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The Adaptive Flexibility of Rhythmic Attentional Sampling in Attending to Multiple Targets

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Recent behavioral and neural imaging studies revealed a rhythmic sampling in the theta-band (3–8 Hz) of attention. Such observation indicates that visual attention sequentially visits attended locations rapidly and periodically to cover multiple spatial locations, which is believed driven by a general sampling mechanism with a sampling rate invariant to the number of targets. However, a general sampling mechanism with a fixed rate would lead to the consequence that it would take longer time for attention to revisit the same item when attention needs to cover more items, which could impair perceptual continuity. It is unclear whether and how the attentional sampling mechanism can flexibly adapt to varying task demand to balance between covering more items and maintaining stable perception. Here with five behavioral experiments, we investigated how the sequential sampling mechanism adapts to the need of attending to from one to four locations. With state-of-the-art analysis methods, results show clear evidence of sequential sampling in attending to multiple locations, that both theta-band oscillations and phase-shift among different locations were observed in the behavioral performance. At each location, the oscillation period increased when the attended locations increased from one to three, maintaining a relatively stable attention-dwelling time at each location. Critically, oscillation period remained essentially the same from three to four, suggesting a flexible task-driven acceleration of attentional sampling to keep the revisiting duration within a reasonable range. Thus, our results reveal that the generally stable rhythmic attention mechanism could flexibly adjust its sampling rate to accommodate increased attentional demands.

Public Significance Statement

When individuals attend to multiple items simultaneously, visual attention sequentially visits these items rapidly and periodically, without individuals being aware of the process. Such sequential visiting of attention with multiple targets is believed to be driven by a general sampling mechanism with a fixed sampling rate. However, could the sampling mechanism be flexible? The fixed attentional sampling rate predicts that the temporal interval for attention to revisit the same item would get longer with increased number of items to attend to, which could impair perceptual continuity. It is unclear whether attention could speed up its sampling rate to balance between covering more items and maintaining stable perception. In the current study, we observed a fixed attentional sampling rate when attending to three or fewer targets, and accelerated sampling with more than three targets. Our results demonstrate the flexibility of attentional sampling faced with varying task demands.

Keywords: attention, oscillation, sampling, flexibility

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Attention distributes limited resources to the most task-relevant information processing to optimize behavioral performances. A key feature of attention is that it could be distributed adaptively based on priority, task relevance, and number of attended items. Recent behavioral and neural evidence indicate that attention boosts perception rhythmically rather than continuously during attention deployment (Busch & VanRullen, 2010; VanRullen et al., 2007), and such rhythmic attentional enhancement is believed to be driven by a general attentional sampling mechanism with a fixed sampling rate. While this sampling mechanism allows attention to cover multiple items, it is relatively rigid in that attention will take longer to revisit each item as the number of items increases. The prelonged absence of attention on any item could be detrimental to perceptual continuity in a dynamic environment. Given the conflict between the apparent rigid temporal sampling mechanism and the need for flexibility during attention deployment, it is unclear whether and how the rhythmic sampling mechanism could flexibly adapt to the task demands to optimize performance.

When observers tried to attend to two locations at the same time, counter-phase oscillations in behavioral performance are observed between the two locations (Fiebelkorn, Saalmann, & Kastner, 2013; Landau & Fries, 2012; Song et al., 2014). Rhythmic behavioral fluctuations have also been observed even when observers attended to a single location (Landau & Fries, 2012; Re et al., 2019; VanRullen et al., 2007; Zhang et al., 2019). Interestingly, although the oscillation frequencies of both tasks fell into the theta-band (3–8 Hz), the oscillation frequency in the single location task was higher than that in the two locations task (Landau & Fries, 2012; Re et al., 2019). These results reveal a potential cognitive mechanism that visual attention sequentially visits potential target locations rapidly and periodically to cover multiple spatial locations, and the sequential sampling process for multiple locations may share a common sampling mechanism with a relatively fixed sampling rate (Holcombe & Chen, 2013; Jensen et al., 2014; Jia et al., 2017).

The sequential sampling mechanism with fixed rate supplied a general cognitive model to explain how attention covers multiple items, but such a general model also has limitations. If the sampling time for an item is fixed, then with an increasing number of attended items, it will take longer for attention to revisit the same item, resulting in a slower performance oscillation at each attended location. However, with multiple items, the long revisiting interval may diminish the perceptual continuity of targets and may lead to failed tracking of moving targets (Holcombe & Chen, 2013; Verstraten et al., 2000). Thus there is a conflict between extending the oscillation period to cover more items and limiting the oscillation period to preserve perceptual continuity. It is unclear whether a sequential sampling mechanism can adapt to the task demand by changing its sampling rate, and if so, how does the sequential sampling mechanism flexibly balance the need to cover more items and at the same time maintain perceptual stability?

In the current study, with five behavioral experiments, we examined the oscillation mechanism in spatial attention tasks with attending to locations ranging from one to four, to address the question of whether attentional sampling time for an item could be flexibly modulated depending on the task. Time-resolved performance data were obtained for each attended location under different task demands. Frequency spectrum analysis of the behavioral data revealed a theta-band oscillation in all tasks, as well as a phase shift among different locations, showing the general applicability of the sequential sampling mechanism in spatial attention. A longer oscillation period was observed with more locations to attend to, up to three. However, from three to four locations, the oscillation period remained essentially the same. These results revealed that the sequential sampling mechanism of attention has a relatively stable sampling time when it needs to attend to no more than three items, but can also flexibly adopt a short sampling time when it has to attend to more than three items, demonstrating both stability and flexibility of attention.

Experiment 1: Attentional Oscillation When Attending to Two Locations

Method

Participants

Seventeen individuals (eight females, nine males) participated in Experiment 1. All participants were between the ages of 21 and 27 and had normal or corrected-to-normal visual acuity. The M_{age} of individuals was 22 ($SD = 1.57$). The behavioral oscillations induced by attentional sampling have been observed in multiple independent studies with similar sample sizes (Fiebelkorn, Saalmann, & Kastner, 2013; Huang et al., 2015; Landau & Fries, 2012), showing that the sample size used could effectively reveal attentional oscillation. Thus, we adopted similar sample sizes in our experiments and indeed the attentional oscillation was clearly observed in all of them, confirming that the sample size we used was adequate. All participants were recruited from the local college community with informed consent and received payments for their participation in the experiment. The experiments were approved by the Committee on the Use of Human Subjects at the Institute of Biophysics of the Chinese Academy of Sciences.

