A Wavelet Analysis of Transient Spike Trains of Hodgkin-Huxley Neurons

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Abstract

Transient spike trains consisting of $M (= 1 - 5)$ pulses generated by single Hodgkin-Huxley (HH) neurons, have been analyzed by using both the continuous and discrete wavelet transformations (WT). We have studied effects of variations in the interspike intervals (ISI) of input spikes and effects of random noises on the energy distribution and the wavelet entropy, which are expressed in terms of the WT expansion coefficients. The results obtained by the WT are discussed in connection with those obtained by the Fourier transformation.

Keywords: Wavelet transformation, Wavelet entropy, Hodgkin-Huxley neurons

1 Introduction

During the last half century, extensive experimental and theoretical studies have been made on functions of brain where neurons communicate information by action potentials or spikes. Because of the complexity of spike signals, little is known how information is carried by spikes at the moment [1]-[6]. It has been widely believed that information is encoded in the average firing rate of individual neurons (rate code). Andrian [7] first noted the relationship between neural firing rate and stimulus intensity, which forms the basis of the rate code. Actually firing activities of motor and sensory neurons are reported to vary in response to applied stimuli. In recent years, however, it has been proposed that detailed spike timings play an important role in information transmission (temporal code): information is assumed to be encoded in interspike intervals (ISIs) or in relative timings between firing times of spikes [8]-[10]. Indeed, experimental evidences have accumulated in the last several years, indicating a use of the temporal coding in neural systems [11]-[15]. Human visual systems, for example, have shown to classify patterns within 250 ms despite the fact that at least ten synaptic stages are involved from retina to the temporal brain [15]. The transmission times between two successive stages of synaptic transmission are suggested to be no more than 10 ms on the average. This period is too short to allow rates to be determined accurately.

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Although much of debates on the nature of the neural code has focused on rate versus temporal codes, there are other important issue to consider: information is encoded in the activity of single (or very few) neurons or that of a large number of neurons. A major question on the population code (or ensemble code) concerns how the information is carried by correlation between different action potentials fired by different neurons. The simplest assumption is that little or no amount of information is carried by such correlation and that information is coded in the relative firing rates of the neurons (ensemble rate code). This code model is supported by many experiments [16] and has been adopted in the majority of analysis of neural coding [6][18]. On the contrary, it is assumed that relative timings between spikes in ensemble neurons may be used as an encoding mechanism for perceptual processing (ensemble temporal code) [19]-[21]. A number of experimental data supporting this code have been reported in recent years [22]-[25]. For example, data have demonstrated that temporally coordinated spikes can systematically signal sensory object feature, even in the absence of changes in firing rate of the spikes [23]. It is currently controversial what kind of code is employed in the real neural systems [1]-[6].

This shows the importance of studying how spike signals may convey information with the sub-millisecond resolution. The response of spikes to stimulus has been best studied when it is periodic in time, for which the Fourier transformation (FT) method is usually adopted for its analysis. The FT decomposes a signal into its constituent components. The information theory provides a powerful tool for analyzing the nature and quality of a neuronal code. A natural approach to quantify the degree of order of a complex signals is to consider its spectral entropy, as defined from the FT power spectrum [26]. The spectrum entropy shows how the FT power spectrum is concentrated or widespread; an ordered activity with a narrow peak in the frequency domain yields a low entropy while a disordered activity with a widespread frequency distribution leads to higher entropy.

The FT requires that a signal to be examined is stationary, not giving the time evolution of the frequency pattern. Actual biological signals are, however, not necessarily stationary. It has been reported that neurons in different regions have different firing activities. Furthermore even within a given region, firing property depends on its states. The typical example is found in thalamus, which is the major gateway for the flow of information toward the cerebral cortex. In arousal spikes with gamma oscillations (30-70 Hz), mainly 40 Hz, are reported, whereas spindle oscillations (7-14 Hz) and slow oscillations (1-7 Hz) are found in early sleeping and deep sleep states, respectively [27]. In hippocampus, gamma oscillation occurs in vivo, following sharp waves [28]. In neo-cortex, gamma oscillation is observed under conditions of sensory signal as well as during sleep [29]. Spike signals in cortical neurons are generally not stationary, rather they are transient signals or bursts [30], whereas periodic spikes are found in systems such as auditory systems of owl [31] and the electrosensory system of electric fish [32].

The limitation of the FT analysis can be partly resolved by using a short-time Fourier transform (STFT). Assuming the signal is quasi-stationary in the narrow time period, the FT is applied with time-evolving narrow windows. Then STFT yields the time evolution of the frequency spectrum. The STFT, however, has a critical limitation violating the uncertainty principle, which asserts that if the window is too narrow, the frequency resolution will be poor whereas if the window is too wide, the time resolution will be less precise. This limitation becomes serious for signals with much transient components, like...
spike signals.

The disadvantage of the STFT is overcome in the wavelet transform (WT) [33]. In contrast to the FT, the WT offers the two-dimensional expansion for a time-dependent signal with the scale and translation parameters which are interpreted physically as the inverse of frequency and time, respectively. As a basis of the WT, we employ the mother wavelet which is localized in both frequency and time domain. The WT expansion is carried out in terms of a family of wavelets which is made by dilation and translation of the mother wavelet. The time evolution of frequency pattern can be followed with an optimal time-frequency resolution.

