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Review

Wavelet analysis in biomedical research: A versatile tool for multiscale signal characterization and functional connectivity analysis

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ABSTRACT

Biological systems exhibit oscillatory dynamics across spatial and temporal scales. From intracellular signaling to organ-level physiology, these rhythms support coordinated regulation and collective behavior. The resulting signals are nonstationary and reflect the superposition of multiple physiological processes, posing challenges for conventional analytical approaches. By providing time-frequency localization, wavelet analysis offers a powerful framework for characterizing transient oscillations and their scale-dependent organization. Recently, its integration with functional connectivity enabled quantification of time- and frequency-resolved interactions among biological units and the construction of frequency-specific functional networks. In turn, multilayer representations provide a foundation for examining network organization across frequency bands and their interrelations. Motivated by these developments, this review provides an integrated overview of the principles of wavelet analysis and its applications in biomedical research. Using examples from cardiovascular physiology, neuroscience, and pancreatic islet calcium dynamics, we illustrate how wavelet-based methods extend from the time-frequency characterization of individual signals to the analysis of functional interactions and collective network dynamics. Overall, wavelet analysis emerges as a versatile framework for linking nonstationary multiscale dynamics with physiological coordination and network organization. Advances in experimental resolution, computational methodology, and data-driven analysis are likely to extend its value, particularly when wavelet-derived features are integrated with functional connectivity, multilayer network models, and machine learning approaches. Such combinations may transform complex physiological recordings into interpretable representations of coordinated function across scales. Wavelet-based analysis thus has the potential to become a key

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methodological tool for studying complex biological systems, from intracellular processes to organs, in health and disease.

1. Introduction

Oscillatory phenomena span multiple levels of biological organization and temporal scales, reflecting the inherently multiscale nature of living systems. From the molecular to the organ level, biological signals often consist of superimposed rhythms operating at distinct frequencies, each carrying functional significance and often interacting in nontrivial ways. For instance, in excitable cells such as pancreatic β-cells, slow metabolic oscillations modulate faster electrical bursting at the membrane along with intracellular calcium (Ca^{2+}) oscillations, jointly shaping insulin secretion patterns [1–3]. Similarly, cyclic adenosine monophosphate oscillations in neural ensembles exhibit a modulatory role, influencing membrane excitability and Ca^{2+} spike timing [4]. At the organ level, the interplay between rhythms becomes even more evident. In the cardiovascular system, respiratory and cardiac oscillations are not only coexistent but also dynamically coupled [5,6], contributing to phenomena such as respiratory sinus arrhythmia [5,7]. In the brain, oscillatory activity spans multiple coexisting frequency bands, which interact across hierarchically organized circuits to support cognitive function, sensory processing, and motor coordination, as demonstrated by electroencephalography (EEG) and other electrophysiological and imaging approaches [8–10]. These examples underscore a central principle in modern biophysics: biological rhythms do not exist in isolation, but rather manifest themselves as intertwined oscillatory processes, whose mutual interactions are essential for physiological function and adaptability.

Understanding such multiscale interactions requires analytical tools that are sensitive to both the time- and frequency-specific nature of signals, a requirement well addressed by wavelet analysis [6,11]. Wavelet analysis offers a powerful framework for decomposing complex signals into their constituent frequency components while retaining information about when in time these components occur [11–14]. Unlike classical Fourier analysis, which assumes signal stationarity and provides only global frequency information, the wavelet analysis enables time-frequency localization, making it ideally suited for biological signals characterized by transient, nonstationary, and multiscale dynamics [12,15]. This property has proven particularly valuable in a variety of biomedical domains. In the cardiovascular system, wavelet analysis has been used to study heart rate variability, allowing for the detection of dynamic shifts in autonomic tone by separating low- and high-frequency components over time [16,17]. In neuroscience, wavelet-based methods have advanced the analysis of EEG data by enabling real-time tracking of frequency-specific brain activity, which is essential for understanding phenomena such as event-related synchronization/desynchronization or cross-frequency coupling [9,18]. At the cellular level, wavelet analysis has facilitated the dissection of cellular dynamics, separating slow oscillatory trends from faster oscillations or rapid spiking events, and revealed condition-dependent modulations of activity in various cellular populations [19,20].

In biomedical systems, complex oscillatory dynamics often arise not only from the interplay between distinct oscillatory subsystems but also from interactions among individual components that are functionally or physically coupled. Consequently, the emergent behavior of the system is frequently shaped by networked interactions, which give rise to collective dynamics. To characterize and study such systems objectively, the field of network science has emerged over the past two decades as a powerful methodological framework [21,22]. In the analysis of empirical data, the concept of functional connectivity has proven particularly effective. This approach treats individual dynamic units as nodes in a network, and defines edges based on the statistical interdependence—most commonly, correlation or coherence—between their activity profiles. The generality of this framework has enabled its application across a wide range of domains, including ecological [22–24], energy [25], and economic systems [26], as well as transportation networks [27]. Within biomedicine, functional connectivity analysis has gained particular prominence. The most well-established examples come from neuroscience, where the principles of functional brain networks [28,29] have matured to the point of clinical application [30,31]. Other notable biomedical applications include the analysis of musculoskeletal coordination networks [32–34], descriptions of inter-organ interactions in physiological networks [35], and the objective mapping of multicellular dynamics across a variety of tissues [36].

Dynamic interactions within such intertwined systems often unfold across multiple temporal scales and frequency bands. This multiscale nature of interdependence motivates the integration of wavelet analysis with functional connectivity, leading to time- and frequency-resolved measures of interaction. Among these, wavelet coherence has emerged as a central metric, quantifying the local correlation between two signals in the joint time-frequency domain. By computing pairwise wavelet coherence between dynamic entities, such as cells, or organ subsystems, researchers can construct frequency-specific functional networks, capturing connectivity patterns that are invisible to purely time- or frequency-domain methods. This naturally leads to multilayer network representations, enabling the study of cross-frequency coupling between oscillatory processes operating on different temporal scales [9,37,38], and the temporal evolution of connectivity patterns [39,40]. In neuroscience, wavelet-based functional connectivity has enabled the investigation of transient interactions across brain regions, facilitating insights into time-resolved network reconfiguration, task-induced synchrony, and cross-frequency coupling [40]. These approaches have proven especially useful in clinical and cognitive contexts, where dynamic reorganization of brain networks is a hallmark of development, learning, and pathology [9,41,42]. Beyond the brain, wavelet-based functional connectivity has also been applied to cellular systems, particularly in neuronal cultures. Studies combining wavelet coherence with time-resolved correlation analyses have demonstrated the ability to track dynamic network reconfiguration during chemically induced activity, as well as to capture frequency-dependent differences in connectivity patterns across experimental conditions [43–45]. These findings illustrate that wavelet-domain approaches are well suited for resolving transient and scale-specific

interactions not only at the organ level, but also within multicellular assemblies.

Modern wavelet theory was laid in the early 1980s, particularly as an alternative to classical Fourier-based spectral analysis. Initial applications were primarily directed toward technical fields such as geophysics [46], image compression (including the JPEG2000 standard) [47,48], signal denoising [49], and numerical modelling [50,51]. At the turn of the millennium, however, wavelet methods began gaining traction in biomedical research, particularly in cardiovascular physiology [15,17,52,53] and neuroscience [6,18,40], where nonstationary and multiscale signal characteristics are the norm rather than the exception. While the theoretical foundations of wavelet analysis have been comprehensively treated in various textbooks and methodological reviews [11,14,54], recent advances in both experimental techniques—such as laser Doppler fluxmetry (LDF) and high-resolution multicellular Ca^{2+} imaging—as well as in conceptual frameworks, notably the integration with network science, have opened new avenues of application. Despite these advances, there remains a lack of integrative overviews that connect core wavelet methodology with emerging biomedical applications and the analysis of functional interactions.

In this review, we address this gap by providing a concise introduction to the core concepts of wavelet analysis and reviewing recent advances in its application to the characterization of complex biological signals. Particular emphasis is placed on the integration of wavelet-based approaches with modern experimental techniques, functional connectivity analysis, and network-based frameworks, which together enable time- and frequency-resolved investigation of coordinated biological dynamics. Beyond surveying individual applications, the central contribution of this review is to show how wavelet-derived representations can be integrated with functional connectivity and multilayer network frameworks, thereby linking local signal dynamics to collective biological organization across temporal scales and levels of biomedical complexity. To demonstrate these concepts explicitly, we examine three representative areas in which wavelet-based methods have shown particular potential: cardiovascular physiology, brain dynamics, and multicellular Ca^{2+} dynamics in pancreatic β-cells. By combining a broader synthesis of the literature with focused examples from these domains, we aim to demonstrate both the methodological versatility of wavelet analysis and its capacity to uncover multiscale organization and functional interactions across different levels of biological complexity.

2. Interpreting multiscale dynamics with wavelet analysis

Biological signals are inherently nonstationary, reflecting the superposition of multiple oscillatory processes whose frequencies and amplitudes evolve over time, often in a context-dependent manner. The coexistence and interaction of physiological processes operating at distinct characteristic time scales give rise to multiscale dynamics, which is expressed in experimentally recorded time series as multiple frequency components whose relative contributions and organization change over time. When signals are recorded simultaneously from spatially distributed cells, regions, or physiological subsystems, their time- and scale-dependent interdependence can additionally reveal patterns of functional organization. A central analytical challenge is therefore not only to determine which frequencies are present, but also when they occur and how they interact, a question that cannot be adequately addressed using conventional approaches such as the Fourier transform, which provide only global frequency information and disregard temporal localization. Wavelet analysis directly addresses this limitation by providing a time-frequency representation of the signal, enabling the identification of transient oscillations and their temporal organization. At the same time, reliable implementation and interpretation require careful consideration of the wavelet choice, sampling rate and accessible frequency range, frequency-band definition, edge effects, and appropriate statistical validation. These methodological considerations are discussed in greater detail in the context of specific applications in the subsequent sections.

The core idea of wavelet analysis is conceptually simple. Instead of representing a signal using infinitely extended sinusoids, as in Fourier analysis, it relies on localized oscillatory functions known as wavelets. A single prototype function (the mother wavelet) is scaled and shifted along the signal, allowing it to probe the data at different temporal positions and frequencies. By correlating the signal with these localized oscillations, we obtain a map of how oscillatory activity evolves over time. Intuitively, this can be understood as a "sliding and zooming" oscillatory probe, where shifting determines when in time a feature occurs, while scaling determines at which frequency it is observed.

Wavelet transforms can be broadly divided into two main classes: the continuous wavelet transform and the discrete wavelet transform, which differ in how the scale and translation parameters are sampled. The continuous wavelet transform evaluates the signal across a continuum of scales and time shifts, producing a highly redundant but detailed time-frequency representation that is particularly well suited for exploratory analysis of complex signals. In contrast, the discrete wavelet transform operates on a discrete set of scales, typically arranged on a dyadic grid, and provides a compact representation that is widely used for signal compression, denoising, and feature extraction [11,12,14]. In the context of physiological time series, where the primary objective is to characterize multiscale oscillations, including transient events and frequency modulation, the continuous wavelet transform is most commonly employed due to its superior time-frequency resolution and interpretability. Formally, the continuous wavelet transform of a signal $x(t)$is defined as [17,55]:

$$W(a,b) = \frac{1}{\sqrt{a}} \int_{-\infty}^{\infty} x(t)\, \psi^{*}\left(\frac{t-b}{a}\right) dt \tag{1}$$

In Eq. (1), t denotes physical time in the units of the experimental recording (seconds in the examples considered below), b specifies the temporal position, and $a > 0$ is the wavelet scale. The argument $\eta = \frac{t-b}{a}$ of the mother wavelet is dimensionless. Each scale can be associated with a corresponding physical frequency based on the central frequency of the selected wavelet; for sampled signals, this

relationship also accounts for the sampling interval. The wavelet transform thus provides a natural mapping between temporal and frequency domains.

The choice of the mother wavelet determines how the signal is analyzed and reflects an inherent trade-off between temporal and frequency resolution: wavelets that are more localized in time provide better temporal precision but poorer frequency resolution, and vice versa. In biomedical applications, commonly used wavelets include the Morlet, Mexican hat, and Gaussian wavelets [11]. Among these, the Morlet wavelet is particularly well suited for oscillatory signals, as it consists of a complex sinusoidal carrier modulated by a Gaussian envelope which ensures simultaneous localization in both time and frequency [56]:

$$\psi_{\text{Morlet}}(\eta) = \pi^{-1/4} e^{-\eta^2/2} e^{2i\pi f_0 \eta} \tag{2}$$

In Eq. (2), η is a dimensionless normalized coordinate and f_0 is the dimensionless central frequency of the mother wavelet. The Gaussian envelope confines the wavelet in time, effectively limiting how far it extends, while the sinusoidal carrier defines a characteristic frequency. As a result, the wavelet transform captures both when an oscillatory component occurs (through temporal localization) and which frequency it corresponds to (through the oscillatory structure). This combination makes the Morlet wavelet particularly effective for analyzing nonstationary oscillatory signals, as it provides a balanced resolution in both domains. Consequently, it is a natural choice for physiological signals, where oscillatory components are both transient and frequency-specific.

To illustrate the principles of wavelet analysis in practice, we consider a synthetic signal composed of multiple oscillatory components with time-varying amplitudes and frequencies (Fig. 1). In the time domain, the signal appears as a complex superposition in which individual components are not readily distinguishable. Such behavior is characteristic of many physiological systems, where processes operating on distinct temporal scales coexist and dynamically modulate one another, including cellular dynamics, neural population activity, and cardiovascular rhythms. The corresponding wavelet transform, shown as a scalogram in Fig. 1, reveals how these components are organized in the time-frequency domain. Distinct oscillatory modes appear as horizontal bands at specific frequency ranges, while their temporal evolution is reflected in changes in power. Variations in band intensity indicate modulation of amplitude or intermittency, whereas curved or shifting structures reveal frequency changes over time. More specifically, the lowest-frequency component forms a broad band that exhibits a gradual decrease in frequency over time, visible as a slight downward shift in the scalogram. At intermediate frequencies, a clearly defined band displays periodic modulation, indicating slow variations in instantaneous frequency. In contrast, the highest-frequency component appears only intermittently, emerging as short-lived bursts that are temporally aligned with the maxima of the underlying slower oscillation. As illustrated in the zoomed segments, fast oscillations manifest as narrow, rapidly varying features, while slower components appear as broader structures extending over longer time intervals. This representation enables the separation of overlapping oscillatory processes and the tracking of their temporal evolution within a unified framework, directly linking signal dynamics to their multiscale organization. In the following sections, we apply this approach to experimental data, where such structure emerges from underlying physiological mechanisms rather than being imposed synthetically.

