PAPER

Weak Coupling Causes Non-monotonic Changes and Bifurcations in the Interspike Intervals in the BVP Model with High-Frequency Input and Noise

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SUMMARY Effects of high-frequency cyclic input and noise on interspike intervals in the coupled Bonhoeffer-van der Pol (BVP) model are studied with computer simulation. When two BVP elements are weakly coupled and cyclic input or noise is added to the first element, the interspike intervals of the second element decrease non-monotonically as the amplitude of the input increases. Further, complicated bifurcations in the interspike intervals are caused by cyclic input in the coupled BVP model in the oscillating state. Effects of the coupling on small rotations due to noise and the interruption of oscillations due to cyclic input, which occur when the equilibrium point is close to the critical point, are also studied. The non-monotonic changes and bifurcations in the interspike intervals are attributed to the phase locking of the coupled elements.

key words: *coupled BVP model, non-monotonic change, high-frequency input, noise*

1. Introduction

Responses of a neuron to various stimuli have been of wide interest since they are fundamental to the understanding of the function of the nervous system. In general a neuron has two states: an excitable state and an oscillating state. The former describes the generation of spikes by adding stimuli and the latter corresponds to spontaneous firing.

In the excitable state, it is known that the spikes generated by periodic pulses show the phase locking and complicated bifurcations when the period of the input lies in the refractory period in a simple neuron model [23], the BVP model [1], [27], the Hodgkin-Huxley model [29] and the squid giant axon [30]. Computer simulation has shown that high-frequency sinusoidal input fails to generate spikes and blocks the propagation of spikes in the Hodgkin-Huxley model [26].

Recently, effects of noise on neuronal activity have much attention in the context of stochastic resonance in excitable media [6] (and references therein). Coherence resonance (stochastic resonance without signals) [7], [25], the phenomenon in which the regularity of spikes is optimal at intermediate noise strength, was also found in the BVP model [19], [24], the Plant model [20] and the Hodgkin-Huxley model [18]. Further, several results have been obtained on coherence resonance in the coupled BVP model [12], [13], [15], [16].

In the oscillating state, periodic stimuli cause bifurcations and chaos similar to those in the excitable state. Sinusoidal input the period of which lies in the refractory period causes chaotic responses in the Hodgkin-Huxley model and the squid giant axon [3], [17] (and references therein). High-frequency sinusoidal input decreases the period of the BVP oscillator [14].

Concerning effects of noise, experimental and simulation studies on actual and model neurons have shown that the noise causes various changes in the oscillation period of the repetitive firing of a neuron. It is expected that the oscillation period decreases as the noise strengthens since the firing of a neuron is regarded as a relaxation oscillator [8]. It was shown that the oscillation period decreases when the noise is added to stimulus currents in experiments on the giant squid axon [9] and the crayfish stretch-receptor neuron [2] under spontaneous firing. However, the noise either decreases or does not change or even increases the oscillation period of afferent nerve fibers of the guitarfish [21]. It can also be seen from computer simulation with stochastic versions of the Hodgkin-Huxley model that fluctuations in opening and closing of Na (K) channels cause increases (decreases) in the oscillation period [28], while white noise has little effects on the mean of the oscillation period [32]. Further, computer simulation on the BVP model showed that the oscillation period decreases (increases) by adding the noise to the fast (slow) variable [11], [14].

In this study, effects of coupling on the response of the BVP model to high-frequency cyclic input and noise are studied with computer simulation. Concerning the coupled BVP model in the excitable state with noise, coherence resonance with multiple peaks has been reported elsewhere [13]. We then focus on the excitable state with high-frequency input as well as the oscillating state with noise or high-frequency input. It is shown that non-monotonic changes and bifurcations in the interspike intervals or the oscillation periods occur in the coupled BVP model when the coupling between the elements is weak.

Model equations and simulation method are given

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in Sect. 2. Non-monotonic changes in the interspike intervals generated by high-frequency sinusoidal input in the coupled BVP model are shown in Sect. 3. In Sects. 4 and 5, it is shown that non-monotonic changes and bifurcations in the period of the coupled BVP oscillators are caused by noise and high-frequency sinusoidal input. Further, effects of the coupling in the BVP oscillators close to the excitable state are considered in Sect. 6. It is shown that increases in the oscillation period due to small rotations caused by noise are suppressed and complicated patterns in the oscillation period with cyclic input are caused by weak coupling. Discussion on mechanism causing non-monotonic changes in the interspike intervals is given in Sect. 7.

2. Simulation Method

A couple of simplified versions of the Bonhoeffer-van der Pol (BVP) model [4], [5] with sinusoidal input and noise are used.

$$
\begin{aligned}
dv_1(t)/dt &= D(v_2(t) - v_1(t)) + f(v_1(t)) - w_1(t) \\
&\quad + A\sin 2\pi t/T_{in} + \sigma n(t) \\
dw_1(t)/dt &= \varepsilon v_1(t) \\
dv_2(t)/dt &= D(v_1(t) - v_2(t)) + f(v_2(t)) - w_2(t) \\
dw_2(t)/dt &= \varepsilon v_2(t) \quad (\varepsilon = 0.001)
\end{aligned} \tag{1}
$$

where $f(v)$ is a cubic function:

$$f(v;\Delta) = -(v-\Delta)(v-1-\Delta)(v+1-\Delta) \tag{2}$$

and $n(t)$ is Gaussian white noise with zero mean.

$$
\begin{aligned}
&E\{n(t)\} = 0 \\
&E\{n(t_1)n(t_2)\} = \delta(t_1 - t_2)
\end{aligned} \tag{3}
$$

Two identical BVP elements are linearly coupled to each other with the coupling strength D. Sinusoidal input with the amplitude A and the period T_{in} or Gaussian white noise with the strength σ is added to the fast variable v_1 of the first element. Equation (1) is numerically integrated using the simple Euler method with the time step $\Delta t = 0.1$. It was confirmed that similar results are obtained in simulation with $\Delta t = 0.2$.

