Graduate Training Centre of Neuroscience
Neural Information Processing

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Dissociating periodic and aperiodic neural dynamics during attention

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Abstract

Electrophysiological signal consist of two components: a periodic part generated by neural oscillation and an aperiodic part following the power law. Studies have shown it will be problematic without dissociating these two components. These two parts have been linked to many cognitive processes, for example, attention. Although there are many investigations on the periodic parts, however, they have never been jointly studied. Here we dissociated these two components from local field potential data in V1 and V4 during covert attention task. We found fast timescale was shorter in V4 during attention. Power of low frequency range oscillation was decreased during attention, while high frequency power was increased. These findings shed light on the functional role of aperiodic and periodic components during covert attention, paving the way for further studies into these two linked signals in human cognition.

Contents

1 Introduction

Periodic neural activity, neural oscillation, plays an essential role in numerous perceptual and cognitive processes, including attention (Jia et al., 2022; van Kerkoerle et al., 2014; Gilbert and Li, 2013). A large body of literature analyzes oscillations in different canonical frequency bands and defines their functional roles (Yuasa et al., 2023; Ferro et al., 2021). For example, low-frequency oscillation, which carries feedforward information, has been proposed to suppress irrelevant unattended information during visual attention. While high-frequency gamma-band oscillation, modulated by feedback projections, increases the task-relevant signal (Mejias et al., 2016).

In addition to the functional role of periodic signals, studies nowadays have focused on interpreting non-oscillatory or aperiodic neural activities in cognition (Donoghue et al., 2020; Gao et al., 2020; Zeraati et al., 2022). The intrinsic timescale (τ) of aperiodic signals characterizes synaptic and cell-intrinsic properties, and the dynamics of neural interaction in cognitive processes. Zeraati et al. (2021) found attentional modulation of timescales on V4 in a visual-spatial attention task.

Emerging studies of aperiodic signals indicate problems in the traditional analysis of neural oscillations (Donoghue et al., 2020). Simply classifying neural activities in canonical frequency bands can conflate oscillations and aperiodic activities, increasing false-positive rates. Given these new findings, dissociating periodic and aperiodic neural dynamics is crucial to define the functional role of different neural oscillations and timescales in a cognitive process. However, so far there's no study jointly analyzing periodic and aperiodic components during attention.

Here, we built an in-house model to dissociate these two components and designed a fitting procedure based on 'Fitting Oscillations & One Over F' (FOOOF) (Donoghue et al., 2020). Compared to FOOOF, our algorithm significantly improved the goodness of fitting. We then examined how the changing state of attention affected the periodic and aperiodic components of local field potential (LFP) in the visual cortex. We analyzed LFP data recorded from cortical columns in primate areas V1 and V4 during a covert, feature-guided spatial attention task Ferro et al. (2021). For neural oscillations, the alpha-band oscillation was suppressed during attention, while the power of gamma-band oscillation increased. The fast timescale was shorter for the aperiodic neural dynamics when the monkey attended to the receptive fields of the recorded neurons in V4. These findings support the crucial function of alpha and gamma band neural oscillation during attention (van Kerkoerle et al., 2014). They also provide insights into the neural mechanism of faster information processing with voluntary attention.

2 Methods

2.1 Dissociating periodic and aperiodic components

For the investigation of periodic and aperiodic components, it is essential to separate the two parts. Among several toolboxes aiming to dissociate aperiodic and periodic components, FOOOF is the most popular(Donoghue et al., 2020; Wen and Liu, 2016). FOOOF fits neurophysiology data with aperiodic and periodic components in the

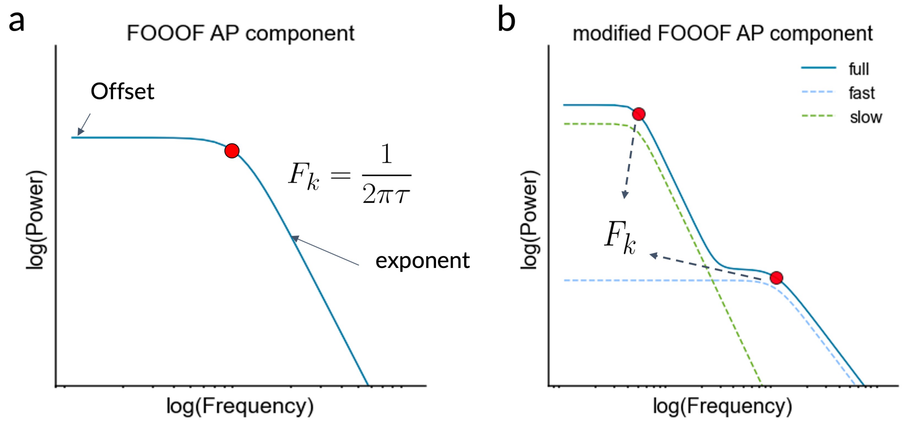

Figure 1: Aperiodic components in FOOOF and our model.

