

# Rhythmic Sampling within and between Objects despite Sustained Attention at a Cued Location

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## Summary

The brain directs its limited processing resources through various selection mechanisms, broadly referred to as attention. The present study investigated the temporal dynamics of two such selection mechanisms: space- and object-based selection. Previous evidence has demonstrated that preferential processing resulting from a spatial cue (i.e., space-based selection) spreads to uncued locations if those locations are part of the same object (i.e., resulting in object-based selection), but little is known about the relationship between these fundamental selection mechanisms. Here, we used human behavioral data to determine how space- and object-based selection simultaneously evolve under conditions that promote sustained attention at a cued location, varying the cue-to-target interval from 300 to 1100 ms. We tracked visual-target detection at a cued location (i.e., space-based selection), at an uncued location that was part of the same object (i.e., object-based selection), and at an uncued location that was part of a different object (i.e., in the absence of space- and object-based selection). The data demonstrate that even under static conditions, there is a moment-to-moment reweighting of attentional priorities based on object properties. This reweighting is revealed through rhythmic patterns of visual-target detection both within (at 8 Hz) and between (at 4 Hz) objects.

## Results

The brain filters the multitude of stimuli within cluttered visual environments (e.g., Times Square in New York) using various selection mechanisms. Perhaps the best understood of these mechanisms, space-based selection, can bias the brain's limited processing resources toward stimuli that occur at a behaviorally relevant location [1]. However, preferential processing of stimuli based on their location is just a single step in a dynamic, ongoing process. Following the deployment of space-based selection, the competition for limited processing resources can be further resolved by object properties [2–7]. Egly et al. [8], for example, demonstrated that preferential processing spreads from cued to uncued locations if those locations are part of the same object (i.e., encompassed by the same visual boundaries). Such object-based selection has now been confirmed using varied methodologies and experimental designs [7, 9–12]. Object-based selection, like space-based selection, thus represents a fundamental step in the cascade of effects that determines which aspects of

the visual environment gain access to the brain's limited processing resources. Yet, the relationship between space- and object-based selection remains poorly understood. These selection mechanisms might reflect a single set of neural processes that is successively guided by location and object properties [9] or, alternatively, separable neural processes, perhaps governed by different networks [8, 13, 14].

One way to disentangle these selection mechanisms is to investigate their temporal dynamics. Attention changes the temporal alignment of oscillations in local field potentials, typically increasing synchronization within and between neural ensembles [15–20]. The characteristic frequencies where such synchronization occurs depend on the nature of attentional deployment [21–24]. Divergence in the temporal dynamics of neural activity under different conditions of attentional deployment suggests separable underlying neural processes, whereas convergence suggests common underlying neural processes.

Busch and VanRullen [25] reported a link between the pre-stimulus phase of theta oscillations (at 7 Hz) and the likelihood of visual-target detection under conditions of space-based selection (with no such phase-detection relationship observed when stimuli were presented at an unattended location). If space- and object-based selection arise from common underlying neural processes, then visual-target detection under conditions of object-based selection should reflect a similar phase-detection relationship (i.e., in the theta range). On the other hand, if object-based selection engages different (or additional) neural processes than space-based selection, phase-detection relationships might emerge at different frequencies. In the present study, we therefore used an established behavioral approach [26–29] to compare the temporal dynamics of visual-target detection at cued (i.e., under conditions of space-based selection) and uncued locations within the same object (i.e., under conditions of object-based selection), varying the cue-to-target interval from 300 to 1100 ms (Figure 1A). We also tracked visual-target detection in the absence of space- and object-based selection, at an uncued location on a different object (Figure 1B).

