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NERVE EXCITATION AND CHAOS

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ABSTRACT

Periodically forced oscillations in nerve membranes are analysed numerically with the Hodgkin-Huxley equations and experimentally with squid giant axons. It is clarified that chaotic oscillations in the nerve membranes are produced through dynamical processes of stretching, folding and compressing. Physiological implication of the nonlinear oscillations is also discussed.

1. INTRODUCTION

The brain is a large-scale network of neurons. The neurons generate and propagate trains of nervous impulses carrying information in the brain.

The functions of the neurons are realized by nonlinear dynamics inherent in the nerve membranes. The nonlinear neural dynamics can produce various attractors and bifurcations according to far-from-equilibrium conditions. For example, a stable limit cycle representing a self-sustained oscillation, or spontaneous repetitive excitation in the nerve membranes bifurcates through a subcritical Hopf bifurcation point with changing some parameters regulating the far-from-equilibrium conditions of the nerve membranes.[1-5] In this study, response characteristics of the nonlinear neural oscillator to periodic force are analysed numerically with the Hodgkin-Huxley equations[6] and experimentally with squid giant axons.

2. THE HODGKIN-HUXLEY EQUATIONS

The Hodgkin-Huxley equations (the H-H eqs.) can describe various phenomena on nerve excitation in squid giant axons phenomenologically.[6] The H-H eqs. are nonlinear ordinary differential equations with four variables of the membrane potential V, the sodium activation m, the sodium inactivation h and the potassium activation n.[6] The H-H eqs. and the values of the parameters used in the numerical analisis are as follows:

$$dV/dt = I - 120m^3h(V-115) - 40n^4(V+12) - 0.24(V-10.613) \quad (1)$$

$$dm/dt = (1-m)\alpha_m(V) - m\beta_m(V) \quad (2)$$

$$dh/dt = (1-h)\alpha_h(V) - h\beta_h(V) \quad (3)$$

$$dn/dt = (1-n)\alpha_n(V) - n\beta_n(V) \quad (4)$$

$$I = 20 + A\sin(2\pi Ft) \quad (5)$$

where $\alpha_i(V)$'s and $\beta_i(V)$'s are functions of the membrane potential V.[6] The term I in eqs.(1) & (5) corresponds to the sinusoidal forcing stimulation to the self-sustained neural oscillator. The amplitude A and the frequency F of the sinusoidal force in eq.(5) are used as the bifurcation parameters in the following analysis. The H-H eqs.(1)-(5) were numerically calculated with the Runge-Kutta method on AICOS 850 Computer at the

Computer Center of Tokyo Denki Unoversity. The behaviors of the periodically forced neural oscillator were analysed by a kind of Poincaré mapping, or the stroboscopic plot.[7-9] Namely, the periodically forced oscillations were observed at a fixed phase of the sinusoidal force.

3. NUMERICAL ANALYSIS ON THE HODGKIN-HUXLEY EQUATIONS

The periodically forced oscillations in the H-H eqs. are classified into three types, i.e. (1) synchronized oscillations, (2) quasi-periodic oscillations and (3) chaotic oscillations.[8-9]

Fig.1 shows an example of a harmonically synchronized oscillation in the H-H eqs. In this oscillation, the forced oscillation is entrained to the sinusoidal force; one nervous impulse is produced during each one period of the force. As the period of the forced oscillation equals to that of the sinusoidal force, each stroboscopic plot in Fig.1-(b) is composed of a single point. Moreover, different n/m-synchronized oscillations defined below can be observed in the H-H eqs.[8-9]

<u>Definition</u> A n/m-synchronized oscillation is a periodic oscillation such that

(1) the period of the forced oscillation just equals to m times the period of the sinusoidal force,

(2) n nervous impulses are generated during m cycles of the sinusoidal force,

where m and n are positive integers but not always relatively prime.

The number n/m of a n/m-synchronized oscillation is physiologically called the average firing rate and corresponds to the rotation number of the oscillation.[10] Regions of n/m-synchronized oscillations are distributed in the shapes of Arnold tongues[11] in the bifurcation parameter space A x F.

Fig.2 shows an example of the second type of forced oscillation, or the quasi-periodic oscillation in the H-H eqs. There co-exist both the rhythm of the natural oscillation and the forcing rhythm in the quasi-periodic oscillations.[8-9] As the two frequencies are relatively irrational, a closed curve emerges asymptotically[8-9] on the stroboscopic plot as shown in Fig.2-(b). The stroboscopic plots in Fig.2-(b) show that the attractor of the quasi-periodic oscillation is in the form of a 2-dim torus.

