Chaos in neurons

Kazuyuki Aihara (2008), Scholarpedia, 3(5):1786. doi:10.4249/scholarpedia.1786

Dr. Kazuyuki Aihara, Institute of Industrial Science, University of Tokyo

Chaos, or deterministic chaos, is ubiquitous in nonlinear dynamical systems of the real world, including biological systems. Nerve membranes have their own nonlinear dynamics which generate and propagate action potentials, and such nonlinear dynamics can produce chaos in neurons and related bifurcations.

Examples

Squid giant axons have been widely used for electrophysiological experiments to clarify nonlinear dynamics in nerve membranes since the first half of the 20th century. In 1952, A.L. Hodgkin and A.F. Huxley proposed, as a mathematical model of nerve membranes, nonlinear differential equations based on their electrophysiological experiments with squid giant axons (Hodgkin & Huxley, 1952), which are now famous...
as the Hodgkin-Huxley equations. Thus, nonlinear dynamics of nerve membranes has been intensively studied by experimentally with squid giant axons and theoretically with the Hodgkin-Huxley equations.

Chaos in nerve membranes is observed both experimentally and theoretically. Figure 1 and Figure 2 show examples of chaos in nerve membranes, which were electrophysiologically observed with a squid giant axon and numerically obtained with the Hodgkin-Huxley equations, respectively.

Nonlinear dynamics in nerve membranes

Resting and oscillatory states

Squid giant axons are usually in a resting state with the constant resting potential of about $-60mV$.|

By changing the external ionic concentrations surrounding the axons in an in vitro experiment, for example, by reducing the calcium concentration, it is possible to induce self-sustained oscillations with spontaneously repetitive firing of action potentials (Huxley, 1959; Aihara & Matsumoto, 1982). In such a situation, a nerve membrane behaves as a neural oscillator like a pacemaker neuron in biological neural systems.

The resting state and the oscillatory one of axons correspond to a stable equilibrium point and a stable limit cycle, respectively, from the viewpoint of dynamical systems theory.

 Forced neural oscillations

Let us consider a situation that a neural oscillator with the natural frequency $f_N$ is stimulated by an externally applied periodic stimulation with the frequency $f_F$ such as a sinusoidal current $A \sin(2\pi f_F t)$ and a periodic-pulse current with strength $A$ and period $1/f_F$. |

Generally speaking, when $f_F$ is close enough to a simple rational number $m/n$ times $f_N$ with small irreducible natural numbers $m$ and $n$, the neural oscillator responds to the periodic stimulation with an $n/m$-entrained (or phase-locked) oscillation. Here, the $n/m$-entrained (or phase-locked) oscillation is a periodic oscillation in which $n$ |
action potentials are generated with locked phases during the fundamental period of the forced oscillation that is equal to \( m \) times the forcing period \( 1 / f_F \).

Even if a self-sustained neural oscillator is forced by a periodic stimulation, its response is not necessarily periodic. A typical example of such nonperiodic response is a quasiperiodic oscillation with multiple independent frequencies (two frequencies here) that are incommensurate each other. When the amplitude \( A \) of the periodic force is sufficiently weak, a quasiperiodic oscillation is generally observed because the external force is not strong enough for entraining a neural oscillator to a phase-locked oscillation, and two coexisting independent frequencies of the natural frequency \( f_N \) and the forcing one \( f_F \) are generically incommensurable each other or irrationally related. Thus, the quasi-periodic oscillation is nonperiodic but without sensitive dependence on initial conditions.

**Chaos and bifurcations**

Nonperiodic oscillations with orbital instability that are more complex than quasiperiodic oscillations can be observed when the amplitude \( A \) and the frequency \( f_F \) of the periodic force stimulating squid giant axons are adjusted either in the self-sustained oscillatory state or in the resting one. These kinds of nonperiodic oscillations have been classified as chaotic oscillations, namely chaos in nerve membranes (Aihara

Figure 1: A chaotic oscillation with \( f_N = 186 \text{Hz} \), \( f_F = 270 \text{Hz} \) and \( A = 2 \mu \text{A} \) in a squid giant axon. (a) The waveforms (above: the sinusoidal stimulation, below: the response of the membrane potential). (b) The stroboscopic plots where the number in each frame shows the phase at which the response is stroboscopically observed.
et al., 1981; Matsumoto et al., 1984; Aihara et al., 1985, 1986; Aihara & Matsumoto, 1986; Matsumoto et al., 1987; Mees et al., 1992; Aihara, 1994, 1995); an example is shown in Figure 1.

The stroboscopic plots in Figure 1 (b) show that the reconstructed attractor keeps almost cylindrical structure but a part of the surface is pinched like a beak, stretched, folded like a wing, and compressed during one forcing period. Such transformation with stretching, folding, and compressing produces sensitive dependence on initial conditions peculiar to chaotic systems. This kind of chaotic attractors with structure of beaks and wings are also observed in various forced oscillators such as the forced Van del Pol oscillator and called the Birkhoff-Shaw chaotic attractor (Abraham & Shaw, 1984; Thompson & Stewart, 1986).

