Discrete Structure of the Brain Rhythms

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Neuronal activity in the brain generates synchronous oscillations of the Local Field Potential (LFP). The traditional analyses of the LFPs are based on decomposing the signal into simpler components, such as sinusoidal harmonics. However, a common drawback of such methods is that the decomposition primitives are usually presumed from the onset, which may bias our understanding of the signal’s structure. Here, we introduce an alternative approach that allows an impartial, high resolution, hands-off decomposition of the brain waves into a small number of discrete, frequency-modulated oscillatory processes, which we call oscillons. In particular, we demonstrate that mouse hippocampal LFP contain a single oscillon that occupies the $\theta$-frequency band and a couple of $\gamma$-oscillons that correspond, respectively, to slow and fast $\gamma$-waves. Since the oscillons were identified empirically, they may represent the actual, physical structure of synchronous oscillations in neuronal ensembles, whereas Fourier-defined “brain waves” are nothing but poorly resolved oscillons.

Neurons in the brain are submerged into a rhythmically oscillating electrical field, created by synchronized synaptic currents. The corresponding potential, known as local field potential (LFP) is one of the principal determinants of neural activity at all levels, from the synchronized spiking of the individual neurons to high-level cognitive processes. Attempts to understand the structure and function of LFP oscillations, and of their spatio-temporally smoothed counterparts—the electroencephalograms (EEG), continues almost a century and a systematic understanding of their roles begins to take shape.

The possibility to identify true physiological functions of the LFP depends fundamentally on the mathematical and computational tools used for its analysis. The majority of the currently existing methods are based on breaking the signal into a combination of simpler components, such as sinusoidal harmonics or wavelets, and then correlating them with physiological, behavioral and cognitive phenomena. For example, wavelet analysis is most appropriate for studying time-localized events, such as ripples or spindles, whereas for the general analyses, the oscillatory nature of LFPs suggests using discrete Fourier decomposition into a set of plane waves with a fixed set of frequencies $\omega$, $2\omega$, $3\omega$, $\ldots$. The latter approach has dominated the field for the last several decades and now constitutes, in effect, the only systematic framework for our understanding of the structure and the physiological functions of the brain rhythms. However, a common flaw of these methods is that the decomposition primitives are presumed from the onset, and the goal of subsequent analyses reduces merely to identifying the combination that best reproduces the original signal. Since no method can guarantee a universally good representation of the signals’ features and since the physiological structure of the LFPs remains unknown, obtaining a physically adequate description of the brain rhythms is a matter of fundamental importance.

Below we propose a novel approach of LFP analysis based on a recent series of publications, in which an optimal set of frequencies $\omega_1, \omega_2, \ldots$, is estimated, at every moment of time $t$, using the Padé Approximation Theory. In contrast with the Fourier method, these adaptively optimized values can freely change within the sampling frequency domain, guided only by the signal’s structure. The resulting harmonics are highly responsive to the signals’ dynamics and capture subtle details of the signal’s spectrum very effectively, as one would expect from a Padé Approximation based technique. We call the new method Discrete Padé Transform (DPT), to emphasize certain key correspondences with the traditional Discrete Fourier Transform (DFT).

Applying DPT analyses to LFP rhythms recorded in mouse hippocampi reveals a new level in their structure—a small number of frequency-modulated oscillatory processes, which we call oscillons. Importantly, oscillons are observed in the physiologically important theta ($\theta$) and gamma ($\gamma$) frequency domains, but are much sharper defined. For example, in the Fourier approach, the $\theta$-rhythm is loosely defined as a combination of the plane waves with frequencies between 4 and 12 Hz. In contrast, our method suggests that there exists...
a single frequency-modulated wave—the \( \theta \)-oscillon—that occupies the entire \( \theta \) frequency band and constitutes the \( \theta \)-rhythm. Similarly, we observe oscillons in the low and high \( \gamma \)-frequency domains. The superposition of the oscillons reproduces the original LFP signal with high accuracy, which implies that these waves provide a remarkably sparse representation of the LFP oscillations. Since oscillons emerged as a result of empirical analyses, we hypothesize that they represent the actual, physical structure of synchronized neuronal oscillations, which were previously approximately described as the Fourier-defined “brain waves.”