Fig.3 shows an example of the third type of forced oscillation, or the chaotic oscillation in the H-H eqs.[8-9] The waveform of the chaotic oscillation is apparently non-periodic and the stroboscopic plots depict strange attractors. The stroboscopic plots in Figs.3-(b)&(c) clearly show that a part of a tubular attractor is pinched, stretched, folded amd compressed during one period of the force. These dynamical processes, which make the forced oscillation chaotic, are similar to those observed in the forced nonlinear oscillator such as the forced Van der Pol system.[12-13]

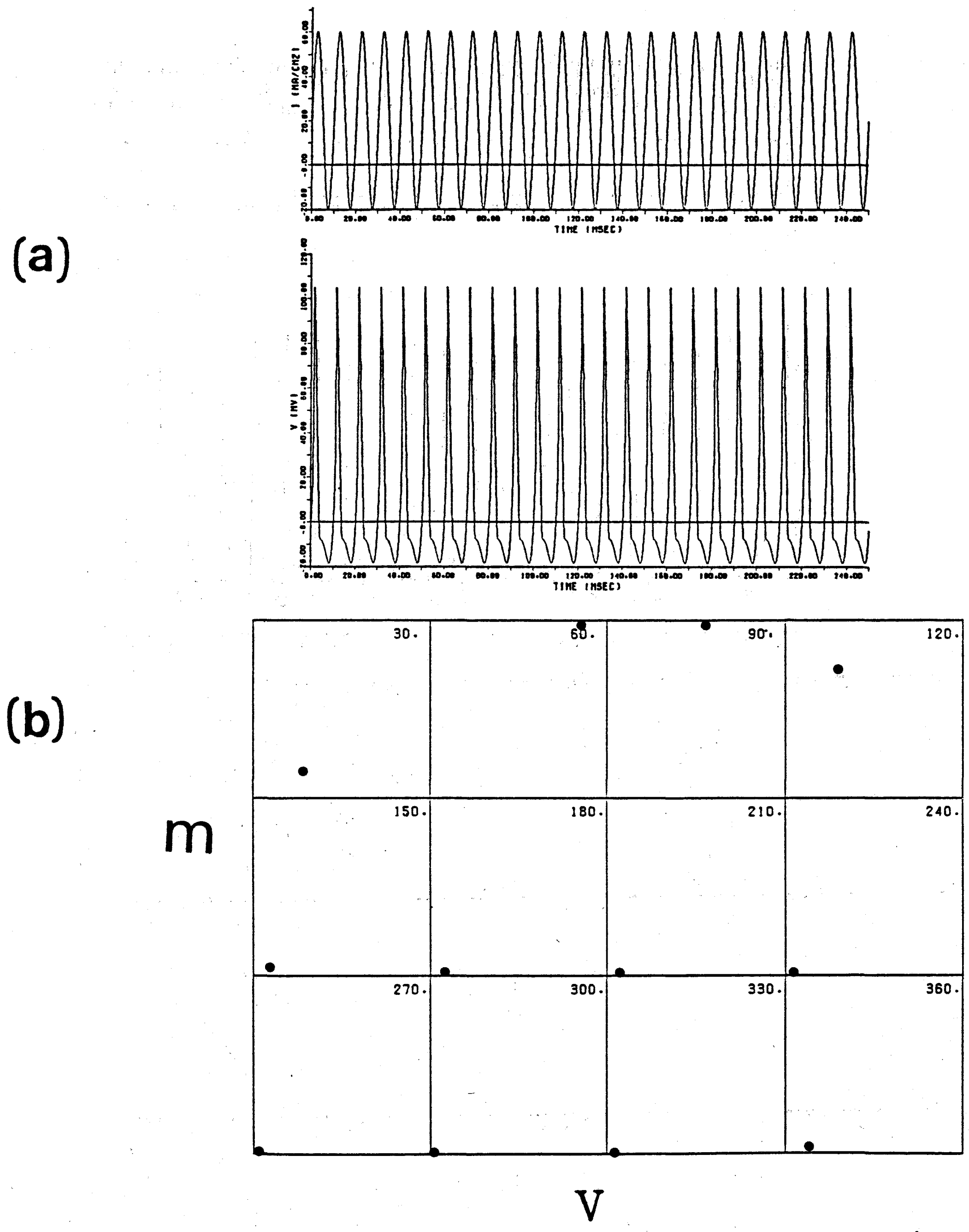


Fig.1 A harmonically synchronized oscillation in the H-H eqs.(A= 40.0μA/cm^2& F=100.0Hz). (a)The waveforms of the sinusoidal force I(above) and the membrane potential V (below). (b)The stroboscopic plots on the plane V(the membrane potential) x m(the sodium activation) at each 30° phase of the sinusoidal force. The number in each stroboscopic plot shows the corresponding phase(°) of the sinusoidal force.