3. High-Frequency Input to the Coupled Excitable BVP Model

Effects of high-frequency sinusoidal input on the interspike intervals of the coupled BVP model in the excitable state are considered. We take 0.6 as Δ ($\Delta = 0.6$) in $f(v;\Delta)$ in Eq. (2) so that the equilibrium point $(v, w) = (0, f(0))$ is stable and the BVP elements are in the excitable state. A value of the period T_{in} of sinusoidal input is taken to be 50.0, which is much smaller than the absolute refractory period of the BVP elements, the order of which is $O(10^3)$. (The strength σ of noise is set to be 0.)

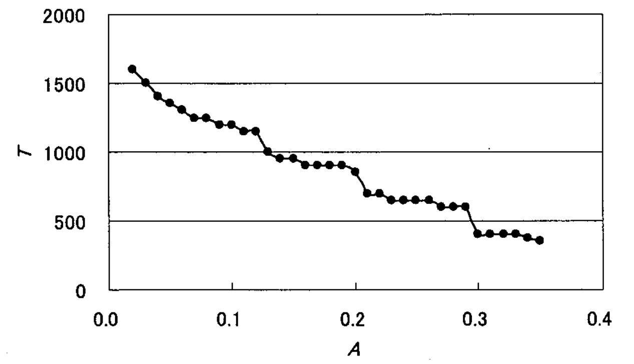
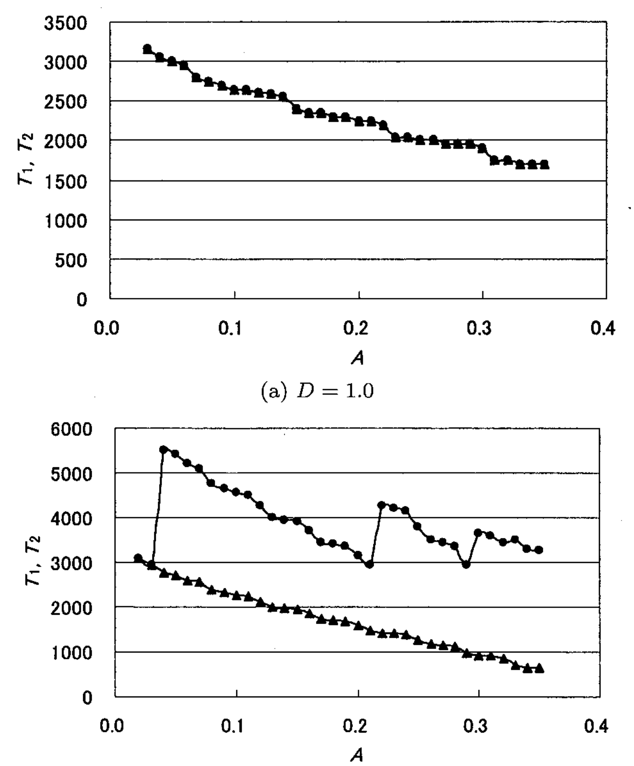


Fig. 1 Mean interspike interval T vs. amplitude A of sinusoidal input in a single BVP model.

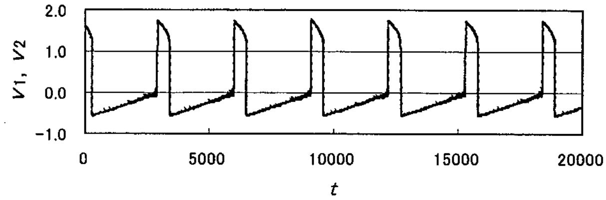


(a) $D = 1.0$

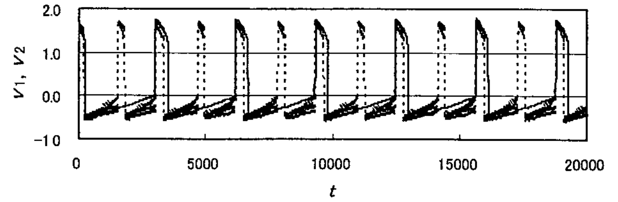
(b) $D = 0.01$

Fig. 2 Mean interspike interval T_1 (triangles) of the first element and T_2 (circles) of the second element vs. amplitude A of sinusoidal input in the coupled BVP model.

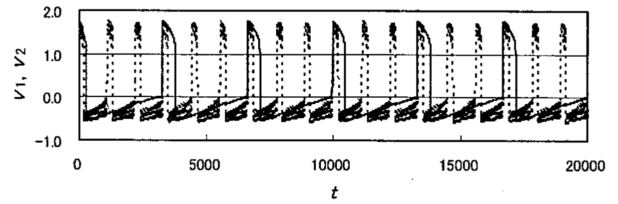
First, changes in the interspike intervals of a single BVP model ($D = 0$) due to high-frequency input are shown for comparison. Spikes are generated by adding the sinusoidal input of $A \geq 0.02$. Figure 1 plots the mean of the interspike intervals T from 11th to 30th against the amplitude A of the sinusoidal input. The interspike intervals of the generated spikes decrease as the amplitude of the sinusoidal input increases. The generated spikes are periodic, i.e., the interspike intervals are constant, except for those at a few values of the amplitude of the sinusoidal input (in which the in-



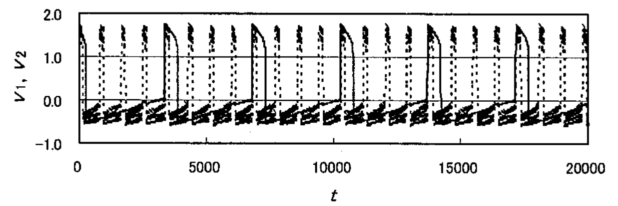
(a) $A = 0.02$



(b) $A = 0.2$



(c) $A = 0.28$



(d) $A = 0.32$

Fig. 3 Time series $v_1(t)$ (dashed lines) and $v_2(t)$ (solid lines) of the coupled BVP model.

terspike intervals are 2-periodic).

