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Attention Samples Stimuli Rhythmically

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Summary

Overt exploration or sampling behaviors, such as whisking, sniffing, and saccadic eye movements [1, 2], are often characterized by a rhythm. In addition, the electrophysiologically recorded theta or alpha phase predicts global detection performance [3, 4]. These two observations raise the intriguing possibility that covert selective attention samples from multiple stimuli rhythmically. To investigate this possibility, we measured change detection performance on two simultaneously presented stimuli, after resetting attention to one of them. After a reset flash at one stimulus location, detection performance fluctuated rhythmically. When the flash was presented in the right visual field, a 4 Hz rhythm was directly visible in the time courses of behavioral performance at both stimulus locations, and the two rhythms were in antiphase. A left visual field flash exerted only partial reset on performance and induced rhythmic fluctuation at higher frequencies (6–10 Hz). These findings show that selective attention samples multiple stimuli rhythmically, and they position spatial attention within the family of exploration behaviors [1].

Results

Temporal Structure of Detection Performance

Many studies have documented temporal properties of endogenous, as well as reflexive, spatial attention, such as the time course to buildup [5, 6] and its decay profile [7]. However, spatial attention extends in time beyond the traditional single trial event. During continuous visual input, akin to natural viewing, attentional performance typically fluctuates. These fluctuations have sometimes been regarded as measurement noise yet recently are considered informative [8, 9]. In the present study, we investigated fluctuations in spatial attention using a detection task. Participants viewed two drifting gratings presented on either side of a central fixation (Figure 1A). Their task was to report the appearance of a brief contrast decrement, the target event (Figure 1C). A single target event occurred at an unpredictable time in a trial, in either one or the other grating (Figure 1). Contrast decrements were pre-adjusted in a separate experimental procedure to equate detection performance across individuals. Trials were terminated by participants' responses and lasted no longer than 3.8 s. Ten percent of trials contained no target (referred to as catch trials). The critical manipulation was a task-irrelevant flash of four dots (Figure 1B) around either one of the gratings. The flash was employed to capture attention to one location at a given moment during the trial [10], and it allowed for the

systematic and finely spaced probing of detection performance thereafter. To achieve a continuous assay of performance, the target event could appear at one of 105 intervals, in steps of 16.7 ms, from 750 ms before to 1,000 ms after the irrelevant flash. Flash and target occurred either in the same or opposite visual fields (referred to as same or opposite relative location, respectively). Target-detection rates were analyzed as a function of the target-to-flash interval. This generated an accuracy time course for each relative location condition (same versus opposite). The resulting time course was subsequently analyzed for oscillatory components (see Experimental Procedures for further details).

We first consider trials with the flash in the right visual field (RVF), because they showed the most pronounced effects (Figures 2A and 2B; Figures S1A and S1B available online). Consistent with previous masking literature, targets presented at the same relative location as the flash event were near invisible when they preceded the flash at short intervals [11] (Figure 2A, red line). Importantly, after the flash, target detection in the same visual field fluctuated rhythmically at approximately 4 Hz (Figure 2B; $p < 0.05$ for 3.5–4.12 Hz). In the visual field opposite to the flash, a similar rhythm was found (Figures 2A and 2B, blue line; $p < 0.05$ for 4.12–4.8 Hz). A direct comparison between the peak frequencies for same- versus opposite relative location revealed that they were not significantly different. The two rhythms had a phase relation that was not uniformly distributed across subjects and clustered around a mean of 222° with a distribution that was significantly different from 0° (i.e., in-phase relationship), and not significantly different from 180° (i.e., antiphase relationship; Figure 2B). This is consistent with the two attended locations being sampled in alternation: higher performance in one location was associated with lower performance in the other ($p < 10^{-210}$ for nonuniform distribution of phase relations; not significant for comparing the mean phase relation to 180°). In the left visual field (LVF), the spectral analysis revealed a significant peak for the same relative location at 7 Hz ($p < 0.05$ for 6.2–7.45 Hz) and a significant peak for the opposite relative location at 9.7 Hz (Figure 2C; $p < 0.05$ 9.4–9.95 Hz). Although an alternating sampling mechanism would suggest peaks at the same frequency with antiphase relationship, the pattern observed for LVF is still consistent with, for example, partial reset after the flash event as explained below. In some conditions, a rhythmic pattern seems to emerge in the time course prior to flash onset. This is likely because, in many trials, the flash intervened between target and behavioral response, such that it could still influence target detection and/or reporting. We have obtained control data (14 subjects) with timing parameters adjusted to focus on an extended pre-flash period. The average over trials with responses before flash onset revealed no significant spectral peaks (Figure S1).