The WT appears to be an ideal tool for analyzing signals of a non-stationary nature. In recent years the WT has been applied to an analysis of biological signals [34], such as electroencephalographic (EEG) waves [47]-[48], and spikes [49]-[52]. EEG is a reflection of the activity of ensembles of neurons producing oscillations. By using the WT, we can obtain the time-dependent decomposition of EEG signals to $\delta$ (0.3-3.5 Hz), $\theta$ (3.5-7.5 Hz), $\alpha$ (7.5-12.5 Hz), $\beta$ (12.5-30.0 Hz) and $\gamma$ (30-70 Hz) components [47]-[48]. It has been shown that the WT is a powerful tool to the spike sorting in which coherent signals of a single target neuron are extracted from mixture of response signals [49]-[51]. The WT has been proved [49] to be superior than the conventional analysis methods like the principal component analysis (PCA) [53].

Besides the FT, another useful way to describe the dynamical behavior of stationary signals is to use Lyapunov exponents and correlation dimensions [54]. Lyapunov exponents, which were initially introduced for an analysis of chaos, measure the rate at which nearby points on an attractor diverge or converge along nearby trajectories. Correlation dimensions are meaningful quantities to examine whether a given signal is chaotic or not. We must note, however, that these quantities are defined only for stationary signals.

It is the purpose of the present paper to make a WT analysis of transient spike signals which have not been quantitatively discussed so far. We have analyzed spike trains consisting of $M$ (=1-5) pulses, generated by the Hodgkin-Huxley (HH) neuron model [55]. We have calculated the energy distribution and the wavelet entropy which are expressed in terms of the WT expansion coefficients. The WT is classified to the continuous wavelet transform (CWT) and the discrete wavelet transform (DWT). The former treats the scale and translation parameters as continuous variables while the latter adopts the variables only at the discrete points. Both the CWT and DWT have advantages. The CWT provides us with the intuitively clear results. On the contrary, the DWT, which is based on the ortho-normal basis, can be quickly performed by using the multi-resolution analysis.

Our paper is organized as follows: In the next § 2.1, we describe the HH neuron model [55], which is considered to be the most realistic neuron model among proposed theoretical models. In § 2.2, we briefly mention the CWT and DWT, presenting expressions for the energy distribution and the wavelet entropy. The results of WT analysis of spike signals by using both CWT and DWT are presented in § 3, where the effect of ISI of spike signals and of noises are studied. The final § 4 is devoted to discussions and conclusion.

## 2 Calculation Method


2.1 HH Neuron Model

In order to generate spike trains, we adopt a single HH model [55]. The neuron is assumed to be in the environment with the independent Ornstein-Uhlenbeck (OU) noises. Dynamics of the membrane potential $V$ of the HH neuron is described by the non-linear differential equation given by

$$ \bar{C} \frac{dV}{dt} = -I_{\text{ion}}(V,m,h,n) + I_{\text{ps}} + I_n, $$

where $\bar{C} = 1 \mu F/cm^2$ is the capacity of the membrane. The first term of Eq.(1) expresses the ion current given by

$$ I_{\text{ion}}(V,m,h,n) = g_{Na}m^3h(V-V_{Na}) + g_Kn^4(V-V_K) + g_L(V-V_L). $$

Here the maximum values of conductivities of Na and K channels and leakage are $g_{Na} = 120 \text{ mS/cm}^2$, $g_K = 36 \text{ mS/cm}^2$ and $g_L = 0.3 \text{ mS/cm}^2$, respectively; the respective reversal potentials are $V_{Na} = 50 \text{ mV}$, $V_K = -77 \text{ mV}$ and $V_L = -54.5 \text{ mV}$. Dynamics of the gating variables of Na and K channels, $m$, $h$ and $n$, are described by the ordinary differential equations, whose details have been given elsewhere [56].

The second term in Eq.(1) denotes the postsynaptic currents given by

$$ I_{\text{ps}} = g_s(V_a - V_s) \alpha(t - t_{im}), $$

with the alpha function $\alpha(t)$:

$$ \alpha(t) = (t/\tau_s) e^{-t/\tau_s} \Theta(t), $$

where $\Theta(t) = 1$ for $x \geq 0$ and $0$ for $x < 0$. Equation (3) expresses the postsynaptic current of the neuron, which is induced by the presynaptic spike-train input given by

$$ U_i(t) = V_a \sum_{m=1}^{M} \delta(t - t_{im}). $$

where $V_a$ means its magnitude, $M$ the number of input pulses and $t_{im}$ is the $m$-th firing time of the input. The interspike interval (ISI) of input signal is defined by

$$ T_{im} = t_{im+1} - t_{im}. $$

The third term in Eq.(1) denotes the OU noise given by

$$ \tau_n \frac{dI_n}{dt} = -I_n + \xi(t), $$

with the Gaussian white noise $\xi(t)$:

$$ <\xi(t)> = 0, $$

$$ <\xi(t)\xi(t')> = 2D \delta(t-t'), $$

where the bracket $<X>$ denote the time average. The intensity and the correlation time of white noises are given by $D$ and $\tau_n$, respectively.
Differential equations given by Eqs.(1)-(9) are solved by the fourth-order Runge-Kutta method by the integration time step of 0.01 ms with double precision. Some results are examined by using the exponential method. We incorporate OU noises given by Eqs.(7)-(9) using the method of Fox, Gatland, Roy and Vemuri [57]. The initial conditions for the variables are given by

\[ V(t) = -65 \text{ mV}, m(t) = 0.0526, h(t) = 0.600, n(t) = 0.313, \text{ for } t = 0, \quad (10) \]

which are the rest-state solution of a single HH neuron. We adopted parameters of \( V_a = 30 \), \( V_c = -50 \text{ mV} \), and \( \tau_s = \tau_n = 2 \text{ ms} \), with which the HH neuron is excitable receiving suprathreshold inputs.