frequency domain (Equation 1-3). The aperiodic component $L(F)$ is parameterized by a offset, exponent and a timescale τ ($\tau = \frac{1}{2\pi f_k}$), following a power law in log scale (Equation 2). The periodic component $G(F)_n$ has a variable number of peaks (putative oscillation), while each peak is a Gaussian distribution with central frequency, power and bandwidth (Equation 3).

$$NPS(F) = L(F) + G(F)_n \tag{1}$$

$$L(F) = b - log(k + f_\chi) \tag{2}$$

$$G(F)_n = a * exp(\frac{-(F-c)^2}{2 * \omega^2}) \tag{3}$$

FOOOF assumed one intrinsic timescale of neural activity in all cognitive processes, resulting in a bent curve of the aperiodic component (Figure 1a). However, studies using electrocorticography (ECoG) data revealed a flat plateau at the intermediate frequency range and two distinctive power law functions at very low and higher frequencies (Freeman and Zhai, 2009; Chaudhuri et al., 2018). This shape implies there might be multiple intrinsic timescales (Zeraati et al., 2021). This inconsistency might lead to underestimate of exponent and bias towards larger timescale (Gerster et al., 2022). To address this issue, we built a model of the aperiodic component with a function including two timescales (Equation 4-5) (Figure 1b).

$$AP = 10^{b_0} * (\frac{1}{f_{k_1}^{\chi_1} + F^{\chi_1}} + \frac{b_1}{f_{k_2}^{\chi_2} + F^{\chi_2}}) \tag{4}$$

$$L(F) = b_0 + log(f_{k_2}^{\chi_2} + F^{\chi_2} + b_1 * (f_{k_1}^{\chi_1} + F^{\chi_1})) - log(f_{k_1}^{\chi_1} + F^{\chi_1}) - log(f_{k_2}^{\chi_2} + F^{\chi_2}) \tag{5}$$

To characterize signals using the model, we designed an algorithm based on FOOOF (Figure 2). The algorithm first estimates the aperiodic component and removes it from the original signal. Then it iteratively fits neural oscillations characterized by their center frequency, power and bandwidth until the remaining signal falls below the noise threshold. After extracting the periodic component, the algorithm

