



There Is More Evidence of Rhythmic Attention than Can Be Found in Behavioral Studies: Perspective on Brookshire, 2022

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Abstract

Recent research indicates periodicity in attention-related sampling and switching, with some of the initial findings coming from behavioral studies. Brookshire [Brookshire, G. Putative rhythms in attentional switching can be explained by aperiodic temporal structure. *Nature Human Behaviour*, 2022, <https://doi.org/10.1038/s41562-022-01364-0>], points out that widely used approaches to testing for rhythms in behavioral time series can misclassify consistent aperiodic patterns in temporal structure as

periodic patterns. Evidence for rhythmic attention, however, is not limited to behavioral data. Here, I briefly discuss (i) issues with differentiating periodic and aperiodic structure in both behavioral and neural time series, (ii) findings from neural data that are consistent with rhythmic sampling and switching during attentional deployment, and (iii) whether alternative approaches to establishing periodicity in behavioral time series, recommended by Brookshire are appropriate for this particular research topic. ■

INTRODUCTION

Selective attention is a collection of mechanisms through which behaviorally relevant aspects of the environment receive preferential processing. The deployment of selective attention is associated with changes in neural activity (e.g., changes in spike rate, changes in neuronal tuning, changes in the temporal structure of neural data) and improvements in behavioral performance (e.g., better accuracy and faster RTs; Moore & Zirnsak, 2017; Reynolds & Chelazzi, 2004; Desimone & Duncan, 1995; Posner, 1980). Whereas classic studies of spatial attention largely assumed that these neural and behavioral effects are continuous during attentional deployment, recent work has provided considerable evidence of consistent fluctuations in attention-related neural and behavioral effects (Fiebelkorn & Kastner, 2019). For example, we have reported evidence (i) that behavioral performance during attentional deployment fluctuates over time, and (ii) that these behavioral fluctuations are related to the phase of neural signals on multiple timescales, with theta-rhythmic neural activity (~4–8 Hz) coordinating higher-frequency activity associated with different sensory and motor functions (Fiebelkorn, Pinsk, and Kastner, 2018, 2019; Helfrich et al., 2018; Fiebelkorn, Saalman, & Kastner, 2013). We have proposed that such temporal dynamics during attentional deployment reflect a balancing act between attention-related sampling and attentional shifting (or switching; Fiebelkorn & Kastner, 2019). That is, attentional deployment, even during tasks that promote sustained

attention, is characterized by interdigitated periods when it is seemingly easier to switch attention from a presently attended aspect of the environment (e.g., a specific location) to another aspect of the environment (e.g., a different location). Such windows of opportunity for attentional switching would prevent us from becoming overly focused on any single location in the environment, creating critical cognitive flexibility. Of note, theta-rhythmic patterns are not only apparent in attention-related neural and behavioral effects but also in the probability of orienting movements in primates (e.g., eye movements; Hogendoorn, 2016; Lowet, Roberts, Bosman, Fries, & De Weerd, 2016; Wutz, Muschter, van Koningsbruggen, Weisz, & Melcher, 2016; Bosman, Womelsdorf, Desimone, & Fries, 2009; Otero-Millan, Troncoso, Macknik, Serrano-Pedraza, & Martinez-Conde, 2008) and rodents (e.g., whisking; Berg & Kleinfeld, 2003; Fanselow & Nicolelis, 1999). That is, theta-rhythmic neural activity has been broadly linked to environmental sampling, regardless of whether that environmental sampling is occurring covertly or overtly (Benedetto, Morrone, & Tomassini, 2019; Fiebelkorn & Kastner, 2019; Schroeder, Wilson, Radman, Scharfman, & Lakatos, 2010).

BEHAVIORAL EVIDENCE OF RHYTHMIC ATTENTION

Some of the initial evidence for theta-rhythmic sampling and switching during selective attention came from behavioral studies that measured behavioral performance as a function of the time from a spatial cue (Song, Meng, Chen, Zhou, & Luo, 2014; Fiebelkorn et al., 2013; Landau & Fries,

2012). A recent publication, Brookshire (2022), argues that the significant results reported by those studies could be attributable to consistent aperiodic patterns rather than consistent periodic (i.e., rhythmic) patterns in behavioral performance (but see Re, Tosato, Fries, & Landau, 2022). Although Brookshire (2022) reminds us of some important points about widely used methods applied to both behavioral and neural time series data, Brookshire's findings do not nullify the substantial literature supporting the existence of periodic structure in attention-related sampling and switching.