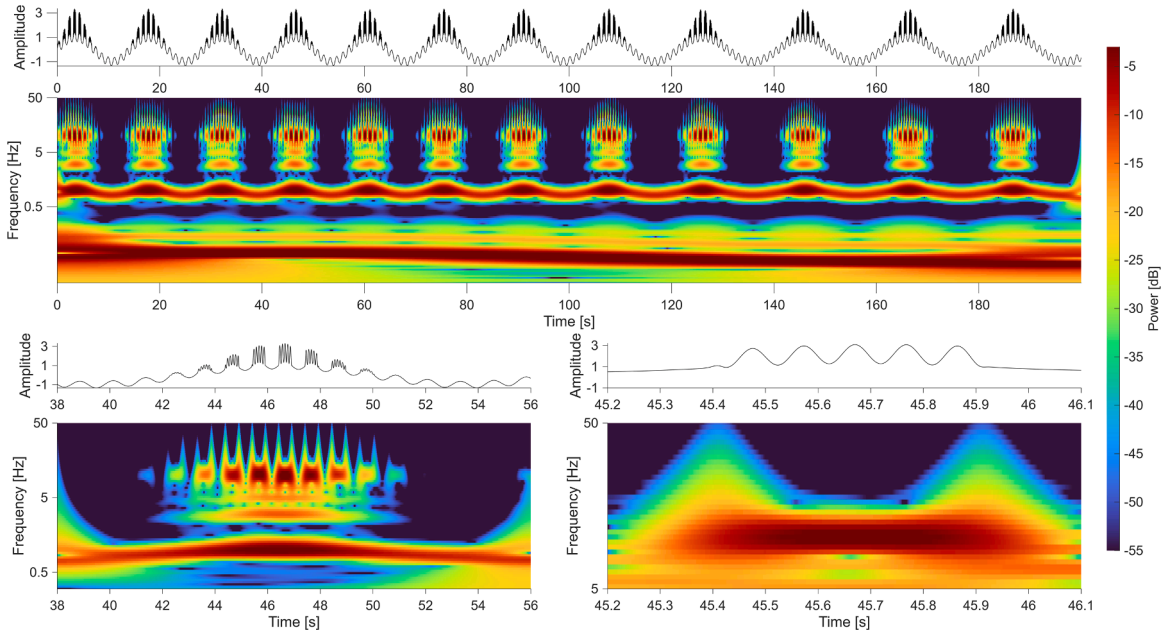

Fig. 1. Continuous wavelet transform of a synthetic multiscale oscillatory signal. The top panels show the full time-domain signal (0–200 s) and its corresponding wavelet power scalogram. The lower panels present a selected segment (38–56 s) and a zoomed interval (45.2–46.1 s), together with their respective scalograms. The decomposition highlights distinct frequency bands and their time-varying modulation across multiple temporal scales.

3. Wavelet approaches to multiscale cardiovascular regulation

The cardiovascular system represents one of the most influential domains for the application of wavelet-based signal analysis in physiology. Although cardiovascular dynamics exhibit pronounced rhythmicity, they are continuously modulated by endogenous regulatory processes and external perturbations, giving rise to transient and nonstationary oscillatory patterns in both cardiac and vascular signals. Wavelet-based approaches are therefore particularly well suited for resolving the time-varying, multiscale organization of cardiovascular regulation. One of the first physiological parameters where the wavelet analysis has been applied to assess the time-frequency distribution was heart rate variability, reflecting modulation of the sinus cardiac rhythm by the autonomic nervous system [57–60]. Application of the wavelet analysis to heart rate variability enabled time-resolved characterization of autonomic cardiovascular regulation by revealing transient changes in low- and high-frequency oscillatory components. This represented one of the first steps toward viewing cardiovascular regulation as a dynamic multiscale process rather than as a collection of isolated components [58,60,61]. More recently, the wavelet-based framework supported a broad range of translational applications, from wavelet-derived heart rate variability indices proposed for cardiovascular risk stratification and prognosis [62–65] to time-frequency-based classification of arrhythmias from electrocardiographic recordings [61] and wavelet-based detection of heart murmurs from phonocardiographic signals [66]. Furthermore, the application of wavelet analysis has expanded beyond electrophysiological signals toward advanced cardiac imaging, including cardiac mesh reconstruction from magnetic resonance imaging [67] and improved strain estimation in three-dimensional echocardiography [68], demonstrating its potential across diverse cardiovascular measurements.

Systemic hemodynamic oscillations generated by cardiac and respiratory activity interact in the microcirculation with locally generated vasomotor rhythms. Microvascular regulation therefore reflects a complex interplay among neurohumoral, metabolic, endothelial, and intrinsic myogenic mechanisms that collectively ensure appropriate tissue perfusion, nutrient delivery, and waste removal. This makes the microcirculation a particularly suitable model system for investigating multiscale cardiovascular regulation using wavelet approaches. Among microvascular beds, the skin microcirculation has been studied most extensively in vivo because it is readily accessible and can serve as a surrogate marker of generalized microvascular function and dysfunction [69,70], thus providing a unique physiological model system for investigating multiscale cardiovascular regulation.

Classical noninvasive approaches for assessing skin microvascular hemodynamics include photoplethysmography and its modifications [71], near-infrared spectroscopy [72], LDF [73], or more advanced laser Doppler imaging techniques [74–76]. These

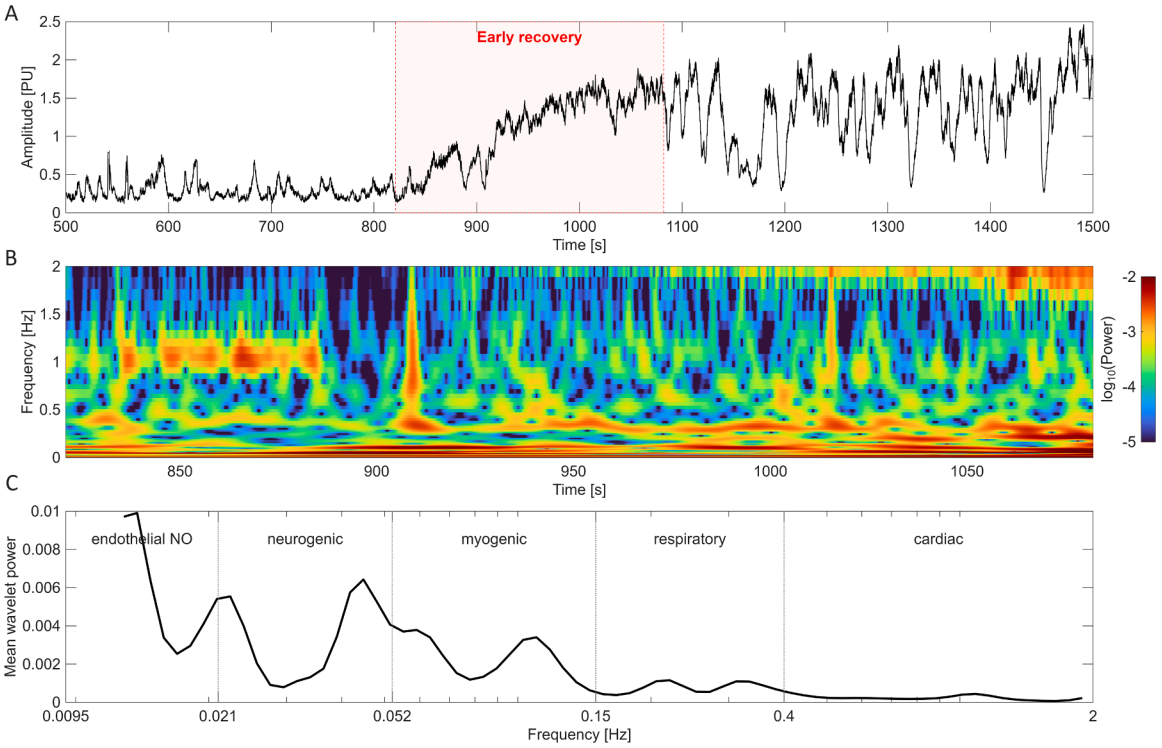

Fig. 2. Representative wavelet-based analysis of a laser Doppler fluxmetry (LDF) signal recorded during graded dynamic exercise. (A) Representative finger pulp LDF signal, with the shaded region indicating the early recovery phase selected for wavelet analysis. (B) Wavelet scalogram of the selected early recovery segment, illustrating the temporal evolution of oscillatory activity across frequencies. (C) Time-averaged wavelet power spectrum of the same segment, showing characteristic frequency ranges commonly interpreted as predominantly reflecting endothelial nitric oxide (NO)-dependent, neurogenic, myogenic, respiratory, and cardiac regulatory activity.

complementary methods provide semi-quantitative, real-time data on skin microcirculatory blood flow and related hemodynamic changes [12,69,75,77]. Despite exhibiting a certain degree of complementarity [78,79], photoplethysmography appears to be too robust to trace the small vessels as it relies on assessment of pulse wave; accordingly, LDF and its up-to-date derivations are best suited to detect the very microcirculation, and especially low-frequency oscillations thereof, attributable to the endothelial component of vascular tone regulation.

Wavelet analysis of LDF signals provides a physiologically interpretable time-frequency representation of microvascular oscillations, allowing transient changes in regulatory activity to be followed over time [12,80,81]. Within a simplified interpretive framework for cutaneous microcirculation, the LDF signal can be decomposed into characteristic frequency ranges commonly interpreted as predominantly reflecting endothelial nitric oxide-dependent (0.0095–0.021 Hz), neurogenic (0.021–0.052 Hz), myogenic (0.052–0.15 Hz), respiratory (0.15–0.4 Hz), and cardiac (0.4–2.0 Hz) regulatory activity [82]. In addition, an even lower-frequency endothelial component (0.005–0.0095 Hz) has been proposed, which may reflect endothelium-dependent regulatory processes mediated by signaling pathways distinct from those associated with the higher endothelial frequency interval [81–83]. However, no individual frequency band can be attributed exclusively to a single physiological mechanism, as multiple regulatory systems are tightly interconnected, and their oscillatory contributions partially overlap. This is particularly evident around 0.1 Hz, a frequency range traditionally associated with sympathetic activity but increasingly recognized to reflect the combined influence of several regulatory processes [84]. Consequently, interpretation based solely on predefined frequency bands remains limited.

Despite these limitations, wavelet analysis has proven to be a highly sensitive tool for detecting subtle changes in microvascular regulation that may remain inconspicuous in raw LDF traces or conventional time-domain measures. As illustrated in Fig. 2, it can be applied to characterize the early recovery phase following exercise, during which the LDF signal exhibits pronounced transient and nonstationary oscillations reflecting the dynamic interplay of multiple regulatory mechanisms. In the associated analysis, early recovery was characterized by an increased contribution of endothelial nitric oxide-dependent activity, likely reflecting enhanced endothelial activation associated with exercise-induced shear stress, together with a transient reduction in the myogenic component, suggesting reduced vascular smooth-muscle activity during this phase [85]. This represents one example of the broad physiological and pathophysiological applications of wavelet analysis in skin microcirculation, spanning studies of endothelial function, ageing, cardiovascular disease, diabetes, thermal regulation, and pharmacological interventions, as reviewed by Kralj and Lenasi [12].

Beyond the decomposition of local oscillatory components, wavelet-based phase and coherence measures can quantify time- and frequency-specific coupling between central cardiovascular rhythms and peripheral microvascular dynamics. Such interactions are altered by ageing and disease, including hypertension, highlighting the value of wavelet approaches for probing integrated cardiovascular regulation [84,86]. Related principles extend naturally to the cerebral circulation, where vascular dynamics are tightly coupled to neuronal activity and shaped by neurovascular coupling as well as by systemic cardiovascular and respiratory influences. The specialized organization of the cerebral microcirculation, including the blood-brain barrier and the close interactions among vascular, glial, and neuronal elements, makes the brain a particularly important setting for studying multiscale hemodynamic regulation. Accordingly, wavelet-based approaches have enabled the investigation of neurovascular interactions by resolving dynamic relationships among cardiovascular, respiratory, and neurophysiological processes across multiple temporal scales. Consequently, they have been widely applied to the study of cerebral blood flow, brain autoregulation, and neurovascular coupling, as well as to elucidate the relationships between arterial blood pressure, local cerebral blood volume, cerebrospinal fluid pulsatility, and other hemodynamic variables [87–89]. For non-invasive human studies, near-infrared spectroscopy provides an accessible window into cortical hemodynamics and oxygenation, whose spontaneous oscillations can be analysed across multiple frequency ranges and related to systemic variables such as arterial blood pressure or transcranial Doppler flow velocity [89,90]. Such analyses have identified altered phase relationships and coherence patterns in pathological conditions, including multiple sclerosis and hypertension [90–93]. Complementary optical approaches combined with wavelet-based time-frequency analysis are also being explored for perioperative monitoring and for characterizing age- and disease-related alterations in cerebral hemodynamics [64,93–95].

An important next step is to regard distributed microvascular recordings not merely as collections of local oscillatory signals, but as dynamically interacting vascular systems. In the renal cortex, high-resolution laser-speckle imaging combined with wavelet analysis has revealed spatially and temporally evolving clusters of synchronized microvessels associated with individual nephrons, demonstrating that renal autoregulation emerges from cooperative dynamics distributed across the nephrovascular network [96,97]. Analogous directions are now becoming feasible in the cerebral circulation, where advances in cortex-wide and microvascular imaging enable simultaneous recordings of blood-flow dynamics across numerous vascular segments and cortical territories. Recent studies have already demonstrated cortex-wide connectivity of rapid blood-flow velocity fluctuations during seizure onset [98], while large-scale optical and ultrasound-based approaches provide multiparametric measurements of vessel diameter, flow velocity, perfusion, and neurovascular responses across the brain [99–101]. Although such data have only rarely been analysed explicitly as scale-specific vascular networks, they provide a natural substrate for wavelet-coherence-based functional mapping and for multilayer representations integrating vascular dynamics with neuronal activity and systemic cardiovascular regulation. When multichannel or imaging-based measurements are available, scale-specific coherence and phase relationships can therefore be used to infer functional vascular networks and relate them to vascular architecture, local tissue demands, and systemic cardiovascular regulation. In this way, wavelet analysis shifts the focus from isolated spectral components to coordinated microvascular dynamics underlying tissue perfusion and organ autoregulation, providing a natural bridge to the functional-connectivity and network frameworks introduced in the following sections.