Then, a couple of the BVP elements with high-frequency sinusoidal input are dealt with. Figure 2 plots the mean interspike interval T_1 of the first element (triangles) and T_2 of the second element (circles) against the amplitude A of the sinusoidal input. Values of the coupling strength are: $D = 1.0$ (a) and $D = 0.01$ (b). When the coupling strength is large ($D = 1.0$ (a)), the two elements are phase locked and the values of the interspike intervals of the two elements are the same. The interspike intervals of both elements decrease as the strength of the sinusoidal input increases in the same manner as a single BVP model. When the coupling strength is small ($D = 0.01$ (b)), however, the mean interspike interval T_2 of the second element is changed in a non-monotonic manner; T_2 once decreases as A increases, but increases suddenly at $A = 0.04$, decreases again until $A = 0.21$ and increases at $A = 0.22$, and so forth. On the other hand, the mean interspike interval T_1 of the first element decreases monotonically as the strength of the sinusoidal input increases.

Figure 3 shows the time series of the fast variables in the coupled BVP model ($v_1(t)$: dashed lines, $v_2(t)$: solid lines). The spikes of the second element are phase locked to those of the first element in the ratios 1/1, 1/2, 1/3 and 1/4 for $A = 0.02$ (a), 0.2 (b), 0.28 (c) and 0.32 (d), respectively. In fact, the mean interspike interval of the second element is double that of the first element for $0.04 \leq A \leq 0.21$, triple for $0.22 \leq A \leq 0.29$, and quadruple for $0.30 \leq A \leq 0.32$. These changes in the ratio of the phase locking result in the non-monotonic changes in the interspike intervals of the second element. (The interspike intervals of the second element are constant at all the values of A, while those of the first element are 2-, 3- or 4-periodic for $A \geq 0.04$.)

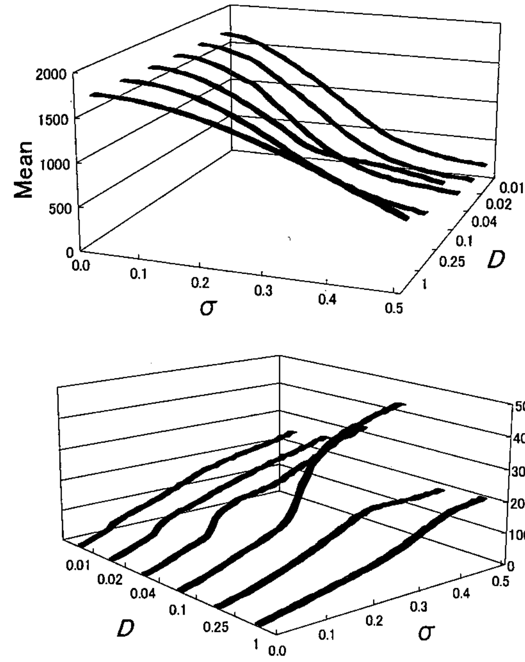
These non-monotonic changes in the interspike intervals due to high-frequency input occur not only in coupled neuron models but also in a nerve fiber model, in which the spatial distribution of nerve membrane is incorporated. It is shown that similar non-monotonic changes in the interspike intervals of propagated spikes in the FitzHugh-Nagumo model [22] appear when the diffusion coefficient is small (Appendix).

4. Noise to the Coupled BVP Oscillators

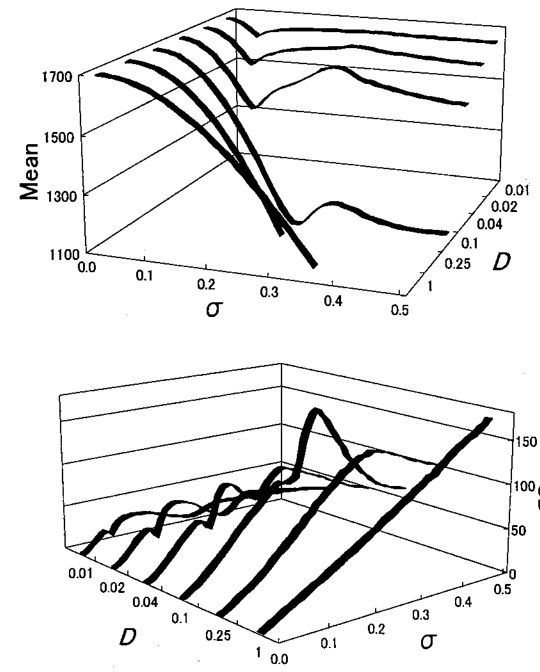
Effects of noise on the coupled BVP model in the oscillating state are considered. We set $\Delta = 0$ in $f(v; \Delta)$ in Eq. (2) so that the equilibrium point of each BVP element is unstable and the stable limit cycle exists. The oscillation periods of the BVP elements were measured by recording the time at which the fast variable v_1 (v_2) crosses the axis $v_1 = 0$ ($v_2 = 0$) from right to left in the upper phase plane $w_1 > 0$ ($w_2 > 0$). The oscillation period without noise is 1681.2. (The amplitude A of sinusoidal input is set to be 0.)