Behavioral time series are constructed from many trials, with each trial contributing a single behavioral observation (e.g., a hit or miss) at a single time point. Behavioral observations are then combined at each time point (e.g., to calculate hit rates) to generate a behavioral time series (Fiebelkorn, 2022). Studies investigating whether there are periodic patterns in behavioral time series have tested whether there are significant peaks in the amplitude spectra, using the discrete Fourier transform (DFT) to represent the behavioral time series in the frequency domain. Statistical significance is then assessed by iteratively shuffling behavioral observations in time and re-applying the DFT to the randomized data. Observed results are compared with the compiled distribution of randomized results to calculate p values. Brookshire (2022) points out two weaknesses of this approach to testing for periodicity in behavioral time series: (i) Reshuffling behavioral observations in time eliminates both periodic and aperiodic temporal structure, and (ii) both periodic and aperiodic temporal structure can lead to peaks in the DFT. Below, I provide a brief discussion of these weaknesses and refute some of the broader implications put forth by Brookshire (2022).

DIFFERENTIATING PERIODIC AND APERIODIC STRUCTURE IN TIME SERIES DATA

The DFT converts a time series into the frequency domain, measuring the sinusoidal components that need to be added together, at specific amplitudes and phases, to

reconstruct that time series. Any time series, periodic or aperiodic, can be decomposed into its sinusoidal components. A peak in the DFT does not necessarily mean that there is periodicity in the time series. For example, there could be a single, high-amplitude bump in the data, and this bump could lead to a theta peak in the DFT (Figure 1). Brookshire (2022) shows that other aperiodic patterns, random walk and AR(1) noise (but see Vinck, Uran, & Schneider, 2022, and Re et al., 2022), can also lead to peaks in the DFT. Typical preprocessing steps, such as detrending and windowing (i.e., combining behavioral data across multiple time points), lead to higher amplitude values at lower frequencies (e.g., in the theta range). It is important to note, however, that these preprocessing steps, akin to filtering the data, should also be applied to the randomized data. That is, there are both higher amplitude values in the observed data at lower frequencies and higher significance thresholds, based on the randomized data, at lower frequencies (see Figures 2 and 3 from Fiebelkorn et al., 2013).

Issues with differentiating periodic and aperiodic temporal structure are not specific to behavioral time series and are not resolved by algorithms, for example, that isolate peaks in the amplitude spectra from the $1/f$ component (e.g., see Figure 1) (Donoghue et al., 2020; Wen & Liu, 2016). It is widely understood that typical signal processing approaches, including the DFT, can measure significant amplitude at specific frequencies, even when there is no true periodicity at those frequencies (Shin, Law, Tsutsui, Moore, & Jones, 2017; Lundqvist et al., 2016; Sherman et al., 2016). Work from Stephanie Jones and colleagues has shown transient (i.e., aperiodic) neural events with a frequency signature in the beta band (Shin et al., 2017; Sherman et al., 2016). When averaged across trials, these behaviorally relevant "beta events" can be mistaken for sustained changes in beta-band amplitude (Jones, 2016). In addition to the existence of transient "beta events," however, there is undoubtedly behaviorally relevant, periodic beta-band activity in neural data (Figure 2A). Typical signal processing approaches, like