Further validation of the observed patterns was found in an ANOVA performed on the same data that was subjected to the spectral analysis with factors time (target-to-flash time interval), relative location (same, opposite), and visual field (LVF, RVF) as within participant factors. Importantly, the interaction of time by relative location was significant, indicat-

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 ing that accuracy fluctuations were different for the same compared to the opposite location ($F_{50,750} = 2.09, p < 0.001$).

Additionally, there was a second-order interaction of visual field, relative location, and time ($F_{50,750} = 2.8, p < 0.001$), supporting the finding that RVF and LVF flashes elicited a different periodic pattern. Following up on the second-order interaction by separate ANOVAs for each visual field flash condition revealed that the interaction of time by relative location was significant for both visual field conditions (LVF: $F_{1,50} = 1.51, p < 0.01$; RVF: $F_{1,50} = 3.52, p < 0.001$). We note that for both RVF and LVF flashes, there was no difference in accuracy between same and opposite relative locations when averaged across time.

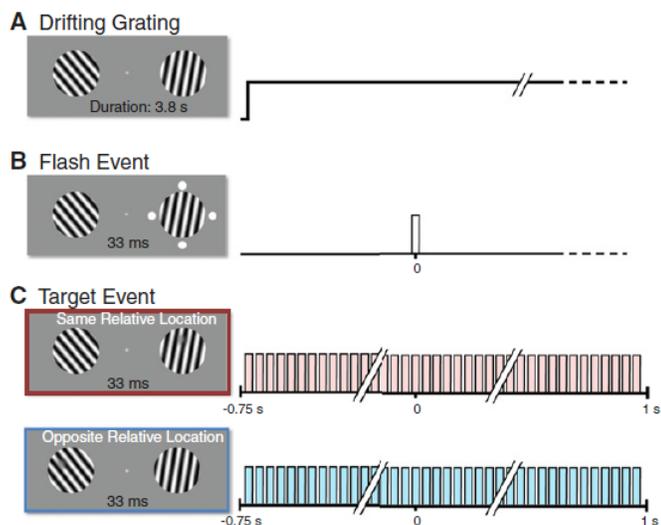


Figure 1. Experimental Procedure and Design

(A) Two gratings were drifting for up to 3.8 s.
 (B) A flash event was displayed for 33 ms at a random time point between 1.25 and 2.5 s relative to grating onset.
 (C) A single target event was displayed for 33 ms, either in the same visual field or in the opposite visual field relative to the flash event (in separate trials). Across trials, the target event could appear at all time intervals, in steps of 16.7 ms, from 750 ms before to 1,000 ms after the irrelevant flash.
 Diagonal cuts along the x axis indicate discontinuities in the timeline. See also Figure S1.

Visual Field Effects

Flash events in both visual fields revealed a rhythmic pattern in detection performance; however, there were observable differences in performance on trials with right versus left visual fields flashes (RVF and LVF, respectively). Notably, the time course of masking for targets appearing shortly before the flash was different when flashes appeared on the RVF versus LVF. When the flash appeared on the RVF, the recovery from masking was prolonged compared to when the flash appeared on the LVF [mean first peak latencies: 229 and 173 ms for RVF and LVF flash, respectively; $t(15) = 3.1, p < 0.01$]. This difference in temporal scope of masking is consistent with asymmetries in the spatial scope of left and right hemispheres in mediating spatial attention [12–15]. Namely, previous studies suggest that the right hemisphere (RH) mediates spatial attention to both visual fields, whereas the left hemisphere (LH) processes only the RVF. Therefore, a unilateral flash presented in the RVF engages attentional mecha-

nisms in both hemispheres dedicated to RVF processing. This generates a perceptual reset event that is more robust and synchronized across hemispheres. A flash presented in the LVF engages only the RH attentional mechanism, limiting the degree of reset to that hemisphere.

Further support for differences in the scope of reset in the two visual fields is provided by a slight difference in the degree of recovery from masking (detection accuracy) following LVF and RVF flash. Accuracy, quantified as hit rate for the first peak after the flash, indicates that performance was slightly worse following a RVF flash (81%) compared to following a LVF flash (89%). Although this difference did not reach significance [$t(15) = 1.95, p = 0.06$], we report the trend to point out that the differences in first peak latencies were not due to a trade-off between time to recovery (from masking) and accuracy, which would predict that faster latencies would be associated with lower accuracy. But rather, the significant delay in peak latency and the trending reduction in accuracy all point to the fact that the RVF flash presents a more robust reset to the visual system. Importantly, when considering performance after the masking effect subsides, both visual fields present with rhythmic performance. Notably, the pattern is clearer following a RVF flash (and therefore more visible even in the time domain plot). This is consistent with the notion advocated in this study, that in order to be able to measure fluctuations in performance, a reset event anchoring attention is required. Consequently, the more robust attentional reset after the RVF flash reveals the ongoing sampling rhythm more clearly. The visual field asymmetries found here are discussed in the context of differential effects of masking. We cannot unequivocally separate visual field asymmetries in the scope of masking from asymmetries in the scope of reflexive attentional capture.