In Fig. 4, the mean and standard deviation ($S.D.$) of the period T_1 of the first oscillator (a) and T_2 of the second oscillator (b) are plotted against the noise strength σ with the coupling strength $D = 1.0$, 0.25, 0.1, 0.04, 0.02 and 0.01. The mean ($S.D.$) of the period T_1 of the first oscillator decreases (increases) monotonically as the noise strength increases. When the coupling strength is large ($D = 1.0$, 0.25), the mean of the period T_2 of the second oscillator also decreases monotonically as the noise strength increases. In the intermediate levels of the coupling strength ($D = 0.1$, 0.04), however, the mean of T_2 once decreases, turns to increase, and decreases again as the noise strength increases. As the coupling weakens further ($D = 0.02$, 0.01), the changes in the mean of T_2 become small. As for the $S.D.$ of T_2, the maximum peaks appear in the intermediate noise strength when the coupling strength is small ($D \leq 0.25$).

Figure 5 shows the time series $v_1(t)$ and $v_2(t)$ of the fast variables of the BVP oscillators with $D = 0.04$, in which the non-monotonic changes in the mean oscillation period of the second oscillator occur. In the first



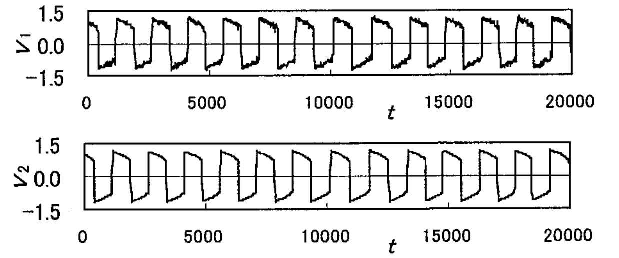
(a) First oscillator



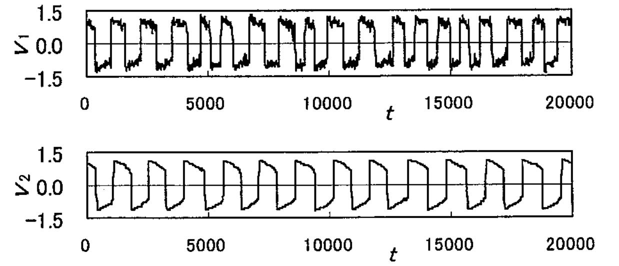
(b) Second oscillator

Fig. 4 Mean and $S.D.$ of the periods T_1 (a) and T_2 (b) of the first and second oscillators vs. noise strength σ (D = 1.0, 0.25, 0.1, 0.04, 0.02 and 0.01).

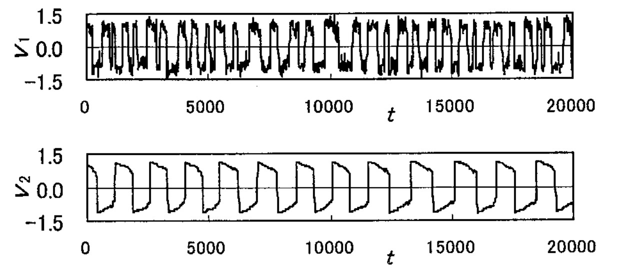
decreasing region ($\sigma = 0.1$) (a), the oscillators are phase locked with each other. In the increasing region ($\sigma = 0.2$) (b), the period of the first oscillator decreases and the second oscillator fails to follow the first oscillator owing to the small coupling strength. Some oscillations still remain phase locked. As the noise strengthens further ($\sigma = 0.3$) (c), the fast variable of the first oscillator has larger variations and works as noisy input to the second oscillator.



(a) $\sigma = 0.1$



(b) $\sigma = 0.2$



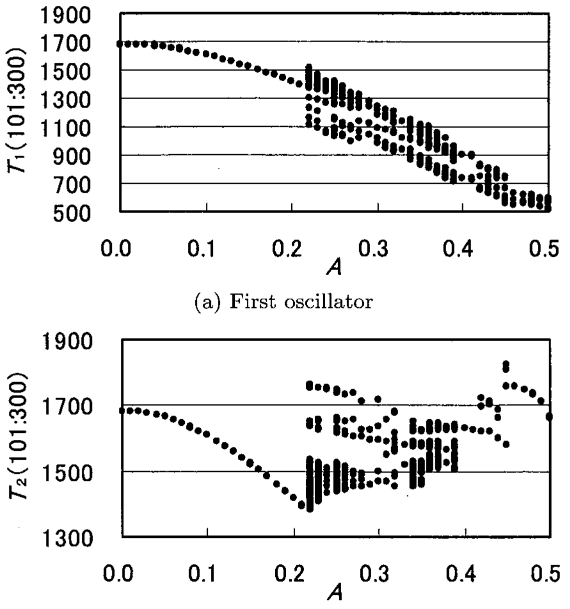
(c) $\sigma = 0.3$

Fig. 5 Time series $v_1(t)$ and $v_2(t)$ of the fast variables of the first and second oscillators with D =0.04 (σ = 0.1 (a), 0.2 (b), 0.3 (c)).