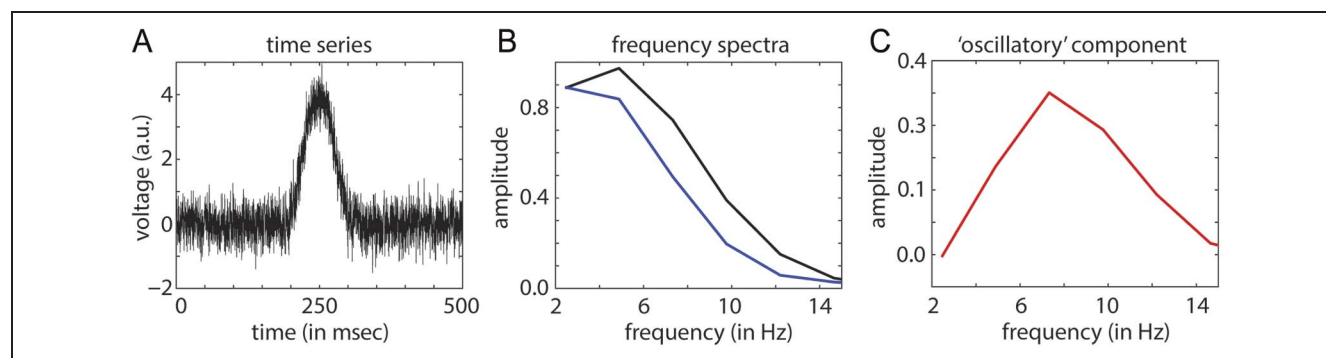


Figure 1. A single bump in time series data is represented as a peak in the frequency spectra that persists after removing the $1/f$ component. (A) Time series data with a single positive deflection was decomposed using the IRASA algorithm (Wen & Liu, 2016), which (B) removes the $1/f$ (or fractal, blue line) component from the full spectra (black line) and isolates (C) the "oscillatory" (red line) component. Although what remains after removing the $1/f$ component is referred to as the "oscillatory" component, it is not necessarily oscillatory (i.e., periodic).