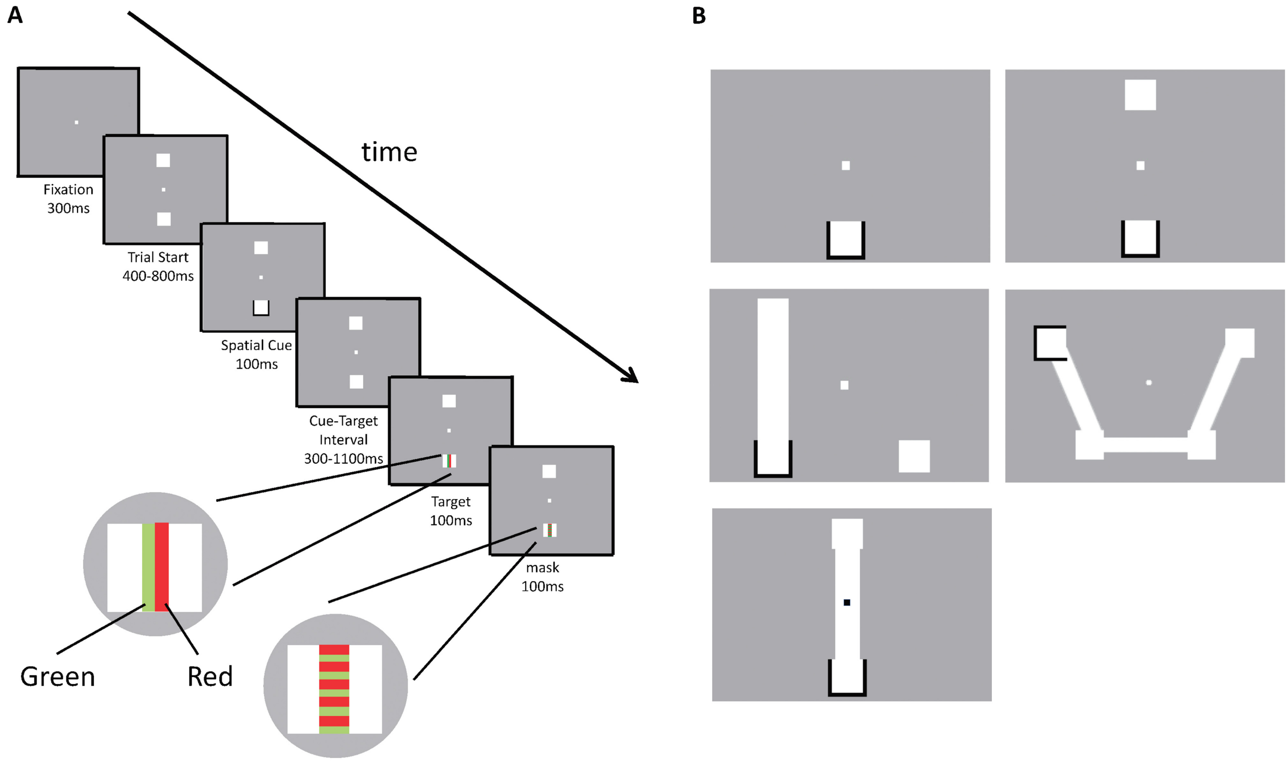
Stimuli and Procedure

In Experiment 1, during each trial, participants were instructed to keep fixating on the center of the screen where a white fixation point ($0.5° \times 0.5°$) was presented on the grey background (Figure 1A). After 300 ms, two squares ($4.4° \times 4.4°$) were presented at 9.4° either above and below or left and right of the fixation. Followed by a random interval between 400 and 800 ms, the outline of one of the squares turned black for 100 ms, serving as an attention cue. The squares marked the potential location where a target could appear. The target appeared at either the cued or uncued square 300–1,100 ms after the cue offset (cue-to-target interval). The target consisted of a pair of adjoining red and green parallel bars ($0.4° \times 4.4°$) presented for 100 ms, followed by 100 ms masking, and the participants were asked to judge whether the red bar was on the left or on the right by releasing the left or right key on the keypad, respectively. An auditory feedback signal was given after each trial to encourage participants to be as accurate as possible. The reaction time (RT) was recorded for each trial. In 70% of the trials, the target appeared at the cued location. Eye movements were monitored during the experiment with an eye-tracker (LiveTrack, Cambridge Research Systems).

Data Analysis

For each participant, RTs outside of three standard deviations across all trials were excluded from further analysis. Next, the

Figure 1
Task Procedure and Experiment Paradigm



Note. (A) An example of a validly cued trial in Experiment 1. Participants were instructed to maintain fixation at the center of the screen. After a random cue–target interval (300–1,100 ms), a target was presented at either the cued or uncued location. Participants were asked to judge the relative position of the red and green bars. (B) Illustrations of the to-be attended locations and cue placement in each experiment. Top left: Experiment 2, attending to one location; top right: Experiment 1, attending to two locations; middle left: Experiment 3, attending to three locations; middle right: Experiment 4, attending to four locations. Bottom left: Experiment 5, attending to two locations connected by a bar. See the online article for the color version of this figure.

RTs were sorted and averaged based on the spatial and temporal locations of the target in each trial, to generate the time courses of RT for each cued and uncued location. Temporal smoothing with a 50 ms time bin and first-order and second-order detrending were applied to each time course (Figure S1 in the online supplemental materials).

The frequency characteristics of the RT time courses were analyzed with the fast Fourier transform (FFT). To increase the frequency resolution, we applied an exponential window and zero padding to each time course. As the variability accumulated over time within each trial, the early period of the time courses aligned better across trials. Thus the exponential window was left shifted to give more weight on the early period during the frequency estimation (see formula below, T is the length of the time course and τ is the decay constant which is 200 ms in the current analysis). Then we performed an FFT on each time course to estimate the frequency spectrum of the behavioral fluctuations at different locations. To further increase the resolution of the FFT analysis, time courses at different locations were concatenated to generate a single time course, and a Hanning window was applied to convert the time course to the frequency domain. Note that to avoid undesired artifact, no exponential window or any other windows was applied to the individual time courses before concatenating. The absolute values of the FFT output were used as the amplitude at each frequency.

$$w(t) = \frac{\text{hanning}(T) \times \exp\left(\frac{t}{\tau}\right)}{\max\left(\text{hanning}(T) \times \exp\left(\frac{t}{\tau}\right)\right)}. \tag{1}$$

To analyze the phase relationships between the cued and uncued locations (Experiments 1, 3, 4, 5), we calculated the individual peak frequency (IPF) for each participant and each experiment around the group-level peak frequency (Experiment 1, 4–7 Hz; Experiment 2, 7–10 Hz; Experiment 3, 2–5 Hz; Experiment 4, 2–5 Hz; Experiment 5, 4–7 Hz). Phase differences between the cued location and each uncued location were then calculated based on complex Fourier outputs for the IPF. Before FFT, a Hanning window and zero-padding were applied to each time course to increase the resolution of the FFT. The Rayleigh test (CricStats MATLAB toolbox, Berens, 2009) was used to examine the nonuniformity of the phase differences, and the average phase differences across participants indicated the relationship between oscillations at the cued location and each uncued location. To estimate if there was a significant phase difference, we computed 95% confidence intervals (CIs; CricStats MATLAB toolbox) of mean phase difference and compared with zero. To reveal the phase relationship of time courses among different locations, we used sinewave functions with a frequency equal to the peak frequency estimated in the FFT analysis to fit individual time courses (using the cftool in MATLAB).