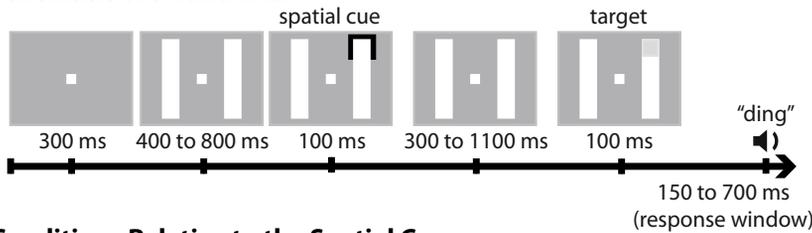
To probe the temporal dynamics of space- and object-based selection, we used an experimental design (Figure 1) based on Egly et al. [8]. The Institutional Review Board of Princeton University approved the study protocol. Participants ( $n = 14$ ) maintained central fixation and reported the occurrence of a near-threshold change in contrast (i.e., a visual target) at the end of one of two bar-shaped objects. On each trial, the bar-shaped objects were randomly oriented, either vertically or horizontally, around central fixation. A spatial cue indicated the location where the visual target was most likely to occur (with 75% cue validity). Following the cue, a valid or invalid target was presented during a randomly sampled 300–1100 ms cue-to-target interval.

Several recent studies have observed periodicity in visual-target detection following a salient or spatially informative event [26–29]. We used a spatial cue both to guide the deployment of space-based selection and to perturb (or reset) the phase of ongoing neural oscillations, causing the timing of high- and low-excitability states to align across trials [17, 18].

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### A Schematic of a Valid Trial



### B Conditions Relative to the Spatial Cue



Figure 1. The Experimental Design

(A) A schematic of a validly cued trial (i.e., the visual target occurred at the cued location). We measured behavioral performance (i.e., detection of a near-threshold visual target) at different cue-to-target intervals. The length of the cue-to-target interval was measured relative to the onset of the cue.

(B) The conditions, which were defined by both the cue and the orientation of the two bar-shaped objects. We tracked visual-target detection at a cued location (i.e., under conditions of space-based selection), an uncued location within the same object (i.e., under conditions of object-based selection), and an uncued location within a different object (i.e., in the absence of space- and object-based selection). The same- and different-object locations were equidistant from the cued location.

As a result of intertrial phase alignment (in response to the spatial cue), we predicted that the likelihood of visual-target detection would depend on the length of the cue-to-target interval, with detection more likely to occur at certain time points (or phases) than others [30–32]. Intertrial phase alignment and significant phase-detection relationships should thus lead to interdigitated periods of enhanced and diminished visual-target detection (i.e., periodicity in visual-target detection).

We tracked visual-target detection under three conditions defined by the spatial cue and the orientation of the bar-shaped objects (Figure 1B): (1) under conditions of space-based selection (i.e., at a cued location), (2) under conditions of object-based selection (i.e., at an uncued, same-object location), and (3) in the absence of space- and object-based selection (i.e., at an uncued, different-object location). Importantly, the same- and different-object locations were equidistant from the cued location, differing only in whether they were linked to the cued location through shared visual boundaries. To estimate the time course of visual-target detection, we calculated location-specific detection rates within 50 ms bins, starting with targets that were presented from 300 to 350 ms after the cue. We then shifted this 50 ms bin forward by 10 ms and calculated the next hit rate (310–360 ms), repeating this procedure throughout the duration of the cue-to-target interval (300–1100 ms). Figure 2A shows the smoothed traces that resulted from this procedure, averaged across all participants. Detection rates fluctuated depending on the length of the cue-to-target interval. In addition to a slow rise in detection rates throughout the cue-to-target interval, there were alternating phases of increased and decreased visual-target detection at each location. The slow rise in detection rates throughout the cue-to-target interval likely reflects a decisional bias, which is typically associated with the increasing conditional probability that a target will be presented at the next time point given that it has not yet been presented (i.e., the hazard rate of target presentation). Here, we removed this slowly developing effect and focused our analyses on periodicity in visual-target detection under different conditions of attentional selection [26]. Detrending the time courses of detection rates more clearly revealed their periodic nature (Figure 2B).