2.2 Wavelet Analysis

2.2.1 Continuous Wavelet Transformation

The continuous wavelet transformation (CWT) for a given regular function \( f(t) \) with a vanishing average is defined by

\[ c(a,b) = \int dt \psi_{a,b}^*(t) f(t) \equiv \langle \psi_{a,b}(t), f(t) \rangle, \quad (11) \]

where \( a \) and \( b \) express the scale change and translation, respectively, and the star denotes the complex conjugate. The wavelet function \( \psi_{a,b}(t) \) is generated by dilation and translation of the mother wavelet \( \psi(t) \) such as

\[ \psi_{a,b}(t) = |a|^{-1/2} \psi \left( \frac{t-b}{a} \right). \quad (12) \]

The parameters of \( a \) and \( b \) in Eqs.(11) and (12) stand for the inverse of the frequency and the time, respectively. Then the CWT transforms the time-dependent function \( f(t) \) into the frequency- and time-dependent function \( c(a,b) \). The mother wavelet is a smooth function with good localization in both frequency and time spaces. A wavelet family given by Eq.(12) play a role of elementary function, representing the function \( f(t) \) as a superposition of wavelets \( \psi_{a,b}(t) \).

The inverse of the wavelet transformation may be given by

\[ f(t) = C_\psi^{-1} \int \frac{da}{a^2} \int db \ c(a,b) \ \psi_{a,b}(t), \quad (13) \]

when the mother wavelet satisfies the following two conditions:

(i) the admissibility condition given by

\[ 0 < C_\psi < \infty, \quad (14) \]

with

\[ C_\psi = \int_{-\infty}^{\infty} d\omega \ |\hat{\psi}(\omega)|^2 / |\omega|, \quad (15) \]

where \( \hat{\psi}(\omega) \) is the Fourier transform of \( \psi(t) \), and
(ii) the zero mean of the mother wavelet:
\[
\int_{-\infty}^{\infty} dt \, \psi(t) = \hat{\Psi}(0) = 0.
\] (16)

**Energy Distribution**

Parseval’s theorem shows that the power spectrum is given by
\[
E_{\text{tot}} = \int dt \, |f(t)|^2 = \int \frac{da}{a^2} \int db \, \epsilon(a, b) = \int \frac{da}{a^2} \, E(a),
\] (17)
where the energy-density distribution \(\epsilon(a, b)\) and the \(a\)-dependent energy is given by
\[
\epsilon(a, b) = C_{\psi}^{-1} |c(a, b)|^2, \quad E(a) = \int db \, \epsilon(a, b).
\] (18) (19)

**Wavelet Entropy**

Equation (17) suggests that the probability of the power spectrum relevant to the states of \(a\) and \(b\) is given by
\[
p(a, b) = \epsilon(a, b) / E_{\text{tot}},
\] (20)
with the normalization condition:
\[
\int \frac{da}{a^2} \int db \, p(a, b) = 1.
\] (21)

We may define the wavelet entropy given by
\[
S = \int \frac{da}{a^2} \int db \, s(a, b) = \int \frac{da}{a^2} \, S_1(a),
\] (22)
where \(s(a, b)\) and \(S_1(a)\) are given by
\[
s(a, b) = -p(a, b) \log_2[p(a, b)], \quad S_1(a) = \int db \, s(a, b),
\] (23) (24)

Alternatively, we may define the wavelet entropy by
\[
S' = \int da \, S_2(a),
\] (25)
with
\[
S_2(a) = -q(a) \log_2[q(a)],
\] (26)
where the probability \(q(a)\) is given by
\[
q(a) = a^{-2} E(a) / E_{\text{tot}},
\] (27)
satisfying the normalization condition:

\[ \int da \, q(a) = 1, \]  

(28)

the prefactor \( a^{-2} \) in Eq.(27) arising from the space factor relevant to the integration with respect to the variable \( a \). Our numerical calculations to be presented in the following subsection shows that \( S_1(a)/a^2 \) defined by Eq.(24) yields similar results as \( S_2(a) \) defined by Eq.(26).

### 2.2.2 Discrete Wavelet Transformation

The discrete wavelet transformation (DWT) is defined for discrete values of \( a = 2^j \) and \( b = 2^j k \) \((j, k: \text{integers})\) as

\[ c_{jk} \equiv c(2^j, 2^j k) = \langle \psi_{jk}(t), f(t) \rangle, \]  

(29)

with

\[ \psi_{jk}(t) = 2^{-j/2} \psi(2^{-j} t - k). \]  

(30)

The ortho-normal condition for the wavelet functions is given by

\[ \langle \psi_{jk}(t), \psi_{j'k'}(t) \rangle = \delta_{jj'} \delta_{kk'}, \]  

(31)

which leads to the inverse DWT:

\[ f(t) = \sum_j \sum_k c_{jk} \psi_{jk}(t). \]  

(32)

In the multiresolution analysis (MRA) of the DWT, we introduce a scaling function \( \phi(t) \), which satisfies the recurrent relation with \( 2^K \) masking coefficients, \( h_k \), given by

\[ \phi(t) = \sqrt{2} \sum_{k=0}^{2^K-1} h_k \phi(2t - k), \]  

(33)

with the normalization condition for \( \phi(t) \) given by

\[ \int dt \, \phi(t) = 1. \]  

(34)

A family of wavelet functions are generated by

\[ \psi(t) = \sqrt{2} \sum_{k=0}^{2^K-1} (-1)^k h_{2^K-1-k} \phi(2t - k). \]  

(35)