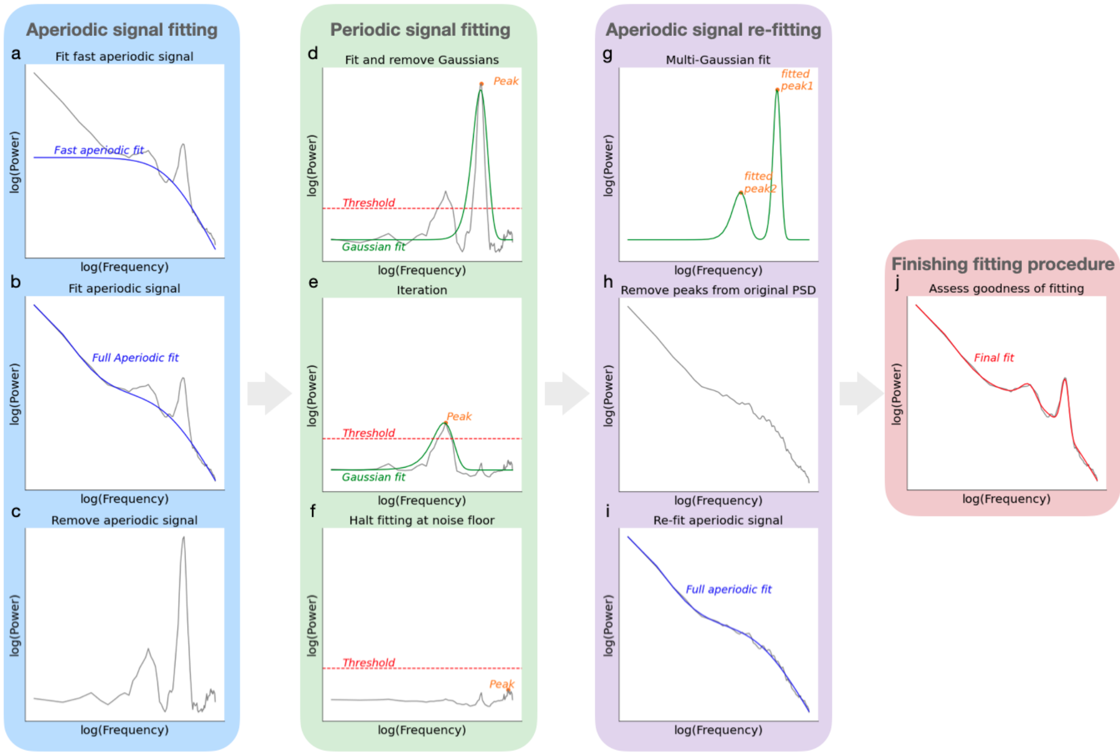

Figure 2: Algorithm schematic on real data.
(a), The PSD is first fit with an estimated fast aperiodic component (blue). (b), The parameters from initial fitting are used to estimate a full aperiodic component (blue). (c), The estimated aperiodic signal is subtracted from original PSD, the residuals are used to generate a threshold in d (red). (d-f), The maximum of residuals is considered as peak (orange). Then we fit a Gaussian with estimated bandwidth on it (green). After that, the estimated Gaussian is removed from signals in d. We find peaks iteratively untill the maximum of residuals is below threshold. (g), Then we sum the multi-Gaussian fit as periodic component. (h-i), The periodic component is removed from original PSD and used to estimate a full aperiodic component (blue). (j) The final fit is the sum of aperiodic and periodic component.

removes it from the original signal and refits the aperiodic component to improve the fitting. Finally, following (Equation 4-5), this re-fit aperiodic component is combined with the periodic component to give the final fit. Overall, this algorithm parameterizes power spectrum density (PSD) using aperiodic and periodic components (Equation 1).

2.2 Experimental data

We used LFP data recorded from V1 and V4 while the money was in a visual spatial attention task (Ferro et al., 2021). In brief, to start a trial, the monkey had to touch a lever and gaze at a centrally placed fixation point (FP). After 500ms of the fixation onset, three moving grating stimuli appeared, coded with different colors and located equidistant from FP. At a random delay after the stimulus onset (between 630 to 960 ms, uniformly distributed), a colored cue occurred at FP, instructing the monkey to monitor the stimulus with the same color. Then after three random delays, the colors of the stimulus were dimmed subsequently (delay for the first dimming ranging from 1160 to 1820 ms, for the second and third dimming from 790 to 1120 ms). The monkey was supposed to release the touch bar when the cued color was dimmed.