To measure periodicity in visual-target detection, we used the fast Fourier transform (FFT) to convert the behavioral time-series data into the frequency domain (after first detrending the data and applying a Hanning window). Figure 2C provides amplitude measurements derived by taking the absolute

value of the complex FFT output. The spectral architecture of visual-target detection under conditions of space- (i.e., at the cued location) and object-based selection (i.e., at the same-object location) was similar. A nonparametric statistical test revealed significant peaks at approximately 8 Hz ( $p < 0.05$ , corrected for multiple comparisons), confirming periodicity in visual-target detection at the cued and same-object locations. There were also peaks at 4 Hz for both the cued and same-object locations, but these peaks did not reach significance after corrections for multiple comparisons. Significant periodicity also occurred at the different-object location, but only at 4 Hz, with no peak at 8 Hz. The spatial cue therefore appeared to only induce 8 Hz periodicity for locations along the same object. These results were similar regardless of whether the bars were oriented either vertically or horizontally (see Figure S1 available online) Busch and VanRullen [25] previously demonstrated a relationship between the phase of theta-band oscillations (at 7 Hz) and the likelihood of visual-target detection under conditions of space-based selection. Here, our findings demonstrate that this phase-detection relationship (in the theta band) is not limited to the cued location but rather spreads to uncued locations that are part of the same object (i.e., share visual boundaries with the cued location). Attention-dependent increases in synchronization at the cued and same-object locations thus seem to arise from common underlying neural processes, operating at a frequency of approximately 8 Hz.

Because the visual target occurred at the cued location (with 75% cue validity) far more frequently than it occurred at the same-object location, it was difficult to make direct comparisons between amplitude measurements. However, we used the following procedure to estimate whether the amplitude of 8 Hz periodicity in detection rates at the same-object location was truly greater than that at the cued location: (1) we downsampled the number of trials at the cued location to equal the number of trials at the same-object location, (2) we used the FFT to estimate the amplitude of periodicity at the cued location (at 8 Hz), and (3) we repeated this procedure 1,000 times to generate a distribution of amplitude measurements at the cued location given the same number of trials as occurred at the same-object location. The observed amplitude of 8 Hz periodicity at the same-object location was greater than 86% of the amplitudes generated by downsampling trials at the cued location. We therefore cannot reject the null hypothesis that the amplitude of 8 Hz periodicity at the cued and same-object locations was equivalent (based on an alpha