Discussion

We probed detection performance at 60 Hz, after a unilateral flash, intended to reset attention to the flashed side. We found that after a RVF flash, performance fluctuated at 4 Hz, and these fluctuations were approximately in antiphase between the two visual fields. After a LVF flash, performance fluctuated at 7 to 10 Hz. We propose that these findings are parsimoniously explained by the following scenario: There is an attentional sampling process that operates at roughly 8 Hz, that is, one location is sampled every 125 ms [9, 16]. As a result of a flash, the sampling process can be temporally reset, and it can be spatially oriented. A RVF flash resets the process, and it orients it to the flashed side. Consequently, with two locations, the 8 Hz sampling becomes apparent as 4 Hz performance fluctuations per location, in antiphase between locations. A LVF flash resets the process and leads to rhythmic performance fluctuations too. Yet, the reset is less efficient, and the orienting goes to either location variably across trials. The performance time courses are constructed from all trials together. Therefore, the 8 Hz sampling becomes apparent as a 7 to 10 Hz rhythm. This scenario does not fully explain the different frequencies after LVF flash, which might be related to the overall less clear LVF-flash effects (as seen in the reduced masking effect). Yet, the scenario does provide a uni-

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 fied interpretation of the results with a relatively small set of assumptions.

The discovery of rhythmic temporal structure in psychophysical performance was possible here because of the exogenous-flash event (for a demonstration of rhythmic structure in appearance without a flash event see [17]). Although the use of the exogenous flash was merely a technique to reset and thereby reveal the existing temporal structure in performance, possible links can be drawn between the findings reported here and attentional capture. When a salient cue highlights a portion of a display, previous work has documented transient performance benefits at that location compared to others [10]. The most common and agreed-on benefits are the acceleration of reaction times in easy detection or discrimina-

tion tasks [18–21]. Performance benefits in accuracy measures (as those reported here) are somewhat more controversial and by and large are not affected by attentional capture directly [18–21]. The typical time course of reflexive attention entails a transient RT benefit, followed by an RT slowing (inhibition of return; [7]). Whereas this pattern is consistent with the present data and interpretation, the current study goes further and shows several cycles of behavioral accuracy enhancements and, at least for right visual field flashes, an antiphase relationship between the two relative locations. Notably, the time course that we measure in accuracy seems to be somewhat delayed compared to other attentional capture time courses, a consequence attributed to the masking effects present in our design.