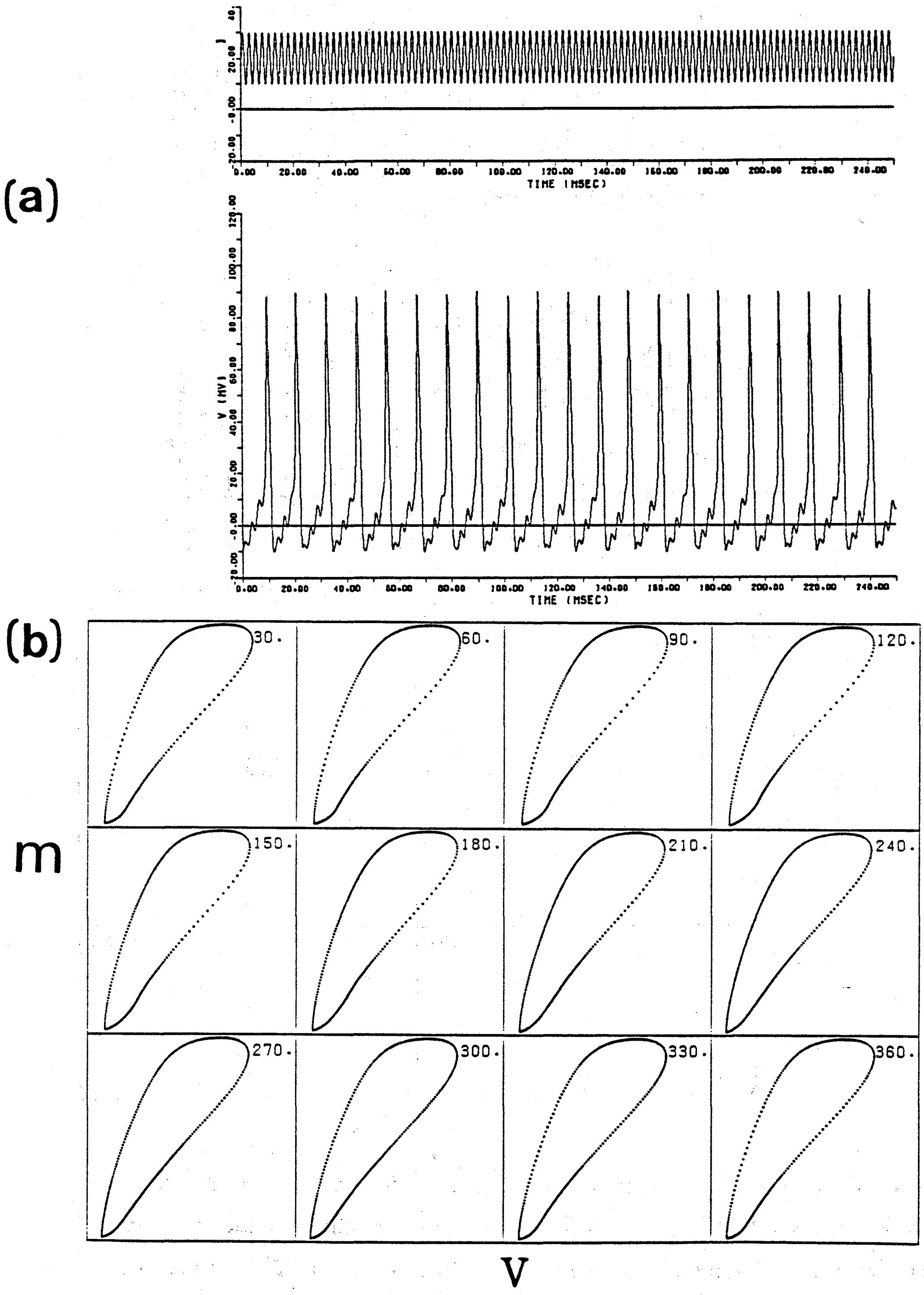
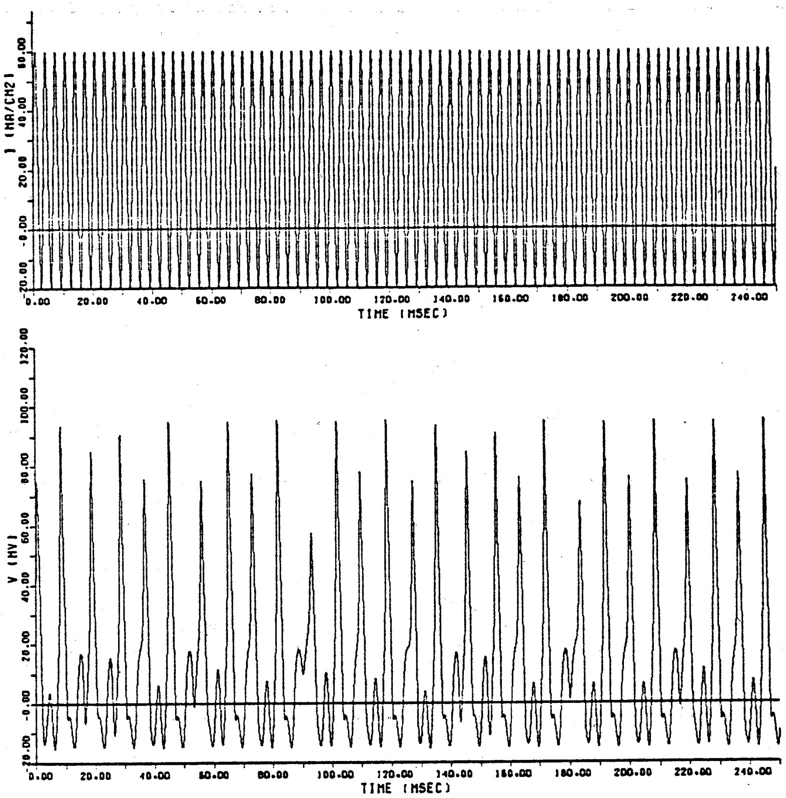