5. High-Frequency Input to the Coupled BVP Oscillators

Changes in the oscillation period of the coupled BVP oscillators caused by high-frequency sinusoidal input are shown. The BVP elements are in the oscillating state with $f(v; 0)$ and sinusoidal input with the period $T_{in} = 10.0$ is added to the fast variable of the first BVP oscillator. (The strength σ of noise is set to be 0.)

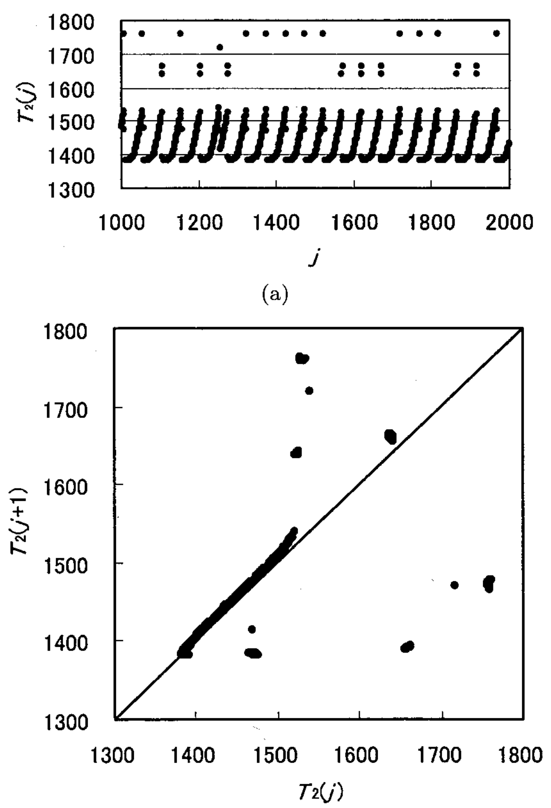
Figure 6 shows the period T_1 of the first oscillator (a) and T_2 of the second oscillator (b) against the amplitude A of the sinusoidal input when the coupling strength D is 0.04. Two hundred periods from 101st to 300th are plotted for each value of A. Note that the coupling strength lies in the values at which the oscillation period changes non-monotonically as the noise strengthens, shown in Sect. 4. The oscillation periods of both oscillators decrease as the amplitude of the sinu-



(a) First oscillator

(b) Second oscillator

Fig. 6 Bifurcation diagram of the periods T_1 (a) and T_2 (b) of the first and second oscillators vs. amplitude A of sinusoidal input (T_{in} = 10.0, D = 0.04).



(a)

(b)

Fig. 7 Series (a) and return map (b) of the oscillation periods T_2 of the second oscillator with sinusoidal input of A = 0.2173 (T_{in} = 10.0, D = 0.04).

soidal input increases from $A = 0$ to 0.21. The series of the oscillation periods cause bifurcations at $A \approx 0.217$ and show complicated patterns as A increases further. Irregular series of the oscillation periods are observed at some values of A.

Figure 7(a) plots the series $T_2(j)$ ($1001 \leq j \leq 2000$) of the periods of the second oscillator at $A = 0.2173$. It can be shown that $T_2(j)$ is not periodic until $j < 10000$. The period T_2 of the second oscillator increases phase locked to that of the first oscillator from $T_2 \approx 1380$ to 1530 gradually. The phase lock is then lost and T_2 changes mainly as $T_2 \approx 1760$, 1480, 1380 or $T_2 \approx 1640$, 1660, 1390. The phase lock is then recovered and the gradual increase in T_2 is repeated again. The return map of $T_2(j)$ (the jth of T_2 vs. the j+1st of T_2, $1001 \leq j \leq 6000$) is shown in Fig. 7(b). It is expected that the tangent bifurcation occurs and causes the intermittency in the series of the periods of the second oscillator.

Similar bifurcations in the oscillation periods appear in about the same range of the coupling strength as the noise causes the non-monotonic changes. The break of the phase locking of the oscillators causes the periodic and complicated patterns in the series of the oscillation periods.

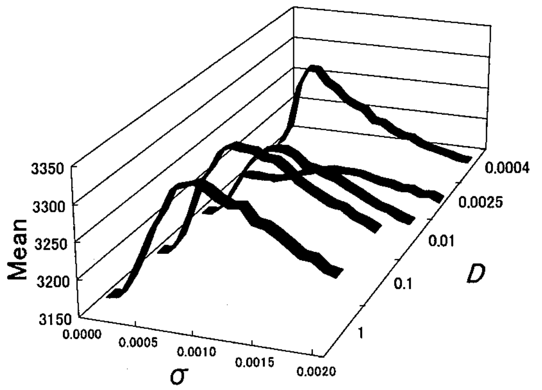
6. Coupled BVP Oscillators Close to the Excitable State

The coupled BVP oscillators close to the excitable state, in which the unstable equilibrium point is close to the minimal point of $w = f(v)$, are considered. We let Δ be 0.577 in $f(v; \Delta)$ so that the equilibrium point (0, $f(0; \Delta)$) is unstable and the stable limit cycle of spike-like form exists. (The oscillation period is 3150.6). Effects of noise and high-frequency sinusoidal input added to the first oscillator coupled to the second oscillator are studied.

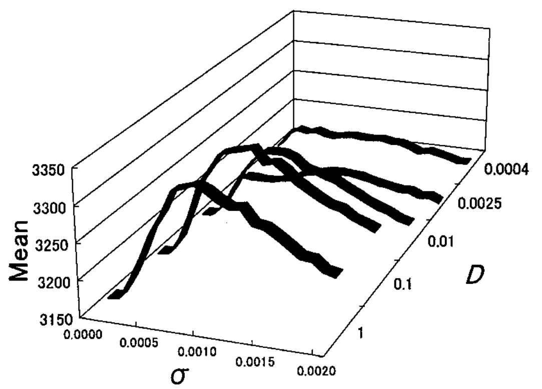
First, it is known that small noise causes small rotations at the equilibrium point and the mean oscillation period increases consequently in a single BVP oscillator close to the excitable state [14].