To examine the significance of the power amplitude at each frequency, a permutation test was applied by shuffling the raw RT time course data for each location and each participant. Then, we analyzed the randomized data using a similar FFT procedure as described above, with this procedure repeated 2,000 times to create the distribution for each frequency. To correct for multiple comparisons, the maximum amplitude among all frequency bins was used as the significance threshold.

To investigate the influence of microsaccades, we reanalyzed the data from the experiment but excluded trials that had microsaccades during stimulus presentation. An eye-tracker was used to obtain the gaze position and pupil size during the trial with a 500 Hz sample rate. We calculated the z-score for the pupil size to define the missing pupil data (z-score threshold $= -3$) and excluded them (eye blinks) from subsequent analysis. Gaze position data were demeaned and low-pass filtered (cutoff = 60 Hz). We identified saccades when the velocity time-series exceeded the elliptic threshold (6 *SD*s above the velocity time-series value) for six successive points in both eyes based on an established method (Engbert & Kliegl, 2003; Re et al., 2019). The entire velocity time-series for each participant was used to calculate the threshold to avoid the bias from trial length. Trials with a peak velocity more than 3 *SD*s above the mean velocity (in either eye) were excluded from further analyses. We allowed only one saccade within 50 ms and got the largest saccade within this range. We compute saccade amplitude using the Euclidean distance between the most eccentric to the least eccentric position of gaze within a saccade, averaged between two eyes. We found microsaccades with the amplitude of saccades were smaller than 2°. For controlling microsaccades influence, we excluded trials with microsaccades, the data from Experiment 1 were reanalyzed. For individual participants, excluding microsaccades may cause missing data at some time points (for most participants, 3%–10% of time points were missing after excluding trials with microsaccades), which were replaced by the averaged RT from other time points.

In order to remove the influence of the aperiodic structure on the spectrum statistics, we applied a first-order autoregressive model to generate a surrogate distribution based on an established method (Brookshire, 2022). First, we used the detrended time course for each location in the analysis described above to fit an AR(1) model and generated surrogate time courses for 2,000 times. Surrogate time courses have the same AR parameter and noise variance. Then, we analyzed the surrogate data using the same FFT procedure as described above for each location and averaged the frequency spectrum among different locations. Finally, we created the distribution for each frequency based on the AR(1) model. For multiple comparisons, we used a one-sided cluster-level statistic test to correct p values across frequencies (cluster threshold, 0.05; cluster statistic, summed z score; Brookshire, 2022). Frequency points were included in a cluster if their z values exceed the one-tailed cluster threshold (for $\alpha = .05$, $Z_{\text{threshold}} = +1.64$). For each frequency spectrum (the experiment data and each surrogate data), the cluster statistics was the total Z-score within each cluster. Corrected p values were computed for the proportion of surrogate data in which the maximum cluster statistics was greater than or equal to the cluster statistic in the experiment data.

Transparency and Openness

We report how we determined our sample size, all data exclusions, all manipulations, and all measures in the study. The data, analysis code, and research materials are available at https://github.com/Jiangyong1994/attention_oscillation/. Data were analyzed using MATLAB, version R2018a, Python, Version 3.6, package CircStats (Berens, 2009) and package oscina (Brookshire, 2022). This study's design and its analysis were not preregistered.

Results

In the attending to two locations task, with data from 17 participants, the results revealed counter-phase theta-band oscillations of behavioral performance between the cued and uncued location (Figure 2A), suggesting a rhythmic and alternating sampling of attention between cued and uncued locations. For cued and uncued locations, the FFT analysis for each location showed peak frequency around 6 Hz, which was significant at both locations (ps $< .001$). The averaged frequency spectrum showed the peak frequency at 6 Hz ($p = .002$, corrected; Figure 2B). To locate the oscillation peak more precisely, the time courses of behavioral performance from different locations were concatenated and the frequency analysis showed peak frequency at 5.8 Hz ($p = .005$, corrected; Figure 2C).

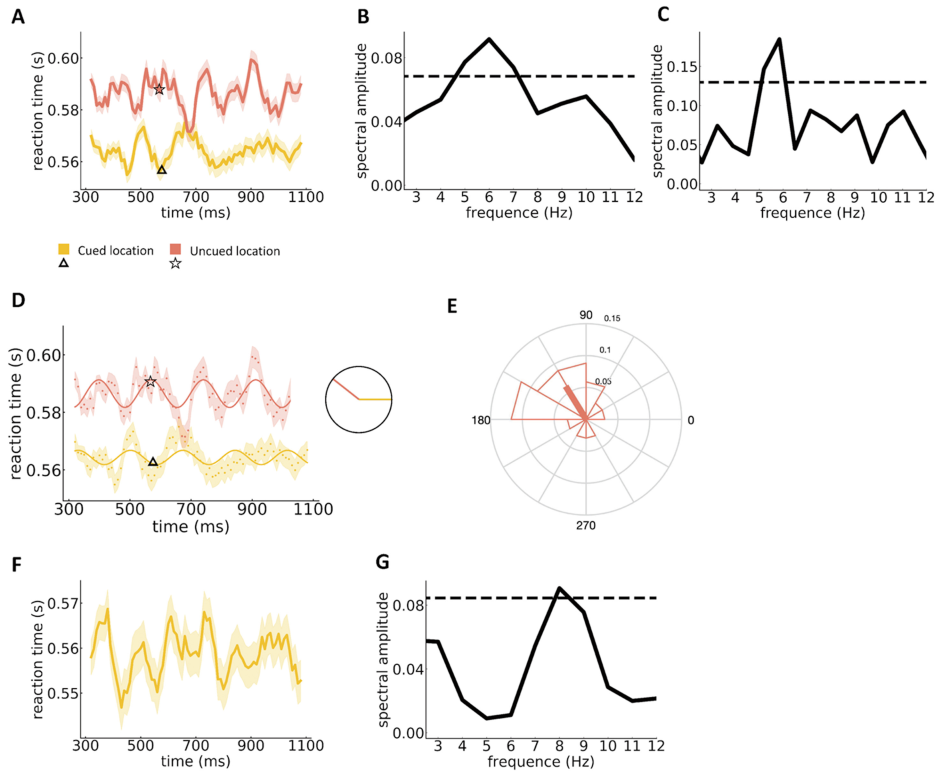
A recent study argued that the aperiodic temporal structure in the time course could impact the estimation of the periodic structure, which leads to potential false positives (Brookshire, 2022). Therefore, a parametric bootstrap approach with autoregressive models (AR surrogate, see more details in Brookshire, 2022) was also used to examine the significance of the oscillation in the current study. The results showed that the peak frequency was also significant in the permutation test with the AR surrogate ($p = .016$, corrected; Figure S3B in the online supplemental materials).