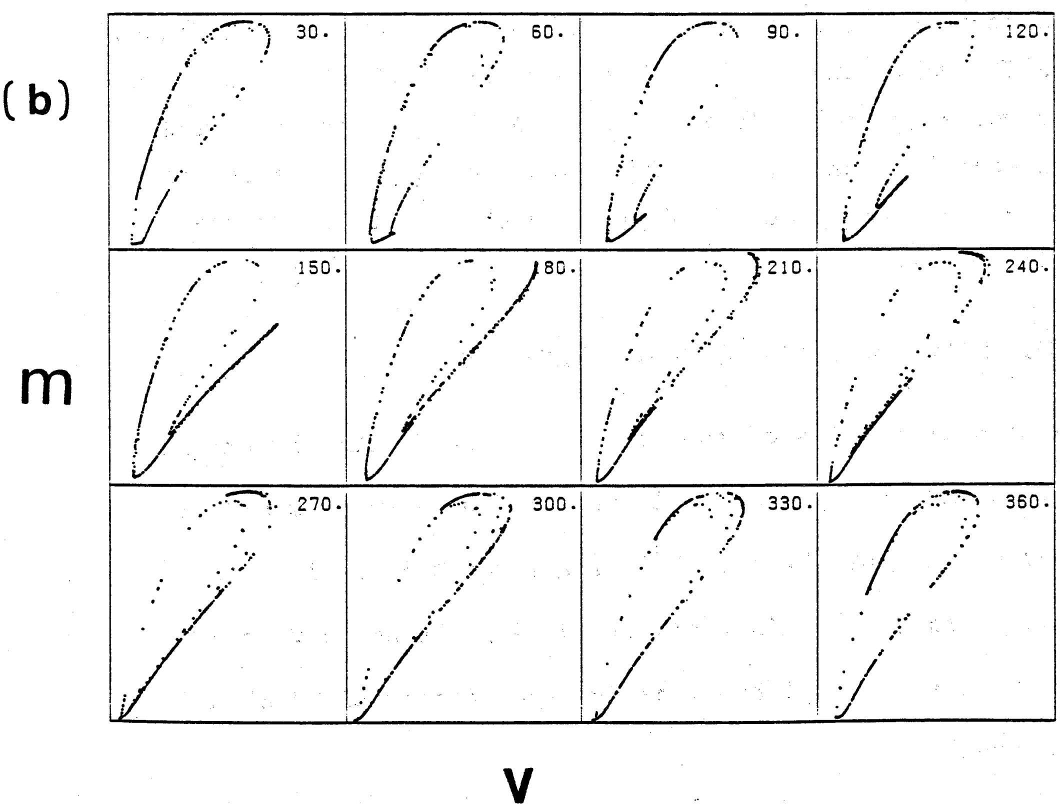