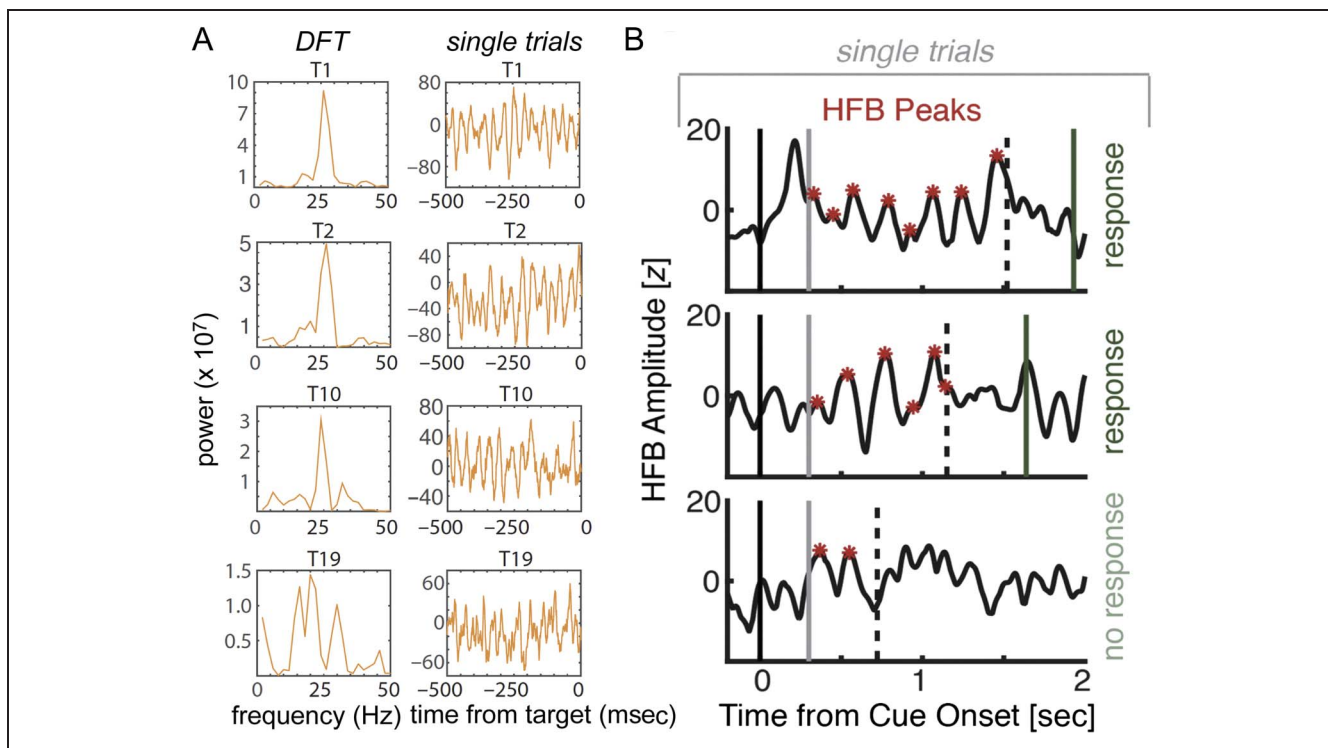


Figure 2. Examples of single trial data showing periodic neural activity at different frequencies. (A) Single trial data recorded from the FEFs of a monkey, from a single recording session during attentional deployment (adapted from Fiebelkorn & Kastner, 2021). The first column shows the amplitude spectra (i.e., DFT results) for the two trials with the strongest beta peak (T1 and T2) and the trial with the weakest beta peak (T19). A trial around the midpoint of beta amplitude (T10) is also shown. The second column shows the single trial data associated with each of the amplitude spectra. (B) Single trial data recorded from an electrode over parietal cortex in a human intracranial patient, during attentional deployment (adapted from Helfrich et al., 2018). The gray vertical line represents cue offset, and the dashed black line represents target onset. High-frequency band (HFB) activity fluctuates at a theta frequency.

the DFT, cannot easily differentiate these different beta signatures (i.e., transient and sustained). Unlike behavioral time series, however, which are constructed across multiple trials (Fiebelkorn, 2022), neural time series can be examined at the level of single trials. We are therefore often asked to show evidence of periodicity at the level of single trials (e.g., Figure 2A and 2B), which helps to differentiate periodic from aperiodic temporal structure.

WHAT DOES THAT MEAN FOR BEHAVIORAL EVIDENCE OF RHYTHMIC ATTENTION?

While we are unable to examine behavioral time series at the level of single trials, we can at least examine the shape of the function that was submitted to the DFT. So, what does the behavioral data supporting rhythmic attentional sampling and switching look like? Figure 3 shows our behavioral data, both averaged across humans ($n = 14$) and from two different animals (tested across experimental sessions; Fiebelkorn, 2022; Fiebelkorn et al., 2013). These data show the difference in performance between two potential target locations (i.e., attentional switching). There are highly consistent peaks and troughs across species and across individuals (i.e., the two animals). Moreover, these peaks and troughs have very consistent

temporal separation, occurring at a theta frequency (~ 4 Hz). A critical component of behavioral evidence that is not discussed by Brookshire is the antiphase relationship between sampling at two potential target locations (e.g., see Figures 2 and 3 from Fiebelkorn et al., 2013). That is, peaks in performance at one location are associated with troughs in performance at the other location (Fiebelkorn et al., 2013; Landau & Fries, 2012). The results shown in Figure 3 were observed during a variation of the Egly-Driver task (Egly, Driver, & Rafal, 1994). Similar results have been observed using different task designs (Landau & Fries, 2012). How changes in different aspects of a behavioral task (e.g., cue validity and the number of target locations) might lead to changes in rhythmic attentional sampling is a topic of ongoing research (Holcombe & Chen, 2013).

One place we can look for verification of periodic structure is in neural signals. This has indeed been done in the rhythmic sampling and switching literature. That is, there is behaviorally relevant theta-rhythmic neural activity, for example, in the network that directs spatial attention (Fiebelkorn & Kastner, 2021; Fiebelkorn et al., 2018, 2019; Helfrich et al., 2018). The link between behavioral performance and theta-rhythmic neural activity in this “attention network” seems to be related to the presence