4. Time-frequency analysis of brain activity using wavelet methods

Whereas the preceding section focused primarily on cardiovascular and hemodynamic signals, recordings of brain activity present the same fundamental analytical challenge in a different physiological context: they are nonstationary, span multiple temporal scales, and reflect interactions among distributed neural populations. EEG, in particular, comprises multiple rhythmic components whose frequency-specific organization provides important information about functional activity across brain regions. These properties have made neuroscience one of the paradigmatic domains for the application of wavelet-based analysis. One of the most direct and effective uses of wavelets in EEG research is detecting and analyzing specific patterns [102–106]. This field leverages the fundamental properties of wavelets and highlights their primary areas of use. Early neurobiological studies employing wavelet transforms focused on characterizing the time-frequency structure of various EEG patterns [107,108]. In subsequent years, more refined techniques were elaborated to quantify statistical properties of non-stationary signals. These include, for example, wavelet entropy, time-varying wavelet coherence, and other related measures [109,110]. Further wavelet-based investigations aimed to identify specific interactions between the cardiovascular system and the central nervous system using EEG and electrocorticography (ECoG) [6,111]. This progression reflects a broader shift from the characterization of transient oscillatory activity toward the investigation of dynamic interactions between distributed brain regions, thereby providing an important conceptual bridge to the functional connectivity approaches discussed in later sections of this review.

Wavelet analysis is particularly well suited for the time-frequency examination of specific forms of rhythmic activity associated with distinct brain functions and behavioral states, such as epileptic episodes, sleep stages, etc. As a result, wavelet-based tools are now widely employed for the automatic detection of oscillatory patterns and various physiological rhythms in prerecorded EEG signals. Simple approaches for automatic pattern recognition in EEG (e.g., threshold-based detection or template matching) often fail to achieve reliable performance. This is primarily due to several challenges: high levels of background noise, the inherent non-stationarity of EEG signals, and/or the strong variability in the time-frequency structure of patterns [112–114]. In contrast, wavelet analysis offers a number of key properties that make it particularly advantageous for automatic EEG processing:

- Time-frequency localization of transient EEG events: Wavelets allow simultaneous localization of signal features in both the time and frequency domains, which is essential for capturing transient oscillatory events.
- Applicability to short EEG epochs: Wavelets can efficiently analyze short segments of data containing only a limited number of oscillatory cycles, which is valuable for detecting brief transient events.
- Adaptability of the analyzing wavelet: The mother wavelet can be selected to match the temporal and spectral characteristics of the EEG pattern of interest, including relatively sharp transient events or more sustained oscillatory rhythms.
- Support for feature extraction in noisy recordings: Wavelet decompositions can facilitate the extraction of informative features, such as band-specific energy or entropy measures, and can support denoising procedures before subsequent detection or classification.

A widely used strategy for the automated processing of prerecorded EEG signals is to estimate wavelet energy within characteristic frequency bands, using either standard or adaptive bases, and subsequently use these features for detection or classification. One of the most actively investigated challenges in modern EEG analysis is the online identification of specific oscillatory patterns [115–118]. Progress in this area is important both for real-time monitoring of human brain activity and for the development of specialized brain-computer interfaces [119–121]. In the context of brain activity monitoring, a particularly important goal is the detection of precursors to epileptic seizures [122–124], which are characterized by the appearance of high-amplitude spike-wave discharges (SWDs) in the EEG. Each SWD consists of a sharp, high-amplitude spike followed by a slower wave component. Seizures associated with absence epilepsy are typically preceded by brief episodes of delta- and theta-range oscillatory activity in the cortex and thalamus. Notably, this specific combination of precursor oscillations is rarely observed during control, non-preictal periods. The presence of such precursor activity indicates that SWDs are not abrupt events, but rather emerge through gradual preictal processes.

Using wavelet-based analytical tools, researchers can identify such coordinated precursor activity within the cortico-thalamocortical network by analyzing multichannel ECoG recordings. In the domain of brain-computer interfaces, wavelets have proven useful across a wide range of tasks, including the automatic detection of SWDs [125]. A fundamental difficulty in this field is that EEG patterns associated with distinct functional or pathological states may exhibit similar overall spectral characteristics. Effective pattern-recognition methods must therefore distinguish not only their frequency content but also their temporal organization and transient structure. Moreover, to be suitable for online EEG analysis, such a tool must also be computationally efficient enough to enable hardware or software implementation. Wavelet-based representations offer a powerful solution to these challenges. For example, wavelet-derived measures can help distinguish brain activity associated with actual motor execution from motor imagery [126]. This capability is important for brain-computer interfaces designed to assist individuals with mobility impairments, as it enables the translation of imagined movements into control commands without requiring real physical movement.

Epilepsy represents one of the most extensively studied forms of pathological brain dynamics. A hallmark of this condition is the hypersynchronization of the thalamocortical network during seizure activity. However, synchronous activity across different areas of the cerebral cortex is not limited to epilepsy but can also occur in normal physiological states (e.g., during cognitive tasks) and may be altered in other neurological and psychiatric conditions [127–129]. To characterize such dynamics, continuous wavelet transform with complex wavelets provides a useful framework for estimating time- and frequency-resolved phase relationships and coherence across multiple EEG or ECoG channels, as it enables the identification of transient intervals and frequency bands in which synchronization is enhanced even in short recordings [18]. Moreover, this approach exhibits considerable robustness against errors in estimating the

characteristic frequencies of the processes under study: a property that is particularly valuable for the automatic processing of neurophysiological signals. It is now well established that rhythmic components in the EEG reflect the synchronized activity of large neuronal populations integrated into functional networks. In this context, wavelet analysis offers additional practical applications. For instance, it can be used to evaluate the effects of pharmacological agents on the time-frequency structure of various EEG patterns, including sleep spindles and oscillations in the 5–9 Hz range, which are distinct from spindle oscillations [122].

More recently, wavelet-based analysis has also been combined with concepts from extreme-event theory to examine the statistical organization of epileptic activity. In WAG/Rij rats, SWDs were associated with a sharp increase in wavelet energy in the dominant 6–9 Hz frequency range and its second harmonic at approximately 12–18 Hz [130]. Within this specific band, the resulting wavelet power transform exhibited properties characteristic of extreme events, whereas no such extreme behavior was observed at other frequencies. Furthermore, in the 6–8 Hz range, wavelet power demonstrated long-range correlations. Their presence is typical of systems operating near a critical point, where even small fluctuations can grow with increasing instability. This phenomenon, termed prebifurcation signal (or noise) amplification, has been revealed in systems of different origin [131–133]. Noise in EEG signals gradually increases prior to seizure onset. Based on this observation, Karpov et al. [134] hypothesized that generalized epileptic seizures in humans represent extreme events arising from instability, accompanied by preictal noise amplification by analogy with that observed in other dynamical systems. Figs. 3A) and 3B) illustrate a representative EEG segment containing an epileptic seizure and its corresponding wavelet scalogram. In Fig. 3B), the solid curve traces the dominant oscillatory component, which exhibits a gradual frequency shift over the course of the seizure. Figs. 3C) and 3D) display the normalized wavelet power during both the seizure episode and the baseline EEG period, along with a comparison of the mean normalized wavelet power values in the 1–5 Hz and 5–10 Hz frequency bands. Finally, Fig. 3E) illustrates a long-term wavelet power time series, which includes extended intervals of background activity punctuated by brief epileptic seizure episodes (highlighted by rectangular frames).

Beyond its utility in pathological brain dynamics, the wavelet transform has also been widely employed in research on cognitive processes [117,135]. For instance, Nikolaev et al. [136] used a wavelet-based correlation method to investigate short-lived interactions between cortical regions during cognitive tasks. Their approach quantified synchronization of EEG activity across short time intervals, on the order of 100 ms, comparable to the duration of individual mental operations. Similarly, continuous wavelet transform of EEG data has also been applied to the study of rapid cognitive processes underlying human face recognition. In one such study by Iakovenko et al. [137], short 800-ms EEG segments were considered following the presentation of emotionally valenced stimuli, specifically angry versus neutral facial expressions. Using the complex Morlet wavelets, cortical activity was analyzed over the 1–30 Hz frequency range to characterize its amplitude dynamics. Statistical analyses focused on alpha- and theta-band components, revealing that interindividual differences in facial-expression perception were associated with wavelet coefficients in these frequency ranges. Changes in alpha and theta activity were most prominent during stimulus perception, whereas emotional responses were more closely associated with theta-band dynamics. These findings illustrate how wavelet analysis can resolve brief, frequency-specific changes in evoked EEG activity and their variability across individuals and task stages. Another promising application of wavelet-based analysis is the study of perceptual decision-making and sustained attention. Behavioral performance during prolonged cognitive tasks fluctuates

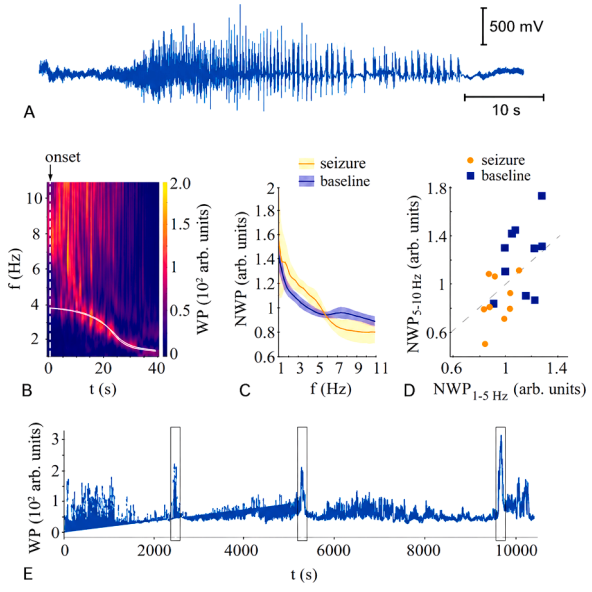

Fig. 3. Wavelet-based analysis of epileptic EEG activity. (A) Representative EEG segment containing an epileptic seizure. (B) Time-frequency representation of wavelet power (WP) during the seizure episode. (C) Normalized wavelet power (NWP) for both the seizure and baseline periods (group mean ± standard error of the mean). (D) Comparison of NWP in the 1–5 Hz and 5–10 Hz frequency bands. Individual subject data are shown as symbols. (E) Time series of WP in the 5–10 Hz band, where sharp peaks correspond to seizure episodes, identified as extreme events. Source: Reproduced from [134] by permission from the American Physical Society.

over time, reflecting changes in the underlying brain state. Wavelet-based time-frequency analysis can characterize these changes by tracking oscillatory activity around stimulus presentation. In a prolonged visual classification task involving ambiguous stimuli, Kuc et al. [138] applied the continuous wavelet transform using complex Morlet wavelets to analyze EEG activity in the 4–40 Hz frequency range, finding a progressive increase in prestimulus 9–11 Hz activity, primarily over right temporal regions. Higher prestimulus power in this range was associated with shorter decision times for low-ambiguity stimuli and fewer perceptual errors for highly ambiguous stimuli. Overall, these findings demonstrate how wavelet-derived spectral features can reveal preparatory brain-state changes relevant for subsequent behavioral performance.

Time-frequency analysis of brain activity is not restricted to electrophysiological recordings such as EEG or ECoG. Functional magnetic resonance imaging (fMRI) provides a complementary perspective by measuring blood oxygenation level-dependent (BOLD) signals, which reflect the slower hemodynamic consequences of underlying neural activity. Accordingly, fMRI captures brain dynamics on substantially longer time scales than electrophysiological methods, predominantly in the range of seconds and low-frequency fluctuations. Nevertheless, BOLD time series are not temporally uniform: they contain task-evoked responses, spontaneous fluctuations, and physiological contributions whose amplitude and spectral composition may vary over the course of a recording. Wavelet-based methods therefore provide a useful framework for characterizing time-varying and scale-specific features of fMRI signals [139]. In resting-state fMRI, particular attention has been devoted to low-frequency BOLD fluctuations, typically below 0.1 Hz, which exhibit reproducible spatial patterns resembling those observed during task-related activation [140–142]. Such slow hemodynamic responses have been detected in brain areas involved in motor, auditory, and visual processing [143–145]. A useful approach for quantifying these responses is time-frequency coherence analysis based on the wavelet transform [146]. This method has been successfully applied to fMRI data in several contexts: to study resting-state network nodes during a working-memory task, to investigate temporal variability in phase relationships between brain areas during a visual task [147], etc. Beyond these applications, wavelets have also proven valuable in cognitive neuroscience for detecting transient responses associated with cognitive processes such as memory retrieval or motor task performance [148]. In clinical diagnostics, wavelet-based approaches can help identify atypical time-frequency signatures characteristic of neurodegenerative diseases [149]. Furthermore, noise filtering with wavelets has proven highly effective at isolating true activation maps from fMRI noise while preserving the temporal dynamics of the underlying signal [150].

Functional near-infrared spectroscopy provides another hemodynamic measure of brain activity that is well suited for wavelet-based analysis. Similar to fMRI, functional near-infrared spectroscopy captures relatively slow changes in cerebral oxygenation rather than fast electrical activity. However, the recorded signals are inherently multicomponent, reflecting not only task-evoked changes in oxygenated and deoxygenated hemoglobin concentrations, but also systemic physiological contributions arising from vascular, respiratory, cardiac, and metabolic processes. Because these components overlap in time and frequency and may vary throughout an experiment, wavelet-based methods provide a useful framework for their time-resolved characterization and separation. Applications of wavelets in functional near-infrared signal processing include the identification of task-related hemodynamic responses and the filtering of physiological noise [151,152]. Wavelet-based approaches can help distinguish very low-frequency fluctuations, myogenic activity, respiration, and cardiac pulsation from cortical hemodynamic responses, thereby facilitating the interpretation of oxygenated and deoxygenated hemoglobin signals. In particular, wavelet coherence can be used to identify time-frequency regions dominated by global physiological contamination, while wavelet-domain filtering can suppress these components before signal reconstruction [152]. More generally, wavelet analysis has been used for denoising, for characterizing the temporal evolution of frequency-specific hemodynamic activity, and for identifying time windows in which oscillatory components become prominent in prefrontal or motor cortical regions during cognitive tasks.