Fig.2 A quasi-periodic oscillation in the H-H eqs.($A=10.0\mu A/cm^2$ & $F=400.0Hz$). (a)The waveforms of the sinusoidal force(above) and the membrane potential(below). (b)The stroboscopic plots on the plane V x m at each 30° phase of the sinusoidal force.

(a)


I (MA/CM2)
TIME (MSEC)
V (MV)
TIME (MSEC)

(b)


30.
60.
90.
120.
150.
180.
210.
240.
270.
300.
330.
360.
m
V

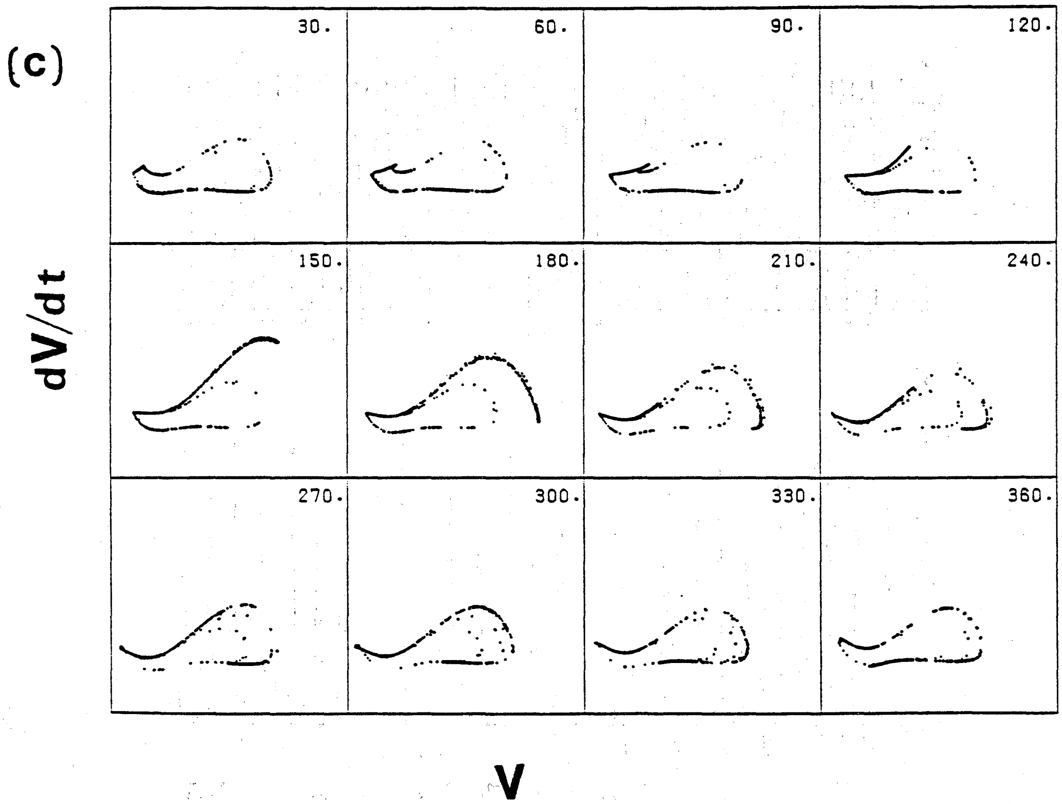


Fig.3 A chaotic oscillation in the H-H eqs.(A=40.0μA/cm^2& F=300.0 Hz). (a)The waveforms of the sinusoidal force(above) and the membrane potential(below). (b)The stroboscopic plots on the plane V x m at each 30° phase of the sinusoidal force. (c)The stroboscopic plots on the plane V x dV/dt at each 30° degree of the sinusoidal force.

4. EXPERIMENTAL ANALYSIS ON SQUID GIANT AXONS

The characteristics of the nonlinear forced oscillations in the H-H eqs. can be experimentally verified with giant axons of squid (Doryteuthis bleekeri).[9,14] The stroboscopic plots on the nonlinear forced oscillations in squid giant axons were displayed on the 2-dim plane V(the membrane potential) x dV/dt(its time differential).

Fig.4, Fig.5 and Fig.6 correspond to a 4/5-synchronized oscillation, a quasi-periodic oscillation and a chaotic oscillation in squid giant axons, respectively. The stroboscopic plots in Fig.6 show that the dynamical processes producing the chaotic oscillation are composed of stretching, folding and compressing. The structures of the attractors in the space V x dV/dt x S^1 will be reported in detail elsewhere.[15)]