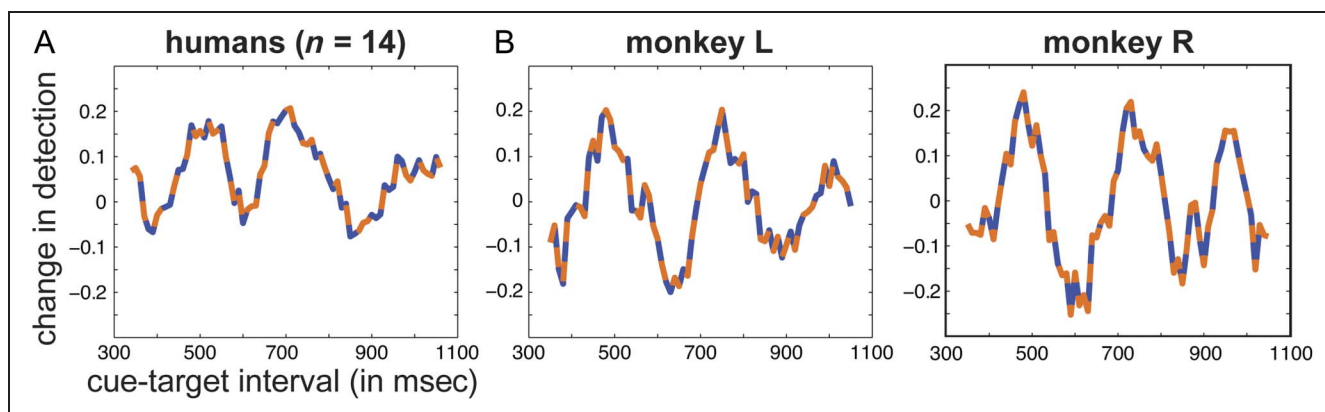


Figure 3. Behavioral time series during attentional deployment are highly consistent within and between species. (A) The difference in detection between two potential target locations as a function of the time between a spatial cue and a low-contrast visual target. These behavioral time series were averaged across 14 human participants. (B) The same results for two different monkeys, collected during performance of a nearly identical task (adapted from Fiebelkorn et al., 2013, and Fiebelkorn, 2022).

of alternating attentional states (Fiebelkorn & Kastner, 2019). These theta-coordinated, alternating attentional states promote either sampling (i.e., sensory functions of the attention network) or switching (i.e., motor functions of the attention network). Landau and Fries (2012) also followed-up their behavioral evidence of rhythmic sampling and switching by confirming a link between behavioral performance and theta-rhythmic neural signals (Landau, Schreyer, van Pelt, & Fries, 2015). There is, in fact, a considerable number of studies linking periodic neural activity to attention-related changes in behavioral performance (e.g., Gaillard et al., 2020; Benedetto et al., 2019; Fiebelkorn & Kastner, 2019; Dugue, Roberts, & Carrasco, 2016; Dugue, Marque, & VanRullen, 2015; Busch & VanRullen, 2010). Taken together, previously published behavioral and neural studies provide strong evidence for periodic structure in attention-related sampling and switching. I have written elsewhere about the importance

of linking behavioral observations to neural signals (Fiebelkorn, 2022).

WHAT ABOUT OTHER METHODS FOR DIFFERENTIATING PERIODIC AND APERIODIC TIME SERIES?

In agreement with Brookshire (2022), it would undoubtedly be better to have measures that could unambiguously differentiate between consistent periodic and aperiodic temporal structure (Re et al., 2022; Tosato, Rohenkohl, Dowdall, & Fries, 2022; Vinck et al., 2022). Such measures would avoid any subjectivity, particularly in behavioral time series, where we are unable to look for further evidence of periodicity on single trials. Brookshire (2022) presents some alternative measures, “AR surrogate” and “Robust estimate,” but are these alternative measures the right measures? Based on Figure 4 (adapted from