To further examine the temporal relationship between attention fluctuations at cued and uncued locations in the two-location task, two analyses were used to reveal the phase relationship in the oscillation of behavioral performances. In the first analysis, a sinewave function with a peak frequency of 5.8 Hz was used to fit the temporal fluctuation from each location and the goodness of fit was significant at both locations (cued, $R^2 = 0.17$, $p < .001$; uncued, $R^2 = 0.35$, $p < .001$). The results showed that the phase of the uncued location lagged 141° behind the phase of the cued location (Figure 2D). In the second analysis, for each participant, the IPF was estimated within 4–7 Hz, and a complex FFT was used to extract phases of the IPF at each location. A significant phase coherence was found between the cued and uncued locations ($p = .009$, Rayleigh test for cross-condition phase coherence). The group-averaged phase difference showed that the attentional oscillation at the uncued location significantly lagged behind the cued location about 123° (Figure 2E, $p < .05$, for phase delay, 95% CI = [85, 161]). The averaged IPF across participants was 5.59 Hz.

The mechanisms for attention control and eye movement are closely related. To control the potential behavioral effect driven by eye movements during the task, in the two locations experiment, in addition to asking participants to keep fixating at the center of the screen, eye-tracking was used to eliminate the trials in which participants failed to maintain fixation. However, recent studies had

Figure 2

Attentional Oscillation in Attending to One and Two Locations Tasks (Experiments 1 and 2)



Note. (A) Group averaged time courses of RT for cued and uncued location in attending to two locations task. The shaded regions reflect ± 1 *SEM*. (B) Averaged frequency spectrum of different locations. The dashed line indicates the significance threshold ($p < .05$) estimated by permutation test and was corrected for multiple comparisons. (C) Frequency spectrum of the concatenated time course of RT in attending to two locations task. The dashed lines indicate the significance thresholds ($p < .05$) estimated by permutation tests and were corrected for multiple comparisons. (D) Sinewaves fit time courses at peak frequency in (C). The phase relationship between cued and uncued locations is showing on the right. (E) Histogram of the phase difference between oscillations at the cued and uncued location at the IPF. (F) Group averaged time course of RT for attending to one location. (G) Frequency spectrum of the time course of RT in attending to one location task. The dashed lines indicate the significance thresholds ($p < .05$) estimated by permutation tests and were corrected for multiple comparisons. IPF = individual peak frequency; RT = reaction time; SEM = standard error of the mean. See the online article for the color version of this figure.

revealed that microsaccades could be related to the spatial distribution of attention (Bosman et al., 2009; Hafed, 2013), thus may potentially drive the behavioral fluctuation. To eliminate the effect from microsaccades, we excluded trials with detectable microsaccades from the beginning of the trial to the target presentation and reanalyzed the data, and observed very similar results (Figure S2 in the online supplemental materials, behavioral oscillation frequency peaking at 4–7 Hz, $p = .002$, oscillation at uncued location lagged 143° behind cued location; for more details, see Method section and online supplemental materials).

Experiment 2: Attentional Oscillation When Attending to One Locations

Experiment 1 demonstrated a sequential sampling mechanism of attention when attending to two items. Theoretically, if there is a common sampling mechanism of attention, we would expect similar behavioral oscillations in tasks where observers attended to different numbers of items, including in a single-item attention task, but with a higher oscillation frequency.

Method

Participants

Nineteen individuals (10 females, nine males) participated in Experiment 2. The M_{age} of individuals was 22 ($SD = 2.29$). All participants were recruited from the local college community with informed consent and received payments for their participation in the experiment. The experiments were approved by the Committee on the Use of Human Subjects at the Institute of Biophysics of the Chinese Academy of Sciences.

Stimuli and Procedure

In Experiment 2, only one square was presented in each trial at one of the four locations (above, below, left, or right of the fixation). The cue (black outline) was shown together with the square and was removed after 100 ms. After a 300–1,100 ms of the cue offset, the target appeared in the square. Other parameters and procedures were the same as in Experiment 1 (Figure 1B).

Data Analysis

Similar analyses as in Experiment 1 were used to examine the behavioral oscillation during the attention task.

Results

In the attending to one location task, with data from 19 participants, the temporal fluctuation of behavioral performance showed an obvious oscillation (Figure 2F), suggesting a rhythmic sampling of attention even with only one attended item. The frequency analysis revealed that such oscillation peaked around 8 Hz ($p = .035$, corrected for multiple comparisons; Figure 2G). Such peak frequency was also significant in permutation test with the AR surrogate ($p = .018$, corrected; Figure S3A in the online supplemental materials). For each participant, the IPF was estimated within 7–10 Hz and the average IPF across participants was 8.79 Hz.

Experiment 3: Attentional Oscillation When Attending to Three Locations

The results from Experiments 1 and 2 support the idea that the oscillation in behavioral performances in single- or two-item attention task was driven by a general attention sampling mechanism. To further examine whether such a mechanism would be adopted when attending to more than two items, Experiment 3 was designed to evaluate the behavioral oscillation when individuals attended to three locations.

In behavioral oscillation studies, it is critical to induce attention to sample different items in the same order across different trials, thus the behavioral performances could be averaged across trials to reveal the attentional oscillation. To help align the potential attentional sampling sequence, we took advantage of the object-based attention selection bias (Fiebelkorn, Saalmann, & Kastner, 2013; Müller & Kleinschmidt, 2003; Wannig et al., 2011) by connecting two of the three locations with a bar (i.e., object), and the spatial cue would always be presented at one of the locations on the bar. With such a manipulation, the spatial cue would reset attention initially to the cued location, then if attention next sampled the uncued locations, presumably attention would more likely sample the uncued location also on the bar due to the object-based selection bias, followed by the uncued location, not on the bar.

Method

Participants

Fourteen individuals (six females, eight males) participated in Experiment 3. The M_{age} of individuals was 23 ($SD = 2.16$). Two participants were excluded from the analysis because of very low accuracy and frequent failure to maintain fixation during the task. All participants were recruited from the local college community with informed consent and received payments for their participation in the experiment. The experiments were approved by the Committee on the Use of Human Subjects at the Institute of Biophysics of the Chinese Academy of Sciences.

Stimuli and Procedure

In Experiment 3, in each trial, squares were presented at three of four potential locations 9.4° from the fixation point (see Figure 1B), two of them were connected with a bar (horizontally or vertically). After 300 ms, the cue was presented at one of the squares at the end of the bar, and the target appeared at one of the three squares (60% at the cued location, 20% at each uncued location) after a random interval between 300 and 1,100 ms. Other parameters and procedures were the same as in Experiment 1.

