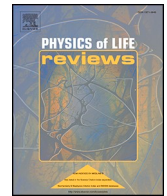




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Revealing hierarchical organization via frequency oscillations: Comment on: “Dark brain energy: Toward an integrative model of spontaneous slow oscillations” by Gong & Zuo

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The human brain is characterized by both spatial and temporal organizational principles. In recent years, novel perspectives—particularly structural eigenmodes [1] and spatiotemporal traveling wave dynamics [2,3]—have emerged in Magnetic Response Imaging (MRI) research to elucidate the spatial-temporal principles underlying cortical organization. Although these approaches differ in definition and implementation, they share a common conceptual framework: decomposing cortical organization (whether anatomical surfaces or functional connectomes) into fundamentally distinct subcomponents. This concept aligns intrinsically with the classical neural oscillation theory, in which time series are decomposed into multiple frequency bands. Whereas the neural oscillation theory [4] has established a comprehensive framework in Electroencephalogram (EEG) research [5], how brain function is organized in the frequency domain has not been reconciled with hemodynamics-based functional MRI (fMRI) observations. Advancing time–frequency analyses in fMRI studies is therefore as crucial as proposing new theoretical frameworks.

In the target paper, Gong and Zuo reviewed the limitations of current multi-band frequency analyses in fMRI research and propose a theoretical model (i.e., the three-layer SSO integrative model) that assigns potential cognitive functions to each frequency band based on the classical neural oscillation theory. It aims to integrate existing discrete findings across frequency bands into a systematic framework by incorporating a cutting-edge hierarchical perspective.

Currently, several factors limit the direct translation of brain oscillation theory from electrophysiological findings to blood oxygen level-dependent (BOLD)-based fMRI studies. First, intrinsic divergences between these imaging techniques result in the fact that fMRI can only sample the spontaneous slow oscillations (SSOs). Second, fMRI data preprocessing pipelines often include arbitrary filtering of raw BOLD time series, which may distort or even remove frequency-domain information, leading to divergent results in multi-band frequency analyses. While these issues can be mitigated through moderate denoising strategies [6], a theoretical framework that disregards technical characteristics—such as scale-specific properties embedded in low-frequency BOLD signals—still limits the ability to accurately characterize time-frequency organization in fMRI data. Moreover, beyond advancing frequency decomposition methods, understanding how cortical functional organization and information propagation relate to specific frequency components is equally essential for establishing a comprehensive framework that accounts for the spatiotemporal characteristics of the human brain.

Gong and Zuo advocated applying the well-proven natural logarithm linear law (N3L), proposed by Penttonen and Buzsáki [7], to reveal the scale-free properties of neural activity underlying BOLD signals. Unlike electrophysiological studies that normally use fixed frequency boundaries, N3L provides an adaptive way for BOLD signal decomposition, allowing frequency boundaries to vary with

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fMRI scan parameters. This approach may mitigate potential divergence across studies caused by differences in signal sampling rates and data preprocessing strategies. Nonetheless, comparisons across studies should be made cautiously. It is more appropriate to characterize these signals using band sequences (e.g., slow-1 ~ slow-6 SSOs) rather than directly referencing specific frequency ranges (e.g., 0.001 Hz to 0.01 Hz).

Based on the N3L-derived frequency components, Gong and Zuo integrate a cutting-edge hierarchical perspective [8–10] to characterize scale-specific properties at the network level. Leveraging the advantages of spatial resolution, existing fMRI studies have accumulated substantial evidence that the cortical surface can be organized into functionally distinct brain areas. These areas can further cluster into large-scale networks, forming a sophisticated hierarchical brain system. Most existing frameworks primarily focus on spatial organization—for instance, proposing that information processing follows a principle of propagation from lower-order sensory networks to higher-order cognitive networks along the cortical sheet [9,10]. Gong and Zuo extend this view and propose a theoretical model, suggesting that such integration occurs not only across spatial dimensions but also extends to the time-frequency domain through frequency-specific components.

The proposed three-layer SSO integrative model links frequency bands to distinct levels of brain functions. Specifically, relatively higher-frequency components (Slow1–3 SSOs) are primarily associated with sensation and perception, characterized largely by bottom-up processing. Slow4 SSO functions as a core transition module, coordinating multiple computational channels associated with different cognitive functions. The slowest components (Slow5–6 SSOs) modulate cross-subsystem integration, forming a general basis for global brain states such as consciousness and awareness/attention. Notably, the decrease in oscillation frequency corresponds to the increase of signal propagation distance along the cortical surface, extending from local to long-range connections. This frequency–distance relationship, well established in electrophysiology, is also evident in recent studies employing structural eigenmodes [1]. These eigenmodes, derived from anatomical topological organization, can be conceptualized as ‘spatial Fourier basis functions’, suggesting that common organizational principles may govern both anatomical and functional architectures across spatial and temporal domains.

Importantly, leveraging the hierarchical organization perspective, this three-layer model posits that Slow4 SSO form a mechanistic bridge between localized and global neural processing, enabling transitions from specific cognitive functions to global mental states. The fMRI-based multi-band frequency analysis allows these frequency components to be spatially mapped across functional parcellations and networks. Gong and Zuo report that the highest-ranking values in Slow4 SSO (figure 6A in the target paper) predominantly occur at the boundary between the attention network and the cognitive control network. These observations suggest that functional transitions in the brain do not depend on specific brain areas or isolated networks, but rather preferentially emerge at spatial network boundaries, with the strongest modularity in Slow4 SSO driven by high within-network connectivity.

Developmental evidence also supports the existence of an intermediate modulation layer in the cortical hierarchy. The action network [11] – previously termed the cingulate-opercular network [12] and largely overlapping with the ventral attention network [13] – features comprehensive functionality supporting both stimulus detection and attention maintenance. This network is proposed to reside at an intermediate level of the cortical hierarchy. During the maturation of the cortical hierarchy from childhood to adolescence [14], enhanced within-network connectivity in the default network and decreased between-network connectivity in the ventral attention network coordinate the refinement of long-range connections with reduced local connectivity [15]. This developmental trajectory ultimately reinforces the dominance of the transmodal cortex within the brain’s hierarchical structure. These patterns also parallel frequency-specific observations: slow-5 and slow-6 SSOs exhibit preferential recruitment of long-range connections, while within-network connectivity predominates in the default network, cingulo-opercular network, and ventral attention network at the slow-5 frequency band.

In summary, the three-layer SSO integrative model proposed by Gong and Zuo not only addresses key gaps in fMRI multi-band frequency research, but also advances the frequency framework into a comprehensive spatiotemporal hierarchical system theory. Future studies could enhance the model’s robustness by addressing three key questions: (1) whether cortical networks maintain fixed or flexible spatial profiles within specific frequency bands; (2) how SSO patterns vary across individuals in relation to global BOLD activity; and (3) whether functional distinctions across frequency bands can predict individual differences in cognitive abilities. Addressing these questions could strengthen the theoretical basis of the three-layer SSO model and promote its applications to explaining individual variability in cognitive functions through the spatiotemporal signatures of slow oscillations.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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