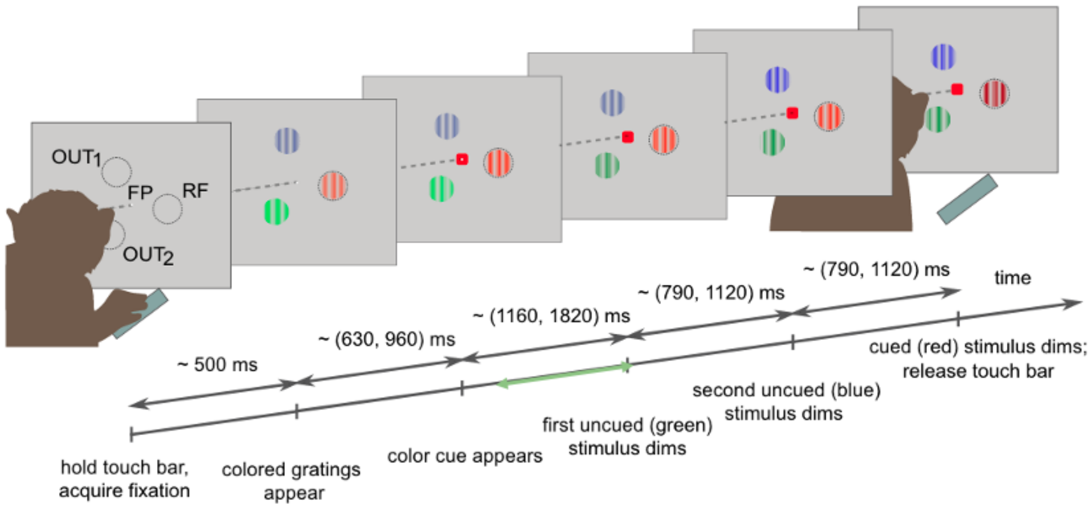

Figure 3: Covert, feature-guided visuo-spatial attention task

The LFP data were recorded over 32 sessions from different laminar (supra-granular, granular, and infra-granular) in V1 and V4. We used the signals from the time window of 1s before the first dimming (N=1024 time points at 1017.375Hz sampling rate) in correct trials. For 1/3 of the trials in each session, the receptive field of the recorded neurons was cued. This yielded 1/3 of the trials during covert attention (attention), while the rest trials were not cued (control). We generated PSD for attention and control conditions separately for each session. Specifically, we performed discrete Fourier Transform (DFT) on each trial in the attention condition and half of the trials in control condition, then averaged spectrum in each condition. Then we fitted the power spectrum in each session using our algorithm described in the previous section.

3 Results

3.1 Goodness of fitting

Our algorithm achieved a better fitting result compared to FOOOF. As shown in Fig. xa, our model fitted the low-frequency range (4-13 Hz) better by introducing the power law function in a slow timescale. Global goodness-of-fit measure R^2 was significantly improved in all our fitting (Figure 4).

3.2 Power and central frequency of periodic components

In line with previous studies, we analyzed the power and central frequency of periodic components. We performed the analysis within widely used frequency ranges, namely theta-band below 8 Hz, alpha-band from 8 to 13 Hz, beta-band from 13 to 25 Hz, low gamma-band from 25 to 50 Hz, and high gamma-band from 50 to 80 Hz.

In V1, attention increased beta and low gamma-frequency peak power (Figure

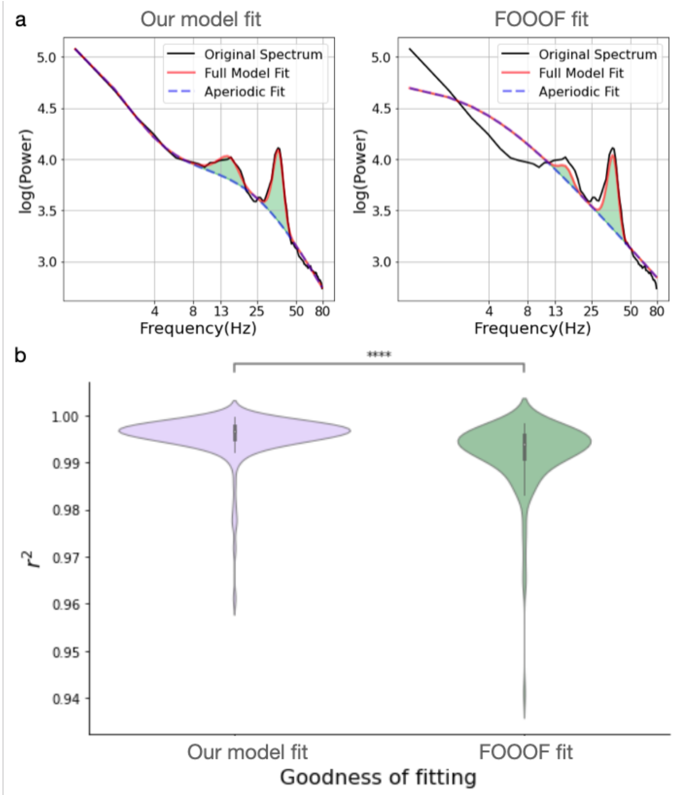

Figure 4: Goodness of fitting.
(a), Fitting result of our model and FOOOF model on LFP data in one session during attention.
(b), Goodness-of-fit measure R^2 on all sessions.

5a,c). Attending to the RF also resulted in a lower peak location in beta and a higher location in low gamma-frequency band compared to control conditions (two-sided Wilcoxon signed-rank test).

Increases in beta-frequency peak power and decreases in alpha-frequency power were found in V4 (Figure 5b,d). The peak location in beta frequency was also shifted towards a higher frequency (two-sided Wilcoxon signed-rank test).

3.3 Shorter fast timescale during attention

For the aperiodic component, we found the fast timescale is shorter during attention (Figure 6). This difference is significant for all laminar in V4 and infragranular in V1 (n=32, paired t-test with Bonferroni correction). There is no significant change in the slow timescale during attention.

