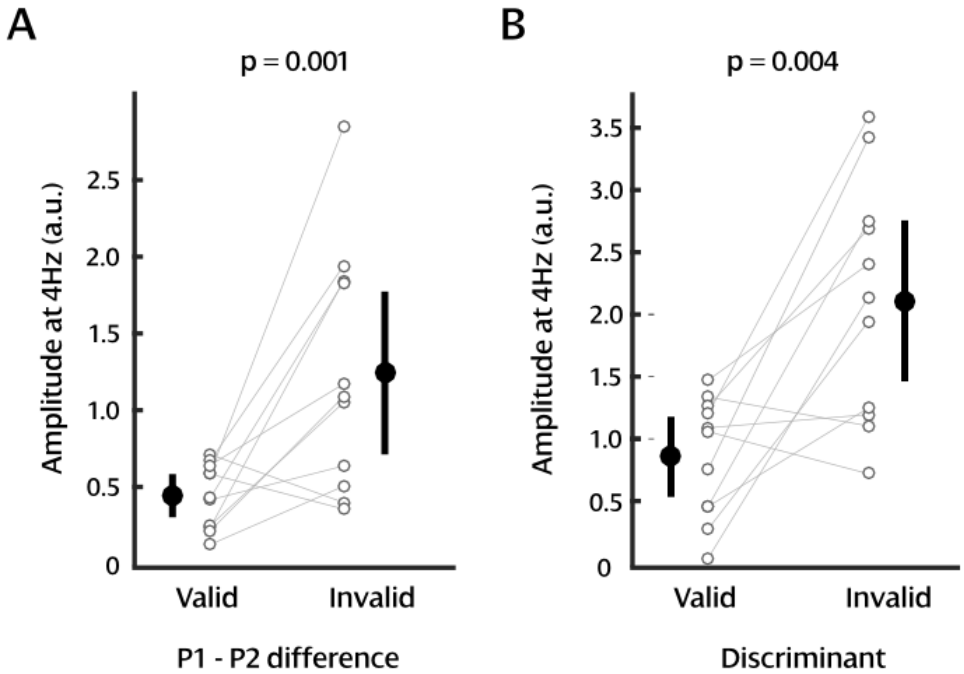

Figure 3. Amplitude of the 4 Hz component for individual observers. *An FFT was performed for each observer separately for both the P1-P2 difference (A) and the Discriminant (B), for valid and invalid conditions. Empty black circles represent the amplitude of the 4 Hz component for individual observers. Black filled circles represent the average across observers. Error bars reflect 95% confidence intervals. The difference between valid and invalid conditions was significant for both the P1-P2 difference ($t(10) = 3.86$, $p = 0.001$, Cohen's d = 1.647) and the Discriminant ($t(10) = 3.36$, $p = 0.004$, Cohen's d = 1.383).*

Finally, we performed the same analysis as in **Fig2C** for trials in which both probes were presented on the same quadrant, i.e. on the same side as the target (**Fig4A**) or the distractor (**Fig4B**). The results show no periodic modulation in the valid trial condition. However, in the invalid trial condition, we observe a significant periodic modulation of the P1-P2 difference at ~11 Hz when both probes were presented on the distractor side (p=0.0074) and marginally significant at 10 Hz when they were presented on the target side (p=0.0110). We argue that this result suggests that the 11 Hz periodicity reflects a sensory, ongoing sampling of visual information in each quadrant and not attentional deployment.