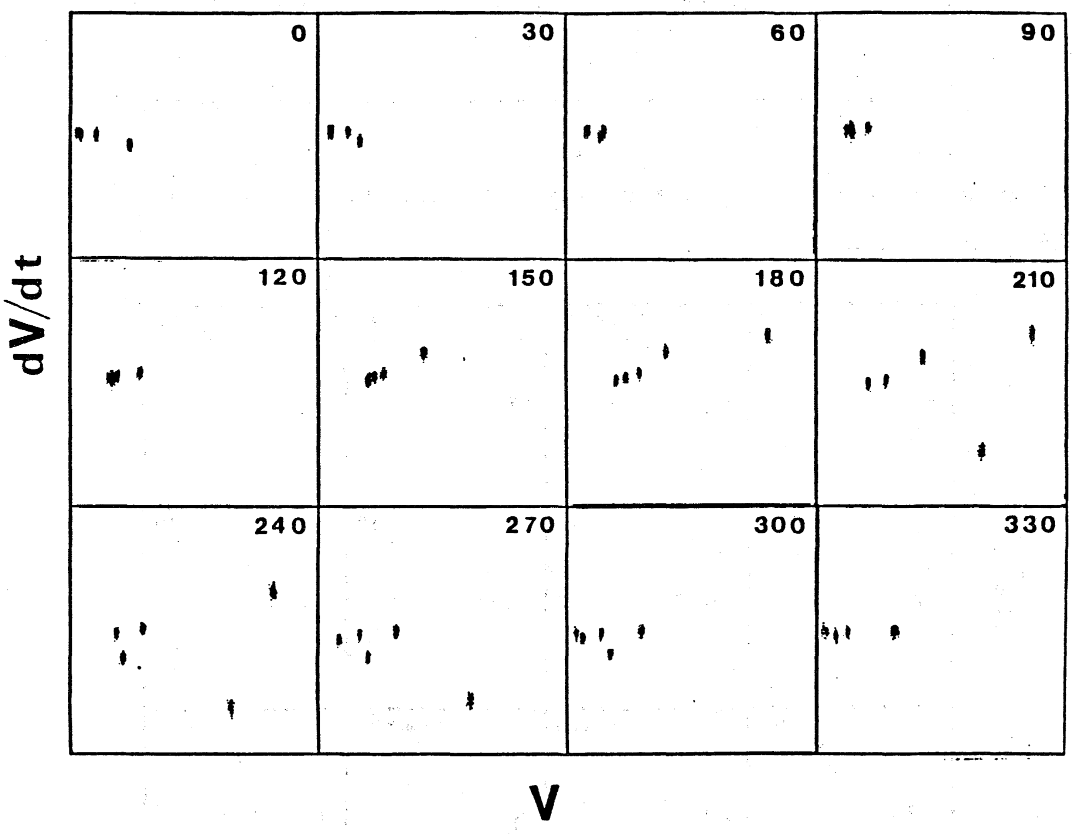


Fig.4 The stroboscopic plots of a 4/5-synchronized oscillation in squid giant axons. The number in each stroboscopic plot shows the corresponding phase(°) of the sinusoidal force.

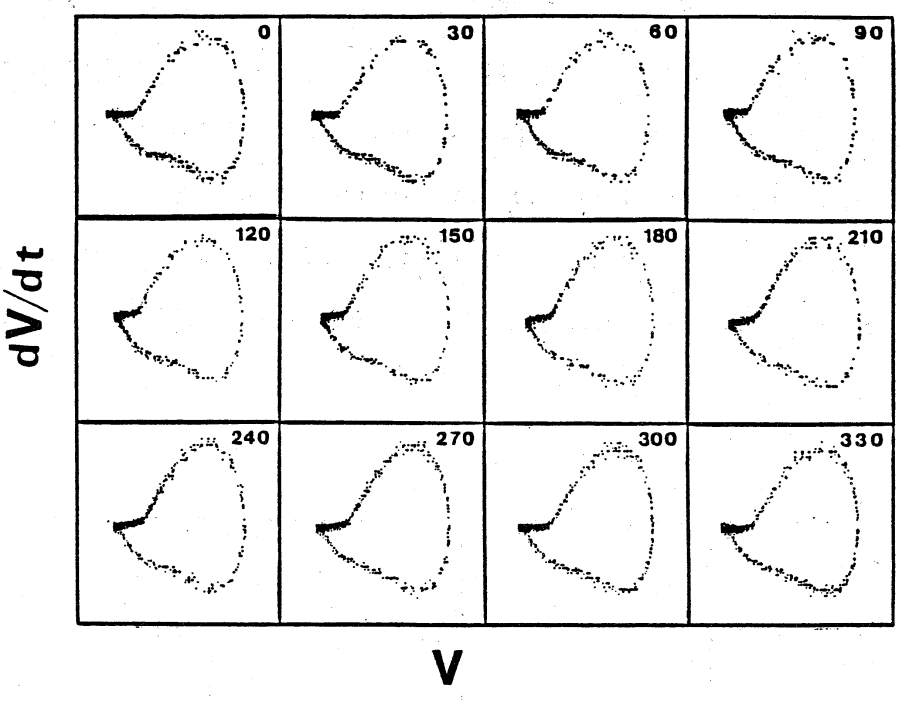


Fig.5 The stroboscopic plots of a quasi-periodic oscillation in squid giant axons.