Data Analysis

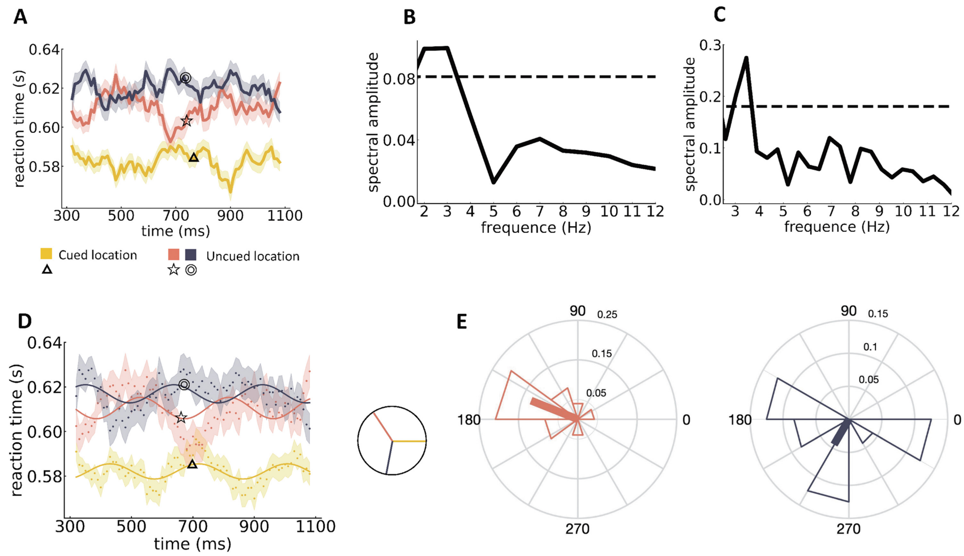
Similar analyses as in Experiment 1 were used to examine the behavioral oscillations in Experiment 3. As more time courses were collected for each individual (three locations), the mean time course was subtracted from time courses of each location to further remove the general trend.

Results

In Experiment 3, participants needed to attend to three locations simultaneously (Figure 1B). Since attentional oscillation across different items could only be revealed from averaged data, we need to make sure that the potential attentional sampling followed the same sequence in different trials. Each participant finished the whole experiment in 2 days, completing 896 trials in each day. The results from 12 participants again revealed clear temporal oscillations in performance with different phases for each location (Figure 3A). The FFT analysis for behavioral fluctuation from each location all showed a peak frequency around 3 Hz, which was significant at cued location ($p = .037$) and uncued Location 1 ($p < .001$), but not at uncued Location 2 ($p = .223$). The averaged frequency spectrum peaked at 3 Hz ($p = .005$, corrected; Figure 3B). Such peak frequency was also significant in the permutation test with the AR surrogate ($p = .045$, corrected; Figure S3C in the online supplemental materials). The more precise FFT analysis with concatenated time courses found the peak frequency of attention oscillations at 3.5 Hz ($p < .001$, corrected; Figure 3C). Sinewave functions with 3.5 Hz oscillation were used to fit the fluctuations at each location and the goodness of fit was significant at all locations (cued location, $R^2 = 0.22$, $p < .001$; uncued Location 1, $R^2 = 0.24$, $p < .001$; uncued Location 2 $R^2 = 0.33$, $p < .001$). The mean fluctuations of two uncued locations lagged 123° and 259° behind the fluctuation of the cued location, respectively (Figure 3D). With IPF analysis (2–5 Hz), for the uncued location on the bar, the phase of oscillation lagged 158° behind the phase at the cued location ($p = .009$, Rayleigh test for nonuniformity; $p < .05$, for phase delay, 95% CI = [120, 196]). For the other uncued location, the phase lagging was more variable across participants, averaging to about 239° behind the cued location ($p = .225$, Rayleigh test; $p < .05$, for phase delay, 95% CI = [149, 329]; Figure 3E). The average IPF across participants was 3.25 Hz. These results clearly show that, for three locations, attention still sequentially samples each location in sequence, but

Figure 3

Attentional Oscillation in Attending to Three Locations Task (Experiment 3)



Note. (A) Group averaged time courses of RT for cued location and two uncued locations. The shaded regions reflect ±1 *SEM*. (B) Averaged frequency spectrum of different location. The dashed line indicates the significance threshold ($p < .05$) estimated by permutation test and was corrected for multiple comparisons. (C) Frequency spectrum of the concatenated time course of RT. The dashed line indicates the significance threshold ($p < .05$) estimated by permutation test and was corrected for multiple comparisons. (D) Sinewaves fit time courses at peak frequency in (C). The phase relationship among cued and uncued locations is showing on the right. (E) Histogram of the phase difference at the IPF between oscillations at the cued and bar-connected uncued locations (left), and between cued and standing alone uncued locations (right). IPF = individual peak frequency; RT = reaction time; SEM = standard error of the mean. See the online article for the color version of this figure.

with a longer revisiting cycle at each location than that in the two-location task.

Experiment 4: Attentional Oscillation When Attending to Four Locations

The previous three experiments showed that the rhythmic sampling mechanism was adopted in tasks when one to three items need to be attended to, and the frequency of behavioral oscillation varied depend on the number of items. To further test such rhythmic sampling, in Experiment 4, behavioral oscillations were tested with four locations. To help align potential attentional sampling sequence across trials, bars were used to connect different locations. Therefore, in Experiment 4, the four locations were connected by three bars, and the cue would only appear at one of the two open ends (Figure 1B).

Method

Participants

Nineteen individuals (nine females, 10 males) participated in Experiment 4. The M_{age} of individuals was 23 ($SD = 1.99$). Two participants were excluded from the analysis because of very low accuracy and frequent failure to maintain fixation during the task. All participants were recruited from the local college community with informed consent and received payments for their participation in the experiment. The experiments were approved by the Committee on the Use of Human Subjects at the Institute of Biophysics of the Chinese Academy of Sciences.

Stimuli and Procedure

In Experiment 4, four squares linked by three bars (one horizontal, two tilted) were presented on the screen (see Figure 1B), and the distances of squares from the fixation were either 10.2° or 12.1°. After 300 ms, the cue was presented at one of the two terminal squares. The target appeared at one of the four squares (60% at the cued location, 13% at each uncued location) after a random 300–1,100 ms interval. Other parameters and procedures were the same as in Experiment 1.