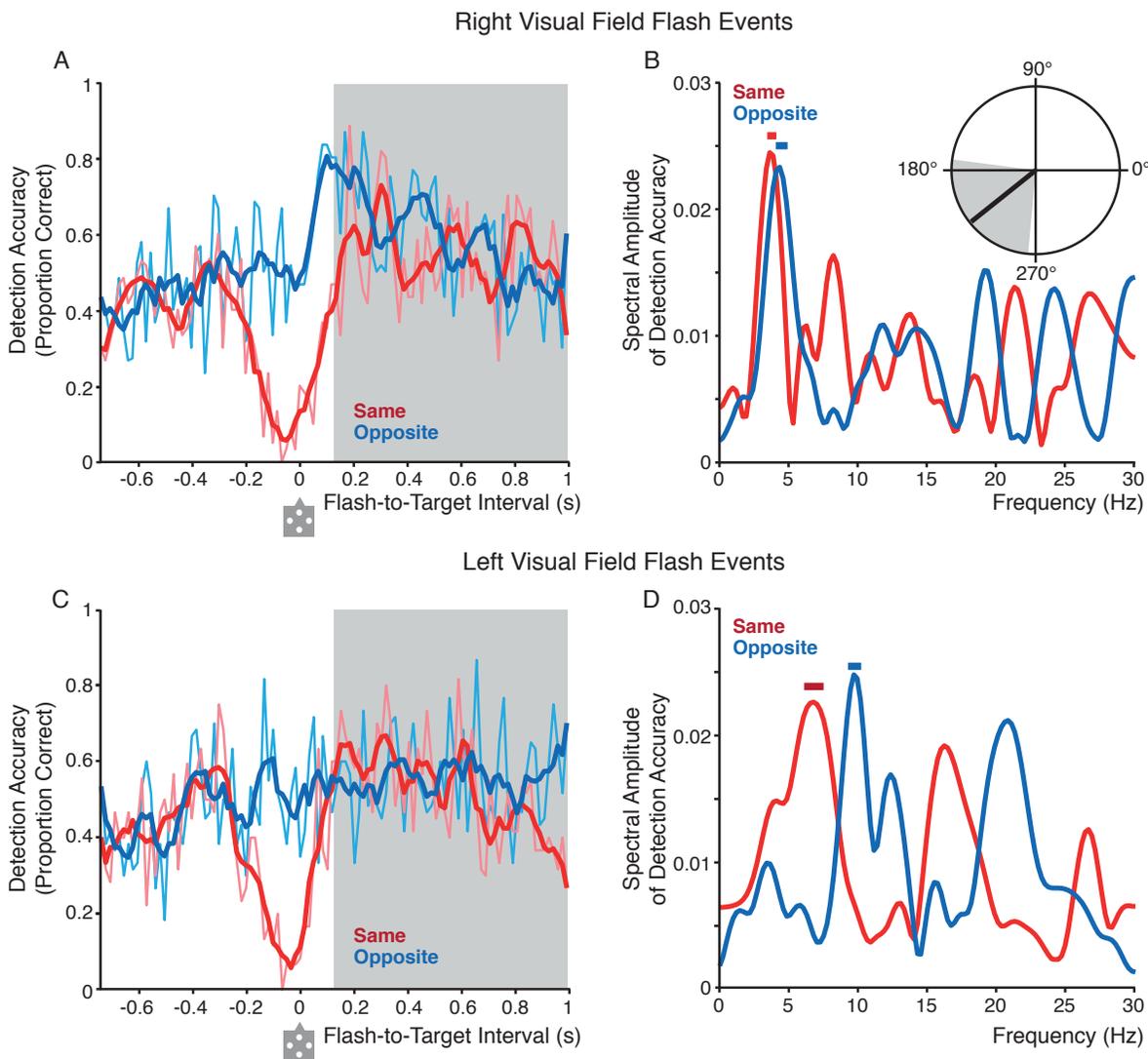


Figure 2. Experimental Results

(A and C) Detection performance as a function of temporal interval between target event and flash event. Zero point denotes onset of flash event; negative values denote trials in which the target preceded the irrelevant flash. Red (blue) line: Detection for targets appearing in the same (opposite) visual field as the flash. Average for trials with flash events on the right visual field (A), and average for trials with flash events on the left visual field (C). Shaded region corresponds to the portion of data subjected to spectral analysis presented in (B) and (D). Smoothed time courses are overlaid (in saturated lines) on the unsmoothed raw data (desaturated lines).

(B and D) Spectra for same- and opposite-relative locations (red and blue lines, respectively). Thick horizontal red and blue lines indicate the significant peak frequencies for same- and opposite-relative locations ($p < 0.05$ Bonferroni corrected). Polar plot shows mean phase relation between the rhythms (3.6–4.8 Hz) in the two relative locations (thick black lines; gray segments indicate 62 SEM).

We would like to consider the possibility that the temporal structure measured here reflects an ongoing endogenous rhythm and is present regardless of the resetting event. Accordingly, in the absence of a reset, a temporal structure of attention can only be inferred indirectly through the measurement of physiological brain rhythms. Previous studies reported post hoc relationships between the electrophysiologically recorded phase of theta- or alpha-rhythms and the subsequent detection performance on a single stimulus [3, 4, 22, 23]. These studies did not address whether theta or alpha phase affects processing globally or whether it corresponds to a spatially selective process. In the present study, we probed performance for two stimuli simultaneously and, after RVF flashes, found performance enhancements to alternate, thereby establishing a spatially specific sampling mechanism. Hence, this rhythmic sampling is indeed a mechanism of spatial attention, rather than global fluctuations in performance.

A recent study by Fiebelkorn et al. [24] reported an investigation of temporal structure in visual performance following the presentation of an auditory reset stimulus. This study probed performance at one location and only at 2 Hz, compared to two locations at 60 Hz here. Therefore, it could not reveal the spatially specific sampling rhythm found here, at frequencies above 2 Hz.

An important line of work in the field of rhythms for perception has focused on utilizing entrainment [25]. In entrainment experiments, a temporal structure present in the stimulus imposes corresponding structure in brain activity [26] and performance [27]. The rationale of such experiments is that the rhythmic stimulation is repeatedly resetting ongoing processes allowing us to better measure them. Shared to the logic of such studies, we also utilize a resetting event. However, the current study diverges from entrainment studies in an important way: we used a single resetting event that does not define any particular frequency. Nevertheless, the reset was followed by a rhythmic behavioral pattern. This rhythmicity is therefore orthogonal to any temporal structure in our stimulus.