The scaling and wavelet functions satisfy the orthogonal relations:

\[ \langle \phi(t), \phi(t - m) \rangle = \delta_{m0}, \quad \langle \psi(t), \psi(t - m) \rangle = \delta_{m0}, \quad \text{and} \quad \langle \phi(t), \psi(t - m) \rangle = 0. \]  

(36)

The set of masking coefficients \( h_j \) are chosen so as to satisfy the conditions shown above.
The simplest wavelet function for \( K = 1 \) is the Harr wavelet for which we get \( h_0 = h_1 = 1/\sqrt{2} \) and
\[
\psi_H(t) = \begin{cases} 
1 & \text{for } 0 \leq t < 1/2 \\
-1 & \text{for } 1/2 \leq t < 1, \\
0 & \text{otherwise.}
\end{cases}
\]

(37) (38) (39)

In the more sophisticated wavelets like the Daubechies wavelet, an additional condition given by
\[
\int dt \, t^\ell \psi(t) = 0, \quad \text{for } \ell = 0, 1, 2, 3\ldots L - 1
\]

(40) is imposed for the smoothness of the wavelet function. Furthermore, in the Coiflet wavelet, for example, a similar smoothing condition is imposed also for the scaling function as
\[
\int dt \, t^\ell \phi(t) = 0, \quad \text{for } \ell = 1, 2, 3\ldots L' - 1
\]

(41)

In principle the expansion coefficients \( c_{jk} \) in DWT may be calculated by using Eq.(29) for a given function \( f(t) \) and an adopted mother wavelet \( \psi(t) \). This integration is, however, inconvenient, and in an actual fast wavelet transformation, the expansion coefficients are obtained by a matrix multiplication with the use of the iterative formulae given by the masking coefficients and expansion coefficients of the neighboring levels of indices, \( j \) and \( k \).

Energy Distribution

Parseval’s theorem for the DWT is given by
\[
E_{\text{tot}} = \int dt \, |f(t)|^2 = \sum_j \sum_k \epsilon_{jk} = \sum_j E_j,
\]

(42) where \( \epsilon_{jk} \), the energy distribution specified by \( j \) and \( k \), and the \( j \)-dependent energy \( E_j \) are given by
\[
\epsilon_{jk} = |c_{jk}|^2,
\]

(43) \[
E_j = \sum_k \epsilon_{jk}.
\]

(44)

Wavelet Entropy

We may define the wavelet entropy as
\[
S = \sum_j S_j,
\]

(45) with
\[
S_j = -\sum_k p_{jk} \log_2 p_{jk},
\]

(46) where the probability \( p_{jk} \) is given by
\[
p_{jk} = \epsilon_{jk}/E_{\text{tot}},
\]

(47)
satisfying the normalization condition:
\[ \sum_j \sum_k p_{jk} = 1. \]  
(48)

An alternative definition of the entropy is given by
\[ S' = \sum_j S'_j, \]  
(49)

with
\[ S'_j = -q_j \log_2 q_j, \]  
(50)

where \( q_j \) expresses the probability given by
\[ q_j = \frac{E_j}{E_{tot}}, \]  
(51)

with the normalization condition:
\[ \sum_j q_j = 1. \]  
(52)

A comparison between \( S_j \) and \( S'_j \) will be numerically made in the following section.

Hereafter, time, voltage, current, noise intensity (\( D \)), energy (\( E_{tot} \)) and entropy (\( S \)) are expressed in units of ms, mV, \( \mu \)A/cm\(^2\), \( \mu \)A\(^2\)/cm\(^4\), mV\(^2\) · ms and bits, respectively.

### 3 Calculated Results

Clustered spike trains to be analyzed are generated by using the HH neuron which receives input signals consisting of \( M (=1-5) \) pulses with the ISI of \( T_{im} = 25 \) ms \((m=1-4)\). Pulse clusters are separated by the longer interval of 100 ms. We choose this ISI value of 25 ms because \( \gamma \)-wave spikes with the average frequency of about 40 Hz are ubiquitous in brain [27]-[29]. The time dependence of \( U_i \), input potential \( I (= I_{ps} + I_n) \) and membrane potential \( V \) is shown in Fig. 1. Spikes fire after an injection of input pulses with a delay of about 2 ~ 3 ms.

Generated spike trains have been analyzed with the use of the WT. One of the advantages of the WT over the FT is that we can choose a proper mother wavelet depending on the shape of signals to be examined. Among many candidates of mother wavelets, we have adopted the Coiflet because its shape is similar to that of spikes. Compromising the accuracy and the computation effort, we have decided to adopt the Coiflet of order 3 as the mother wavelet for our analysis.

We analyze the time-dependent membrane potential \( V(t) \) by setting the signal to be
\[ f(t) = V(t) - < V(t) > \]  
in Eqs.(11) and (29), \( < V(t) > \) being the time average of \( V(t) \). Spike signals \( V(t) \) are assumed to be given at the sampled \( t \) values with a sampling time of \( \Delta t = 1 \) ms, and are analyzed by both the CWT and DWT with the use of MATLAB wavelet tool box.