Altogether, wavelet analysis is now an established component of neurophysiological signal processing, particularly in applications where oscillatory activity is transient, nonstationary, or distributed across multiple temporal scales. Its practical use nevertheless requires careful methodological choices, including the selection of the analyzing wavelet, the treatment of edge effects and noise, the definition of relevant frequency ranges, and appropriate statistical validation of time-frequency features. These considerations are particularly important in clinical and biological sciences, where novel mathematical techniques must undergo rigorous testing, careful adaptation, and extensive validation before they can be deemed suitable for practical use. It is important to emphasize that wavelet analysis is not only well suited for neurophysiological signal processing but can be integrated into more advanced algorithms. Such integration can significantly enhance the overall efficiency and effectiveness of data analysis in neurophysiological studies, ultimately facilitating more robust and insightful research outcomes. More broadly, wavelet-based approaches provide a flexible framework for linking time-resolved signal structure to the underlying physiological processes that generate it. Although the examples discussed above focused on large-scale brain recordings, the same core analytical problem recurs in cellular systems, where nonstationary activity spans multiple temporal scales and emerges from interacting ionic, biochemical, and metabolic processes. The following section therefore turns to multiscale cellular dynamics, before subsequent sections extend the analysis from individual signals to functional interactions and network organization.

5. Multiscale cellular oscillations and their time-frequency structure

Oscillatory dynamics are a ubiquitous feature of living cells. Across diverse cell types the intracellular activity rarely unfolds as stationary or single-frequency behavior. Instead, cellular signals emerge from nested feedback loops operating on distinct temporal scales, where fast ionic processes, intermediate biochemical pathways, and slower metabolic or gene-regulatory mechanisms interact nonlinearly. Such multilevel organization gives rise to multiscale oscillatory dynamics in which oscillations of different characteristic frequencies coexist, modulate one another, or become transiently synchronized. Because of this inherent nonstationarity, wavelet-based approaches have increasingly been employed to investigate biological signals ranging from molecular data to intracellular

dynamics. Early applications include the analysis of ion-channel recordings, genomic sequences, protein structural profiles, and gene-expression dynamics, where wavelet transforms enable the detection of multiscale patterns and transient features in biological data [55].

Wavelet analysis has been extensively applied in neuronal contexts, where the combination of fast electrical dynamics and slower modulatory processes naturally gives rise to cross-scale interactions. In intracellular recordings from single neurons, continuous wavelet transform-based approaches have been used to characterize membrane potential oscillations, particularly in the gamma band, and to quantify their transient and nonstationary nature. For example, wavelet spectrograms derived from intracellular recordings reveal that neuronal oscillations often occur as short-lived bouts rather than sustained rhythms, with phase-locking and coherence emerging transiently during these events [153]. Moreover, wavelet-based phase extraction enables the quantification of cross-frequency coupling, such as delta-beta interactions, where beta-band power is modulated as a function of the phase of slower delta oscillations [154]. In addition, wavelet-based approaches have been applied to study intracellular Ca^{2+} dynamics in neurons, revealing spatial heterogeneity of oscillatory activity across subcellular compartments [155]. Beyond neurons, similar approaches have been used to investigate cellular dynamics in astrocytes in vitro and in vivo, demonstrating that astrocytic Ca^{2+} activity exhibits distinct temporal dynamics compared to neuronal signals, including delayed and spatially propagating responses that reflect intracellular integration mechanisms rather than direct coupling to neuronal firing [156,157]. In parallel, wavelet-based approaches have been used to characterize the temporal structure of intracellular Ca^{2+} signaling in neurons, enabling the detection of spontaneous transient events. For example, in gonadotropin-releasing hormone neurons, wavelet-based denoising and event detection uncovered intrinsic, episodic Ca^{2+} transients arising from intracellular store-dependent mechanisms [157,158]. Such analyses further reveal that neuronal intracellular dynamics are inherently multicomponent and temporally structured, involving interactions across multiple frequency bands. For instance, double-wavelet analysis of neuronal signals demonstrates the presence of distinct frequency components and their mutual interactions through frequency and amplitude modulation, reflecting coordinated regulatory processes across different temporal scales [159].

Beyond neuronal systems, wavelet-based methods have been widely applied to other cell types, particularly in the analysis of intracellular Ca^{2+} signaling dynamics. For example, in cultured cell lines such as HEK-293 cells, wavelet analysis of fluorescence

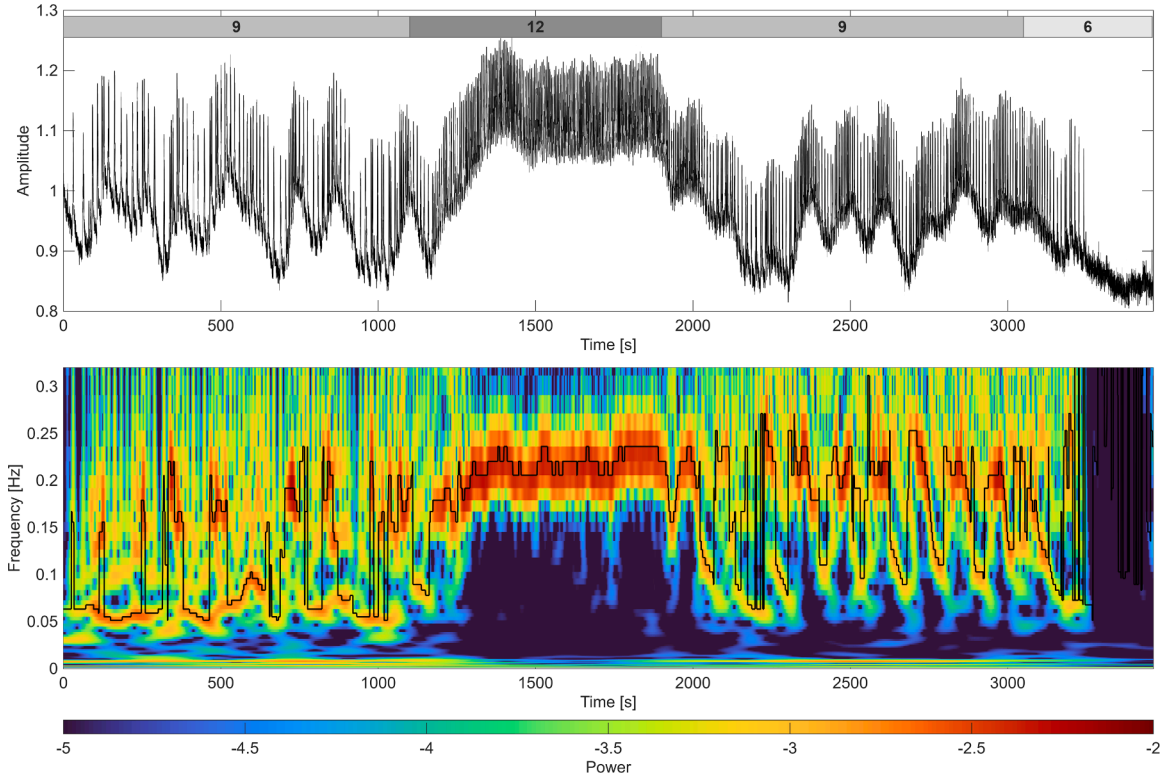

Fig. 4. Multiscale oscillatory dynamics of β-cell calcium (Ca^{2+}) activity revealed by wavelet analysis. Top: Average intracellular Ca^{2+} signal across cells in a pancreatic islet during a glucose stimulation protocol (9–12–9–6 mM). The signal exhibits nested oscillations, where faster calcium-related oscillations are modulated by a slower component associated with metabolic activity. Bottom: Continuous wavelet transform of the same signal shown as a log-power scalogram, illustrating the temporal evolution of spectral power across frequencies. The logarithmic scaling enhances the visibility of both strong and weak oscillatory components by compressing the dynamic range of the wavelet power. Warmer colors indicate higher power, and the black ridge marks the dominant instantaneous frequency. The analysis highlights the multiscale structure of β-cell activity and illustrates how wavelet analysis captures time-varying oscillatory dynamics.

recordings has enabled time-resolved quantification of Ca^{2+} oscillation frequencies and their modulation by extracellular conditions, highlighting the advantages of wavelet approaches for analyzing inherently nonstationary intracellular signals [19]. In immune cells, wavelet-based methods have further been used to characterize the temporal structure of Ca^{2+} signaling at the single-cell level. In T lymphocytes, wavelet-based detection of oscillatory events revealed heterogeneous Ca^{2+} flux patterns, where the frequency of oscillations correlates with the strength of receptor stimulation, enabling functional discrimination of activation states based on intracellular dynamics [160]. In addition, wavelet-based approaches have also been applied to electrophysiological recordings in endocrine cells, where stationary wavelet transforms enable real-time denoising and detection of low-amplitude electrical activity in pancreatic islet cells recorded with multi-electrode arrays [161].

Finally, wavelet-based approaches have proven particularly powerful in the study of metabolic and mitochondrial dynamics, where oscillations occur on slower timescales and often involve transitions between distinct dynamical regimes. In single cells, using combined continuous and discrete wavelet transform has enabled the identification of frequency components, time-localized transitions, and distinct dynamical regimes of mitochondrial membrane potential oscillations [162]. At a finer scale, wavelet analysis has revealed that individual mitochondria in cardiac myocytes exhibit heterogeneous, time-dependent oscillatory dynamics, with frequencies that vary over time [163]. Similarly, in metabolic oscillations measured through reduced nicotinamide adenine dinucleotide autofluorescence, wavelet ridge extraction has enabled the reconstruction of instantaneous phase and frequency, providing insight into the dynamical stability and perturbation resilience of intracellular biochemical oscillators [164].

This capacity to resolve nonstationary dynamics across temporal scales makes wavelet analysis particularly well suited for cellular systems in which electrical, Ca^{2+}, and metabolic oscillations coexist. Pancreatic β-cells represent a prominent example of such multiscale organization. In response to stimulatory glucose, β-cells generate rhythmic electrical bursting accompanied by oscillations in intracellular Ca^{2+} concentration and metabolic activity, which together shape pulsatile insulin secretion [3,165–167]. These dynamics unfold across nested temporal scales. At the slower timescale (periods of several minutes), oscillations are closely associated with rhythmic variations in metabolic fluxes, particularly within glycolysis and mitochondrial pathways, which modulate the adenosine triphosphate/adenosine diphosphate (ATP/ADP) ratio and thereby regulate ATP-sensitive potassium channel activity [1,168,169]. Superimposed on this slow component are faster bursting oscillations (periods of seconds to tens of seconds), driven by membrane depolarization and Ca^{2+} influx through voltage-dependent Ca^{2+} channels. These fast oscillations primarily arise from nonlinear feedback loops in which Ca^{2+} both activates Ca^{2+}-dependent potassium channels and influences metabolic processes via ATP consumption and mitochondrial regulation [3,168,170]. Simplistic as well as contemporary integrative models, such as the Dual Oscillator and Integrated Oscillator frameworks, demonstrate that electrical and metabolic subsystems do not operate independently but instead form a symbiotic dynamical unit, where either subsystem can dominate depending on physiological conditions [1,2,168]. The resulting activity therefore reflects a hierarchy of coupled feedback mechanisms linking metabolism, membrane excitability, and Ca^{2+} handling,

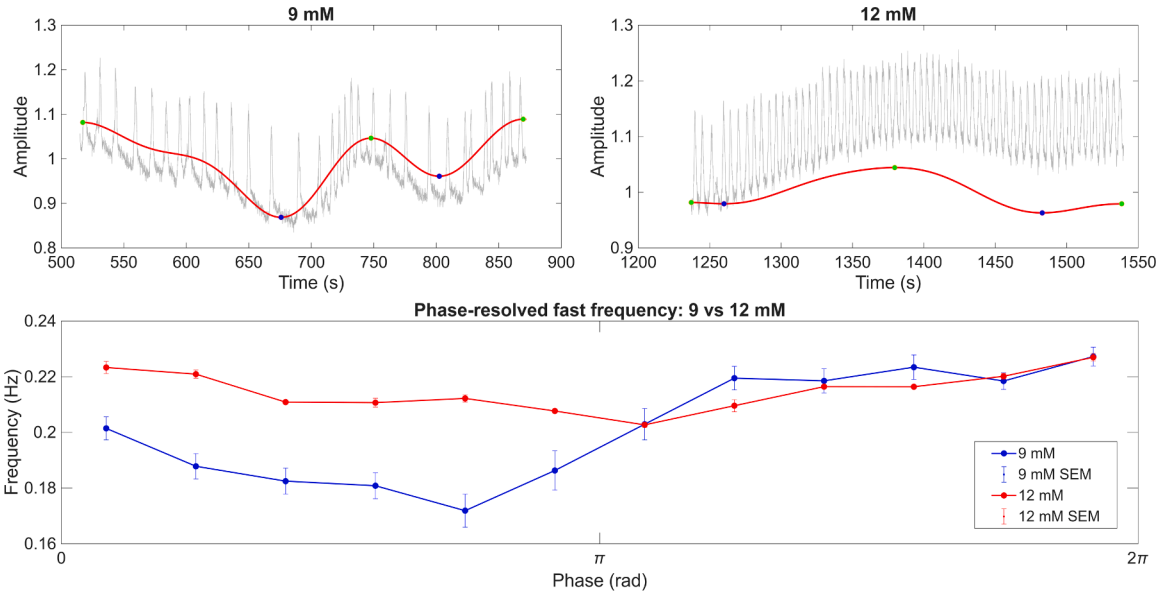

Fig. 5. Phase-resolved Ca^{2+} fast oscillation frequency at different glucose concentrations. Top panels show representative Ca^{2+} traces used to define the slow phase. The left panel corresponds to the 9 mM glucose condition, where slow oscillations are clearly present, while the right panel shows the 12 mM glucose condition, where slow oscillations are reduced. The bottom panel shows the average fast oscillation frequency as a function of the phase of the slow Ca^{2+} oscillation (0 = slow maximum, π = minimum, 2π = next maximum). The slow cycle was divided into 12 phase bins, and the dominant fast frequency (ridge frequency) was averaged across cells (mean ± standard error of the mean). Fast Ca^{2+} oscillation frequency showed pronounced phase-dependent modulation at 9 mM glucose, with the lowest frequencies near phase π and the highest frequencies near 0 and 2π. The same trend was markedly attenuated at 12 mM glucose, indicating weaker modulation of fast activity by the slow oscillatory component under high stimulation.

rendering β-cells a canonical example of multiscale cellular oscillations.