**Results**

**The oscillons.** We implemented a “Short Time Padé Transform” (STPT), in which a short segment of the time series (that fits into a window of a width \( T_w \)) is analyzed at a time. This allows us to follow the signal's spectral composition on moment-to-moment basis and to illustrate its spectral dynamics using Padé spectrograms (the analogues of the standard Fourier spectrograms\(^{18,19}\)).

Applying these analyses to the hippocampal LFPs recorded in awake rodents during habituation stage\(^{20}\), we observed that there exist two types of time-modulated frequencies (Fig. 1). First, there is a set of frequencies that change across time in a regular manner, leaving distinct, continuous traces—the spectral waves. As shown on Fig. 1A, the most robust, continuous spectral waves with high amplitudes (typically three or four of them) are confined to the low frequency domain and roughly correspond to the traditional \( \theta \)- and \( \gamma \)-waves\(^{13,16}\). The higher frequency (over 100 Hz) spectral waves are scarce and short, representing time-localized oscillatory phenomena that correspond, in the standard Fourier approach, to fast \( \gamma \) events\(^{21}\), sharp wave ripples (SWRs)\(^{22}\) or spin-dles\(^{23}\). Second, there exists a large set of “irregular” frequencies that assume sporadic values from one moment to another, without producing contiguous patterns and that correspond to instantaneous waves with very low amplitudes.

From the mathematical perspective, the existence of these two types of instantaneous frequencies can be explained based on several subtle theorems of Complex Analysis, which point out that the “irregular” harmonics represent the signal’s noise component, whereas the “regular,” stable harmonics define its oscillatory part (see\(^{24–27}\) and the Mathematical Supplement). Thus, in addition to revealing subtle dynamics the frequency spectrum, the DPT method allows a context-free, impartial identification of noise, which makes it particularly important for the biological applications\(^{28,29}\).
As it turns out, the unstable, or “noisy,” frequencies typically constitute over 95% of the total number of harmonics (Fig. 1A). However, the superposition of the harmonics that correspond to the remaining, stable frequencies captures the shape of the signal remarkably well (Fig. 1B). In other words, although only a small portion of frequencies are regular, they contribute over 99% of the signal’s amplitude: typically, the original LFP signal differs from the superposition of the stable harmonics by less than 1%. If the contribution of the “irregular” harmonics (i.e., the noise component $\xi(t)$) is included, the difference is less than $10^{-6}$ of the signal’s amplitude.

These results suggest that the familiar Fourier decomposition of the LFP signals into a superposition of plane waves with constant frequencies,

$$r(t) = \sum_{p=1}^{N} a_p e^{i\omega_p t},$$

should be replaced by a combination of a few phase-modulated waves embedded into a weak noise background $\xi(t)$,

$$s(t) = \sum_{q=1}^{M} A_q e^{i\omega_q t} + \xi(t),$$

which we call oscillons. We emphasize that the number $M \ll N$ of the oscillons in the decomposition (2), their amplitudes $A_q$, their phases $\phi_q$, and the time-dependent frequencies $\omega_q(t) = \partial_t \phi_q(t)$ (i.e., the spectral waves shown on Fig. 1A) are reconstructed on moment-by-moment basis from the local segments of the LFP signal in a hands-off manner: we do not presume a priori how many frequencies will be qualified as “stable,” when these stable frequencies will appear or disappear, or how their values will evolve in time, or what the corresponding amplitudes will be. Thus, the structure of the decomposition (2) is obtained empirically, which suggests that the oscillons may reflect the actual, physical structure of the LFP rhythms.

