# Period-doubling bifurcations and chaos in the decremental propagation of a spike train in excitable media

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(Received 6 December 1993)

Decremental propagation of a spike train in an excitable medium is studied using a computer simulation of the FitzHugh-Nagumo model. Period-doubling bifurcations and chaos in the propagation length of the spikes occur as the period of the stimulus pulses decreases.

PACS number(s): 87.10.+e, 05.45.+b, 87.22.Jb

When stimulus pulses are added to one end of an excitable medium, e.g., a nerve fiber, spikes are generated and are propagated toward the other end of the medium. The propagated spikes keep their proper shape when the medium has a normal excitability. However, the spikes are diminished and disappear during propagation, i.e., the spikes are decrementally propagated, when the excitability of the medium is lowered.

Decremental propagation has been observed in a narcotized nerve fiber [1,2]. Computer simulation of the Hodgkin-Huxley model has also shown that reduction of the excitability of the nerve membrane, e.g., because of decreases in channel conductance, causes decremental propagation [3–5].

I consider a decrementally propagated spike train generated by periodic stimulus pulses. Experiments on the squid giant axon [6,7] and analyses of neuron models [8–10] have shown that, in media of normal excitability, the refractory period has considerable effects on spike generation and causes chaotic responses. The firing rate, the ratio of the number of spikes generated to the number of stimulus pulses, is characterized by a chaotic Cantor-like function. Computer simulation of the FitzHugh-Nagumo model shows that the successive propagation lengths of the spikes period-double as the period of the stimulus pulses decreases.

The FitzHugh-Nagumo model is one of the simplest models of excitable media [11,12]. It is described

$$\begin{aligned} \partial v(x,t)/\partial t &= \partial^2 v(x,t)/\partial x^2 + f(v(x,t)) - w(x,t) , \\ \partial w(x,t)/\partial t &= b[v(x,t) - dw(x,t)] , \\ f(v) &= -v(v-a)(v-1) , \end{aligned} \quad (1)$$

where $v(x,t)$ corresponds to an excitation variable and $w(x,t)$ corresponds to a recovery variable.

The excitability of the medium depends on parameters $a$, $b$, and $d$ [13]. In the simulation, these values were set to $a=0.2$, $b=0.005$, $d=1.0$, so that no stationary traveling wave solutions exist and spikes were decrementally propagated. The explicit finite-difference method was used to solve (1) numerically. The space $x$ was discretized into $\Delta x=0.2$ and the time $t$ was discretized into $\Delta t=0.01$. [Calculation with coarser step size ($\Delta x=1.0$, $\Delta t=0.4$) gives similar results.] The total length of the medium was taken to be 80.0. A sealed-end boundary condition (a zero flux condition) was assumed at both ends. Periodic stimulus pulses were added at $x=0$ to generate spikes propagated toward the other end. The amplitude of each stimulus pulse was 1.0 and its duration was 4.0.

A spatial form of a decrementally propagated spike is shown in Fig. 1, in which $v(x,t)$ is plotted from $t=10.0$ to 250.0 at intervals of 40.0. The spike decreases in height during propagation and disappears at $x=65.8$.

Figure 2 shows the trajectory $\{t_j(x)\}$ of a propagated spike train in the $x$-$t$ plane, where $t_j(x)$ is the time at which the front of the $j$th spike crosses $v=0.3$ at position $x$. When the period $T$ of the stimulus pulses is large [$T=360.0$ (a)], all spikes except for the first spike disappear at the same position: $x=65.0$. That is, the propagation length $X_j$ of the $j$th spike ($j>1$) is the same.

As the period of the stimulus pulses decreases, however, patterns of $\{t_j(x)\}$ vary. A pattern with period 2 is obtained at $T=180.0$ (b). The sequence of the propagation length $X_j$ converges to a two-cycle (58.4, 11.2). A four-cycle pattern with $X_j=(59.0, 2.4, 10.2, 2.4)$ is obtained at $T=90.0$ (c).

The trajectory $\{t_j(x)\}$ does not converge to any cyclic pattern at $T=80.0$ (d). The corresponding sequence $\{X_j\}$ $(1\le j\le 100)$ of the propagation length is plotted in Fig. 3(a). It varies in an irregular manner. The irregularity in $\{X_j\}$ continues up to $j=5200$. The power spectrum $S(\omega)$ of $\{X_j\}$ $(1001\le j\le 5096)$ is continuous and does not have clear peaks [Fig. 3(b)]. The return map of $\{X_j\}$ $(201\le j\le 5200)$ is also plotted in Fig. 3(c). It has a one-dimensional structure with a narrow steep hump and a wide flat region, though it is not perfectly single valued. The sequence is thus considered to be chaotic.