The analyzed spike train is depicted in Fig. 2(a) and the pattern of the expansion coefficients \( c(a, b) \) obtained by the CWT is shown in the \((a, b)\) space of Fig. 2(b), where
the medium dark tone denotes the zero level and the black (white) expresses the negative (positive) value. Note that $1/a$ and $b$ physically stand for the frequency and time, respectively. The pattern of the energy-density distribution $\epsilon(a, b) = |c(a, b)|^2$ by setting $\hat{C}_\psi = 1$ in Eq.(18) hereafter is shown in Fig. 2(c), where black and white denote the minimum (zero) and maximum levels, respectively. Patterns near the both sides along vertical axis in Fig. 2(b) and (c) are due to the edge effect and should not be taken seriously. Figure 2(c) shows that for a single ($M = 1$) spike signal, the energy-density pattern shows a cone which is progressively broader at larger $a$. For spike signals with multiple $M$, cones of spikes are separable for small $a$ whereas they merge for larger $a$, yielding intriguing structure in the pattern. Figure 3 shows the $b$ dependence of the expansion coefficients $c(a, b)$ for $a = 2, 4, 8, 16, 32$ and 64. We notice that the CWT coefficients for smaller $a$ oscillates with shorter period. The magnitudes of $c(a, b)$ are largest for $a \sim 8 - 16$ in Fig. 3: note vertical scales for $a= 2$ and 64 to be different from those for the other $a$ values.

In what follows, we pay our attention to the $M = 3$ spike in order to perform more detailed analysis. Figure 4(a) shows the $M = 3$ spike signal to be analyzed. The energy-density distribution analyzed by the CWT is depicted in Fig. 4(b). At small $a$ each pulse yields a characteristic cone pattern. At $10 \lesssim a \lesssim 20$, cones arising the consecutive pulses separated by $T_o = 25$ msec, begin to merge. At larger $a \approx 40$ cones originating from the first and the last pulses, which are separated by $2T_o = 50$ msec, begins to correlate. The pattern has structures near both end sides of vertical axis because of the edge effect.

Figure 5 expresses the $b$ dependence of the expansion coefficients of $c(a, b)$ for typical $a$ values calculated in the CWT. As noticed in Fig. 3, the magnitudes of $c(a, b)$ is most significant for $a \sim 16$. This is more clearly seen in the $a$-dependence of the energy-density distribution $E(a)$ shown in Fig. 6(a) which has a peak at $a \sim 20$. However, when taking into account the space factor $a^{-2}$ in the integration with respect to the variable $a$ [see Eq.(17)], we note that $E(a)/a^2$ has a peak at much a lower value of $a = 4$.

The $a$-dependent average $[\mu(a)]$ and root-mean-square value $[\sigma(a)]$ of CWT coefficients are plotted in Fig. 7(a) and (b), respectively. A rise in $\mu(a)$ at $a > 30$ is due to the edge effect. We note that $\sigma(a)$ has a peak at $a \sim 20$. When the space factor $a^{-2}$ is included, the peak position of $\sigma(a)/a^2$ moves to the lower value of $a = 4$.

So far we have employed the CWT. When we apply the DWT to the signal shown in Fig. 4(a), we get the $j-$ and $k$-dependent energy distribution, $\epsilon_{jk}$, which is plotted in Fig. 4(c). Because the scale ($a = 2^j$) and translation ($b = 2^j k$) parameters are discrete in the DWT, the energy distribution, $\epsilon_{jk}$, defined by Eq.(43) are depicted by the blocks in the $(a, b)$ space. The DWT decomposition of the spike signal: $V = \sum_{j=1}^{6} a_j + d_6$, is shown in Fig. 8. A contribution from $j = 2$ ($a = 4$) to $V$ seems to be predominant. This is supported by the calculated $j$-dependent energy $E_j$ plotted in Fig. 6(c), which has the maximum at $j = 2$ ($a = 4$). The $j$ dependence of the average $[\mu_j]$ and RMS value $[\sigma_j]$ of the DWT coefficients are plotted in Fig. 7(c) and (d), respectively. The maximum in $\sigma_j$ is realized at $2^j = 8$ ($j = 3$), which should be compared with the maximum at $a = 4$ in $\sigma(a)/a^2$. These comparisons show that the $a$ dependence of $E(a)/a^2 [\sigma(a)/a^2]$ in the CWT are in fairly good agreement with the $j$ dependence of $E_j [\sigma_j]$ in the DWT.

Next we discuss the wavelet entropy calculated in terms of the WT expansion coefficients. Figure 9(a) shows the contour map depicting the entropy density $s(a, b)$ defined by Eq.(23) with the CWT. Figure 9(b) shows the $a$ dependence of $s(a, b)$ for typical values
of $a = 103, 109$ and $115$, which are indicated by vertical, dashed lines in Fig. 9(a). $s(a, b)$ has peaks at $a \sim 10$, $a \sim 15$ and $a \sim 20$ for $b = 103, b = 109$ and $b = 115$, respectively. Figure 9(c) expresses the $b$ dependence of $s(a, b)$ for $b = 10, 20$ and $30$ ms, which are shown by horizontal, dashed lines in Fig. 9(a). Although $s(a, b)$ for $a = 10$ has the maximum peaks at the firing times $t_{on} (= 103, 128$ and $153$ ms), it has also side-peaks before and after $t_{on}$. For $a = 20$ and $30$, $s(a, b)$ has peaks not only at $t_{on}$ but also between the firing times. The $a$ dependence of the CWT entropy $S_1(a)$ defined by Eq.(24) is plotted in Fig. 6(b), which has a peak at $a = 20$, just as $E(a)$ shown in Fig. 6(a). We note, however, that $S_1(a)/a^2$ has a peak at a lower value of $a = 3$, which may be compared with the peak position at $a = 4$ of the entropy $S_2(a)$ defined by Eq.(26).

The DWT entropies, $S_j$ and $S'_j$, defined by Eqs.(46) and (50), are shown in Fig. 6(d). Although $S_j$ is about two times larger than $S'_j$, both entropies have a similar $j$ dependence with the maximum at $a = 4$ ($j = 2$).