Figure 8 plots the mean of the period T_1 of the first oscillator (a) and T_2 of the second oscillator (b) against the noise strength σ with the coupling strength D = 1.0, 0.1, 0.01, 0.0025 and 0.0004. (The amplitude A of sinusoidal input is set to be 0.) When the coupling strength is large (D = 1.0, 0.1), the mean oscillation period shows a peak at small strength of the noise ($\sigma \approx 0.001$). As the coupling weakens (D = 0.01, 0.0025), the height of the peak decreases. For extremely small coupling strength (D = 0.0004), the phase locking of the oscillators is lost. Then the peak in the mean oscillation period of the first oscillator reappears while that of the second oscillator is less changed.

The second oscillator works to prevent the occurrence of the small rotations at the equilibrium point of the first oscillator. That is, when the point of the first

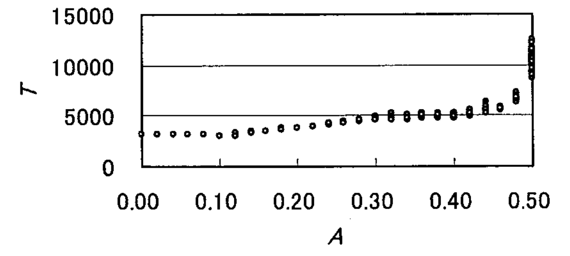


(a) First oscillator

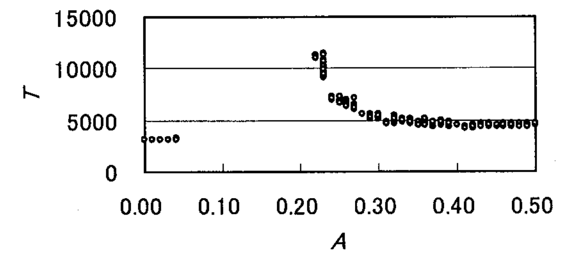


(b) Second oscillator

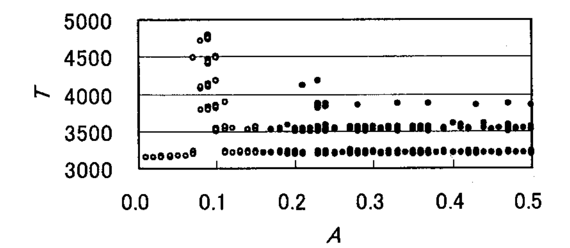
Fig. 8 Mean of the periods T_1 (a) and T_2 (b) of the first and second oscillators close to the excitable state vs. noise strength σ (D = 1.0, 0.01, 0.0025 and 0.0004).



(a) $D = 0.25$



(b) $D = 0.1$



(c) $D = 0.001$

Fig. 9 Periods T_1 (open circles) and T_2 (closed circles) of the first and second oscillators close to the excitable state vs. amplitude A of sinusoidal input of T_{in} = 10.0. D = 0.25 (a), 0.1 (b), 0.001 (c).

oscillator turns to the left in the phase (v-w) plane to rotate at the equilibrium point, the point of the second oscillator is located on the right-hand side. The coupling term $(D(v_2(t) - v_1(t)))$ in Eq. (1) then has a positive sign and tends to make the sign of $dv_1(t)/dt$ positive so that the point of the first oscillator turns to the right and moves away from the equilibrium point. This prevention of the small rotations of the first oscillator due to the second oscillator occurs in the intermediate ranges of the coupling strength (D = 0.01, 0.0025). (The oscillators are phase locked to each other when the coupling strength is large; thus the system reduces to a single oscillator (D = 1.0, 0.1). The first oscillator is hardly affected by the second oscillator and acts as a single oscillator when the coupling is extremely weak (D = 0.0004).)

Next, it is known that, when high-frequency sinusoidal input is added to a single BVP oscillator close to the excitable state, the oscillation is ceased as the amplitude of the sinusoidal input crosses over some threshold value ($A \approx 0.015$). It can be shown that the oscillation is recovered by adding noise of small strength ($\sigma \approx 10^{-4}$). It is expected that the coupling of the oscillators causes fluctuations and also recovers the oscillation.

Figure 9 shows the periods of the oscillators against the amplitude A of sinusoidal input of period T_{in} = 10.0 with the coupling strength D = 0.25 (a), 0.01 (b) and 0.001 (c). (The strength σ of noise is set to be 0.) Two hundred periods from 101st to 300th are plotted for each value of A with open circles for the period T_1 of the first oscillator and closed circles for the period T_2 of the second oscillator. The oscillations of both oscillators are still maintained in the wide ranges of the amplitude of the sinusoidal input ($0 \leq A \leq 0.5$) for D =0.25 (a). When the coupling strength decreases (D = 0.1 (b)), the oscillations are once ceased at A = 0.05, then recovered at A = 0.22, and maintained with the period decreasing. For extremely small coupling strength (D = 0.001 (c)), the oscillation of the first oscillator is ceased at A =0.15, while the oscillation of the second oscillator is maintained as A increases.