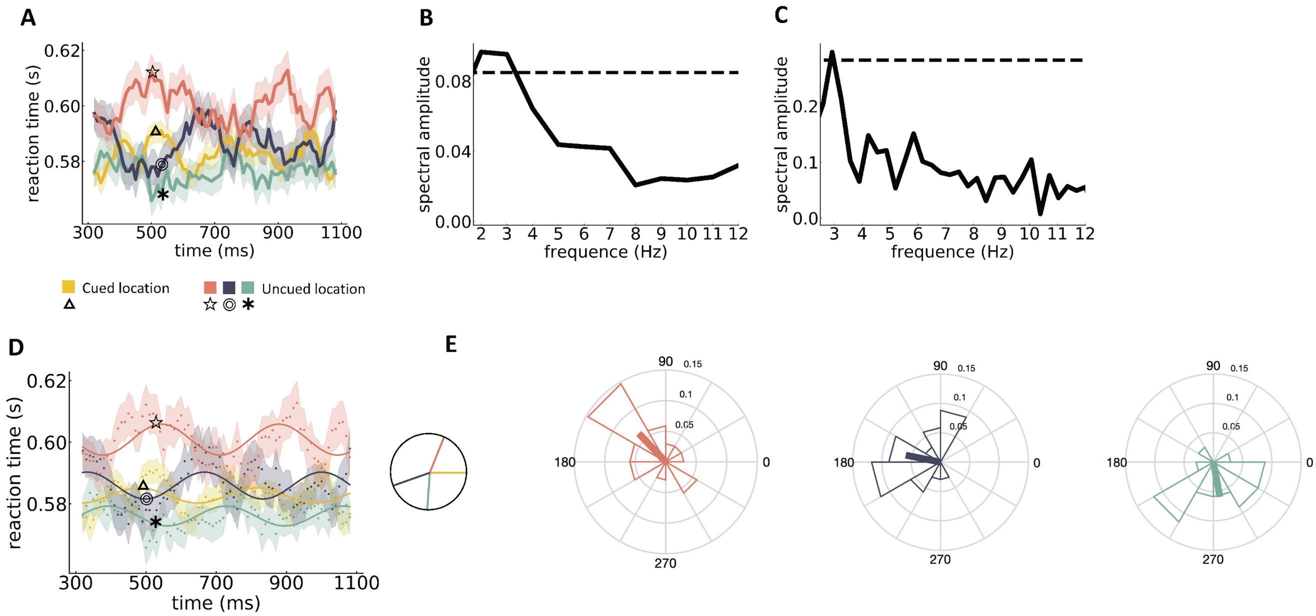
Data Analysis

Similar analyses to Experiment 3 were used to determine the temporal characteristics of attentional oscillation.

Results

In Experiment 4, the target could appear at one of four locations. Each participant finished the experiment in 3 days, completing 896 trials for each day. The results from 17 participants revealed a

Figure 4
Attentional Oscillation in Attending to Four Locations Task (Experiment 4)



Note. (A) Group averaged time courses of RT for cued location and three uncued locations. The shaded regions reflect ±1 *SEM*. (B) Averaged frequency spectrum of different location. The dashed line indicates the significance threshold ($p < .05$) estimated by permutation test and was corrected for multiple comparisons. (C) Frequency spectrum of the concatenated time course of RT. The dashed line indicates the significance threshold ($p < .05$) estimated by permutation test and was corrected for multiple comparisons. (D) Sinewaves fit time courses at peak frequency in (C). The phase relationship among cued and uncued locations is showing on the right. (E) Histogram of the phase difference at the IPF between oscillations at the cued and three uncued locations. IPF = individual peak frequency; RT = reaction time; SEM = standard error of the mean. See the online article for the color version of this figure.

significant theta-band oscillation in performance, peaking around 3 Hz for each location, which was significant at cued location, uncued Location 1, and uncued Location 2 ($ps < .026$), but not at uncued Location 3 ($p = .38$). The averaged spectrum of all locations also peaked around 3 Hz ($p = .019$, corrected; Figure 4A and B). Such peak frequency was also significant in the permutation test with the AR surrogate ($p = .027$, corrected; Figure S3D in the online supplemental materials). Analysis of the concatenated time courses showed the peak frequency at 3 Hz ($p = .042$, corrected; Figure 4C), which is very similar to the peak oscillation frequency in Experiment 3. Again, the 3 Hz sinewave functions significantly fitted the fluctuations at each location (cued location, $R^2 = 0.13$, $p < .001$; uncued Location 1, $R^2 = 0.34$, $p < .001$; uncued Location 2 $R^2 = 0.21$, $p < .001$; uncued Location 3 $R^2 = 0.32$, $p < .001$). The mean fluctuations of the three uncued locations lagged 68°, 199°, and 266° behind the fluctuation of the cued location, respectively (Figure 4D). Similarly, with IPF analysis (2–5 Hz), all three uncued locations showed significant phase coherence relative to the cued location (Figure 4E, $p = .036$, $p = .009$, $p = .010$, respectively, Rayleigh test). The phase differences indicated that the oscillations at the three uncued locations lagged 134°, 169°, and 281° behind that at the cued location, respectively (Figure 4E, in all conditions $p < .05$, for phase delay, 95% CI = [95, 172], [130, 208], [242, 320], respectively). The average IPF across participants was 3.24 Hz. In other words, the temporal oscillations in behavior performance reveal that attention sequentially sampled the four attended locations.

Experiment 5: Attentional Oscillation When Attending to Two Connected Locations

With the four experiments described above, the frequencies of attentional oscillation had been estimated in tasks with different numbers of attended locations. However, while in three- and four-location tasks, bars were used to connect different targets so that object-based attention was involved in guiding the sequential sampling of attention, but no bar was used in the two-location task as the sampling sequence was highly predictable between two locations. Such a manipulation meant that object-based attention was not involved in switching between the two locations, unlike in the other tasks. It is unclear whether the object-based attention would modulate the frequency of attentional oscillation. To clarify this question, the two-location experiment was repeated with the same design except that the two locations were connected by a bar (Figure 1B).

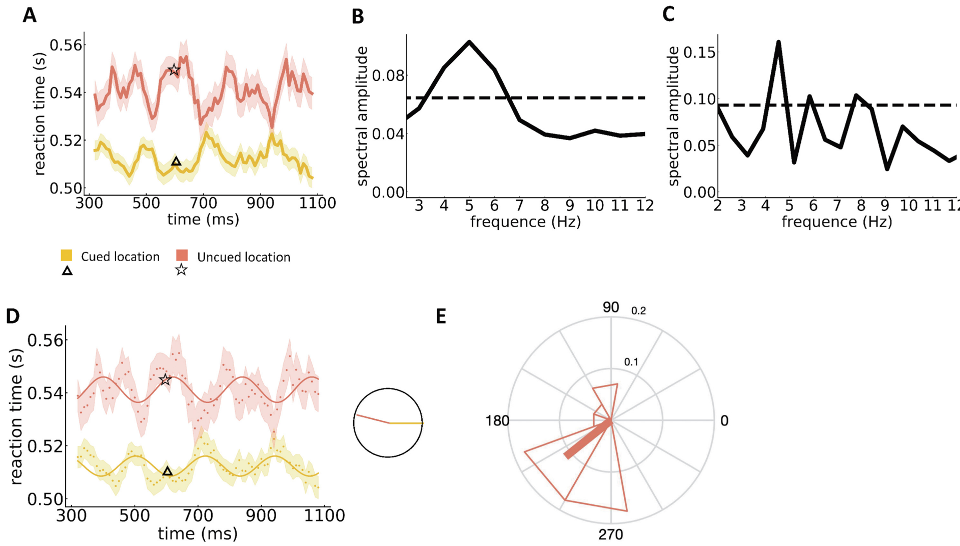
Method

Participants

Fourteen individuals (six females, eight males) participated in Experiment 5. The M_{age} of individuals was 26 ($SD = 2.86$). All participants were recruited from the local college community with informed consent and received payments for their participation in the experiment. The experiments were approved by the Committee on the Use of Human Subjects at the Institute of Biophysics of the Chinese Academy of Sciences.