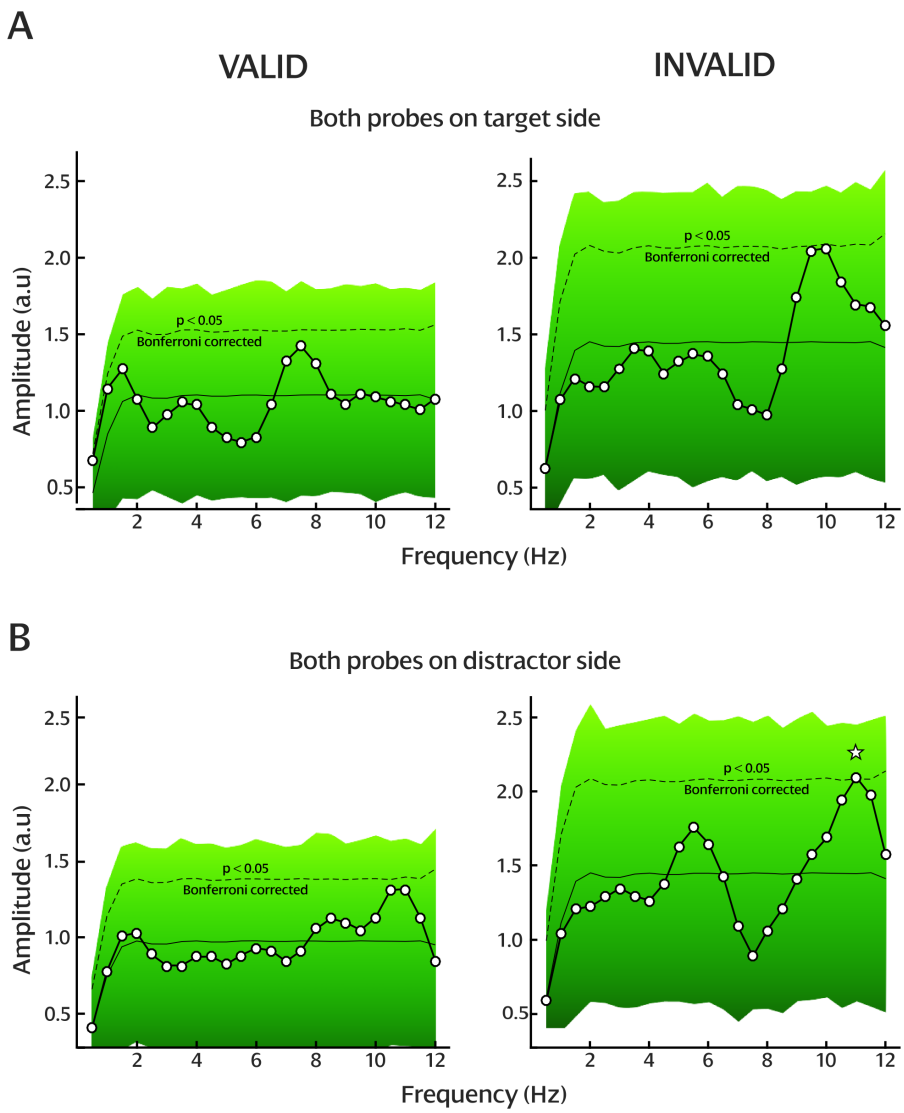

Figure 4. Dynamics of attentional orienting and reorienting when both probes were presented on the same quadrant. *Power spectra of P1-P2 difference and results of the 100,000 surrogate analysis for valid and invalid conditions when (A) both probes are presented on the target side, and (B) both probes are presented on the distractor side. The solid line represents the average of the surrogate analysis. The black-to-green background represents the distribution of surrogate values, i.e. the level of significance of each frequency component. The dashed line represents the p < 0.05 limit (Bonferroni corrected). The star indicates significant effect (p < 0.05 Bonferroni corrected).*

Power analysis

The sequential attentional reorienting interpretation of the results suggests that within a trial the probability of detecting the probe identity is dependent across locations, i.e. that if the observer correctly identifies a probe at one location, they are less likely to identify the probe at another. This dependency is lost if the probe responses to one location are randomly permuted. The result is the same overall percent correct for each probe but probe responses within each trial are independent.