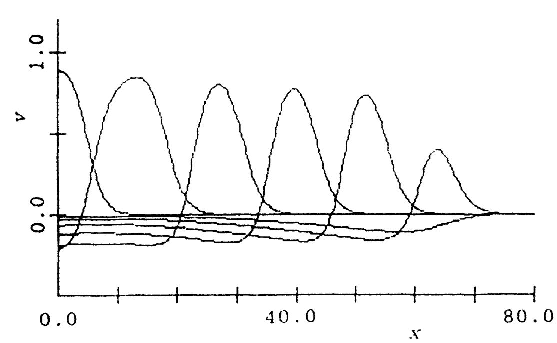


FIG. 1. Spatial form $v(x,t)$ of a decrementally propagated spike.

 

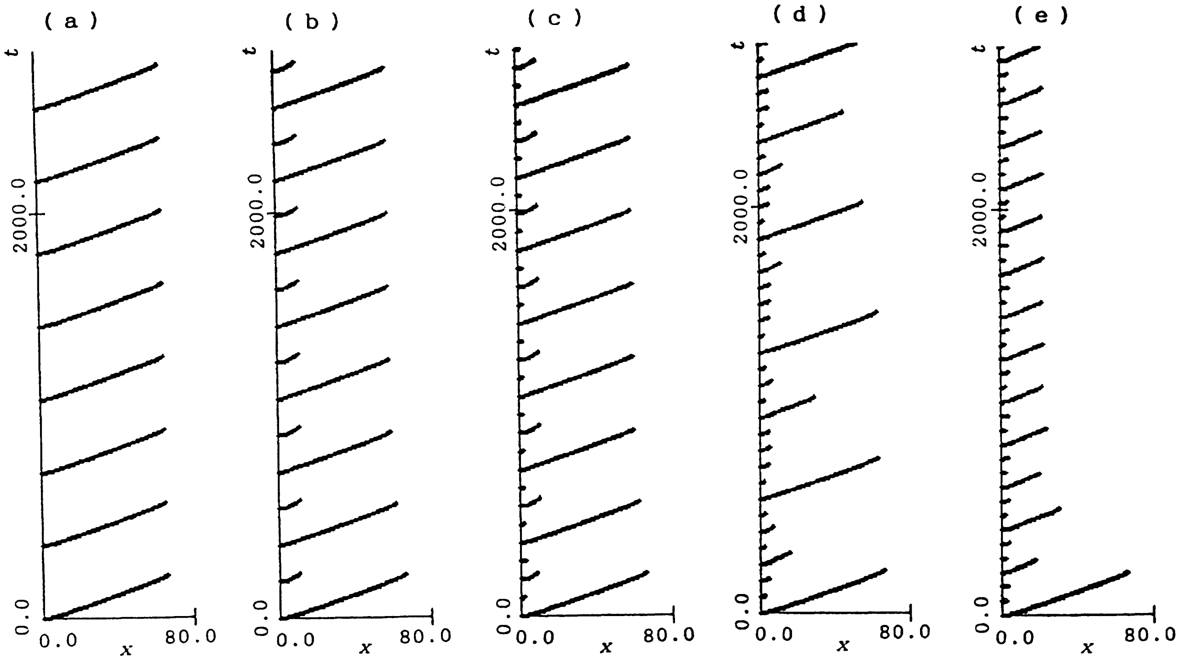


FIG. 2. Trajectory $t_j(x)$ of a spike train generated by stimulus pulses of period $T$. (a) $T=360.0$, stationary; (b) $T=180.0$, two-cyclic; (c) $T=90.0$, four-cyclic; (d) $T=80.0$, chaotic; (e) $T=70.0$, three-cyclic.