From a signal processing perspective, such activity can be viewed as a multiscale time series composed of fast electrical and slower metabolic oscillations that are intertwined. Wavelet analysis provides a natural framework for investigating such multiscale dynamics, as it enables decomposition of the signal into time-resolved frequency components corresponding to the underlying oscillatory processes. This allows identification of dominant oscillatory modes and their temporal variability under different physiological conditions. An illustrative example of this behavior is shown in Fig. 4, where the average intracellular Ca^{2+} signal, obtained using multicellular confocal Ca^{2+} imaging, is recorded from β-cells during a glucose stimulation protocol (9 → 12 → 9 → 6 mM), with 9 mM representing a physiological stimulatory condition, 12 mM an elevated stimulatory condition, and 6 mM a substimulatory regime. Based on the recorded signal shown in the top panel, clear qualitative differences between dynamical regimes can be identified. During physiological stimulation at 9 mM glucose, the activity exhibits pronounced slow oscillations with superimposed fast components whose occurrence and temporal organization vary over time. Increasing glucose to 12 mM shifts the response toward a more sustained activity pattern, characterized by diminished slow modulation and more regularly recurring fast oscillations. Importantly, the fast activity appears to be organized by the slower oscillatory component, suggesting an intrinsic coupling between the two temporal scales.

This multiscale organization becomes particularly evident in the time-frequency representation obtained via the continuous wavelet transform. The corresponding scalogram in the lower panel reveals a distinct low-frequency band (≈0.01–0.025 Hz) during 9 mM glucose, which becomes markedly attenuated during the high-glucose phase. At the same time, the fast component exhibits pronounced temporal variability in the physiological-stimulation regime, with frequencies dynamically shifting between approximately 0.07 and 0.22 Hz, whereas under 12 mM glucose it becomes more confined and stable, predominantly within the 0.16–0.22 Hz range. Furthermore, the temporal evolution of spectral power suggests that fast oscillations are strongly modulated by the phase of the slow component, an effect that will be examined in more detail in continuation.

To further characterize the interaction between the slow and fast components, we systematically examined the relationship between the phase of the slow, metabolically driven oscillations and the instantaneous frequency of the electrically driven fast component, separately for normal (9 mM) and high (12 mM) stimulatory glucose conditions. The slow component of the average signal was first extracted using inverse wavelet transform within a low-frequency band, and its phase was defined based on successive maxima and minima, mapping each oscillatory cycle to the interval [0, 2π]. The signal was then partitioned into twelve discrete phase intervals. For each cell, the continuous wavelet transform was computed, and the dominant frequency of the fast oscillatory component was determined at each time point by tracking the ridge of maximal wavelet power within a predefined frequency band. These instantaneous frequencies were then averaged within each phase interval of the slow oscillation to obtain the phase dependence of the mean fast oscillation frequency.

The results are presented in Fig. 5. The representative Ca^{2+} traces in the top panels illustrate the differences in slow oscillatory dynamics between the two glucose conditions. At 9 mM glucose, pronounced slow oscillations are clearly visible, with distinct minima

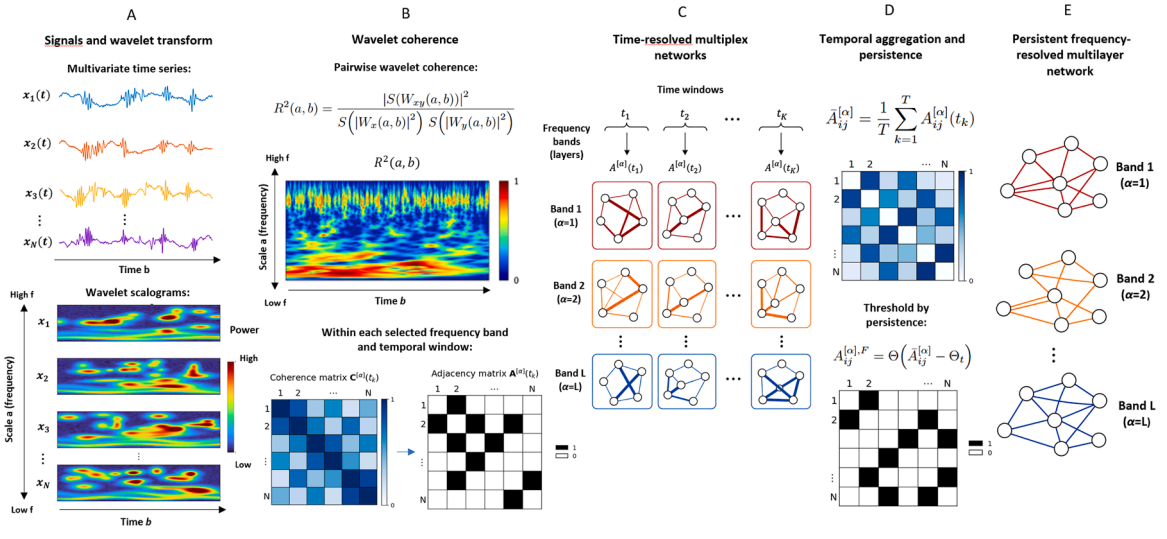

Fig. 6. Schematic workflow for constructing frequency-resolved functional connectivity and multilayer network representations from multivariate time series. (A) Individual signals $x_i(t)$ are decomposed using the continuous wavelet transform to obtain their time-frequency representations. (B) Pairwise wavelet coherence is calculated and evaluated within selected frequency bands α and temporal windows t_k, yielding band- and time-specific coherence matrices $C^{[\alpha]}(t_k)$, which are thresholded to obtain adjacency matrices $A^{[\alpha]}(t_k)$. (C) These matrices define time-resolved functional networks for each frequency band. (D) Temporal aggregation quantifies the persistence of individual connections across successive time windows, and a persistence threshold Θ_t is applied to retain recurrent links. (E) The resulting persistent frequency-specific networks constitute the layers of a multilayer representation, in which corresponding nodes represent the same signal source across frequency bands. Interlayer identity links are omitted for clarity.

and maxima that modulate the fast-spiking activity. In contrast, at 12 mM glucose, the slow component is reduced in amplitude, and the signal appears more plateau-like, indicating weaker slow modulation despite persistent fast oscillations. Consistent with these observations, the phase-resolved analysis (bottom panel) reveals a pronounced phase-dependent modulation of fast dynamics under normal stimulatory conditions (9 mM glucose). The fast oscillation frequency is lowest near the midpoint of the slow cycle (around phase π) and increases toward the maxima (phases near 0 and 2π). In contrast, under high stimulation (12 mM glucose), this modulation is markedly reduced and persists only to a limited extent. Notably, the maximal fast oscillation frequencies are comparable in both conditions, suggesting that glucose primarily affects the depth of modulation rather than the upper frequency bound of the fast component. This behavior is consistent with progressive recruitment and saturation of β-cell electrical activity at higher glucose levels, where cells operate closer to a sustained depolarized plateau and the influence of slower metabolic oscillations becomes less effective in modulating fast dynamics [171].

6. Wavelet-based functional connectivity and multilayer network representations

Despite their different physiological origins and levels of organization, the cardiovascular, neural, and cellular examples discussed above reveal the same fundamental analytical challenge: biological signals are inherently nonstationary, span multiple temporal scales, and reflect interactions among multiple components. Building on the time-frequency decomposition framework introduced above, wavelet analysis can be extended from individual experimental time series to multivariate recordings obtained simultaneously from multiple cells, brain regions, or physiological subsystems. By quantifying their interdependence at distinct temporal scales, it provides a natural basis for constructing functional connectivity patterns that are explicitly scale-resolved. In contrast to conventional approaches, where functional relationships are inferred from raw or band-pass filtered signals, the wavelet transform enables the isolation of interactions that are specific to distinct frequency scales, thereby providing a principled route toward disentangling multiscale coordination mechanisms. In this context, functional connectivity can be derived by quantifying the statistical interdependence between pairs of signals in the wavelet domain. More specifically, for each pair of signals, one can compute measures such as wavelet coherence, phase-locking value, or amplitude correlation within a selected frequency band. This yields a scale-specific connectivity representation, in which links reflect coordinated dynamics at a given temporal scale rather than across the entire signal. Such an approach is particularly advantageous in physiological systems, where multiple oscillatory processes coexist and interact, often in a scale-dependent manner [35,171,172].

In the following, we outline the methodological principles underlying these approaches, following the workflow illustrated in Fig. 6. Functional connectivity between signals can be quantified using wavelet coherence, which provides a normalized measure of localized correlation in the time-frequency domain. For two signals $x(t)$ and $y(t)$, the squared wavelet coherence is defined as

$$R^2(a,b) = \frac{\left|S\left(W_{xy}(a,b)\right)\right|^2}{S\left(\left|W_x(a,b)\right|^2\right) S\left(\left|W_y(a,b)\right|^2\right)} \tag{3}$$

where $W_x(a,b)$ *and* $W_y(a,b)$ denote the continuous wavelet transforms of the two signals, $W_{xy}(a,b) = W_x(a,b)W_y^*(a,b)$ is the cross-wavelet transform, and $S(\cdot)$ represents a smoothing operator in both time and scale. This normalization in Eq. (3) ensures that $0 \leq R^2(a,b) \leq 1$, providing a measure of the strength of coupling between signals at a given scale a and time b. For multivariate recordings, wavelet coherence is evaluated for every pair of signals. Subsequently, for each predefined frequency band α, the corresponding coherence values are assembled to form a coherence matrix $C^{[\alpha]}$, whose elements $C_{ij}^{[\alpha]}$ quantify the interaction strength between dynamical units.

Once pairwise connectivity measures are computed within predefined frequency bands, functional networks can be constructed by assigning nodes to individual dynamical elements and edges based on the strength of wavelet coherence. Each frequency band therefore gives rise to a separate functional connectivity matrix, which naturally serves as the basis for constructing a corresponding network layer. A key conceptual step is to recognize that different frequency bands generally encode distinct interaction mechanisms. Rather than aggregating these into a single network, it is therefore more appropriate to represent the system as a multiplex network, in which each layer corresponds to a specific frequency range. Formally, this yields a set of adjacency matrices

$$\{A^{[\alpha]}\},\ \alpha = 1,\ldots,L \tag{4}$$

where each matrix represents the frequency-specific functional connectivity network associated with a selected frequency band. In physiological systems, this is particularly relevant, as different oscillatory components may reflect distinct coupling mechanisms or modes of communication. Beyond the separate characterization of individual layers, embedding these networks within a multiplex framework enables the assessment of interlayer relationships, including the extent to which functional connections, node roles, or community structure are conserved or reorganized across frequency bands. This provides a principled way to examine whether collective organization is shared across dynamical scales or instead remains frequency specific, an issue that will be addressed further in the following sections.

An additional layer of complexity arises from the fact that functional connectivity is inherently time dependent. Wavelet coherence already provides a time-resolved estimate of interactions, which can be leveraged to construct temporal networks by evaluating connectivity within discrete, typically overlapping temporal windows. Combining this with the frequency-resolved framework leads to a two-dimensional multilayer structure, where one dimension corresponds to frequency layers (multiplex structure), and the other

corresponds to time layers (temporal evolution). This results in a set of adjacency matrices $A^{[\alpha]}(t_k)$ where α indexes frequency bands, t_k denotes the k-th temporal window along the physical time axis of the recording, and k is a dimensionless index. Each adjacency matrix represents a network snapshot capturing the interaction structure between dynamical units within the corresponding time window. Conceptually, this can be viewed as a multiplex temporal network, or equivalently, a temporal sequence of multiplex networks.

While such temporal representations provide detailed insight into the dynamics of interactions, they are often accompanied by substantial variability, as transient or noise-driven connections may appear intermittently. To extract the most robust features of the interaction structure, it is therefore useful to construct an aggregated or time-averaged network that emphasizes only the most persistent connections. This can be achieved by evaluating the temporal consistency of links across the sequence of adjacency matrices. Specifically, one may define an aggregated adjacency matrix as

$$\overline{A}_{ij}^{[\alpha]} = \frac{1}{T}\sum_{k=1}^{T} A_{ij}^{[\alpha]}(t_k) \tag{5}$$

which reflects the average strength (or presence) of interaction between nodes i and j over the observed time interval.

If the adjacency matrices are binarized (e.g., via within-window thresholding that preserves a fixed proportion of strongest connections), Eq. (5) becomes equivalent to measuring the fraction of temporal windows in which a given connection is present, i.e., its persistence, thereby capturing the temporal stability of interactions rather than their average magnitude. In this case, $\overline{A}_{ij}^{[\alpha]}$ directly represents the persistence of connections. This persistence-based representation can then be thresholded to retain only those connections that remain consistently present across time, i.e.,

$$A_{ij}^{[\alpha],\,\mathrm{F}} = \Theta\left(\overline{A}_{ij}^{[\alpha]} - \Theta_{\mathrm{t}}\right) \tag{6}$$

where $\Theta(\cdot)$ is a thresholding operator and Θ_{t} defines the minimal persistence required for a link to be retained. This procedure suppresses transient interactions and isolates the stable backbone of functional connectivity. In the wavelet domain, the resulting networks capture sustained coordination within specific frequency bands and thus provide a compact description of long-term organization. Across bands, this naturally yields a multilayer representation of temporally robust connectivity, emphasizing that functionally relevant interactions are defined not only by their strength, but also by their persistence. This formulation provides a practical and robust approximation of multiscale functional connectivity in empirical data.

While wavelet coherence represents one of the most widely adopted approaches for constructing functional connectivity networks [173], owing to its ability to capture localized, frequency-specific correlations in nonstationary signals, a range of alternative measures can also be employed. For instance, wavelet phase synchrony focuses on phase relationships and is particularly suitable in regimes where interactions are dominated by phase locking rather than amplitude co-variation [174]. In contrast, amplitude-based measures in the wavelet domain, such as cross-wavelet power, emphasize similarities in signal intensity within selected frequency ranges, which may be more appropriate when signal intensity fluctuations carry functional relevance [173,175]. More generally, similarity measures defined directly between scalograms offer additional flexibility in capturing complex interdependencies across scales. However, as a comprehensive comparison of these approaches lies beyond the scope of this review, we focus on wavelet coherence as a representative and well-established framework for constructing scale-resolved functional networks that balances interpretability with sensitivity to localized, scale-specific interactions.