Previous work on exploration behaviors has also pointed to the significance of theta rhythms. In rodents, exploration behaviors, such as sniffing and whisking, are associated with theta oscillations [2]. In humans and primates, saccadic eye movements occur at a theta rhythm [1]. Intriguingly, this saccadic theta rhythm, reflected in the dominant intersaccadic interval, is remarkably stable over a wide range of saccade magnitudes [1]. Because saccades are tightly linked to selective attention, this finding suggests that also attentional sampling rhythms might be invariant to the spatial scale of sampling; that is, we might measure the same rhythm for different spatial configurations. This possibility is supported by studies reporting that attentional shift latencies are invariant for different spatial scales [28, 29].

Finally, most physiological models of spatial attention can readily describe spatial attention to a single item [30, 31]. The present work generates a prediction as to how attention to multiple items might be achieved within these conceptual frameworks. If we consider, for example, communication through coherence (CTC) [30], a single item is selected by virtue of interareal synchronization of gamma-band (40–100 Hz) oscillations. We now document that two items are sequentially sampled at a theta rhythm. It is possible that the theta

rhythm sets the period for gamma-band synchronization. A given (single) location will be selected at a given moment, whereas sampling will provide for the selection of multiple items. Each individual sampling event is achieved by gamma band synchronization. The nesting of gamma into theta realizes the sequential selection of one stimulus at one moment and the next stimulus at a subsequent moment. In other words, if synchronization between a visual area representing one item and other visual areas were to be measured, gamma band synchronization would fluctuate at a slow theta rhythm. In the past decades, researchers have documented systematic relationships between oscillatory activity in different frequencies. The cross-frequency relationship documented most prominently is the nesting of gamma-band activity into the theta phase [32–35]. Many groups have speculated about the function of these nested relationships. CTC elaborated by the behavioral findings presented here suggests that a theta rhythm governs attentional sampling through gamma-synchronized networks, which in turn determine the temporal structure of behavior [30].

To conclude, the findings reported here provide evidence for the relevance of neural oscillations to behavior. They provide for a rich contextualizing view on spatial attention and generate predictions expanding on current models for spatial attention in the brain.

Experimental Procedures

A brief description of experimental procedures is at the beginning of the Results. A complete description can be found in the Supplemental Experimental Procedures.

Supplemental Information

Supplemental Information includes one figure and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2012.03.054.

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Supplemental Information

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Supplemental Inventory

1. Supplemental Figures

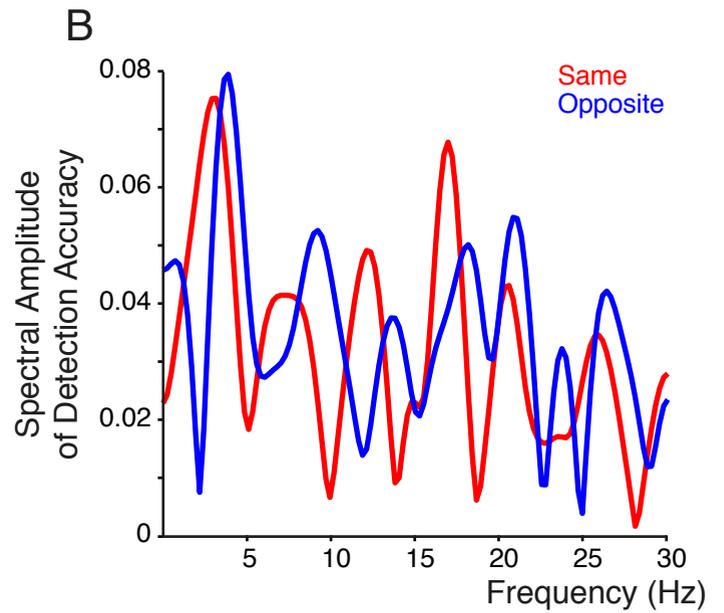
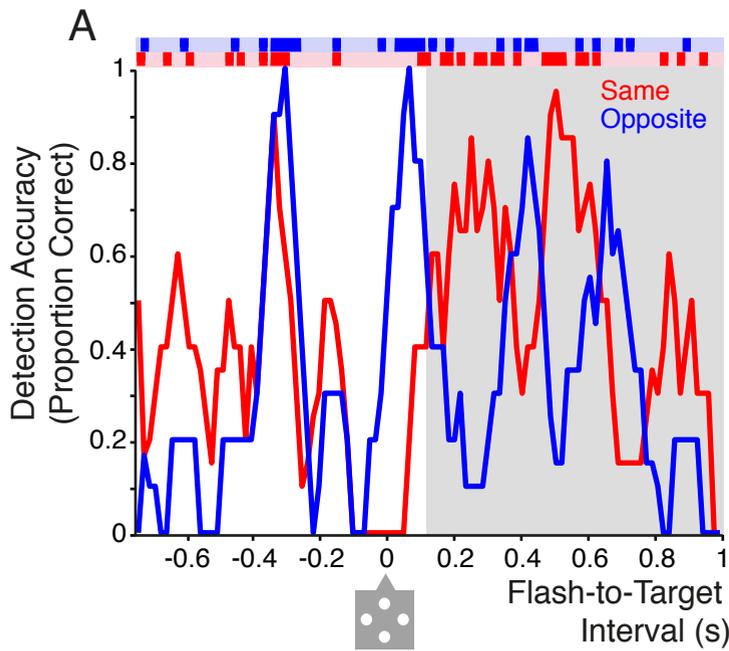
Figure S1, related to Figure 2