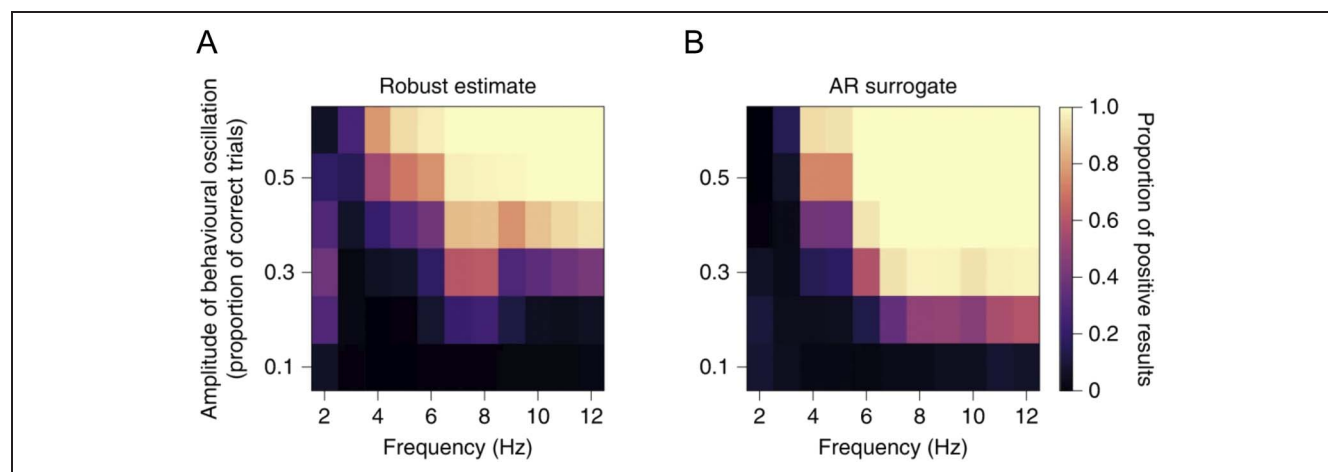


Figure 4. Alternative approaches proposed by Brookshire (2022) fail to identify simulated oscillations at the frequencies of interest for the attentional sampling and switching literature. For example, Landau and Fries (2012) and Fiebelkorn and colleagues (2013) report attentional switching at approximately 4 Hz. The plots show the proportion of simulated experiments that correctly identified an oscillation ($p < .05$) when using either the (A) AR surrogate method or (B) the Robust estimate. Results are plotted by frequency and different amplitudes of simulated behavioral oscillations.

Brookshire, 2022), these measures frequently fail to detect true oscillations in the low-theta (i.e., 4–6 Hz) frequency range, that is, the range typically associated with rhythmic sampling and switching. For several combinations of amplitude and frequency, the proportion of correctly identified oscillations was zero (Figure 4). It would therefore seem that the “AR surrogate” and “Robust estimate” approaches, recommended by Brookshire (2022), are not the right measures for this particular research topic. If these measures fail to detect periodicity in highly consistent, simulated data, then they will not detect periodicity in noisier, less consistent behavioral time series. Given this performance with simulated, sinusoidal data, it was inevitable that these measures would find no evidence of periodicity when Brookshire (2022) reanalyzed behavioral data from four previously published studies (Michel, Dugue, & Busch, 2022; Senoussi, Moreland, Busch, & Dugue, 2019; Davidson, Alais, van Boxtel, & Tsuchiya, 2018; Ho, Leung, Burr, Alais, & Morrone, 2017). That is, the alternative measures proposed by Brookshire (2022) demonstrated poor detection performance at the frequencies of interest for the rhythmic sampling and switching literature. It is therefore unfair to conclude, based on the analyses in Brookshire (2022), that these reanalyzed studies do not demonstrate periodicity in behavioral data.

FINAL THOUGHTS

Brookshire (2022) states: “These results encourage us to question whether attention switches rhythmically after all.” Although it is true that approaches typically used in published behavioral studies can lead to false positives, meaning they conclude there is significant periodic structure (with consistent peak frequencies across subjects) when there is actually significant aperiodic structure, these behavioral studies are just a piece of the puzzle. There is a substantial body of work linking behavioral performance to neural data that further supports the presence of rhythmic patterns in attentional sampling and switching. In addition, a few recent studies have pointed out shortcomings in Brookshire’s analysis of false positives (Re et al., 2022; Tosato et al., 2022; Vinck et al., 2022). These same recent studies recommend different approaches for differentiating periodic and aperiodic patterns in behavioral data (in the absence of neural data), providing guidance for future behavioral studies.

The search for improved analysis methods should certainly continue. Beyond identifying methods that better differentiate periodic and aperiodic patterns, there are other potentially important aspects of behavioral and neural time series that are not accounted for by widely used approaches. For example, variability in the shape and frequency of periodicity in behavioral and neural time series (Cole & Voytek, 2017). Neural oscillations are often nonsinusoidal and variable in their moment-to-moment frequency, but typical analysis methods, including the DFT,

are based on sinusoids. Continued efforts to be more precise about what we mean by “rhythmic” or “oscillatory” would help to better inform debates regarding the temporal dynamics of selective attention and other cognitive functions.

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Author Contributions

Ian C. Fiebelkorn: Conceptualization; Funding acquisition; Writing—Original draft; Writing—Review & editing.

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