4 Discussion

Our investigation focused on how periodic and aperiodic signals are modulated by attention. We used LFP data among laminar within V1 and V4 columns while the monkey was performing a visual-spatial covert attention task. We developed an algorithm to dissociate these two components from LFP signals and analyzed the timescale of neural activities, oscillation power, and central frequency during

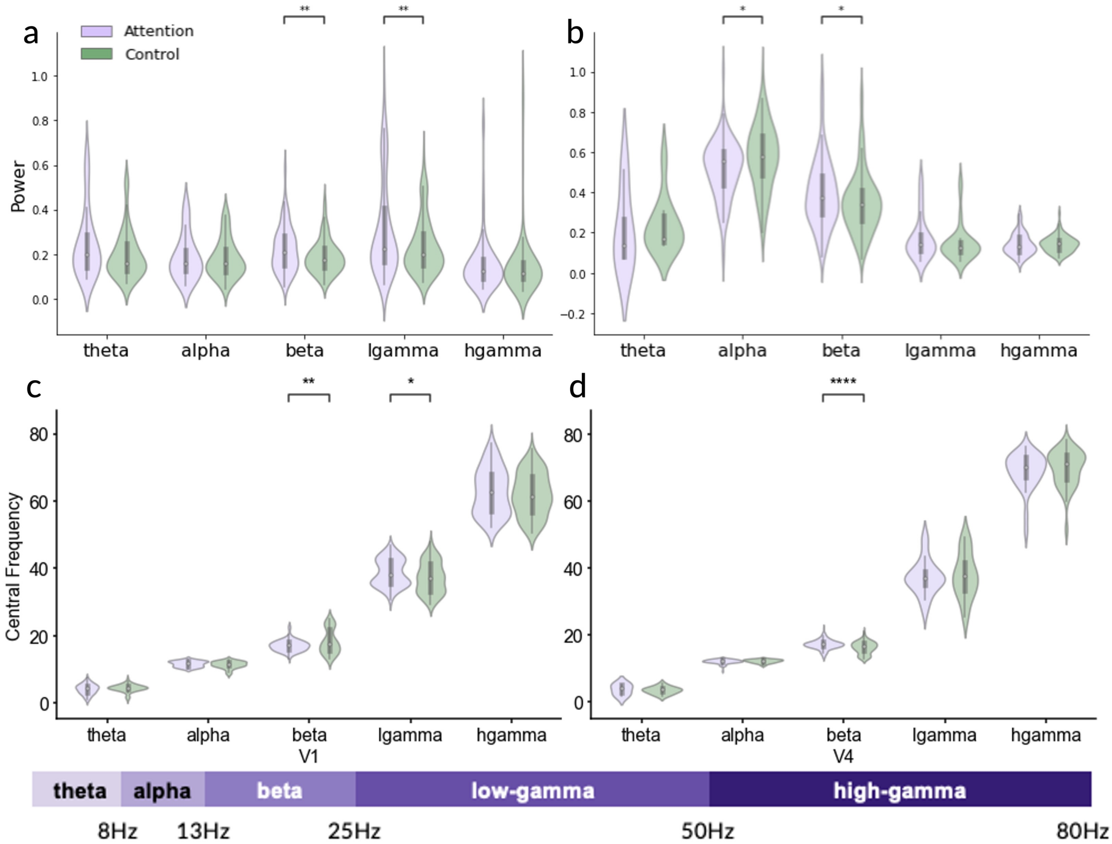

Figure 5: Power and central frequency of periodic components.
(a), Power of neural oscillation between attention and control in V1. (b), Power of neural oscillation between attention and control in V4. (c) Central frequency of neural oscillation between attention and control in V1. (d) Central frequency of neural oscillation between attention and control in V4.