7. Wavelet-based functional connectivity and brain network organization

Among the most prominent applications of wavelet-based connectivity analysis is the study of brain networks reconstructed from empirical recordings. Functional connectivity refers to statistical interdependence between temporally evolving activity signals recorded from distinct brain regions, recording sites, or source-reconstructed neuronal populations, without necessarily implying a direct anatomical connection or causal interaction. In the resulting data-derived functional networks, these neural units are represented as nodes, whereas edges quantify the strength of their statistical relationships within a specified time interval and frequency range. This distinguishes functional connectivity from structural connectivity, for which edges correspond to physical anatomical pathways, such as axonal projections of white matter. At the macroscopic level, the brain comprises several hundred distinct regions connected by numerous such projections, together forming the structural brain connectome [176]. Although this anatomical architecture constrains the possible routes of neural communication, functional connectivity is dynamic and may reorganize across behavioral states, cognitive tasks, and pathological conditions. By enabling time-resolved and frequency-specific assessment of these relationships, wavelet methods are particularly well suited for capturing the dynamic and multiscale organization of neural interactions.

This network perspective is motivated by the recognition that brain functions do not arise solely from isolated regions or individual pathways, but from coordinated interactions within distributed neural systems [28,29]. Despite considerable advances in molecular neurobiology, genetics, and neuroimaging, the principles through which neuronal activity becomes organized across cellular-network, systems, and functional levels remain incompletely understood. In particular, it remains unclear how coordinated activity within distributed brain networks gives rise to functions ranging from motor control and sensorimotor transformations to learning, memory, and consciousness. Data-derived functional networks and theoretical neuronal-network models provide complementary perspectives on these questions. Whereas functional networks characterize patterns of statistical coordination observed in experimental recordings,

theoretical models explicitly prescribe the dynamics of neuronal units and their coupling, thereby allowing researchers to test how cellular excitability, synaptic interactions, excitation-inhibition balance, network topology, and anatomical connectivity generate collective oscillations and scale-specific patterns of coordination. Such models can therefore provide mechanistic interpretations of empirically observed functional-network organization and help examine how this organization may be altered in neurological and neuropsychiatric disorders [177–179]. Although the present Review focuses primarily on functional networks inferred from recorded neural activity, theoretical modeling represents an important complementary framework for understanding the mechanisms underlying their emergence and reorganization.

Bridging the gap between macroscopic recordings, such as EEG and fMRI, and the underlying cellular and network mechanisms requires a framework that relates measurable activity to coordinated dynamics across multiple scales. Rhythmic brain activity provides such a framework, as oscillations emerge from interacting neuronal populations and contribute to functional organization from the cellular to the systems level [8,180]. To explain the rich functional versatility of the brain in the context of a relatively fixed connectome structure, neuroscientists are increasingly focusing on the topology of functional connectivity. These connections are dynamically formed and reconfigured between different brain regions during various cognitive tasks [181,182], sensory processing [183], working memory [184], and even in the resting state [185]. It should be noted, however, that while a statistical relationship between two brain regions is generally interpreted as evidence of functional connectivity, it does not necessarily imply causality [186]. Functional connectivity exhibits non-stationarity, being subject to continual modulation by factors such as sensory stimulation [187], fatigue [188], and cognitive task context [189]. The relevant temporal scale depends on the recording modality: electrophysiological signals can reveal subsecond changes in coordination, whereas fMRI captures slower fluctuations constrained by the temporal properties of the hemodynamic response. This time-varying and frequency-dependent organization motivates the use of wavelet-based approaches, which can quantify functional interactions without averaging over the full duration of a recording [39,190,191].

Building on the methodological framework introduced in Section 6, wavelet-derived functional brain networks are constructed by first decomposing EEG, magnetoencephalography, or fMRI signals into scale- or frequency-specific components and then quantifying statistical dependencies between pairs of regions, sensors, or source-reconstructed signals. Depending on the selected wavelet approach, these dependencies may be quantified either as time-frequency-localized measures, such as wavelet coherence, or as frequency-specific correlations between wavelet-derived signal components. The resulting connectivity matrices can subsequently be thresholded and examined using graph-theoretical measures, thereby linking scale-resolved interactions to network topology. A number of methodological considerations accompany this procedure. Wavelet decomposition transforms brain signals (e.g., EEG signals, fMRI BOLD signals) into time series that capture neurophysiological activity in distinct frequency bands and can be combined with denoising procedures when appropriate [141,192]. However, the resulting connectivity estimates derived from signals remain sensitive to the choice of wavelet transform, filter, scale range, preprocessing strategy, and network-construction procedure. The work by Zhang et al. [193] provided practical guidance on these issues by comparing wavelet methods, filter families and lengths. This work specifically discussed the merits of the maximal overlap discrete wavelet transform and showed that wavelet length strongly influences graph metrics and the sensitivity to differences between groups. This factor affects the estimated graph metrics to a greater extent than the specific wavelet type. A moderate wavelet length is likely optimal, as it combines the benefits of longer wavelets without suffering from their inherent limitations.

One of the earliest applications of wavelets to the construction of functional brain networks was reported by Achard et al. [141]. The authors applied the discrete wavelet transform to resting-state fMRI time series from healthy subjects, producing frequency-dependent correlation matrices among 90 cortical and subcortical regions. Following thresholding, the resulting networks exhibited small-world topology, with particularly pronounced effects in the 0.03–0.06 Hz low-frequency band. The wavelet domain offers a transform space particularly appropriate for the investigation of multiscale systems, given that the wavelet basis set is formed through a self-similar rescaling of a kernel that is delimited in both time and frequency. For example, Billings et al. [194] applied wavelet transforms to assess fluctuations in BOLD-fMRI connectivity as a function of wavelet spectral scale in healthy volunteers at rest. Information-theoretic criteria served to quantify relatedness among spectrally delimited functional connectivity graphs. Voxel-wise comparisons of graph structures across spectral bands illustrated the emergence of preferential functional networks. More recently, Ding et al. [195] proposed a frequency self-adaptive model leveraging wavelet transform that identifies optimally correlated frequency combinations, allowing functional brain networks to be constructed with varying frequency response characteristics. This work was the first attempt to study whether particular brain regions show heightened frequency responses depending on the frequency band under consideration. By pooling different frequency bands from fMRI signals, the authors generated a correlation matrix that incorporates the best-matching frequency combinations, revealing detailed cross-frequency connectivity patterns and interactions. Although this approach does not by itself constitute a formal multilayer network model, it illustrates the growing move beyond fixed, independently analyzed frequency bands toward more adaptive representations of multiscale brain connectivity.

It should be emphasized that the selected frequency range affects network topology, and distinct frequency bands may offer varying degrees of diagnostic or task-relevant information pertaining to different cognitive and clinical states. In an early demonstration of frequency-specific functional networks, Bassett et al. [196] demonstrated that brain networks exhibited a scale-invariant structure and a small-world organization across the 2–37.5 Hz range. During a simple motor task, global topological and dynamical parameters were broadly preserved, whereas additional long-range connectivity emerged in the beta and gamma frequency bands. These observations suggested that scale-invariant small-world topology may contribute to the temporal integration of information distributed across frequency-encoded channels, while allowing spatial reconfiguration during changing cognitive or behavioral states.

The increasing recognition that brain organization varies across frequency, time, and spatial scale has motivated the development of multiscale and multilayer network approaches [29,197,198]. Frequency-specific networks constructed independently within separate bands provide a scale-resolved description of functional organization. A multiplex or multilayer representation extends this

framework by explicitly modelling relationships between network layers, which may represent frequency bands, temporal windows, modalities, or their combinations. In a multiplex network, interlayer links commonly connect replicas of the same brain region across different frequency layers, whereas a more general multilayer framework can additionally accommodate cross-frequency interactions between different regions [199]. Such representations can therefore preserve information that would be lost when frequency-specific networks are analyzed separately or aggregated into a single connectivity matrix. For example, De Domenico [200] demonstrated that different frequency bands carry distinct topological information and that multiplex analysis can identify hub regions not apparent in single-band network representations. More generally, multiscale modelling frameworks have emphasized that neural activity at a given level reflects both local interactions and constraints imposed by processes operating at other scales [201]. Recent applications

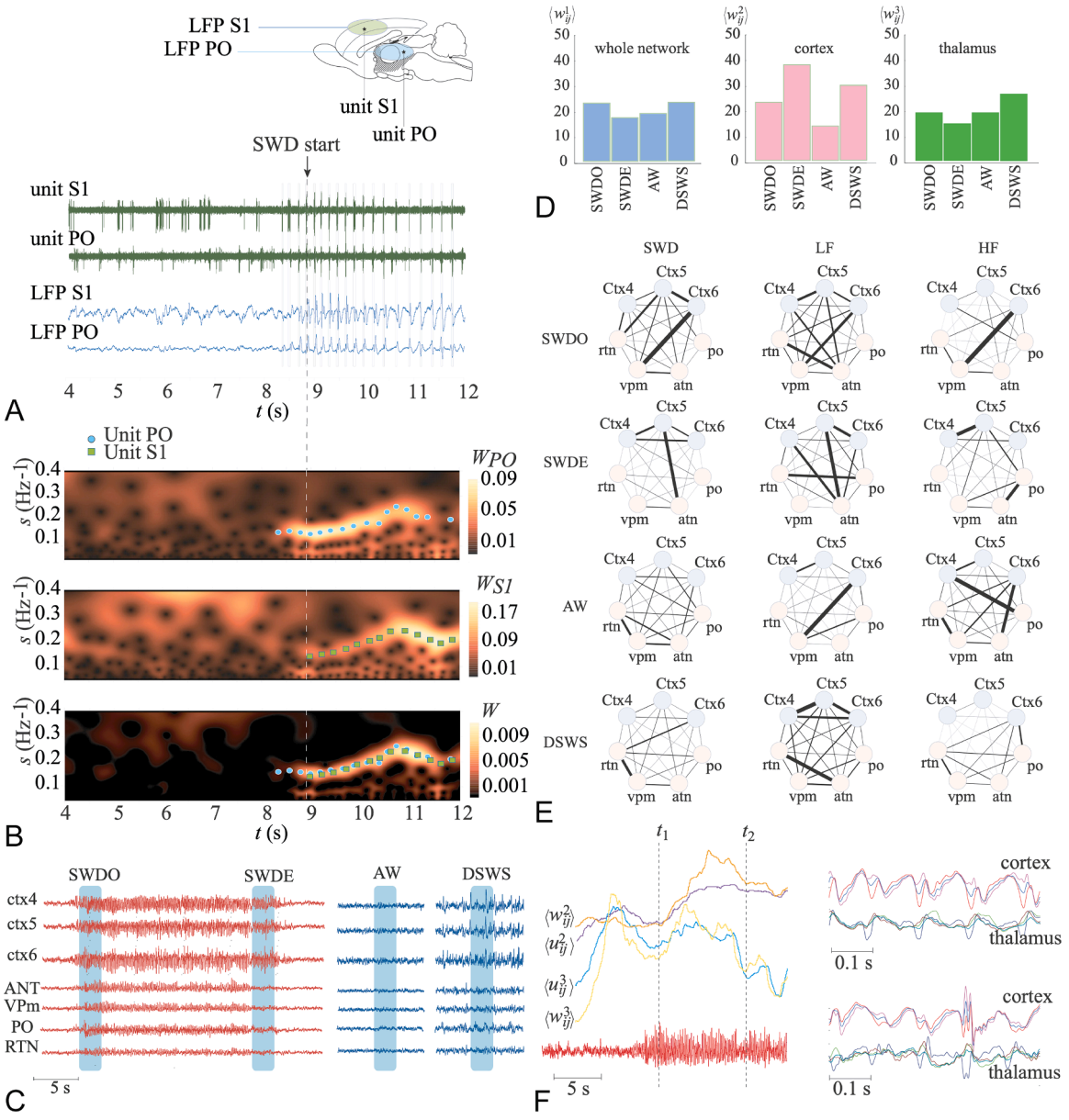

Fig. 7. Wavelet-based functional network analysis of corticothalamic activity. (A) Schematic diagram of the experimental setup and representative neurophysiological recordings, including single-unit activity (unit S1 and unit PO) and local field potentials (LFP S1 and LFP PO) reflecting collective neuronal activity in the cortex and thalamus. (B) Wavelet-based time-frequency decompositions of the macroscopic signals, along with the surface product $W(s,t) = W_{S1}(s,t) \times W_{PO}(s,t)$. (C) Typical raw electroencephalography (EEG) segments recorded during different brain states. (D) Mean interaction strength between various components of the thalamocortical neuronal network. (E) Graphical representation of the degree of functional coupling between different cortical and thalamic areas, with line thickness indicating interaction strength. (F) Mean interaction strength values computed for cortical and thalamic structures, together with corresponding EEG samples. Source: based on data from Maksimenko et al. [222].

illustrate the potential of frequency-integrated and multilayer network analysis in clinical neuroscience. For example, Ke et al. [202] examined the frequency-specific dynamics of multilayer brain networks, highlighting that network organization and its temporal reconfiguration can differ substantially across frequency bands. Complementing the frequency self-adaptive fMRI framework described above, Ding et al. [195] showed that functional interactions between brain regions may be characterized by distinct optimal combinations of frequency components rather than by a single predefined frequency range. In EEG, Cai et al. [203] constructed multiplex networks across both frequency bands and temporal windows to characterize altered functional integration and segregation in Alzheimer's disease, whereas Klepl et al. [204] incorporated both within-band and cross-frequency interactions using cross-bispectral connectivity. Finally, Yu and Meng [205] proposed an effective epilepsy detection method combining multilayer brain networks with deep learning. Their approach employs wavelet packet decomposition and reconstruction to decompose EEG signals into distinct frequency bands, which are subsequently used to construct a multifrequency multilayer brain network, with each layer representing the spatiotemporal feature topology of a specific frequency band. Unlike single-layer networks, this multilayer architecture integrates information across bands, enabling a more complete characterization of brain states.