2. Supplemental Experimental Procedures

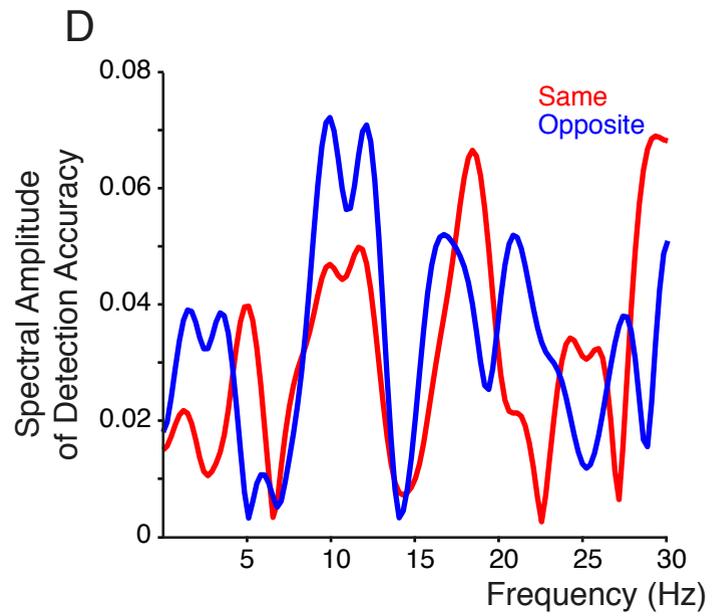
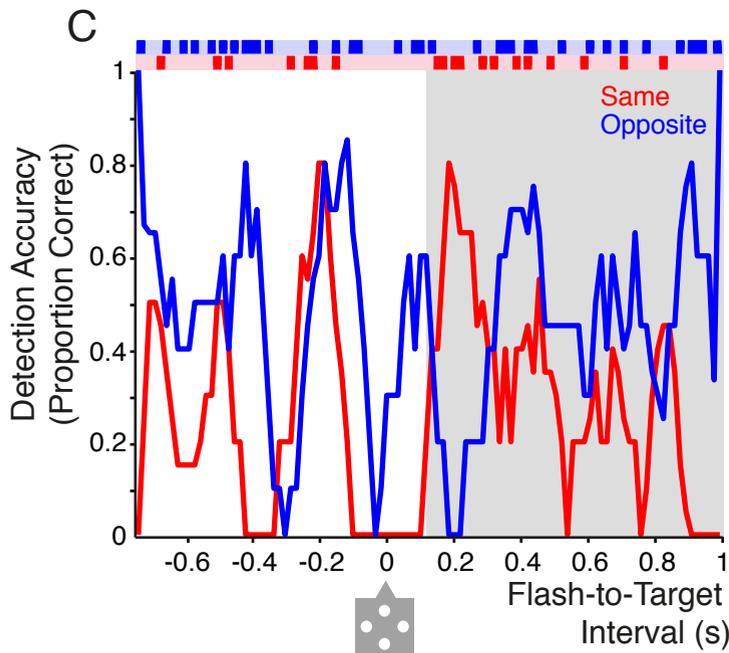
3. Supplemental References

Single Participant Data

Right Visual Field Flash Events



Left Visual Field Flash Events



Control Experiment Data (14 participants)