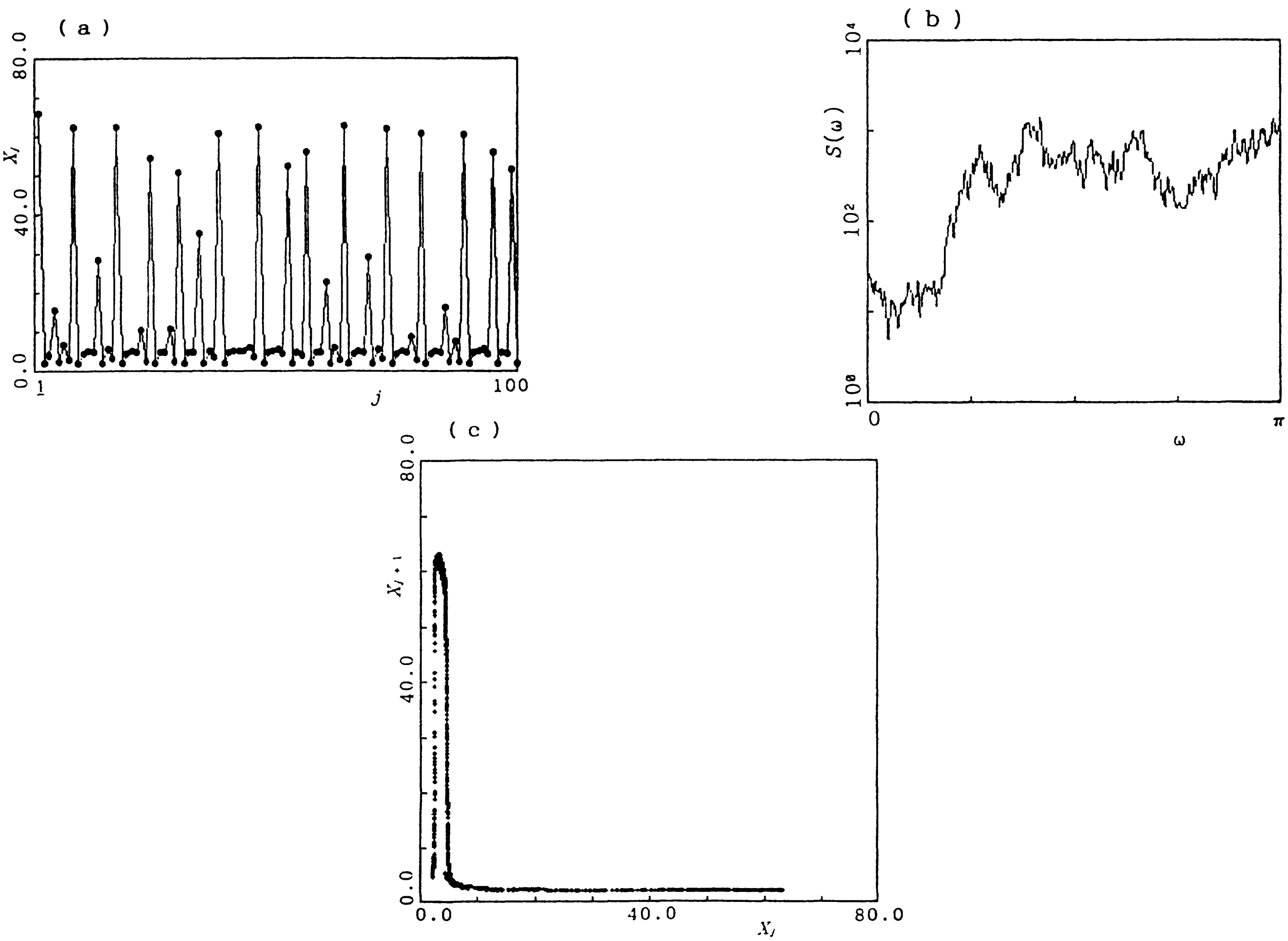


FIG. 3. Chaotic response to stimulus pulses of $T=80.0$. (a) Propagation length $X_j$ of $j$th spike; (b) Power spectrum $S(\omega)$ of $X_j$; (c) Return map of $X_j$.