The practical significance of graph-theoretic metrics in functional brain networks extends well beyond theoretical interest — they are now actively used in clinical diagnostics for conditions ranging from cognitive decline to epilepsy and disorders of consciousness [31,206–208]. Functional brain networks, reconstructed from multichannel neurophysiological data, provide a powerful systems-level framework for quantifying both normal cognitive dynamics and pathological alterations. In this context, graph metrics, such as clustering coefficient, characteristic path length, betweenness centrality, and global efficiency, can capture subtle reorganizations of neural communication patterns [209–211]. However, the interpretation and reliability of such measures critically depend on the method used to estimate connectivity. In addition to pairwise wavelet coherence or phase synchrony, wavelet-based bicoherence can be used to assess time-resolved quadratic phase coupling across frequencies, thereby providing complementary information on nonlinear cross-frequency interactions [212,213]. Even more importantly, the use of complex wavelets allows the extraction of instantaneous phase at each temporal scale, enabling phase synchronization to be assessed as a dynamic process rather than a static average [214,215]. Combined with graph-theoretical analysis, such scale- and phase-resolved measures can provide a richer characterization of functional reorganization during rest, cognitive tasks, and pathological state transitions. More broadly, alterations in the temporal and frequency-specific organization of functional brain networks can provide candidate markers of pathological states, as illustrated by directed SEEG networks in epilepsy [216]. Complementary dynamical models can test how such states emerge, stabilize, and respond to perturbation or intervention [217]. These approaches may support disease characterization and, in selected settings such as epilepsy, the detection or prediction of pathological transitions; however, their broader clinical predictive value remains context-specific and requires prospective validation.

Among various applications, one notable example by Karavaev et al. [218] concerns the relationship between infra-slow oscillations of brain potentials and respiratory rhythms. This research demonstrates that under paced breathing conditions, infra-slow oscillations become phase- and frequency-locked to the respiratory cycle. Such observations enhance our understanding of the origins and behavior of ultra-slow electrical activity in the brain. A more direct example of multiplex brain-network analysis was provided by Makarov et al. [219], who used wavelet phase coherence to construct a multiplex functional network in which distinct EEG frequency bands were represented as interacting layers. During cognitive task performance the transition from rest was associated with a redistribution of shortest paths away from lower-frequency layers and with stronger connectivity in higher-frequency layers. Moreover, shortest paths became more evenly distributed across the brain, indicating a less centralized and more spatially distributed functional organization. Wavelet-derived functional connectivity has also been used to investigate sensory processing. The brain's neuronal network operates as a distributed computational system that continuously reshapes its connectivity to support efficient sensory processing. In a visual-processing paradigm, Pisarchik et al. [220] reported that tasks requiring sustained attention were associated with long-range interactions between parietal and frontal regions, whereas less demanding visual processing primarily involved occipital and parietal areas. The authors further showed that the strongest functional coupling emerged under conditions of coherence resonance. Complementing these observations, Maksimenko et al. [221] demonstrated that cortical responses to visual stimuli give rise to distinct patterns of parieto-occipital coupling depending on the frequency band examined. The study further revealed the temporal evolution of parieto-occipital network interactions during visual perception and early sensory processing. These insights not only illustrate how wavelet-based methods can link spectral dynamics to transient reorganization of functional brain networks, but also offer a valuable extension to current theories regarding the neural aspects of visual information processing.

An illustrative example of how wavelet analysis can link macroscopic recordings to regional interaction patterns is provided in Fig. 7. Maksimenko et al. [222] developed a computationally light and practically feasible method for relating microscale interactions among network elements to the analysis of macroscale recorded signals. Fig. 7A) presents a schematic overview of the experimental setup, together with representative local field potential recordings and the corresponding microscopic neural activity, i.e., single- or few-neuron spiking, captured simultaneously via the same electrodes. Wavelet-based analysis reveals that the onset of an epileptic seizure is associated with the emergence of local synchronization *within* both the cortex and the thalamus, as well as global synchronization *between* these two brain structures, as depicted in Fig. 7B). Furthermore, Fig. 7C) illustrates the characteristic dynamical states of the corticothalamic neuronal network in the epileptic brain. These include SWD at onset and SWD termination, active wakefulness, and deep slow-wave sleep. Fig. 7D) quantifies the mean degree of interaction among cortical areas, thalamic regions, and the entire neuronal network, whereas Fig. 7E) provides a schematic representation of the interaction patterns across the considered brain states and frequency bands. In this panel, interaction strength is encoded by the thickness of the lines connecting the respective brain structures. Finally, Fig. 7F) displays the mean interaction strength between different components of the thalamocortical network, estimated over the time interval corresponding to SWD development, along with representative EEG segments recorded near time points t_1 and t_2.

Applied to a rat model of absence epilepsy, this framework demonstrated that inferred cortical, thalamic, and corticothalamic interaction patterns differ systematically across seizure onset and termination, wakefulness, and deep slow-wave sleep [223]. Related wavelet-based measures of local and global synchrony were subsequently incorporated into a real-time algorithm for predicting absence seizures, in which stimulation was triggered to prevent or interrupt spike-wave discharges [224]. These studies illustrate how time- and frequency-resolved network measures can provide both mechanistic insight into transient brain-state transitions and a basis for real-time intervention.

More broadly, recent developments increasingly combine wavelet-derived multiband connectivity with graph-theoretical analysis and data-driven classification. For instance, Shen et al. [225] constructed multiband EEG functional connectivity matrices using mutual information computed from continuous wavelet transform coefficients obtained with complex Morlet wavelets. These matrices were subsequently analyzed using a modified three-dimensional convolutional neural network based on the VGG architecture, enabling joint learning of spatial and frequency-resolved connectivity patterns for distinguishing Alzheimer's disease and frontotemporal dementia. Similarly, Ding et al. [226] applied wavelet decomposition to fMRI signals, constructed frequency-specific functional connectomes, and integrated their complementary information using a multi-kernel support vector machine for autism spectrum disorder identification. Multiscale graph-theoretical analysis of wavelet-resolved resting-state fMRI networks has likewise been combined with machine learning to distinguish Alzheimer's disease, mild cognitive impairment, and healthy control groups [227]. Related hybrid wavelet- and neural-network-based approaches have also been explored for automated epilepsy diagnosis [228]. These examples reflect a growing methodological shift toward integrated analytical pipelines in which wavelet-based signal decomposition provides frequency-resolved connectivity representations, while graph-theoretical and machine or deep-learning methods extract their organizational and diagnostic content. Beyond improving the characterization of altered brain states, such frameworks may support translational applications in diagnostic assistance, real-time decoding, neurofeedback, brain-computer interfaces, and neurorehabilitation [229,230]. Their clinical utility will nevertheless require validation across independent cohorts, recording settings, and analytical pipelines.

Although the present section focuses on brain networks, the same wavelet-derived framework can be applied whenever multiple dynamic units exhibit time-varying and scale-specific coordination. This is particularly relevant in multicellular systems, where individual cells display activity across multiple temporal scales and where tissue-level function emerges from nontrivial interactions among heterogeneous cellular units. The following section therefore extends these principles to multicellular recordings, in which individual cells, rather than brain regions or recording sites, constitute the network nodes.

8. Wavelet-based functional connectivity in multicellular systems

Beyond applications in large-scale physiological systems, wavelet-derived functional connectivity has also proven valuable for analyzing interactions at the level of individual cells, although such applications remain comparatively less explored. While most developments have been driven by large-scale recordings, neuronal systems provide an important intermediate step, where multicellular measurements with high spatiotemporal resolution allow direct investigation of interactions between individual units. In this setting, wavelet-based approaches have been successfully used to capture dynamic and frequency-specific patterns of connectivity. For example, in hippocampal cultures imaged with wide-field Ca^{2+} imaging, wavelet coherence combined with time-varying correlation enabled tracking of evolving network topology under glutamate stimulation [43]. Similarly, ATP-driven Ca^{2+} dynamics in neuronal monolayers revealed how temporal properties of external cues shape network connectivity through gap junctions while multielectrode array recordings demonstrated frequency-dependent differences in network architecture between cortical and hippocampal cultures using wavelet-based cross-correlogram analysis [45]. Earlier work by Li et al. also demonstrated how wavelet transforms can reveal interaction dynamics among neuronal oscillations [175].

Building on these insights and driven by the growing recognition of the importance of collective cellular activity, together with rapid advances in multicellular imaging techniques, the concept of functional connectivity is increasingly being extended to a wide range of multicellular settings, where coordinated dynamics emerges from interactions among individual units [36,231–239]. In this context, wavelet-based approaches still represent largely untapped potential, offering a powerful framework for resolving time-localized and frequency-specific interactions in complex biological systems. This opens new opportunities for applying such methodologies to a broad range of excitable and non-excitable tissues, including endocrine systems. In the following, we illustrate these principles and their advantages using the example of the pancreatic islet, a prototypical multicellular syncytium of β-cells.

In the context of pancreatic β-cells, it is now increasingly recognized that coordinated activity across the islet is essential for normal glucose homeostasis. Rather than acting as independent units, β-cells operate as a functionally coupled multicellular network, in which interactions across a hierarchical connectivity structure are required for appropriate insulin release. Disruptions of this coordinated activity have been linked to irregular insulin secretion, a hallmark of diabetes [240–243]. At the same time, β-cell dynamics are inherently multiscale. As discussed in Section 5, individual cells exhibit oscillations across distinct temporal regimes, reflecting the interplay between metabolic and electrical processes, while at the multicellular level, cells form intricate yet coherent intercellular activity patterns, including propagating waves and partial synchronization. These features have driven the increasing use of network-based approaches to objectively characterize collective islet activity [36,244–246]. Such analyses reveal a nontrivial organization, including modular structure, small-world properties, and heavy-tailed degree distributions, indicative of specialized subpopulations such as hub and wave-initiating cells [247–250]. However, the inferred functional connectivity depends critically on the temporal scales being analyzed. Given the coexistence of multiple oscillatory components and diverse experimental preparations, insufficient separation of these scales can lead to markedly different interpretations. Time-frequency approaches therefore provide a natural framework to disentangle these interactions, enabling a more consistent and physiologically meaningful characterization of

β-cell functional networks.

As illustrated in Fig. 8, the characteristic multiscale organization of pancreatic β-cells is reflected in distinct patterns of slow and fast activity, which give rise to different modes of collective behavior. Slow Ca^{2+} oscillations form broad, quasi-periodic domains of coordinated activation, consistent with a global modulatory drive that organizes activity across the islet. Fast oscillations, on the other hand, tend to manifest as rapidly propagating fronts of electrical and Ca^{2+} activation across the coupled β-cell population, producing synchronized, recurrent events that traverse the islet. These observations suggest that the two regimes are governed by partially different, yet interconnected synchronization mechanisms: slow dynamics are associated with sustained, long-range coordination, whereas fast dynamics more prominently reflect spatially propagating wave-like events. Importantly, the two regimes are not independent but coexist and interact, indicating that collective β-cell behavior emerges from the interplay between slower metabolic modulation and faster electrically driven activity.

To examine these differences in a systematic manner, we construct wavelet-based functional connectivity networks by computing wavelet coherence separately for the slow metabolic and the fast electrically driven components. The computation is performed within short, overlapping temporal windows, enabling local resolution of interactions while avoiding averaging over nonstationary dynamics that would obscure subtle coupling patterns, with window lengths chosen to capture the characteristic time scales of the selected frequency bands ($\Delta t = 60$ s with 50% overlap for the fast band, and $\Delta t = 1200$ s with 75% overlap for the slow band). Within each temporal window, wavelet coherence is evaluated. For the slow component, estimates are restricted to regions outside the cone of influence, as obtained from the wavelet transform, to mitigate edge effects [81,251]. The resulting coherence values are subsequently averaged over the selected frequency bands and thresholded to retain the strongest interactions (top 3%), yielding a sequence of time-resolved networks. These are further summarized using a persistence-based representation, and only interactions present in at least 20% of the temporal windows are retained to construct the final persistent network.

As illustrated in Fig. 9, the resulting frequency-specific networks exhibit distinct spatial organization. The fast-component network is characterized by spatially localized clusters of interacting cells, whereas the slow-component network displays more extended and cohesive connectivity across the islet. These differences are consistent with wave-like propagation in the fast regime and more sustained, large-scale coordination in the slow regime. To quantify these differences, we analyzed global network properties (Fig. 9, lower panels). Networks derived from the slow component exhibit longer spatial edge lengths, indicating more extended connectivity, while fast-component networks are dominated by shorter, localized interactions. Differences in clustering coefficient and node degree further support distinct organizational patterns, with the slow network appearing more integrated and the fast network more locally

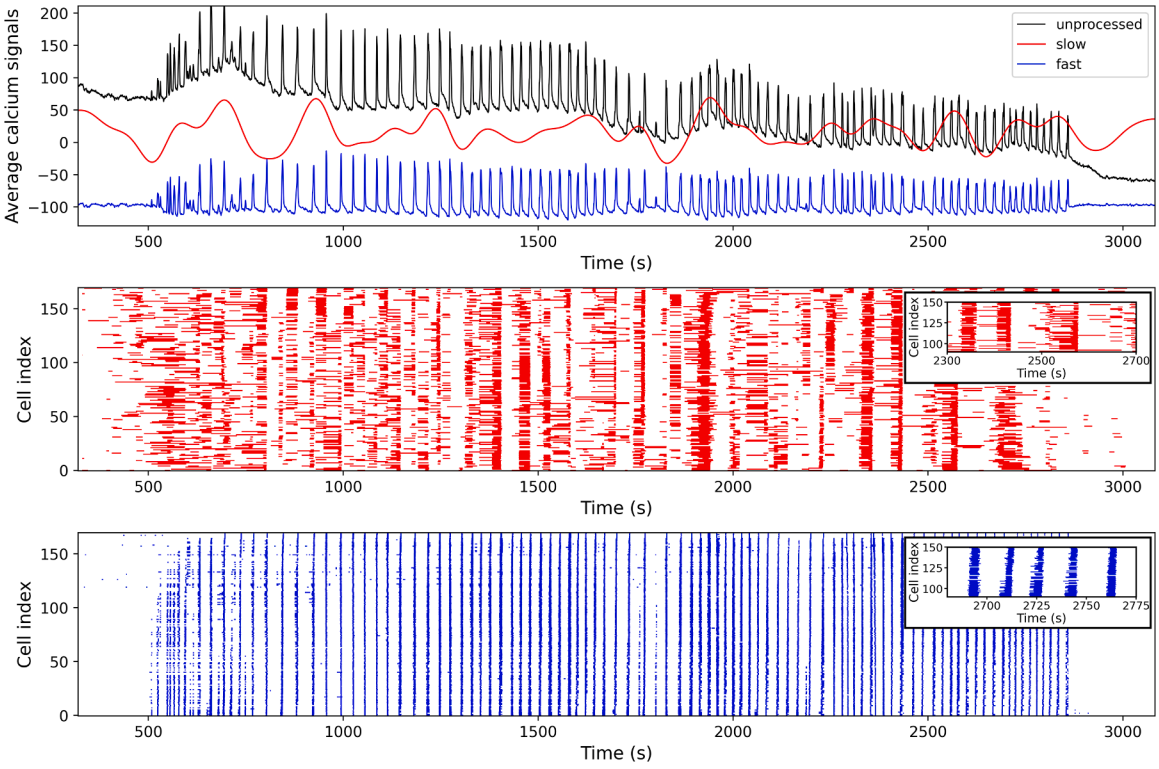

Fig. 8. Multiscale collective dynamics of pancreatic β-cells. Top: Average intracellular Ca^{2+} signal across islet cells during 8 mM glucose stimulation, shown together with its decomposition into slow (red) and fast (blue) components. Middle: Raster plot of the slow component illustrating coordinated low-frequency activity with broad, quasi-periodic temporal organization across the cell population. Bottom: Raster plot of the fast component, highlighting rapid, recurrent activation events that propagate across the islet as intercellular waves. Inset: Zoomed-in segment revealing the fine temporal structure of fast oscillations and the sequential activation of cells during wave propagation.