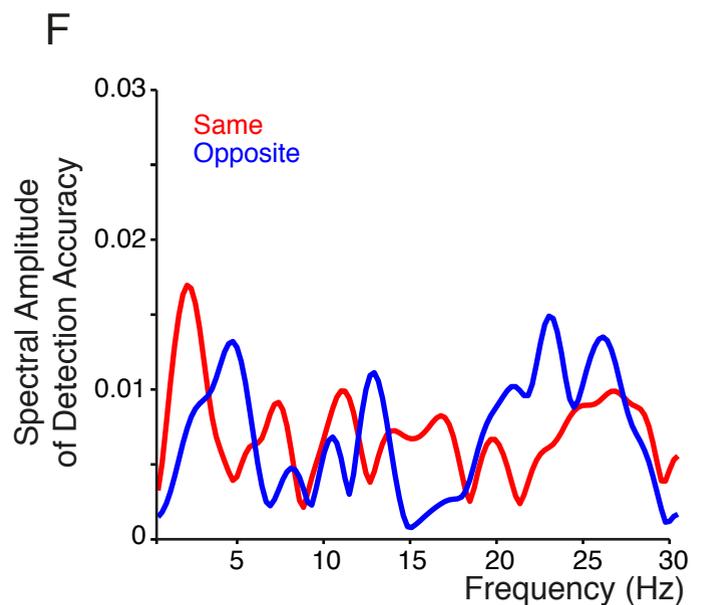
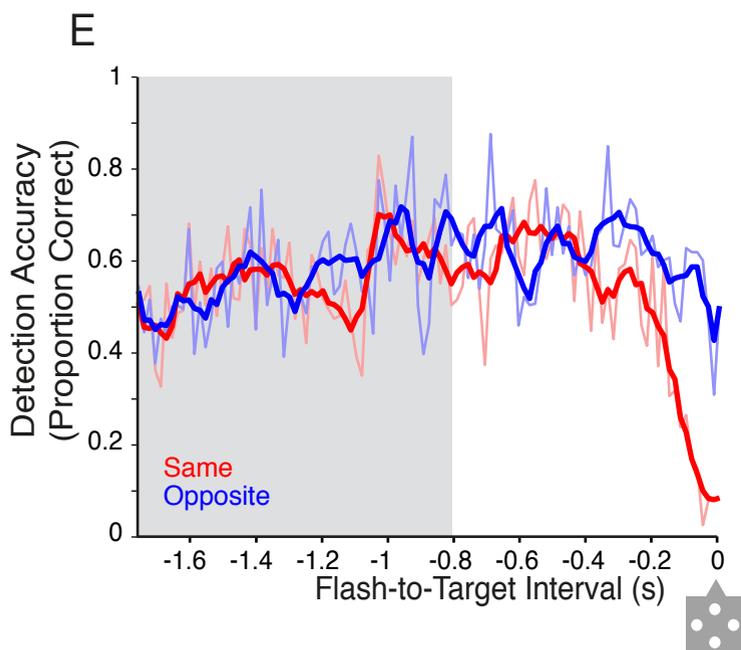


Figure S1, Related to Figure 2.

(A-D) Data from a single participant.

(A,C) Detection performance as a function of temporal interval between target event and flash event. Zero point denotes onset of flash event, negative values denote trials in which the target preceded the irrelevant flash. Red (blue) line: Detection for targets appearing in the same (opposite) visual field as the flash. (A) and (C) shows trials with flash events on the right (left) visual field. Shaded region corresponds to the portion of data subjected to spectral analysis presented in (B) and (D). Line graphs are smoothed time courses. The light red/blue horizontal bands at the top of each time course panel show correct responses as saturated vertical lines for same (red) and opposite (blue) relative locations.

(B,D) Spectra for same- and opposite-relative locations (red and blue lines, respectively).

Detection performance (E) and spectra (F) for the control experiment (14 participants). In the control experiment, targets were presented at a modified time range, from 1.8 s before to 0.1 s after the flash event. Other than that all stimulus and task parameters were kept as in the main experiment. Smoothed time courses are overlaid (in saturated lines) on the unsmoothed raw data (desaturated lines). Shaded region corresponds to the portion of data subjected to spectral analysis presented in (F).

Supplemental Experimental Procedures

Participants

Sixteen individuals (9 females, 2 left handed, average age 31) with normal or corrected-to-normal vision participated in the experiment. The study protocol was approved by the ethics committee of the Medical school at the Johann Wolfgang Goethe-University, Frankfurt. Accordingly, participants gave informed consent before the experimental session and received monetary compensation.

Stimuli

Stimuli were generated using psychophysics toolbox [1,2] version 3 within MATLAB (Mathworks inc., Natick MA). Participants viewed an LCD monitor placed at a viewing distance of 57 centimeters while their heads were stabilized in a chin rest. Eye movements were monitored using an eyetracker (EyeLink 2000, SR research). Responses were delivered by keyboard.