Figure 5

Attentional Oscillation in Attending to Two Connected Locations Tasks (Experiment 5)



Note. (A) Group averaged time courses of RT for cued and uncued location in attending to two connected locations task. The shaded regions reflect ±1 *SEM*. (B) Averaged frequency spectrum of different locations. The dashed line indicates the significance threshold ($p < .05$) estimated by permutation test and was corrected for multiple comparisons. (C) Frequency spectrum of the concatenated time course of RT in attending to two connected locations task. The dashed lines indicate the significance thresholds ($p < .05$) estimated by permutation tests and were corrected for multiple comparisons. (D) Sinewaves fit time courses at peak frequency in (C). The phase relationship between cued and uncued locations is showing on the right. (E) Histogram of the phase difference between oscillations at the cued and uncued location at the IPFs. IPF = individual peak frequency; RT = reaction time; SEM = standard error of the mean. See the online article for the color version of this figure.

Stimuli and Procedure

In Experiment 5, all the experiment designs and parameters were the same as in Experiment 1, except two squares were linked by a bar (see Figure 1B).

Data Analysis

Similar analyses to Experiment 1 were used to determine the temporal characteristics of the attentional oscillation.

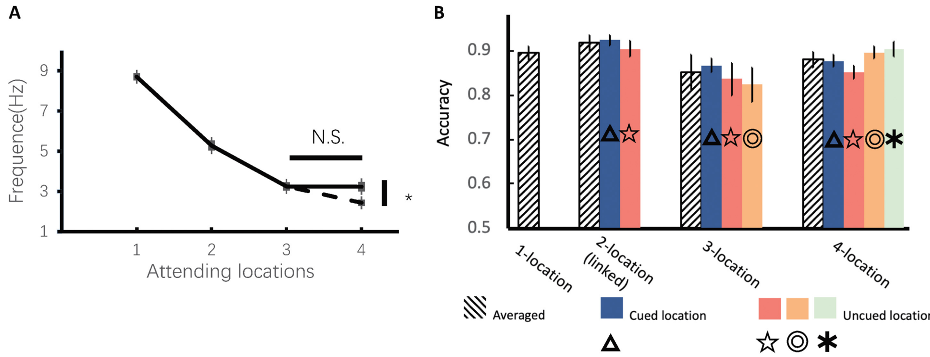
Results

The results from 14 participants revealed a significant theta-band oscillation in performance, peaking around 5 Hz for each location (significant at both locations, $ps < .03$) as well as in the averaged spectrum ($p = .003$, corrected; Figure 5A and B). Such peak frequency was also significant in the permutation test with the AR surrogate ($p = .021$, corrected; Figure S3E in the online supplemental materials). Analysis of the concatenated time courses showed the peak frequency at 4.5 Hz ($p < .001$, corrected; Figure 5C), which is noticeably but insignificantly lower than the peak oscillation frequency in the two-location task without the connecting bar. Again, sinewave functions fitted the fluctuations very well (cued, $R^2 = 0.47$, $p < .001$; uncued, $R^2 = 0.34$, $p < .001$), and the mean fluctuations of the uncued location lagged 162° behind the fluctuation of the cued location (Figure 5D). Similarly, with IPF analysis (4–7 Hz), the uncued locations showed significant phase coherence relative to the cued location (Figure 5E, $p = .001$, Rayleigh test). The phase differences indicated that the oscillations at the uncued locations lagged 219° behind that at the cued location (Figure 5E, $p < .05$, for phase delay, 95% CI = [186, 252]). The average IPF across participants was 5.29 Hz.

To facilitate the comparison of the rhythmic sampling properties in different experiments, we averaged the IPF across participants that were obtained from each experiment, and plotted them as a function of the number of attended locations (Figure 6A, for the two-location task, data from Experiment 5 were used). It is clear that the oscillation frequency decreased from attending to one location to attending to three locations, but stayed essentially the same from attending to three locations to attending to four locations. To examine the relationship of oscillation frequency between the three-location and four-location tasks, the IPFs from these two experiments were compared, and no significant difference was found, $t(27) = 0.04$, $p = .967$. Moreover, for each participant in the three-location task, the expected IPF in the four-location task was estimated based on the sequential sampling mechanism (e.g., say the oscillation frequency in the three-location task is 3.25 Hz, then expected frequency in four-location task should be $3.25 \times 3/4$, which is 2.44 Hz). The observed IPFs in the four-location task (3.24 Hz) were significantly higher than the expected IPFs of 2.44 Hz, $t(27) = 2.42$, $p = .022$, showing an accelerated sampling mechanism in the four-location task. The expected IPF in the four-location task was also estimated by fitting the 1/n function with data from

Figure 6

Attentional Oscillation Frequency and Accuracies in All Four Experiments



Note. (A) The average peak frequency of the attentional oscillation for different number of attended locations in all four experiments. The oscillation frequency systematically decreased from attending to one location to attending to three locations, but was essentially unchanged from attending to three locations to attending to four locations. (B) The response accuracies in each experiment. From left to right: one-location task; two-location (linked) task; three-location task; four-location task. Error bars reflect ± 1 *SEM*; SEM = standard error of the mean; NS = not significant. See the online article for the color version of this figure.

one- to three-location tasks and using the fitted parameter to predict the four-location oscillation frequency. The analysis predicted a 2.28 Hz oscillation in the four-location task, which was very close to the prediction using only the three-location task (2.44 Hz), and significantly lower than the observed frequency (3.24 Hz) in the four-location task ($t = 0.002$, $p = 3.80$)

In addition to the response times, the response accuracies were calculated for each experiment. The targets in the task composed of red and green bars were easy to be detected, but required focused attention to identify their spatial configurations. In addition, the participants were asked to respond as accurately as possible and an auditory feedback of correctness was given at the end of each trial, which encouraged participants to reach their best accuracy. Consistent with the expectation, high accuracies were observed in all tasks (above 82.35%; Figure 6B). While accuracy varied slightly across different tasks, $F(3, 58) = 2.88$, $p = .04$, no gradual change was observed from one- to four-location task, no significant difference between one-location and two-location, $t(31) = 1.53$, $p = .13$; two-location is higher than three-location, $t(24) = 2.98$, $p = .01$; no significant difference between three- and four-location, $t(27) = 1.13$, $p = .27$. In the two-location task, the accuracy in cued location was significantly higher than uncued locations, $t(13) = 3.10$, $p = .008$. In three-location and four-location tasks, there was no significant difference between accuracy at cued and averaged accuracy at uncued locations (ts < 1.09, ps $> .29$).

General Discussion

An important goal of this study is to examine whether and how the rhythmic sampling mechanism of attention could be flexibly implemented to tasks with different attended items. Results from four experiments show that when attending to relatively fewer items (one to three items in Experiments 1–3 and 5), attention adopted a relatively stable sampling rate across different tasks, leading to a decreased oscillation frequency from attending to one to attending to three items. In contrast, when attending to four items (Experiment 4), attention still adopted a sequential sampling mechanism, but with an accelerated sampling rate, resulting in the same oscillation frequency as attending to three items (Figure 6A). The flexibility to speed up the sampling rate allowed attention to maintain a reasonable revisiting interval when attending to more items, which is important for the perceptual continuity. Our findings reconcile the apparent conflict between an apparent rigid attentional sampling mechanism and the needed flexibility of attention in multiple target tasks.