**The spectral waves.** We studied the structure the two lowest spectral waves using high temporal resolution spectrograms (Fig. 2A). Notice that these spectral waves have a clear oscillatory structure,

$$\omega_q(t) = \omega_{q,0} + \omega_q \sin(\Omega_q t + \varphi_{q,1}) + \omega_q \sin(\Omega_q t + \varphi_{q,2}) + \ldots, \quad q = 1, 2,$$

characterized by a mean frequency $\omega_{q,0}$ as well as by the amplitudes, $\omega_q$, the frequencies, $\Omega_q$, and the phases, $\varphi_{q,j}$, of the modulating harmonics. The lowest wave has the mean frequency of about 8 Hz and lies in the domain $2 \leq \omega/2\pi \leq 17$ Hz, which corresponds to the $\theta$-frequency range. The second wave has the mean frequency of...
about 35 Hz and lies in the low-γ domain $25 \leq \omega/2\pi \leq 45$ Hz. Importantly, the spectral waves are well separated from one another: the difference between their mean frequencies is larger than their amplitudes, which allows indexing them using the standard brain wave notations, as $\omega_\theta(t)$ and $\omega_\gamma(t)$ respectively, e.g.,

$$\omega_\theta(t) = \omega_{\theta,0} + \omega_{\theta,1} \sin(\Omega_{\theta,1} t + \varphi_{\theta,1}) + \omega_{\theta,2} \sin(\Omega_{\theta,2} t + \varphi_{\theta,2}) + \ldots, \quad (4)$$

for the θ spectral wave an

$$\omega_\gamma(t) = \omega_{\gamma,0} + \omega_{\gamma,1} \sin(\Omega_{\gamma,1} t + \varphi_{\gamma,1}) + \omega_{\gamma,2} \sin(\Omega_{\gamma,2} t + \varphi_{\gamma,2}) + \ldots\quad (5)$$

for the low-γ spectral wave, etc.

We verified that these structures are stable with respect to the variations of the STPT parameters, e.g., to changing the sliding window size, $T_W$. The size of the sliding window, and hence the number of points $N$ that fall within this window can be changed by over 400%, without affecting the overall shape of the spectral waves (Fig. 2B). The smallest window size (a few milliseconds) is restricted by the requirement that the number of data points captured within $T_W$ should be bigger than the physical number of the spectral waves. On the other hand, the maximal value of $T_W$ is limited by the temporal resolution of STPT: if the size of the window becomes comparable to the characteristic period of a physical spectral wave, then the reconstructed wave looses its undulating shape and may instead produce a set of sidebands surrounding the mean frequency $\omega_\theta/2\pi \approx 34$. This effect limits the magnitude of $T_W$ to abut 50 milliseconds—for larger values of $T_W$, the undulating structure begins to straighten out, as shown on Fig. 1A for $T_W = 80$ msec.

In contrast with this behavior, the values of the irregular frequencies are highly sensitive to the sliding window size and other DPT parameters, as one would expect from a noise-representing component. The corresponding “noisy” harmonics can therefore be easily detected and removed using simple numerical procedures (see Mathematical Supplement). Moreover, we verified that the structure of the Padé Spectrogram, i.e., the parameters the oscillons remain stable even if the amount of numerically injected noise exceeds the signal’s natural noise level by an order of magnitude (about $10^{-4}$ of the signal’s mean amplitude), which indicates that the oscillatory part of the signal is robustly identified.

**Parameters of the low frequency oscillons.** To obtain a more stable description of the underlying patterns, we interpolated the spectral waves over the uniformly spaced time points (Fig. 3A) and then studied the resulting “smoothened” spectral waves using the standard DFT tools. In particular, we found that, for studied LFP signals, the mean frequency of the $\theta$-oscillation is about $\omega_{\theta,0}/2\pi = 7.5 \pm 0.5$ Hz and the mean frequency of the low-
define the dynamics of neuronal synchronization30–32.