Note that the oscillations of both oscillators are ceased in the same manner as a single oscillator for large (D = 1.0) and intermediate (D = 0.01) coupling strength, though not shown. Further, the oscillation of the first oscillator is ceased while the oscillation of the second oscillator is maintained in the limit of small

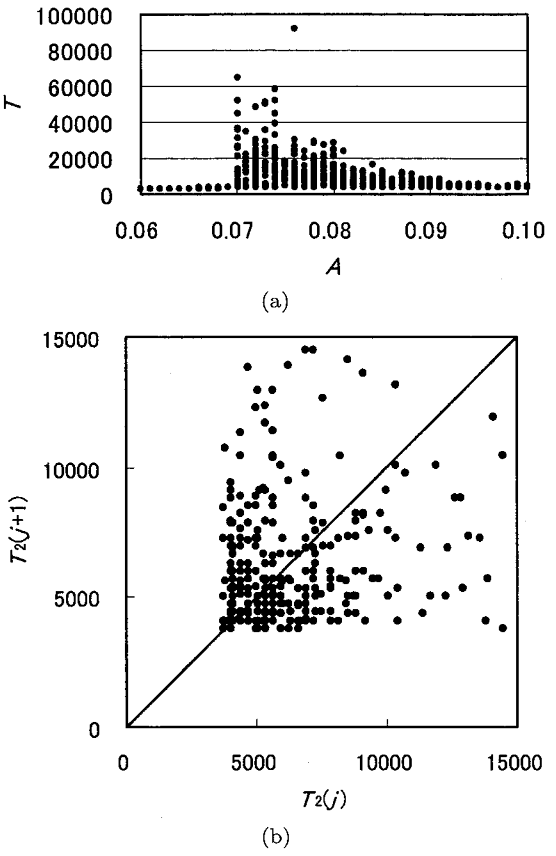


Fig. 10 Oscillation period T_2 of the second oscillators close to the excitable state vs. amplitude A of sinusoidal input (magnified from Fig. 11(c)) (a), and return map of T_2 at $A = 0.082$ (b).

coupling strength. In two distinct regions of the values of the coupling strength ($D \approx 0.25$ and $D \approx 0.001$), the oscillations of the coupled oscillators are recovered.

The region from $A = 0.06$ to 0.1 in Fig. 9(c) ($D = 0.001$) is magnified in Fig. 10(a). Large oscillation periods close to 10^5 exist, which are almost thirty times as large as the oscillation period without input. The time series $v_1(t)$ and $v_2(t)$ of the fast variables of the oscillators at $A \approx 0.07$ then show bursting patterns with rather regular oscillations interrupted by long ceased intervals. The series of the oscillation periods vary sensitively as the amplitude of sinusoidal input changes, while they are periodic. Figure 10(b) shows the return map of the series $T_2(j)$ ($101 \le j \le 400$) of the periods of the second oscillator with sinusoidal input of $A = 0.082$, in which the series has period 294 ($T_2(j) = T_2(j+294)$). Low dimensional structures are not observed from the return map of the oscillation periods. The cause of the occurrence of the bursting patterns is not clear and is a future problem.

7. Discussion

It was shown that the interspike intervals of the spikes in the coupled BVP model are changed non-monotonically as the amplitude of high-frequency cyclic input increases when the coupling strength is small. The decrease in the interspike intervals of the first element due to the high-frequency cyclic input and the changes in the ratio of the phase locking due to the refractory period cause the non-monotonic changes in the interspike intervals of the second element. The interspike intervals of the first element decrease monotonically as the amplitude of the sinusoidal input increases. The spikes in the second element are generated by the spikes in the first element. The interspike intervals of the second element decrease phase locked to the first element in the ratio 1/1, but the ratio of the phase locking is dropped to 1/2, 1/3 and so forth, because of the refractory period of the second element, as the interspike intervals of the first element decrease further. The similar mechanism causes the non-monotonicity in the firing rate with periodic pulses [10] and in the coherence resonance [13] in the coupled BVP model.

These non-monotonic changes in the interspike intervals appear only in the intermediate range of the period (frequency) of the sinusoidal input. Spikes are not generated when the period of the sinusoidal input is small ($T_{in} \le 16$). When the order of the period of the sinusoidal input is equal to that ($O(10^3)$) of the refractory period, generated spikes are phase locked to the sinusoidal input.

Further, it was shown that the noise or high-frequency cyclic input causes the non-monotonic changes and bifurcations in the oscillation period of the coupled BVP oscillators. The noise causes the decrease in the period of the first oscillator. The period of the second oscillator also decreases phase locked to the first oscillator. As the noise strength increases and the period of the first oscillator decreases further, however, the phase locking is lost and the period of the second oscillator increases. The non-monotonic changes appear only when the coupling is weak. The high-frequency cyclic input also makes the oscillation period small. When the coupling is weak, the phase locking of the oscillators is also lost as the amplitude of the input increases and the period of the first oscillator decreases. The tangent bifurcation then occurs and complicated patterns in the series of the oscillation periods appear.

In Sect. 6, the coupled BVP oscillators in which the unstable equilibrium point is close to the minimal point of $w = f(v)$ were dealt with. It is known that small noise causes a peak in the mean of the oscillation period and cyclic input ceases the oscillation in a single BVP oscillator. It was shown that weak coupling makes the height of the peak small and recovers the oscillation. Although these results have little relation to the non-monotonic changes in the interspike intervals and the oscillation period shown in Sects. 3–5, both are caused only in the intermediate ranges of the coupling strength. It should be mentioned that the weak coupling may have various effects on the system near critical states between excitable and oscillatory states.