In our natural environment, there is often the need to monitor many items at the same time, so that a sequential sampling mechanism needs to keep revisiting these items. A possible factor that constrains such a revisiting time could be the decay duration of iconic memory, which is in the order of 200–300 ms (Gilmore et al., 1986; Lu et al., 2005). Often the attended targets in the natural environment are in motion, this adds additional pressure for a sequential sampling mechanism to limit the temporal gap of revisiting the same target, otherwise, it may lose track of the targets (Holcombe & Chen, 2013). Our finding that the oscillation frequency was similar between the three-location and four-location tasks is consistent with the attentional strategy, that there is some sort of acceleration. In theory, such an acceleration could be achieved by only visiting a subset of items during each cycle, or even sampling more than one items at a time (e.g., sampling the last two items together in a cycle). However, our results clearly show that there was a phase shifting among different locations, even between Locations 3 and 4 in the four-location task, which means attention still sampled each location sequentially, though it shortened the sampling duration in the case of attending to four locations. The accuracy data also support the proposal that attention accelerated the sampling rate rather than only sampled a subset of targets during each cycle in the four-location task, as no significant difference on accuracy was found either between the three- and four-location task, or between cued and uncued locations in the four-location task, suggesting that no location was dropped during the sequential sampling in the four-location task (Figure 6B).

When attention samples multiple locations, the flexibility to adjust the sampling rate ensures perceptual continuity. In addition to the number of targets, other factors may also modulate the sampling rate. The results of the two-location tasks (Experiments 1 and 5) showed a roughly 6 Hz oscillation with two separated targets and a roughly 5 Hz oscillation with two connected targets. Although the current data showed that the difference between the two frequencies was not significant, $t(29) = 0.76$, $p = .45$, if connectedness did reduce the sampling rate, one of the possible reasons could be that the connection rendered the two locations part of the same object, so that the changes at the two locations were more correlated. Therefore, with more predictable changes at different locations of the same object, a longer revisit interval was acceptable to maintain perceptual continuity.

Given that object-based attention could potentially slow down attentional oscillation, in Experiment 3, the fact that one of the locations was not connected to the others could presumably lead to a slight overestimation of the oscillation frequency, so the expected oscillation frequency for a fully connected condition would be lower. Such reasoning makes it a stronger case to draw the conclusion from our current data that the oscillation frequency stopped decreasing from the three- to the four-location task. Nevertheless, the current study used object-based attention (bars connecting two targets) to guide attention to sequentially sample different locations in an orderly way across different trials to reveal the attentional oscillation, so the involvement of object-based attention could not be completely excluded. Although Experiments 1 and 5 showed that object-based attention did not fundamentally alter the attentional oscillation, it is still unclear how the attentional sampling mechanism works in a task without object-based attention. Novel designs are needed to answer this question in future studies.

It is also interesting that the transition in sampling strategy occurred between monitoring 3 to monitoring 4 items. There are many cognitive tasks in which "four" items seem to represent the capacity limit (e.g., subitizing range, visual working memory capacity). More related to the turning point at four-location in our results is the four-item capacity limit observed in many multiple object tracking studies (Intriligator & Cavanagh, 2001; Pylyshyn & Storm, 1988; Yantis, 1992). The sequential sampling mechanism, presumably operating in the multiple object tracking tasks, provides an explanation for such a capacity limit (Alvarez & Franconeri, 2007; Holcombe & Chen, 2013; Scimeca & Franconeri, 2015), that the attentional mechanism may not be able to further accelerate its sampling speed when tracking more than four objects. In other words, with the number of attended items go beyond four, the acceleration of sequential attention sampling is no longer a viable strategy, as the sampling duration might be too short for realizing attentional benefit.

The temporal dynamics of sequential attentional sampling may represent a more general capacity limit in attention. Recent evidence supports that sequential sampling also applies to feature attention (Mo et al., 2019; Re et al., 2019), but it remains unknown whether different types of attention have a shared mechanism, or even a common "oscillator." One way to address this question is to examine whether the oscillation frequency in one kind of attention task (e.g., spatial attention) could predict oscillation frequency in other kinds of attention tasks (e.g., feature attention) across individuals. It may also be possible that individuals with a faster attentional sampling rate have a higher capacity in attending to multiple locations.

The behavioral oscillation in the attention task has been found to be associated with neural oscillation in the primate brain. Electroencephalographic and magnetoencephalographic (MEG) studies have revealed behavior performance varied as a function of the phase of theta rhythm neural signal (Busch & VanRullen, 2010; Dugué et al., 2016; Es et al., 2022; Fiebelkorn, Snyder, et al., 2013; Hanslmayr et al., 2013). Further MEG and neurophysiology studies demonstrated the phase of theta-band neural oscillation modulated the amplitude of gamma-band neural activities in early visual cortex, which is highly relevant with visual information processing (Fiebelkorn et al., 2018; Landau et al., 2015; Lisman & Jensen, 2013). Electrocorticography and monkey neurophysiology showed that the theta-band neural oscillation in parietal and frontal cortex may drive the behavioral oscillation in attention tasks (Fiebelkorn et al., 2018; Gaillard et al., 2020; Helfrich et al., 2018). In light of our results, we would expect that the attention-relevant neural oscillation frequency would reflect both the stability (attending to one to three locations) and flexibility (from three to four locations) observed in the behavioral performance.

The current study focuses mainly on the rhythmic sampling mechanism of spatial attention that sequentially visits different locations to facilitate the processing of targets. However, it is important to point out that such a mechanism is not in conflict with the classic observation that attention continuously deploys on specific spatial locations to boost perception in a sustained manner. In fact, the rhythmic and continuous attention mechanisms may work together to optimize the resource distribution for efficient information processing (Buschman & Kastner, 2015; Fiebelkorn, Saalmann, & Kastner, 2013). In our results, in addition to the oscillation at each location, general perceptual facilitations in cued locations were observed over all tested time points, consistent with a continuous attentional benefit elicited by the spatial cues. Thus, both rhythmic and continuous mechanisms need to be considered to fully interpret our data. While there are many unknown properties in rhythmic attentional sampling, it is also important to investigate the interaction between sustained and rhythmic mechanisms during attention deployment in future studies.

Summary

Attention is one of the most important cognitive functions and it is important to understand how it is implemented in the brain, especially how attention distributes limited resources to multiple items. While recent findings showed that attentional enhancement is intrinsically rhythmic, our results suggest that such rhythmic sampling mechanism may be based on a common oscillator, which operates at a relatively stable frequency, but could speed up under pressure to maintain perceptual continuity. Our findings that attention balances stability and flexibility advance our knowledge about rhythmic attentional sampling and bring us closer to a comprehensive understanding of this important attention mechanism.

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