### 3.1 Effects of Variation in ISI

We will discuss in this subsection, how the variation in ISI of the spike signal modifies the result of the WT. Firstly we equally change both $T_{o1}$ and $T_{o2}$ as $T_{o1} = T_{o2} \equiv T_o$. Figure 10(a), (b), (c) and (d) show the analyzed spike signal (upper frames) and the energy-density patterns (lower frames) for $T_{o} = 15, 25, 35$ and $50$ ms, respectively. We note that the size of patterns becomes large almost in proportion to an increase in $T_o$. Figure 11(a) and (b) show the $a$ dependence of the energy-density distribution $E(a)$ and the entropy $S(a)$ in the CWT, respectively. The peak position moves to larger $a$ for the spike signal with larger $T_o$, as expected. The relevant $j$ dependence of $E_j$ and $S_j$ in the DWT is shown in Fig. 11(c) and (d). When $T_o$ is smaller, $E_j$ and $S_j$ have large magnitude for smaller $j$, which is consistent with the result obtained in the CWT.

The FT for a signal $f(t)$ is defined by

$$\hat{F}(\omega) = \int dt \ e^{-i\omega t} f(t).$$

(53)

When $f(t)$ is given by a delta-function-type function:

$$f(t) = \sum_{n=1}^{3} \delta(t - t_{on}),$$

(54)

which is a simplification of our $M = 3$ HH spike with firing times of $t_{on}$, its FT spectrum is given by

$$|\hat{F}(\omega)|^2 = 2 \sum_{n=1}^{3} \cos(2\pi f/f_{on}) + 3.$$

(55)

In Eq.(55) $f = \omega/2\pi$ is the frequency and the fundamental frequencies $f_{on}$ ($n = 1 - 3$) are given by $f_{o1} = 1/T_{o1}$, $f_{o2} = 1/T_{o2}$ and $f_{o3} = 1/(T_{o1} + T_{o2})$.

Figures 12(a), (b) (c) and (d) show the FT frequency spectra of the HH spike signals for $T_o = 15, 25, 35$ and $50$ ms, respectively. When $T_o = 25$, for example, the fundamental frequencies are $f_{o1} = f_{o2} = 40$ and $f_{o3} = 20$ Hz, the former being coincidentally the second harmonics of the latter. The dashed curve in Fig. 12(b) shows the FT spectra given by
Eq. (55) for a delta-function-type signal given by Eq. (54) with \( T_0 = 25 \) ms, which is in good agreement with the FT spectra of the HH spike at \( f < 150 \) Hz.

Next we investigate the effect of ISI on the WT result by changing \( T_{o1} \) but keeping \( T_{o1} + T_{o2} = 50 \) ms. The analyzed spike signals (upper frames) and the pattern of the energy-density distribution (lower frames) for \( T_{o1} = 10, 15, 20 \) and \( 25 \) ms are shown in Fig. 13(a), (b), (c) and (d), respectively. Note that the average ISIs are the same (25 ms) but their RMS are different: \( \langle (T_{on} - \langle T_{on} \rangle^2) \rangle^{1/2} = 15, 10, 5 \) and \( 0 \) ms for \( T_{o1} = 10, 15, 20, 25 \) ms, respectively. For the case of \( T_{o1} = T_{o2} = 25 \) ms, the calculated pattern in Fig. 13(d) is nearly symmetric with respect to the axis of \( b = 128 \) ms, at which the second spike fires. With introducing a small asymmetry in ISI: \( T_{o1} = 20 (T_{o2} = 30) \) ms, the pattern becomes asymmetric, as shown in Fig. 13(c). This is more clearly seen in Fig. 13(a) for the case of \( T_{o1} = 10 (T_{o2} = 40) \) ms: smaller \( T_{o1} \) and larger \( T_{o2} \) yield smaller and larger patterns, respectively. Figure 14(a) and (b) show the \( a \) dependence of \( E(a) \) and \( S(a) \), respectively. In the case of \( T_{o1} = 25 \) ms, \( E(a) \) has a single maximum at \( a \sim 20 \). On the contrary, in the case of \( T_{o1} = 10 \) ms, \( E(a) \) and \( S(a) \) have double maxima: the peak at smaller \( a \) arises from the contribution due to a smaller \( T_{o1} \) and the peak at larger \( a \) from a larger \( T_{o2} \). These features are consistent with the results obtained in the DWT, which are shown in Figs. 14(c) and 14(d). Figures 13 and 14 clearly show that the response of the HH neuron cannot described only by the rate of the input pulses [56], in agreement with experiments [28, 29].

Figure 15 shows the FT spectra for spike signals for \( T_{o1} = 10, 15, 20 \) and \( 25 \) ms. In the case of \( T_{o1} = 15 \) ms, for example, the fundamental frequencies are 66.7, 28.6 and 20 Hz. Although a glimpse of Fig. 15(b) suggests that fundamental frequencies are 60 and 80 Hz, it is not true. The dashed curve in Fig. 15(b) shows the FT spectra given by Eq. (55) for a delta-function signal given by Eq. (54) with \( f_{o1} = 66.7, f_{o2} = 28.6 \) and \( f_{o3} = 20 \) Hz, which is in good agreement with the FT spectra of HH spikes at \( f < 150 \) Hz.

### 3.2 Effects of Noises

We will study, in this subsection, the effect of OU noises given by Eqs. (7)-(9). Figure 16(a), (b), (c) and (d) show the spike signals (upper frames) and the CWT patterns of the energy-density distribution (lower frames) for \( D = 0, 1, 2 \) and \( 3 \), respectively. The result without noises \( (D = 0) \) has been shown previously [e.g. Fig. 4(b)]. When noises are introduced, spike signals lead to fine structures in the CWT patterns. For a large \( D = 3 \), applied noises trigger a spurious spike at \( t = 203 \) ms.