The non-monotonic changes and bifurcations in the interspike intervals and the oscillation periods obtained in this study appear irrespectively of the precise forms of the functions in the BVP model. It can be shown that similar changes occur with a piecewise linear function as $f(v)$, for instance. It is only needed that the values of the small parameter ε and the coupling strength D are sufficiently small. The noise and cyclic input decrease the oscillation period only of relaxation oscillators of small ε. The strength D of the coupling between the oscillators must be small so that the phase locking of the oscillators is lost as the oscillation period decreases.

When the BVP model is in the excitable state, it is known that the coherence resonance occurs, i.e., the regularity of the spikes is optimal at an intermediate level of the noise strength [19], [24]. It has been shown that weak coupling causes multiple maxima in the mean of the interspike intervals [13]. The mechanism causing the multiple maxima is considered to be similar to that shown in this study, i.e., the phase locking of the oscillators. The multiple maxima in the coherence resonance, however, only appear in the BVP model with a piecewise linear function as $f(v)$, not with a cubic function. The non-monotonic relations of the firing frequency of neurons to the noise strength may appear more likely in spontaneously firing neurons than in less firing neurons.

It is known that the mean oscillation period of a single BVP oscillator increases when noise is added to the slow variable w [11], [14]. Weak coupling may suppress this increase in the oscillation period in the same manner as shown in Sect. 6. Further, more complicated patterns in the series of the oscillation periods may appear when the number of the coupled oscillators increases.

The coupled BVP model is a simplified model of interacting neurons. The noise and high-frequency stimuli added to one part of neurons can cause non-monotonic changes in the firing frequency of another part of neurons. It is also regarded as a model of a single neuron of complicated shapes, e.g., bifurcations in dendrites and axon terminals. The mean firing frequency of a single neuron may vary non-monotonically as the strength of the noise and stimuli depending on the location.

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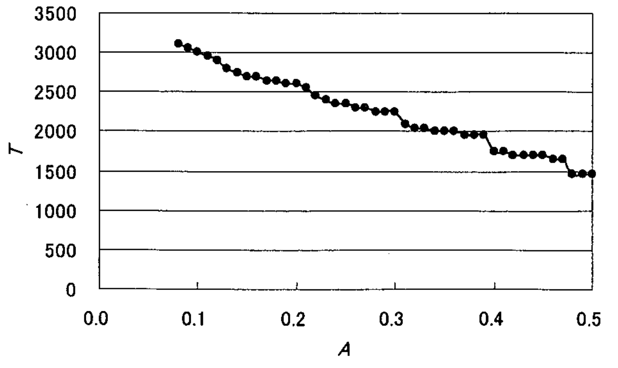
Appendix: High-Frequency Input to the FHN Model

The non-monotonic changes in the interspike intervals due to high-frequency input shown in Sect. 3 occur in propagated spikes in a nerve fiber model, in which the spatial distribution of nerve membrane is incorporated, when the diffusion coefficient is small. Computer simulation is done on the FitzHugh-Nagumo model [22] with cyclic input to the one end.

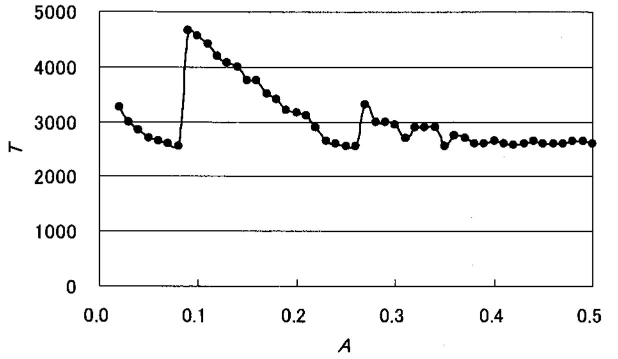
$$\partial v(x,t)/\partial t = D'\partial^2 v(x,t)/\partial x^2 + f(v(x,t)) - w(x,t) + \delta(x) A \sin 2\pi t/T_{in}$$
$$\partial w(x,t)/\partial t = \varepsilon v(x,t) \quad (\varepsilon = 0.001, 0 \le x \le 20) \qquad (A\cdot 1)$$

where D' is the diffusion coefficient, which corresponds to the coupling strength D in Eq. (1). Sinusoidal input with $T_{in} = 50.0$ is added to the one end ($x = 0$) of the fiber. Spikes are generated at $x = 0$ and are propagated to the other end ($x = 20$). Equation (A·1) is spatially discretized with $\Delta x = 1.0$ and is numerically calculated by the Euler method with $\Delta t = 0.1$. The spatially discretized model is equivalent to a linear chain of 20 BVP elements.

Figure A·1 plots the mean interspike interval T of the propagated spikes at $x = 20$ against the amplitude A of the sinusoidal input. Values of the diffusion coefficient are: $D' = 1.0$ (a) and $D' = 0.04$ (b). The mean interspike interval decreases monotonically as the amplitude of the sinusoidal input increases for the large diffusion coefficient ($D' = 1.0$ (a)). When the diffusion coefficient is small ($D' = 0.04$ (b)), however, the mean interspike interval decreases once as A increases, but increases at $A = 0.09$, then turns to decrease and increases again at $A = 0.27$. The non-monotonic changes in the mean interspike interval of the spikes propagated in a nerve fiber are caused by the high-frequency sinusoidal input.

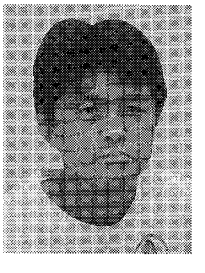


(a) $D = 1.0$



(b) $D = 0.04$

Fig. A·1 Mean interspike interval T of propagated spikes vs. amplitude A of sinusoidal input in the FHN model.



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