The resolution of the latter, which is due to the well-known inherent conflict between the frequency and the tempo-

A method identifies a small number of structurally stable, frequency-modulated oscillons which may reflect the

The Fourier and the Padé decompositions agree in simple cases, e.g., both spectrograms resolve the individual

The amplitudes of the θ and the low γ spectral waves—7.0 ± 1.5 Hz and 10.1 ± 1.7 Hz respectively—define the

The oscillatory parts of the spectral waves are also characterized by a stable set of frequencies and amplitudes:

Importantly, the reconstructed frequencies sometimes exhibit approximate resonance relationships (Fig. 3C),

Discussion

The Fourier and the Padé decompositions agree in simple cases, e.g., both spectrograms resolve the individual

Why these structures were not previously observed via Fourier method? The reason lies in the insufficient

In the specific case illustrated on Fig. 2, the characteristic amplitudes of the spectral waves is about 15–25 Hz.

Producing such frequency resolution in DFT at the sampling rate $S=10\text{ kHz}$ would require some $N=300–500$

In general, the modulating frequencies tend to increase with the mean frequency.

In contrast, the DFT harmonics can decrease in the number of data points necessarily results in an increase of the interval between neighboring dis-

In the case of the LFP signals, this Froissart doubles form a very low amplitude background “dust,” shown in gray. Our main hypothesis is that

The characteristic period of the spectral waves is about 60 msec, which implies that for such
\( T_{\phi}, \) the DFT will not be able to resolve the frequency wave dynamics and will not replace it by an average frequency with some sidebands (see Mathematical Supplement). In contrast, a DFT that uses as few as 80 data points in a \( T_{W} = 8 \) msec wide time window, reliably capturing the shape of the spectral wave, which then remains overall unchanged as \( T_{\phi} \) increases fourfold.

Another key property of the DFT method is the intrinsic marker of noise, which is particularly important in biological applications.\(^{28,29} \) In general, the task of distinguishing "genuine noise" from a "regular, but highly complex" signal poses not only a computational, but also a profound conceptual challenge.\(^{35,36} \) In contrast with the standard \( \text{ad hoc} \) approaches, the DFT method allows a context-free, impartial identification of the noise component, as the part of the signal represented by the irregular harmonics.

The new structure also dovetails with the theoretical views on the origins of the LFP oscillations as on a result of synchronization of the neuronal spiking activity in both the excitatory and inhibitory networks.\(^{30–32} \) Broadly speaking, it is believed that the LFP rhythms are due to a coupling between the electromagnetic fields produced by local neuronal groups.\(^{1} \) If the coupling between these groups is sufficiently high, then the individual fields oscillating with amplitudes \( a_{p} \) and phases \( \phi_{p} \) synchronize, yielding a nonzero mean field \( \Sigma_{p} a_{p} e^{i\phi_{p}} = A e^{i\phi} \) that is macroscopically observed as LFP.\(^{30–32} \) In particular, the celebrated Kuramoto Model\(^{30} \) describes the synchronization between oscillators via a system of equations

\[
\frac{\partial x_{p}}{\partial t} = \omega_{p} + K \sum_{q} \sin(x_{q} - x_{p}),
\]

according to which the oscillators transit to a synchronized state, as the coupling strength \( K \) increases. Eq. (6) directly points out that the synchronized frequency, \( \omega(t) = \partial \phi_{s} \), should have the form (3). However, this form of expansion has not been previously extracted from the experimental data, which may be due to the fact that the Fourier method does not resolve the spectral structure in sufficient detail (Sfig. 2). In contrast, the description of the LFP oscillations produced by the DPT method may provide such resolution and help to link the empirical data to theoretical models of neuronal synchronization.

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**Author Contributions**

L.P. and D.B. developed the method, L.P., J.D. and Y.D. developed the software. Y.D. conceived the project, analyzed data, wrote the manuscript. All authors reviewed the manuscript.

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