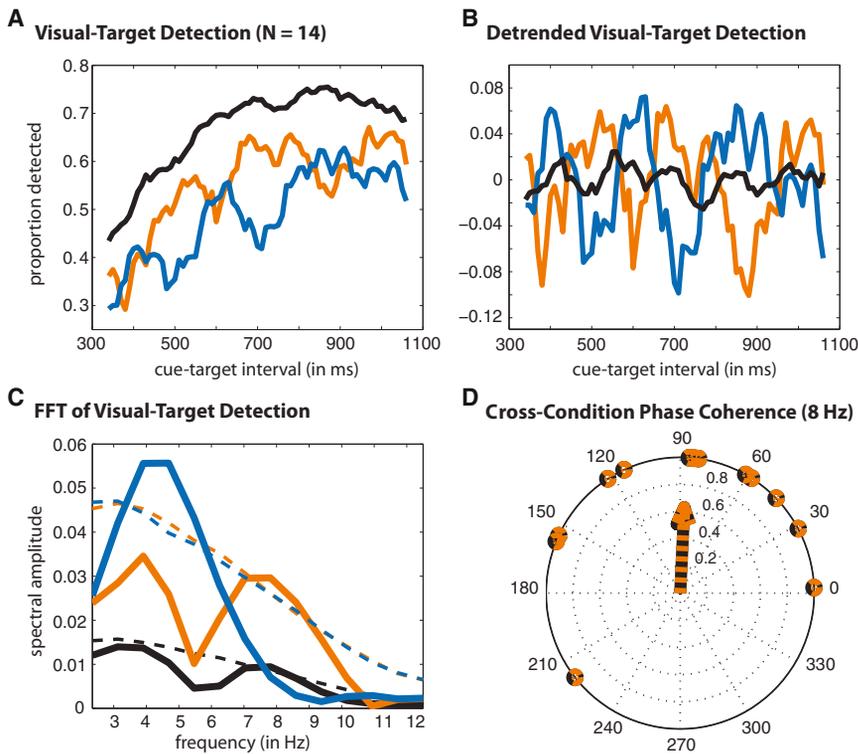


Figure 2. Visual-Target Detection under Conditions of Both Space- and Object-Based Selection Reflects Increased Theta-Band Synchronization (A) Visual-target detection at the cued (black line), same-object (orange line), and different-object (blue line) locations as a function of the cue-to-target interval. (B) Visual-target detection at each location following detrending to isolate periodic effects. (C) A frequency domain representation of the time-series behavioral data shown in (B). The dashed lines represent the cutoff for statistical significance ( $p < 0.05$ ) after corrections for multiple comparisons. (D) Significant cross-condition phase coherence ( $p < 0.05$ ) at 8 Hz between the cued and same-object locations. Each participant's phase difference is plotted on the circle, and the vector points toward the average phase difference.

level of 0.05), consistent with a common 8 Hz generative mechanism influencing both locations.

We next examined whether the observed 8 Hz periodicity had a consistent phase relationship across the cued and same-object locations. That is, we used the complex FFT output to measure whether the phase difference between these locations was consistent across participants, adapting an approach used by Lachaux et al. [33]. Figure 2D illustrates the results of this analysis, indeed highlighting a consistent phase lag between visual-target detection at the cued and same-object locations (at 8 Hz). A circle represents each participant's cross-condition phase difference, with the vector pointing toward the average phase difference. The strength of this phase relationship, indicated by the length of the vector, was significant based on a nonparametric statistical test ( $p < 0.05$ ). A value near zero would indicate a random phase difference across participants, whereas a value near one would indicate a perfectly consistent phase difference across participants. **The phase of 8 Hz periodicity at the cued and same-object locations was consistently offset by approximately 90°, meaning that a peak in visual-target detection at the cued location was followed approximately 31 ms later by a peak in visual-target detection at the same-object location. These results thus suggest that brain regions representing different locations within the attended object are synchronized at a common frequency but have location-specific phases.** Such location-specific phases might preserve an efficient transfer of information between brain regions that represent the same location within the attended object [34] and/or might contribute to the encoding of different locations within the attended object [35].

In the preceding analyses, we compared the temporal structure of visual-target detection under conditions of space- and object-based selection (i.e., we determined whether these selection mechanisms were associated with periodicity in

behavioral performance at the cued and same-object locations (relative to the different-object location) to demonstrate the existence of space- and object-based selection [8, 13, 36–38]. Their findings generally show a gradient of selection effects, such that the boost in behavioral performance is greater and earlier when targets are presented at the cued location, while smaller and later (but still significant) when targets are presented at the same-object location [7, 9, 39, 40]. Little is known, however, regarding how these selection effects evolve under conditions of sustained attention at the cued location. Figure 3A therefore depicts selection-dependent boosts in visual-target detection at different cue-to-target intervals ( $p < 0.05$ , corrected for multiple comparisons). To isolate these selection effects, we subtracted detection rates at the different-object location from those at the cued (i.e., to isolate effects under conditions of space-based selection) and same-object locations (i.e., to isolate effects under conditions of object-based selection). Detection rates under conditions of space-based selection were elevated for all cue-to-target intervals, whereas detection rates under conditions of object-based selection were only periodically elevated.

The difference waves shown in Figure 3A were influenced in part by periodicity in visual-target detection at each location. As shown in Figure 2C, there was significant periodicity at the different-object location at approximately 4 Hz. Subtracting detection rates across the same- and different-object locations enhanced this periodicity (Figure 3B), suggesting the existence of an inverse relationship between the time courses of visual-target detection at these locations (Figures 2A and 2B). Seeking confirmation of this inverse relationship, we next measured whether the phase difference (at 4 Hz) between the same- and different-object locations was consistent across participants. Figure 3C illustrates the results of this analysis, highlighting a consistent antiphase lag (i.e., an approximately 180° difference) between visual-target

visual-target detection at similar or dissimilar frequencies). Next, we compared detection rates under conditions of space- or object-based selection (i.e., at the cued and same-object locations) with detection rates in the absence of these selection mechanisms (i.e., at the different-object location). Previous studies have used relative boosts in