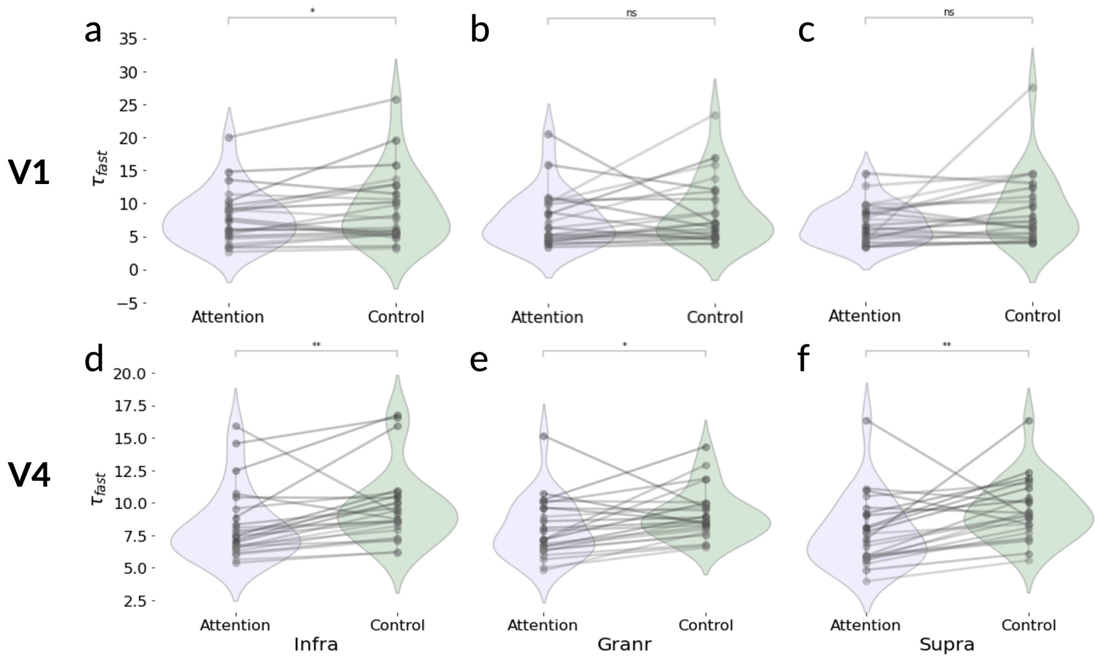

Figure 6: Fast timescale of aperiodic components.
(a), Fast timescale of neural activities between attention and control of infra-granular in V1. (b), Fast timescale of neural activities between attention and control of granular in V1. (c) Fast timescale of neural activities between attention and control of supra-granular in V1. (d), Fast timescale of neural activities between attention and control of infra-granular in V4. (e), Fast timescale of neural activities between attention and control of granular in V4. (f) Fast timescale of neural activities between attention and control of supra-granular in V4.

attention. We found attending to the RF increased the power of neural oscillations in higher frequency ranges and decreased it in lower frequency ranges. Attention also resulted in a peak shift to a higher frequency in V4. Also, the fast intrinsic timescale is shorter during attention among all laminar in V4.

For neural oscillations, we found decreased oscillation power in the low-frequency range and increased power in high frequency during attention. Previous studies have shown gamma oscillations are usually associated with feedforward pathways (Mejias et al., 2016; van Kerkoerle et al., 2014). Also, a study using magnetoencephalogram (MEG) found that increased alpha band power was correlated with prediction errors (Dijk et al., 2008). These findings suggest attention improves perception accuracy by improving discrimination ability and enhancing feedforward communication in V1. Also, peak locations in the low gamma range differed between attention and control conditions. This is consistent with previous studies using electrocorticography surface recording and LFP data Ferro et al. (2021); Xing et al. (2012). Ray and Maunsell (2010) has found that the peak frequency of gamma activity increased with stimulus strength, while Xing et al. (2012) found the peak frequency was higher with increased consciousness. This frequency-shift phenomenon can be explained by changing the timescales of inhibition and excitation, as we discussed below. Increasing vigilance and stimulus strength shorten the timescale of the primary visual network.

We found fast timescale is shorter in V4 during attention, which is inconsistent with Zeraati et al. (2021). This might be due to fitting issues in large time lags. Previous studies have shown that neuronal timescales reflect cell-intrinsic properties and anatomical connectivity and are functionally flexible and relevant to the cognitive state (Gao et al., 2020). Our results are in line with this finding. Besides, studies found the intrinsic timescale modulated by cognitive processes can be simulated by changing recurrent input in a spatial network model (Zeraati et al., 2021; Xing et al., 2012). Together with the results in periodic signals, covert attention changes the spatial connectivity in the primary visual cortex to enhance feedforward signals from attended objects/locations.

Overall, the current work dissociated periodic and aperiodic components in neural signals and studied the neural mechanism of covert attention. These results raise further questions regarding neural dynamics in different behavior demands. On the one hand, intrinsic timescales are flexible with behavior state; on the other hand, timescales are also shaped by macro- and microarchitectural properties. How these two factors modulate cognitive processes together remains to be investigated. Also, further study should look into the information flow during attention. The spatially and temporally detailed picture of neural activities during attention will shed light on recent ideas of computation-through-dynamics.

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