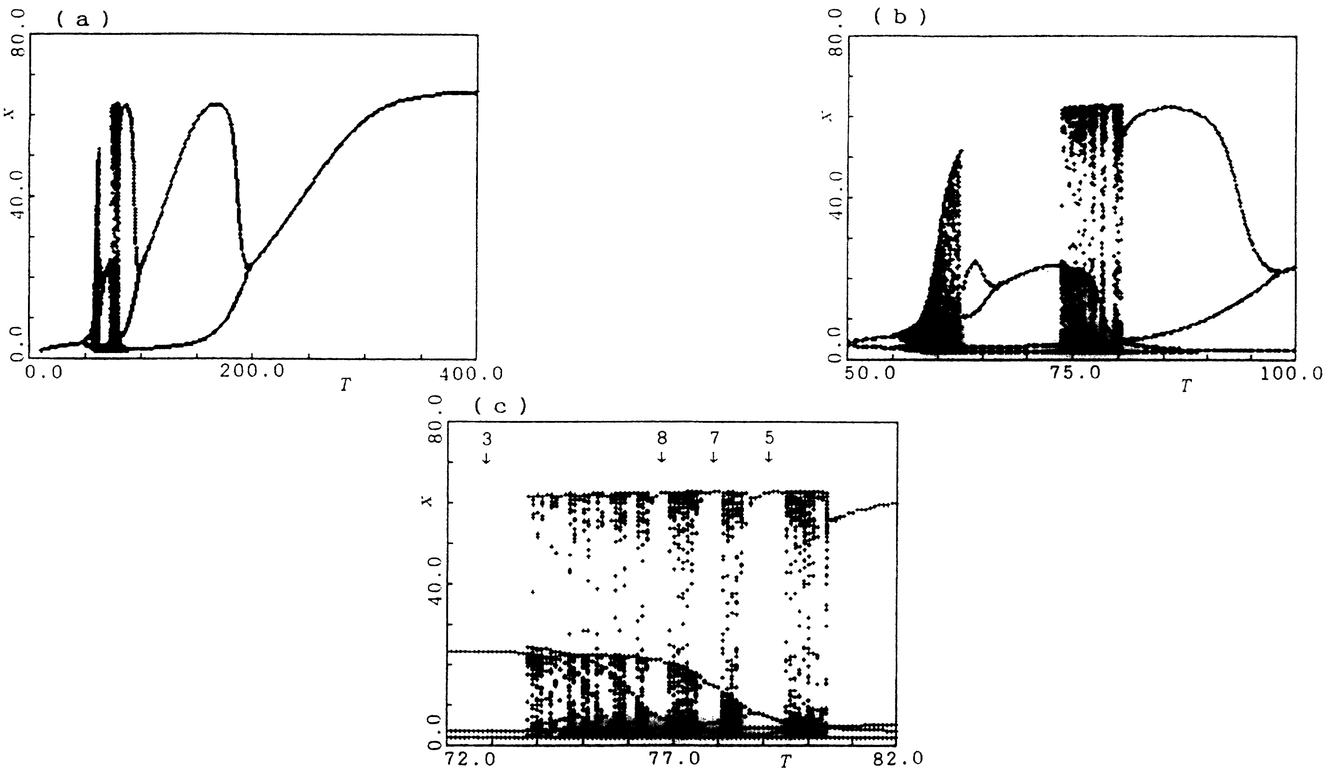


FIG. 4. Bifurcation diagram of propagation length $X_j$. (a) $0 \le T \le 400.0$; (b) $50.0 \le T \le 100.0$; (c) $72.0 \le T \le 82.0$.

For the smaller stimulus period, $T=70.0$, a pattern with period 3 [$X_j=(21.6, 2.0, 3.4)$] is obtained (e).

Figure 4(a) shows the bifurcation diagram of the propagation length $X_j$, in which $\{X_j\}$ ($101 \le j \le 300$) are plotted as the period $T$ of the stimulus pulses decreases from 400.0 to 10.0. The propagation length decreases as the stimulus period decreases. However, the propagation length bifurcates into a pattern with period 2 at $T=200.0$. One branch increases and the other decreases after the bifurcation. The upper branch then decreases, and again bifurcates at $T=98.6$, yielding a pattern of $X_j$ with period 4.

The patterns of $X_j$ in the region in which $X_j$ are widely distributed, i.e., ($73.7 \le T \le 80.1$), ($56.4 \le T \le 62.7$) are magnified in Fig. 4(b). Chaotic sequences are observed in these regions.

A periodic window of period 3 is clear between $62.8 \le T \le 73.6$. Windows of periods 5, 7, and 8 are also denoted in Fig. 4(c).

Further decrease in the stimulus period makes the sequence of the propagation length converge from an eight-cycle ($T=56.3$) to a fixed point ($T=45.6$) through a reversal of the period-doubling cascade.

We are currently studying the mechanism causing the period doubling. In media of normal excitability, the refractory period causes period-doubling bifurcations in the internal state of the media (e.g., in the membrane potential of a nerve fiber) [9]. In media of low excitability, decremental propagation shows period doubling in the propagation length of spikes.

Period-doubling bifurcations and chaos were observed in the decrementally propagated spike train in a simple model of excitable media. Spike generation in media of normal excitability is well described by the one-dimensional circle map; the firing rate is a Cantor-like function of the stimulus period [8–10]. Decremental propagation for low excitability causes qualitative changes in the response of excitable media to periodic stimulus pulses.

This work was partly supported by the Sasakawa Scientific Research Grant from The Japan Science Society.

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