Figure 17(a) and (b) show \( E(a) \) and \( S_1(a) \) for \( D = 0, 1, 2 \) and \( 3 \) calculated by the CWT coefficients. Applied noises provide extra energy contributions in a fairly wide range of \( a \) value. Particularly for \( D = 3 \), \( E(a) \) and \( S(a) \) are much increased by a spuriously triggered spike at \( t = 203 \) ms.

Similar results are obtained in the \( j \)-dependent energy \( (E_j) \) and entropy \( (S_j) \) calculated by the DWT, which are plotted in Fig. 17(c) and (d).

Spike signals with noises are analyzed also by the FT, whose frequency spectra for \( D = 0, 1, 2 \) and \( 3 \) are plotted in Fig. 18(a), (b), (c) and (d), respectively. It is interesting that peaks of the fundamental frequency of 40 Hz and its harmonics are sharpened by noises.
4 Conclusion and Discussion

One of the advantages of the DWT is that we can easily separate noise components from a given signal. As the first example, we discuss the denoising by using the DWT. The key point in the denoising is how to choose which wavelet coefficients are correlated with the signal and which ones with noises. The simple denoising is to neglect some DWT expansion coefficients when reproducing the signal by the inverse wavelet transformation.

In getting the inverse WT by

$$f_I(t) = \sum_j \sum_k c_{jk}^{dn} \psi_{jk}(t),$$

we may assume that the components for $a < a_c$ in the $(a,b)$ plane arise from noises to set the denoising coefficients $c_{jk}^{dn}$ as

$$c_{jk}^{dn} = c_{jk}, \quad \text{for } j \geq j_c (a \geq a_c)$$

$$= 0, \quad \text{otherwise} \quad \text{(Method I)}$$

where $j_c = \log_2 a_c$ is the critical $j$ value. A demonstration of denoising of spike signals with $M = 3$ and $D = 3$ is given in Fig. 19. Figure 19(a) expresses the original output spike, and Fig. 19(b) shows the inverse signals by using the method I [eq.(4.2)] with $j_c = 2$. For a comparison, we show the relevant results for the postsynaptic input $I$: the original signal in Fig. 19(d) and the inverse signal with denoising for $j_c = 2$ in Fig. 19(e).

Since the DWT transforms the original signal to the two-dimensional $(a,b)$ plane, it has much freedom than the FT, which makes it possible for us to adopt the more sophisticated denoising. We may assume that the components for $b < b_L$ or $b > b_U$ at $a < a_c$ in the $(a,b)$ plane are noises to set the denoising WT coefficients as

$$c_{jk}^{dn} = c_{jk}, \quad \text{for } j \leq j_c \text{ or } k_L \leq k \leq k_U$$

$$= 0, \quad \text{otherwise} \quad \text{(Method II)}$$

where $j_c = \log_2 a_c$, and $k_L = b_L 2^{-j}$ and $k_U = b_U 2^{-j}$ are lower and upper critical $k$ values. Figures 19(c) and 19(f) show the denoising signals of the output and postsynaptic signals, respectively, by using the method II [Eq.(4.3)] with $b_L = 40$, $b_U = 220$ and $j_c = 4$. The denoising method II given by Eq. (4.3) is better than the method I given by eq.(4.2) because the magnitude of a spurious spike at $t \sim 200$ ms is much reduced while the signal at $100 < t < 160$ ms is better reproduced in the method II than in the method I.

As the second example using the DWT, we discuss the signal-to-noise ratio (SNR). From the above consideration, we may define the signal component $A_s$ and the noise component $A_n$ by

$$A_s = \sum_j \sum_k |c_{jk}^{dn}|^2,$$

$$A_n = \sum_j \sum_k (|c_{jk}|^2 - |c_{jk}^{dn}|^2)$$

which lead the SNR $\eta$:

$$\eta = \log_{10}(A_s/A_n).$$
The solid curves in Fig. 20(a) and Fig. 20(b) shows the $D$-dependent SNR of output ($V$) and input signals ($I_i$), respectively, with $M = 3$ calculated by the denoising method I given by eq. (4.2) with $j_c = 2$. It might be strange that SNR is finite even for no noises ($D = 0$). This is because signals for $D = 0$ already included in the $j = 1$ component are regarded as noises in the denoising method I though its magnitude is small. On the contrary, the dashed curves in Fig. 20(a) and 20(b) show the SNR as a function of $D$ calculated by the denoising method II given by eq. (4.3) with $b_L = 40$, $b_U = 220$ and $j_c = 4$. Because of the condition imposed for the $a$ variable in the method II, the noise contribution is much reduced for small $D$, yielding a large SNR. With increasing the value of $D$, SNR of the input and output signals decreases as expected.

Finally, we apply the CWT to a signal which is a simplified one of the original HH neuron spike, in order to get some insight how the detailed shape of spikes is relevant to information transmission. As its candidate, we adopt a square pulse with the width of 1 ms, the delta-function-type signal. Figures 21(a) and (b) show the analyzed signal and its energy-density distribution in the CWT, respectively. Comparing Fig. 21(b) with Fig. 4 (b) for the original HH spike, we note that except for very small value of $a$ ($\sim 4$), the CWT pattern for the delta-function-type signal is almost the same as that of the original HH spike. This suggests that information is predominantly carried by firing times of spikes, but not by their detailed structure. This agrees with the conventional wisdom in the neuroscience community.

To summarize, we have analyzed transient spike signals with the use of both the CWT and DWT. The WT has been shown to be more useful than the FT for an analysis of transient signals like spikes. The WT now has a wide-range of applications including the information compression like MPEG and JPEG. It might be possible that real neural systems adopt the WT-like technique for their efficient information transaction.