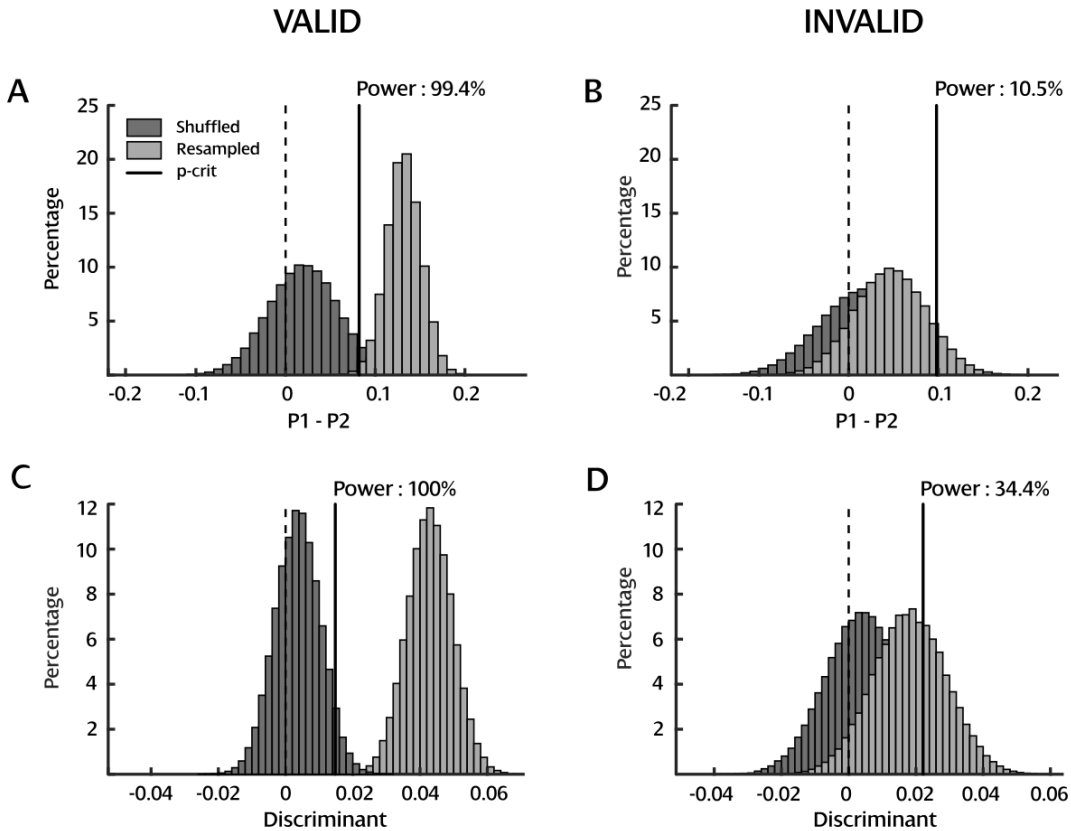

Figure 5. Power analysis. *Distributions of P1-P2 difference and discriminant for resampled and permuted trials, for valid (left panels) and invalid (right panels) conditions. Solid vertical lines in each panel indicate the 95th percentile of the permuted distribution. Proportion of resampled repetitions to the right of the solid line indicates the power achieved.*

To evaluate the statistical power of the analysis, we tested the null hypothesis of no dependency between the two probe responses within a trial. We generated a surrogate distribution under this null hypothesis by repeatedly (10,000 repetitions) permuting the probe responses at one location and performing the quadratic analysis on the resulting pairs of probe responses. This null distribution was then compared to a distribution generated by resampling with replacement trial responses while preserving any existing dependency within a trial (**Fig5**).

The achieved power is the proportion of sampling repetitions from the resampling P1-P2 difference (**Fig5A** and **5B**) and discriminant (**Fig5C** and **5D**) distributions that are greater than the 95th percentile of the permuted distributions. For the P1-P2 difference the achieved power in the valid condition was 99.4%, and in the invalid condition was 10.5%. For the discriminant the achieved power in the valid condition was 100%, and in the invalid condition was 34.4%.

Interestingly, the permuted data does not have a discriminant distribution centered on zero as would be expected if there were no relation between the two probe responses. A possible explanation is that observers had a bias in performance for the first or second probe responses, which is a relation preserved in the permutation method described above.

In conclusion, we show the analysis method of Dugué and colleagues (2015; 2017) to be appropriate and sufficiently powered.

DISCUSSION

We investigated the spatio-temporal dynamics of attentional orienting and reorienting using a psychophysical approach with high temporal resolution. By explicitly manipulating voluntary, endogenous attention, we demonstrated that performance in the invalid condition, when attention needed to be reoriented from the distractor to the target location, was periodically modulated at the theta frequency (~4 Hz). Additionally, we found that information in each quadrant was sampled periodically at the alpha frequency (~11 Hz). Finally, we performed our analysis on another index of attentional deployment (the discriminant; see Methods section) and replicated the effect.

Together with the results of the power analysis (**Fig5**), we found compelling evidence validating our mathematical approach to the study of the attentional and perceptual rhythms.

Interestingly, our mathematical approach not only allowed us to investigate the rhythm of attentional reorienting (i.e. when analyzing trials in which one probe is presented on each stimulus location), but also the rhythm of information sampling at each location (i.e. when analyzing trials in which both probes are presented in each quadrant). We found a functional dissociation between the alpha and the theta rhythm. This result is consistent with a recent review suggesting that the theta rhythm corresponds to attentional sampling while the alpha rhythm rather reflects an ongoing, sensory sampling of information (VanRullen, 2016). Together, our results suggest that an attentional sampling rhythm, i.e. theta (~4 Hz), coexists with an ongoing, sensory rhythm, i.e. alpha (~11 Hz), to sample the visual environment periodically.