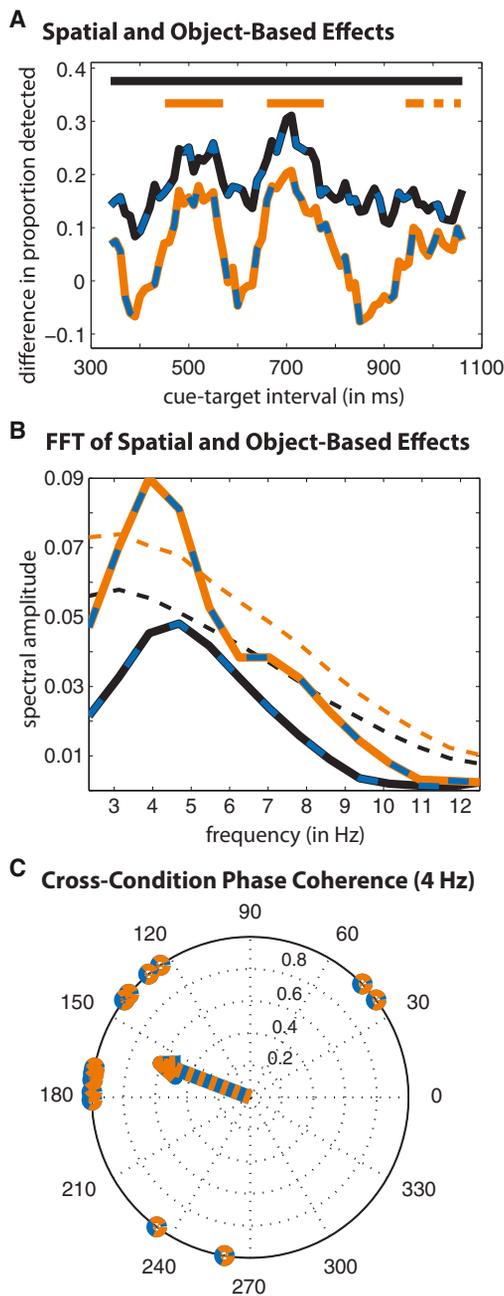


Figure 3. Enhanced Visual-Target Detection under Conditions of Space- and Object-Based Selection

(A) Difference between visual-target detection at the cued and different-object locations (black/blue line) and the difference between visual-target detection at the same- and different-object locations (orange/blue line). The bars above the traces represent time points when the effects of space- (black bar) and object-based (orange bar) selection were significantly greater than zero. The effects of space-based selection on visual-target detection were sustained, whereas the effects of object-based selection were only intermittently significant.

(B) Frequency domain representation of the time-series data shown in (A). The dashed lines represent the cutoff for statistical significance ( $p < 0.05$ ) after corrections for multiple comparisons.

(C) Significant cross-condition phase coherence ( $p < 0.05$ ) at 4 Hz between the same- and different-object locations. Each participant's phase difference is plotted on the circle, and the vector points toward the average phase difference. An antiphase relationship between detection rates at the same- and different-object locations creates periodicity in the effects of object-based selection (at 4 Hz).

detection at the same- and different-object locations. A circle represents each participant's cross-condition phase difference, with the vector pointing toward the average phase difference. The strength of this phase relationship, indicated by the length of the vector, was significant based on a nonparametric statistical test ( $p < 0.05$ ). Periods of elevated visual-target detection at the same-object location were accompanied by periods of decreased visual-target detection at the different-object location (and vice versa). A closer examination of Figure 2A reveals that detection rates at the different-object location remained near or below those at the same-object location for all cue-to-target intervals. These data therefore suggest that periods of preferential processing at the same-object location were interdigitated with periods when the same- and different-object locations were given equal processing weight.

We have described patterns of periodicity between the same-object location and each of the other two locations: (1) there was a consistent phase relationship between detection rates at the cued and same-object locations at approximately 8 Hz (Figure 2D), and (2) there was a consistent phase relationship between detection rates at the same- and different-object locations at approximately 4 Hz (Figure 3C). We next confirmed that these two processes were temporally linked at the same-object location. To this end, we measured whether the phase difference at the same-object location between 4 and 8 Hz was consistent across participants [33, 41]. Figure S2 illustrates the results of this analysis, demonstrating significant cross-frequency phase coherence. The phase difference between these two patterns of periodicity at the same-object location was highly consistent, suggesting that the neural processes underlying these effects were tightly coupled.