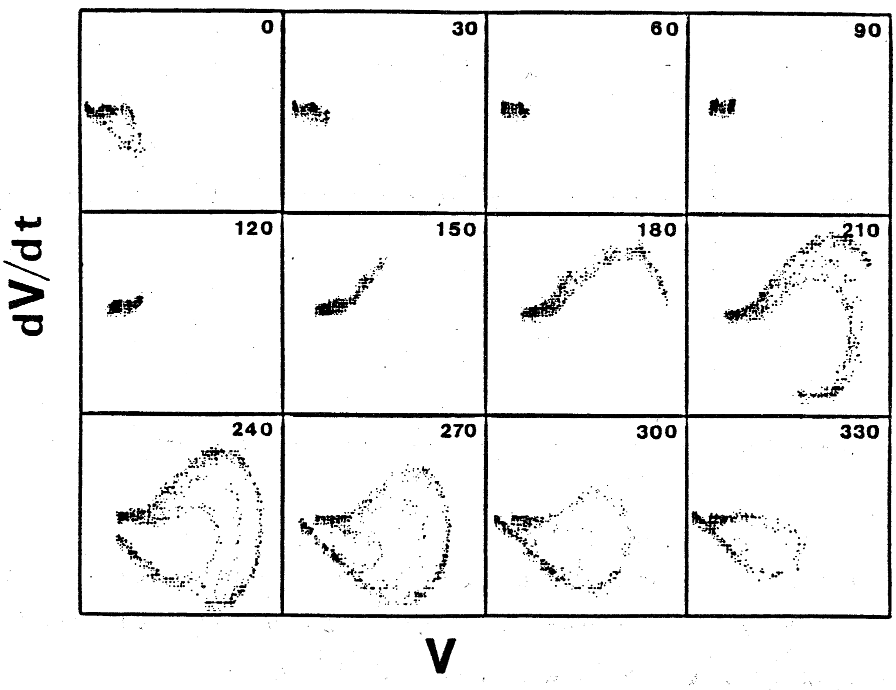


Fig.6 The stroboscopic plots of a chaotic oscillation in squid giant axons.

5. DISCUSSION

The periodically forced oscillations in both the H-H axons and squid giant axons have been classified into (1) the synchronized oscillations, (2) the quasi-periodic oscillations and (3) the chaotic oscillations by examining the ω-limiting sets of the stroboscopic mapping, or the stroboscopic plots. Fig.7 shows the projection of the chaotic trajectory of the H-H eqs. onto the plane V x m. Fig.7 implies that the orbital instability of the chaotic oscillation results from the continuous type of threshold separatrix[16)] in the neural dynamics.

The routes from the synchronized oscillations to the chaotic oscillations in the nerve membranes are successive period-doubling bifurcations and intermittency.[8-9)] Further, there exist the routes from the quasi-periodic oscillations to the chaotic oscillations via collase of the 2-dim torus in the nerve membranes.[9,15)]

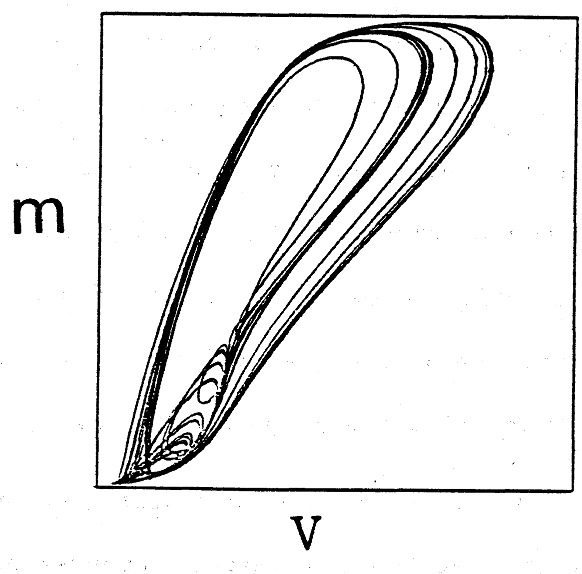


Fig.7 The projection of the chaotic trajectory of the H-H eqs. onto the plane V x m ($A=40.0\mu A/cm^2$ & F=300.0Hz).