Various routes, or bifurcations to chaos have been studied in details (e.g. Thompson & Stewart, 1986; Alligood, Sauer & Yorke, 1996; Strogatz, 2000; Hilborn, 2000; Ott, 2002). The typical routes to chaos so far observed in nerve membranes are (1) successive period-doubling bifurcations, where the period successively increases to infinity in the form of \(2^n\) times, (2) intermittency, where chaotic oscillations are generated intermittently among nearly periodic ones, and (3) collapse of quasiperiodicity, where a chaotic oscillation emerges through collapse of a two–dimensional torus representing a quasiperiodic oscillation (e.g. Aihara & Matsumoto, 1986, 1995).

**Experimental evidence and mathematical modeling of chaos in neurons**

**Chaos in the Hodgkin-Huxley equations**

The Hodgkin-Huxley equations can well describe nonlinear excitable dynamics with a threshold peculiar to nerve membranes. Various phenomena in squid giant axons have been successfully described nearly quantitatively with the Hodgkin-Huxley equations (Hodgkin & Huxley, 1952). Chaotic oscillations and the routes to chaos that are observed in squid giant axons are not exceptions. These chaotic phenomena can be essentially understood with deterministic dynamics of the Hodgkin-Huxley equations (Aihara et al., 1981, 1984; Aihara and Matsumoto, 1986). Figure 2 shows an example of a chaotic oscillation in the forced Hodgkin-Huxley equations. The Poincaré sections in

Figure 2 indicate dynamical structure with beaks and wings peculiar to the Birkhoff-Shaw chaotic attractor, which characteristics are similar to those of the chaotic oscillations in squid giant axons as shown in Figure 1. Figure 3 summarizes classification of attractors and their characteristics in the Hodgkin-Huxley equations.

**Figure 2**: Chaos and Poincaré sections in the forced Hodgkin-Huxley equations.

**Figure 3**: Classification of attractors in dissipative dynamical systems. Trajectories and Poincaré sections are obtained with the Hodgkin-Huxley equations.

### Chaos in neurons and time series analysis

Chaos and related bifurcations are observed in various biological membranes, cells, and neural networks (Degn et al., 1987; Glass & Mackey, 1988; Elbert et al., 1994; Korn & Faure, 2003) as well as in different nerve equations like the FitzHugh-Nagumo.
equations and the Hindmarsh-Rose equations (FitzHugh, 1969; Izhikevich, 2007). Chaotic burst firing and related bifurcations are also intensively studied (e.g. Chay et al., 1995; Rulkov, 2001; Doiron et al., 2001, 2002; Korn & Faure, 2003).

Since it is a complicated problem to distinguish between stochastic processes and chaotic dynamics, tools of time series analysis to characterize chaotic dynamics with attractor reconstruction, the Lyapunov spectrum, fractal dimensions, surrogation etc. are quite important (e.g. Sauer et al., 1991; Ott et al., 1994; Weigend & Gershenfeld, 1994; Abarbanel, 1996; Kantz & Schreiber, 1997).

**Chaotic neuron model**

A chaotic neuron model that qualitatively reproduces chaos in nerve membranes observed in squid giant axons and the Hodgkin-Huxley equations can be described by the following simple 1-dimensional map (Aihara et al., 1990):

$$
y(t + 1) = F(y(t)) = ky(t) - \alpha f\{y(t)\} + a,
$$

where $y(t)|$ is the internal state at discrete time $t$, $l|k|\ is the decay factor, $\alpha|\ is the scaling factor of refractoriness, $a|\ is the bias including both the threshold and the temporally constant input, and output $x(t)| is obtained by $x(t) = f\{y(t)\}$ with, for example, the logistic function

$$f\{y(t)\} = 1/\{1 + \exp(-y(t)/\epsilon)\} .$$

Figure 4 shows the shape of the chaotic neuron map, which is bimodal and similar to return plots of the data of squid giant axons and the Hodgkin-Huxley equations (Aihara, 1994, 1995; Mees et al., 1992). The chaotic neuron map is a piecewise monotone continuous map with two turning points and $(+−+)−$ signs of the slope on the three monotonic intervals (Aihara et al., 1990). While the derivatives on the two $(+−)$-segments, which correspond to resting and firing, are between 0 and 1, those on the middle $(−−)$-segment can be less than $−1|\ if the steepness parameter $\epsilon| of the output function is sufficiently small. This middle branch corresponds to the continuous type of threshold separatrix peculiar to excitable nerve dynamics (FitzHugh, 1969), which
causes orbital instability or the butterfly effect of chaos. Chaotic neural networks composed of the chaotic neurons generate various kinds of spatio-temporal chaos with abilities of parallel distributed processing (Aihara, 2002).

References


Science 81, 221–246.

**Internal references**


**Recommended reading**

**External links**

- Kazuyuki Aihara's website (http://www.sat.t.u-tokyo.ac.jp/index.html)

**See also**

Dynamical systems, Chaos, Hodgkin-Huxley model, FitzHugh-Nagumo model

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Accepted on: 2008-05-17 15:57:07 GMT