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Figure Captions

Fig. 1 The time course of (a) the input potential $U_i$, (b) the postsynaptic potential $I (= I_{ps} + I_n)$ and (c) the membrane potential $V$.

Fig. 2 (a) The analyzed signal, (b) the pattern of the CWT coefficients $c(a, b)$, and (c) that of the energy-density distribution $\epsilon(a, b) \equiv |c(a, b)|^2$. Scales of colors from minimum to maximum in (b) and (c) are shown.

Fig. 3 The $b$ dependence of the CWT coefficients $c(a, b)$ for specified $a$ values.

Fig. 4 (a) The $M = 3$ spike signal, (b) the profile of energy distribution $\epsilon(a, b)$ analyzed by the CWT, and (c) that analyzed by the DWT.

Fig. 5 The $b$ dependence of the CWT coefficients $c(a, b)$ for specified $a$ values.

Fig. 6 (a) The $a$-dependent energy $[E(a)$ and $E(a)/a^2]$ and (b) entropy $[S(a)$ and $S(a)/a^2]$ in CWT. (c) The $j$-dependent energy $(E_j)$ and (d) entropy $(S_j, S_j')$ in DWT, solid lines being drawn only for a guide of eye (see text).

Fig. 7 (a) The $a$-dependent average of $c(a, b) [\mu(a)$ and $\mu(a)/a^2]$, and (b) their RMS $[\sigma(a)$ and $\sigma/a^2]$ in CWT. (c) The $j$-dependent average of $c_{jk} (\mu_j)$, and (d) their RMS $(\sigma_j)$ in DWT, solid lines being drawn only for a guide of eye (see text).

Fig. 8 The DWT decomposition of the signal to various components; $V = \sum_{j=1}^{6} d_j + a_6$.

Fig. 9 (a) The contour map of the entropy distribution $s(a, b)$. (b) The $a$ dependence of $s(a, b)$ for $b = 103$ (solid curve), 109 (dot-dashed curve) and 115 ms (dashed curve), whose positions are indicated by vertical, dashed lines in (a). (c) The $b$ dependence of $s(a, b)$ for $a = 10$ (solid curve), 20 (dot-dashed curve) and 30 (dashed curve), whose positions are indicated by horizontal, dashed lines in (a).

Fig. 10 The time dependence of spikes (upper frames) and the energy-density patterns (lower frames) in the CWT for (a) $T_o = 15$, (b) 25, (c) 35 and (d) 50 ms.

Fig. 11 (a) The $a$ dependence of $E(a)$ and (b) the entropy $S_1(a)$ in the CWT for $T_o = 15, 25, 35$ and 50 ms. (c) The $j$ dependence of $E_j$ and (d) the entropy $S_j$ in the DWT for $T_o = 15, 25, 35$ and 50 ms.

Fig. 12 The FT spectra for (a) $T_o = 15$, (b) 25, (c) 35 and (d) 50 ms. The dashed curve in (b) expresses the FT spectra given by Eq.(55) for a delta-function-type signal given by Eq.(54) with $T_o = 25$ ms.

Fig. 13 The time dependence of spikes (upper frames) and the energy-density patterns (lower frames) in the CWT for (a) $T_{o1} = 10$, (b) 15, (c) 20 and (d) 25 ms.
Fig. 14 (a) The $a$ dependence of $E(a)$ and (b) the entropy $S_1(a)$ in the CWT for $T_{o1} = 10, 15, 20$ and $25$ ms. (c) The $j$ dependence of $E_j$ and (d) the entropy $S_J$ in the DWT for $T_{o1} = 10, 15, 20$ and $25$ ms.

Fig. 15 The FT spectra for (a) $T_{o1} = 10$, (b) 15, (c) 20 and (d) 25 ms. The dashed curve in (b) expresses the FT spectra given by Eq.(55) for a delta-function-type signal given by Eq.(54) with $T_{o1} = 15$ ms.

Fig. 16 The time dependence of spikes (upper frames) and the energy-density patterns (lower frames) in the CWT for (a) $D = 0$, (b) 1, (c) 2, and (d) 3.

Fig. 17 (a) The $a$ dependence of $E(a)$ and (b) the entropy $S_1(a)$ in the CWT for $D = 0, 1, 2$ and 3. (c) The $j$ dependence of $E_j$ and (d) the entropy $S_J$ in the DWT for $D = 0, 1, 2$ and 3.

Fig. 18 The FT spectra for (a) $D = 0$, (b) 1, (c) 2, and (d) 3.

Fig. 19 (a) The original output spike $V$ with $D = 3$, (b) its inverse signal by the denoising method I [eq.(4.2)] with $j_c = 2$, and (c) that by the denoising method II [eq.(4.3)] with $b_L = 40, b_U = 220$ and $j_c = 4$. (d) The original input signal $I_i$ with $D = 3$ (e) its inverse signal by the denoising method I [eq.(4.2)] with $j_c = 2$, and (f) that by the denoising method II [eq.(4.3)] with $b_L = 40, b_U = 220$ and $j_c = 4$.

Fig. 20 The $D$ dependence of SNR of (a) the output spike signal $V$ and (b) the input presynaptic signal $I_i$; the solid curves show the results by using the denoising method I [eq.(4.2)] with $j_c = 2$, and the dashed curves express the results by using the denoising method II [eq.(4.3)] with $b_L = 40, b_U = 220$ and $j_c = 4$ (see text).

Fig. 21 (a) The analyzed delta-function-type signal and (b) the energy-density pattern in the CWT (see text).
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