The display consisted of two gratings presented 5° eccentrically on either side of a fixation. Gratings were drifting at 0.7 cycles per second and the spatial frequency of the grating was 1.4 cycles per degree of visual angle. Drift direction was randomized from trial to trial avoiding configurations that would generate the percept of a bound surface viewed through two apertures. Each grating was 4° in diameter. The fixation point was a white two-dimensional Gaussian subtending 0.5° visual angle. Background was medium gray (128, 128, 128 RGB values)

Flash events were used to reset the location of attention. A flash event consisted of four dots that were briefly presented (33 ms) around one of the gratings (visual field randomized from trial to trial). Each dot subtended 1° of visual angle in diameter and was centered 1.5° away from the edge of the drifting grating. Detection targets were briefly presented (33 ms) Gaussian-shaped decrements in grating amplitude, subtending 1° of visual angle in diameter and occurring at unpredictable locations within part of the respective

grating. The precise amplitude decrement was adjusted for each participant in a separate staircase procedure.

We placed the detection targets onto the drifting gratings for several reasons: 1.) The two gratings clearly demark the two locations that are to be monitored; 2.) The two high-contrast gratings allowed us to maintain performance around 50% while using suprathreshold stimuli akin to natural visual environments; 3.) The use of high-contrast gratings rendered the superimposed targets, which were contrast decrements, relatively non-salient. We chose this scenario to de-emphasize attentional capture to the detection target, in order to minimize interference with the hypothesized ongoing sampling rhythm.

Staircase Procedure

Detection-target amplitude was determined individually using an adaptive staircase procedure (QUEST [3]). A 50% threshold was obtained at the beginning of the experimental session for each visual field separately. Average thresholds were similar for both visual fields ($t < 1$). Stimulus and task parameters for the staircase procedure were identical to the general experimental procedure (below) with the exception that there were no flash events presented when determining the participants' thresholds.

Experimental Procedure

Each trial began with a fixation screen presented for 1000 ms to 1200 ms. Following the fixation period, the two drifting gratings appeared on the screen for 3800 ms at most. Flash events occurred briefly at a random time between 1250 ms and 2500 ms from grating onset. To achieve a continuous assay of performance, the target event could appear at one of 105 intervals, in steps of 16.7 ms, from 750 ms before to 1000 ms after the irrelevant flash. Target events could randomly and with equal likelihood appear on either the same side as flash event or the opposite side (relative location condition). Each time lag on a given relative location repeated two times per subject. Successful detection of targets was coded if the participant delivered a button response within 1 second from the target onset.

Analysis

The analysis was performed using Matlab (Mathworks inc., Natick MA), the FieldTrip toolbox [4] and the CircStat toolbox[5]. For each relative-location condition (same vs. opposite), target detection was analyzed as a function of target-to-flash onset interval. A temporal profile for each relative location was composed of performance accuracy as a function of target to flash interval. One subject was excluded from further stages of analysis due to missing values in a few temporal bins. Spectral analysis was performed on the temporal profiles from 150-1000 ms after the flash event. This 850 ms epoch was Hanning tapered, zero-padded and Fourier transformed. The absolute values of the Fourier spectra gave the amplitude spectra. Figures 2b, and 2d show the amplitude spectra. The conjugate multiplication of Fourier spectra derived from same- and opposite-relative locations gave the phase relations between these two conditions.

Statistical significance of the peaks found in the spectra amplitude was assessed using a randomization procedure [6]. The null hypothesis states that there is no temporal structure in performance, and therefore the time points are exchangeable. Thus, multiple random exchanges between time points generate a randomization distribution against which we can compare the observed data. This corresponds to a random effects analysis in a parametric testing framework. We would like to emphasize that the non-parametric approach that we use does take the cross-subject variance into account, because this variance is the basis for the

width of the randomization distribution. We chose the non-parametric approach, because it does not make any assumptions about the underlying distribution. The random exchange of time points was repeated 500 times. Importantly, for each iteration, time points were exchanged for each participant separately. After each randomization, precisely the same analysis was performed as for the observed data. This resulted, for each frequency bin, in a distribution of 500 amplitude values from which significance thresholds could be determined. The thresholds were set to $p < 0.05$, Bonferroni corrected for multiple comparisons across multiple frequencies.

The analysis of phase relations used a jackknife procedure to estimate the standard error of the mean of the phase relations [7]. Non-uniformity was established using circular statistics on the phase difference values (Rayleigh test for nonuniformity for circular data in CircStats toolbox [5]).

Supplemental References

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