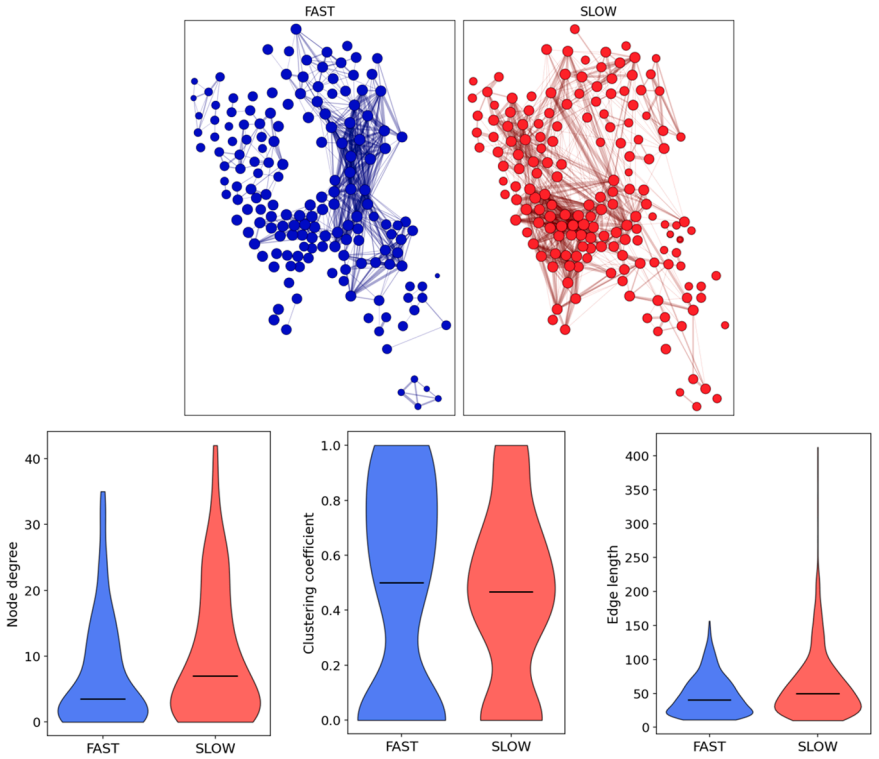

Fig. 9. Frequency-specific functional networks of β-cell activity. Top: Wavelet-based functional connectivity networks constructed from the fast (left) and slow (right) oscillatory components of intracellular Ca^{2+} signals in a pancreatic islet. Nodes represent individual cells, and edges indicate persistent functional interactions, defined as connections that consistently appear across time windows. Bottom: Distributions of node degree (left), clustering coefficient (middle), and spatial edge length (right) for the corresponding networks.

structured. These differences likely reflect distinct underlying physiological mechanisms. Fast-component networks are strongly shaped by direct electrical coupling via gap junctions, which promotes local synchronization and wave propagation, whereas the organization of slow-component networks is more strongly influenced by intrinsic cellular heterogeneity and metabolic variability across the islet [2,252]. This interpretation is further supported by recent experimental and computational studies highlighting the differential contributions of electrical coupling and intrinsic cellular properties to collective β-cell dynamics [253,254]. Importantly, this underscores that the inferred structure of functional connectivity critically depends on the temporal scale at which interactions are evaluated. These findings highlight that wavelet-based functional connectivity provides a framework for linking multiscale signal dynamics to collective β-cell behavior, enabling a consistent characterization of how distinct oscillatory regimes shape coordinated activity in multicellular systems.

To link the observed network organization to underlying signal-level interactions, we next examine time-frequency structure at the level of individual β-cell pairs. Focusing on the fast component, which exhibits more heterogeneous dynamics, we compare representative connected and disconnected pairs defined based on persistence of functional links. As illustrated in Fig. 10, differences between the two cases are already apparent in the raw signals and their scalograms: while both pairs may occupy similar frequency ranges, the temporal organization of activity differs markedly. In the connected pair, oscillatory patterns are well aligned over extended periods, resulting in sustained coherence across a substantial portion of the fast frequency band. In contrast, the disconnected pair exhibits less coordinated fluctuations, with coherence confined to short-lived and irregular patches in the time-frequency plane.

This comparison highlights that the key determinant of functional connectivity is not the mere presence of coherence, but its temporal persistence. Brief episodes of high coherence can occur even between weakly coupled cells, yet such transient events do not survive temporal averaging and thresholding, and therefore do not contribute to stable network links. Consequently, only interactions characterized by sustained coherence are retained in the functional network. This provides a mechanistic explanation for the fragmented and locally organized structure of the fast-component network (Fig. 9), where stable connections emerge only within subsets of cells exhibiting consistent coordination. More broadly, it demonstrates how wavelet-based functional connectivity links time-frequency signal dynamics at the pairwise level to the emergence of collective patterns at the network scale.

9. Conclusions and outlook

Wavelet analysis has evolved from a method for localized time-frequency inspection into a broadly applicable multiresolution language for complex data. Although this Review has focused primarily on biomedical oscillations, the scope of wavelet-based methods

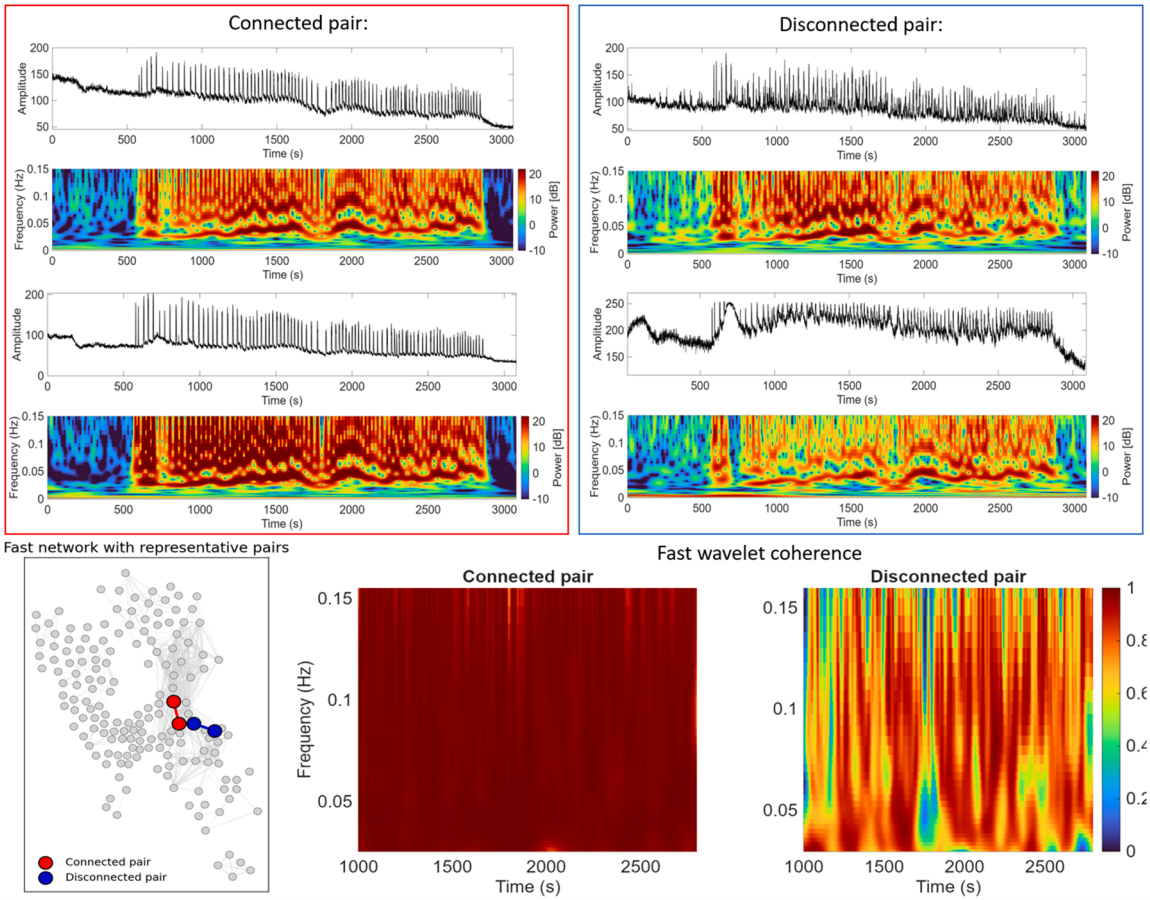

Fig. 10. Linking network connectivity to the time-frequency dynamics in the fast component. Top: Representative connected (left) and disconnected (right) β-cell pairs. For each pair, raw Ca^{2+} time series and corresponding scalograms are shown. Bottom: Corresponding wavelet coherence maps in the fast frequency band. The connected pair exhibits sustained, high coherence over time, whereas the disconnected pair shows fragmented and transient coherence.

is considerably wider. Wavelets have long been used to study nonstationary processes in geophysics, environmental systems, engineering, signal compression and signal denoising [14,47,49–51,255], as well as for image analysis, feature extraction, pattern recognition, and the multiscale characterization of complex structures [13,256]. In biomedicine, this spatial perspective extends naturally to multiscale image processing, tissue morphology, and radiomic descriptions of structural heterogeneity [257]. Likewise, in bioinformatics and computational biology, wavelet approaches have been applied to genomic sequences, gene-expression profiles, protein structures, and other high-dimensional molecular data sets [55]. This breadth reflects a common principle: complex systems frequently contain informative features that are localized not only in frequency or time, but also in space and scale.

Wavelets therefore contribute not only to the interpretation of physiological dynamics, but also to their processing. Denoising, compression, transient detection, feature extraction, and the localization of sharp events are all integral parts of the wavelet toolkit. This is particularly relevant for biological recordings in which relevant activity may appear as brief bursts, spikes, Ca^{2+} transients, epileptiform discharges, or abrupt transitions between dynamical states. Wavelet-based detection methods can enhance the separation of such events from noise and background fluctuations, while retaining their timing and scale-specific properties, thereby making them suitable components of automated and potentially real-time analytical pipelines [258–260].

Within physiology, the value of this framework is especially evident because biological function emerges from interacting processes distributed across multiple temporal and spatial scales. The cardiovascular, neural, and multicellular examples discussed in this Review illustrate that wavelet analysis does not merely identify which frequencies are present in a signal, but reveals when specific oscillatory components emerge, how their properties evolve, and whether their relationships with other components persist, weaken, or reorganize. This capability is essential for interpreting nonstationary biological dynamics, in which transient coordination may be at least as informative as average spectral properties. These capabilities will become increasingly important as advances in high-speed imaging, dense multichannel sensing, and simultaneous multimodal recording generate increasingly comprehensive and spatially resolved time series across cellular, tissue, and organ levels. A key methodological challenge will be to integrate these heterogeneous and data-rich measurements while preserving their temporal and scale-specific information, rather than reducing them to stationary summaries or isolated frequency components. From a network physiology perspective, the same developments create an opportunity

to move beyond individual signals and organs toward time- and scale-resolved descriptions of coordination among physiological systems [35].

Realizing this broader perspective requires characterizing how spatially distributed units and physiological subsystems interact and organize collectively. Wavelet coherence, phase-based measures, and related time-frequency metrics provide a means of quantifying when and at which scales dynamic units become coordinated. When embedded within a network framework, these measures link local signal-level relationships with system-level organization. In this context, multilayer and temporal network representations are particularly promising: different layers may encode frequency bands, temporal windows, physiological variables, imaging modalities, or spatial scales, whereas interlayer links can capture cross-frequency, cross-modal, or cross-scale dependencies. Such representations offer a route toward a more holistic description of biological systems, in which electrical, metabolic, mechanical, and chemical processes interact rather than operate as isolated dynamical modules [21,199,204,261,262]. Wavelet-based measures are particularly well suited for this purpose, as they provide a natural bridge between multiscale signal dynamics and the layered organization of collective biological activity.

The integration of wavelet analysis with machine learning and deep learning provides a further opportunity to link interpretable, scale-resolved signal features with data-driven models of physiological states, disease progression, and responses to intervention [263,264]. Combined with functional and multilayer network representations, such hybrid approaches may support automated event detection, clinical decision support, neurofeedback, brain-computer interfaces, and closed-loop therapeutic technologies [265,266]. Realizing this potential will require robust performance across recording conditions and a meaningful connection between predictive accuracy and physiological interpretation. As biomedical recordings become increasingly multimodal, spatially resolved, and data rich, wavelet analysis should not be viewed simply as a transform for visualizing time-frequency content. Its integration with advanced experimental techniques, functional connectivity, network science, and data-driven methods will provide an increasingly powerful framework for linking transient local dynamics to coordinated biological function across scales. Its future role will lie not only in identifying which rhythms are present, but also in revealing when and where biological interactions emerge, at which scales they operate, and how their reorganization relates to physiological adaptation, disease, and responses to intervention.

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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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