## Discussion

The present findings demonstrate dynamic changes in detection rates despite task conditions that promoted sustained attention at a cued location. We propose that the rhythmic patterns observed here under different conditions of attentional deployment were attributable to the following: (1) the spreading of preferential processing from a cued location to an uncued location that was part of the same object (i.e., shared visual boundaries with the cued location), and (2) a periodic reweighting of attentional prioritization that creates windows during which events associated with an uncued location on the same object (i.e., on the same object as the cued location) and an uncued location on a second object are monitored with equal importance. With regard to the first point, periodicity in detection rates emerged at a frequency of approximately 8 Hz at both the cued and the same-object locations (Figure 2C). These results are thus consistent with common neural processes influencing visual-target detection under conditions of space- and object-based selection [8, 9]. That is, these two selection mechanisms seem to be attributable to a single set of neural processes that is successively guided by location and object properties. With regard to the second point, the antiphase relationship between detection rates at the same- and different-object locations (at 4 Hz) might represent the timescale of attentional switching between objects that would occur under normal viewing conditions (i.e., in the absence of sustained attention at a cued location). Here, we have suggested that both attentional spreading and attentional switching were present during every trial; however, it should be noted that we investigated the temporal dynamics

of space- and object-based selection by compiling behavioral data across trials. It therefore remains possible that attentional spreading and attentional switching each occurred during a nonoverlapping subset of trials (i.e., attention either spread within an object or alternated between objects on a given trial).

Landau and Fries [27] recently used periodicity in visual-target detection to track attentional selection following a spatially uninformative phase-resetting event. Subsequent targets were equally likely to occur at the same location as the phase-resetting event or at a second location on the opposite side of central fixation (i.e., the phase-resetting event provided no spatial information). Under these conditions, the two locations were alternately sampled, leading to antiphase periodicity in detection rates at a frequency of approximately 4 Hz. Given that there was no reason to favor either location, preferential processing alternated equally between them. In the present experiment, on the other hand, the phase-resetting event was a spatial cue (i.e., the target was far more likely to occur on the object that included the cued location). Periods of preferential processing at the same-object location—rather than alternating with periods of preferential processing at the different-object location—alternated with periods when processing at the two locations was equivalent (Figure 2A). Periodicity between the objects was therefore still apparent, but sustained attention at the cued location seems to have prevented full attentional switching between objects. Although there was a periodic reweighting of attentional prioritization between the same- and different-object locations, detection rates at the different-object location never significantly exceeded those at the same-object location.

To maintain space-based selection at a cued location, participants need to overcome their natural tendency to continuously sample from different regions of the visual environment (a process often guided by the configuration of objects [42]). Suppression of this natural tendency creates conflict between stimulus- and goal-directed selection mechanisms [43]. The present findings indicate, however, that the outcome of this conflict is not always winner-takes-all. The behavioral data show that participants successfully deployed their attention based on the spatial cue (Figure 2A), which was the optimal strategy given that near-threshold visual targets were far more likely to occur at the cued location than elsewhere. Yet, attentional prioritization of the cued location was not absolute. Preferential processing spread from the cued location to the same-object location, and a periodic reweighting of attentional priorities across the two bar-shaped objects provided windows when relevant events (e.g., the occurrence of a visual target) at the different-object location were just as likely to be detected as those at the same-object location.

The present data thus reveal a critical interplay between two fundamental selection mechanisms (i.e., space-based selection and object-based selection) that continuously guide attentional prioritization and strongly influence behavioral outcomes. These selection mechanisms led to complex rhythmic patterns in detection rates, which involved both cued and uncued locations. Many of the behavioral effects associated with “sustained” attention are therefore not so sustained. Even under static conditions (i.e., conditions that promote sustained attention at a cued location), there is rhythmic sampling both within and between objects, clearly demonstrating the fluidity with which the brain directs its limited processing resources. Space- and object-based selection work in concert to influence attentional priorities.

#### Supplemental Information

Supplemental Information includes two figures and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.10.063>.

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