When the bifurcation parameters were changed in the global ranges, alternating periodic-chaotic sequences were observed both in the H-H eqs. and in squid giant axons.[17] For example, the following sequence was obtained in the H-H eqs. when the bifurcation parameter F was changed from f_N(the natural frequency) to $2f_N$[18]: $1 \rightarrow \cdots \; n/(n+1) \cdots \rightarrow 3/4 \rightarrow C \rightarrow 2/3 \rightarrow C \rightarrow 5/8 \rightarrow C \rightarrow 3/5 \rightarrow C \rightarrow 1/2$ where n/m and C correspond to a n/m-synchronized oscillation and a chaotic oscillation, respectively. The average firing rate, or the rotation number of the synchronized oscillations are distributed according to the Farey series of rational numbers.[8,19-22] The average firing rate of the chaotic oscillation is an intermediate value between those of the neighboring synchronized oscillations in the regions of the alternating periodic-chaotic sequences because the waveform of the chaotic oscillation is mainly a mixed pattern of those of the two synchronized oscillations. Then, the neural oscillator can respond smoothly to a change of stimulating frequency by using the chaotic mode in the sense of the average firing rate. Moreover, the forced neural oscillator can generate abundant temporal patterns of graded impulses. The axons, which are active transmission lines of nervous impulses, transform the patterns of impulse trains during the propagation. Fig.8 shows an example of the propagating impulse train in the H-H axon. It is a future problem to clarify the information processing in a kind of non von Neumann computer of the nerve membranes.

(a)

(b)

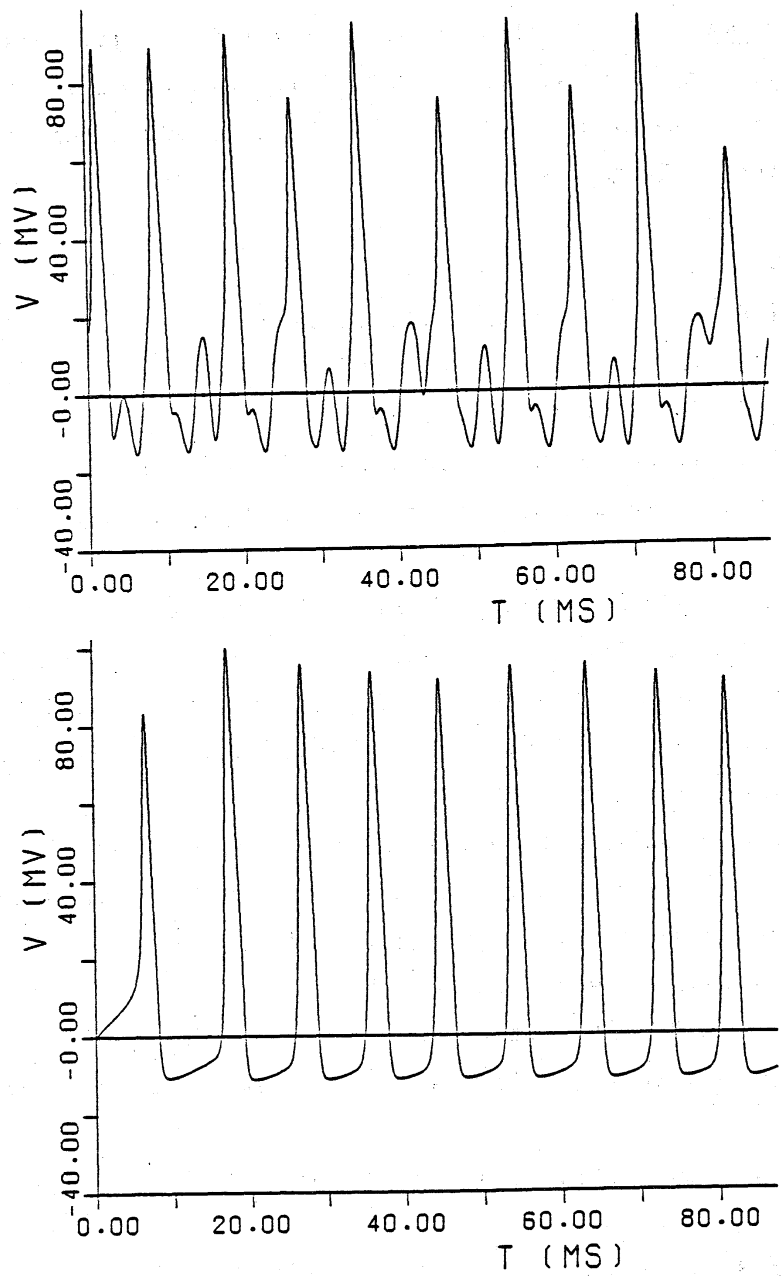


Fig.8 The transformation of the impulse train during the propagation in the H-H axons. The H-H partial differential eqs. with 1-dim diffusion[6,5] were numerically calculated for the axon with the length of 10.0cm and with the radius of 0.025cm. The temporal pattern of the chaotic oscillation in Fig.8-(a) is input at one end of the axon. The boundary condition at the other end was fixed at the resting state. Fig.8-(b) shows the corresponding temporal pattern after the propagation of 8.0cm.

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