Previous studies have demonstrated the role of theta oscillations in attentional exploration of the visual space (Busch & VanRullen, 2010; Dugué et al., 2015; Landau et al., 2015; Rollenhagen & Olson, 2005), consistent with the theta periodicity observed here in the invalid condition. These authors have suggested that the observed behavioral periodicity was due to the intrinsic property of the system, i.e. brain oscillations at the theta frequency would modulate periodically behavioral performance at the same frequency. A recent psychophysics study explicitly manipulated spatial attentional orienting to assess the behavioral periodicity of attentional sampling with a discrimination task (Song et al., 2014). Such task allows assessing whether the effect of attentional cueing reflects changes in sensory (d') rather than decisional (criterion) processing. At the contrary, in detection task, the challenge is to disentangle whether higher performance is due to facilitation of information coding at that location, probability matching, or a decision mechanism (see Dugué, Merriam, et al., 2017). The results of this study suggest that attention samples periodically information at low frequencies (alpha and theta). Unfortunately, the main dependent variable was reaction time, which can reflect perceptual processing speed, motor anticipation (Correa, Triviño, Pérez-Dueñas, Acosta, & Lupiáñez, 2010), and criterion (Carrasco & McElree, 2001). Here, we explicitly manipulated the reorienting of attention to directly address the following question: is the periodicity in behavioral performance due to the sequential sampling by attention of the different stimulus locations or to the independent sampling of each location? We then measured d-prime as main dependent variable to ensure that attention in the 2-AFC orientation discrimination task was successfully manipulated for each participant, with no speed-accuracy trade-off.

Critically, we flashed two stimuli at various delays after the 2-AFC task to probe the state of attentional allocation during the course of the trial. This manipulation allowed us to reveal the intrinsic periodicity of the attentional system during the reorienting of endogenous, spatial attention. Recently, Dugué et al. (2016) employed a similar approach. They used TMS to perturb the reorienting process of attention at various delays during the same 2-AFC orientation discrimination task. They observed that attention periodically reoriented from the distractor to the target location (invalid condition), at the theta frequency (~5 Hz). Here, using a psychophysics approach instead of directly interfering with neural processing, we replicated such finding. Additionally, our result point to a slightly lower frequency of reorienting, i.e. ~4 Hz. Indeed, here we used a high temporal resolution (i.e. 13 different delays; 0.5 Hz resolution) with robust statistical power. We can thus propose that, in this specific 2-AFC orientation discrimination task, attention sequentially samples the two stimulus positions at ~4 Hz.

Interestingly, the specific frequency of attentional exploration, although always in the theta frequency range, varies across studies between 4 and 8 Hz (Busch & VanRullen, 2010; Dugué et al., 2015; Dugué, Xue, et al., 2017; Fiebelkorn et al., 2013; Huang et al., 2015; Landau & Fries, 2012; Landau et al., 2015; Song et al., 2014; van Diepen, Miller, Mazaheri, & Geng, 2016; VanRullen, 2013; VanRullen, Carlson, & Cavanagh, 2007). It is possible that the differences in task parameters could modulate the frequency of the attentional sampling. Recent studies show that the peak frequency of alpha oscillations can be shifted depending on task demands or general cognitive load (Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014; Mierau, Klimesch, & Lefebvre, 2017; Wutz, Melcher, & Samaha, 2018). These studies suggest that a top-down modulation of the alpha peak frequency in occipital areas optimizes sensory sampling and inter-areal communication (see review and model by Mierau et al., 2017). Although these studies do not explicitly suggest a general mechanism that would also be present in other frequency bands, e.g. theta, it would be interesting to investigate whether the differences in the theta modulation of attentional deployment

in our study or in visual categorization, priming, illusory visual experience or visual search (Drewes, Zhu, Wutz, & Melcher, 2015; Dugué et al., 2015; Huang et al., 2015; R. Nakayama, Motoyoshi, & Sato, 2018) could be attributable to differences in task demands, task difficulty or general cognitive load.

We found a periodic modulation in the invalid but not in the valid condition, i.e. when attention was reoriented but not when it was sustained at the initially cued location, consistent with Dugué et al. (2016). Other studies showed modulations in the probability of detecting a target in conditions where attention was sustained (Fiebelkorn et al., 2013; Rollenhagen & Olson, 2005; VanRullen et al., 2007), although different types of attention were manipulated. As argued in Dugué et al. (2016), it is possible that sampling in the valid condition may have been similarly modulated, but with its own spontaneous phase. In this condition, the reorienting process would not have reset the underlying oscillation, and the probes would not bear a phase relation with attention. However, in the invalid condition, the attentional reorienting process would have reset the phase of the oscillation, which could then be revealed by the two probe stimuli.

In conclusion, using a mathematical approach, we not only show that attentional reorienting samples space periodically at the theta frequency (~4 Hz), but also that each spatial location is sampled periodically at the alpha frequency (~11 Hz) by an ongoing, sensory rhythms. This result supports the hypothesis that attention samples space non-uniformly during attentional reorienting (for review see Dugué and VanRullen, 2017). Furthermore our mathematical approach using probability estimation of stimulus identification to probe the state of the attention system is a valuable, sufficiently powered, tool to investigate attentional deployment.

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