Finding unstable periodic orbits in electroreceptors, cold receptors and hypothalamic neurons

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Accepted 18 December 1998

Abstract

Recently, searches for low-dimensional dynamical activity in various biological preparations have become fashionable. In particular, demonstrations of the existence of unstable periodic orbits (UPOs) and bifurcations between unstable and stable states are of interest. Here, we report the detection of UPOs in three diverse preparations: electroreceptor, cold receptor and hypothalamic neurons. Inherent, noise mediated oscillators are common to these temperature sensitive neurons, and the UPOs arise in them in the absence of external periodic stimulation. The external temperature is the bifurcation parameter. Behaviors in response to temperature transients are also shown. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Unstable periodic orbit; Electroreceptor; Cold receptor; Hypothalamic neuron

1. Introduction

In the structural view of dissipative chaos, the dynamics arises from an infinite set of unstable periodic orbits (UPOs) [4,5]. A chaotic trajectory spends much of its time wandering among the high-order periods, but occasionally visits those of low period.
In noise free, stationary, physical systems, periods as high as 95 [8] are experimentally detectable. The relatively recent advent of statistically and topologically based search algorithms [11–16,18] have made it possible to observe UPOs with statistical certainty in various biological preparations including electroreceptors [1] cold receptors [2] synaptic currents [7], bursting hippocampal neurons [10,15,17], human electroencephelographic records [9], and human cardiac dynamics [11]. But because biological preparations are typically non-stationary and include relatively large intensities of dynamical noise, only the first few periods have been experimentally observed in the biological preparations. Since higher-order periods are in general less likely to occur, we here focus only on the period-one orbits.

In the following sections, we describe the first observations of UPOs in preparations from three radically different types of temperature sensitive neurons: catfish electroreceptors, rat facial cold receptors and hypothalamic neurons from the rat brain paraventricular nucleus. We briefly describe the data analysis method, techniques for preparing the neurons, experimental protocols and the results. We conclude with a brief summary.

2. Data analysis method

All our data are in the form of a series of time intervals $T_i$ between neural action potentials. We seek particular sequences of six time intervals interspersed among the rest of the file. These sequences are the signatures of an encounter of the general trajectory with a period-1 UPO. Beginning the analysis, we plot the data on a first return map, $T_{n+1}$ versus $T_n$ as shown in Fig. 1A. On this plot, a periodic point is one which lies on the 45° line, that is $T_{n+1} = T_n$. An encounter with an unstable periodic point is marked by a sequence of points which approach the 45° line with decreasing distances along a direction called the stable manifold followed immediately by a sequence which departs along the unstable manifold with increasing distances. An encounter is defined as the occurrence in the data file of three points which approach
Fig. 2. Data from the catfish electroreceptor showing (top-to-bottom) scatter plots, histogram of encounters, intervals with $K$-values and file segments indicated by the bar lengths, firing rate and temperature time course. Stable and unstable sequences are indicated by squares and circles, respectively, with the mid-point shown by the large diamonds.

followed by three which depart. An example is shown in Fig. 1B. Searching the data file results in $N$ such occurrences. The points encompassing all identified sequences are plotted over the complete files in the examples shown in the top panel of Fig. 2. The noise results in the scattering of these collections of points, but in some cases (where
UPOs are clearly present in significant concentrations) two populations, lying generally along the unstable and stable directions, can easily be identified.

The problem is the noise. If the dynamics contains noise, then the definition of an encounter can be fulfilled by accident. Therefore the question becomes: Is \( N \) a statistically significant number? This question can be answered by comparing \( N \) with the average number \( \langle N_s \rangle \) found using the same encounter definition in randomized, or surrogate files [19]. Proper surrogates will destroy the essential information contained in the definition of an encounter, that is, the sequential order of the seven time intervals. Thus all such sequences except random occurrences will be destroyed by randomly scrambling the order of the time intervals in the data file. To obtain the mean, we scramble each data file 100 times, find \( \langle N_s \rangle \) and the standard deviation \( \sigma \). We then examine the statistic,

\[
K = \frac{N - \langle N_s \rangle}{\sigma}
\]

in units of the standard deviation, sigma. \( K \geq 3 \) sigmas signifies the detection of UPOs in the data file with greater than 99% confidence. The value of \( K \) indicates their concentration. Often statistically significant determinations can be made rapidly from files of only a few hundred time intervals, thus indicating that this algorithm is suitable for on-line determinations of the dynamical state of a preparation including transient changes as described below. Such algorithmic simplicity, and hence speed, is especially important in applications involving chaos control [6,15,3].

3. Experimental methods

In all cases, afferent action potentials were recorded extracellularly. The data analysis was performed off line on the time intervals between the fast rises of sequential pairs of action potentials. For the peripheral neurons – electroreceptors and cold receptors – the surface temperature overlying the receptive field of the neuron was regulated and could be adjusted on demand either in discontinuous steps or swept over a range from 5 to 35°C. In the case of the hypothalamus, the temperature of the fluid in a perfusion chamber containing the brain slice preparation could be adjusted in the same manner.

The electroreceptor experiments were performed on live anesthetized catfish, *Ictalurus nebulosus* immobilized in a Lucite holder and artificially respired [1]. A small chamber containing thermally regulated water was sealed by O-ring over the receptive field. Recording was from the ampullary canal located in the dorsal head region using tungsten microelectrodes and standard extracellular electronics.

The cold receptor experiments were performed on anaesthetized rats [2]. Recordings were made from single afferent fibers of the infraorbital nerve with platinum electrodes. The temperature of the receptive field was controlled by a brass cylinder (3 mm diam. tip) over the range described above.
The hypothalamic recordings were made from brain slice preparations obtained from Sprague-Dawley rats. After decapitation, brain removal and conditioning, a block containing the hypothalamus was cut from the brain. Slices (400 μm thick, 5–7 mm diam.) were obtained and conditioned in oxygenated aCSF solution for at least one hour. The slice preparations were then mounted in a temperature controlled perfusion chamber. Single-unit recordings were made from the paraventricular nuclei (PVN) using glass micropipettes positioned with micromanipulators.

File segments containing several hundred to three thousand time intervals were analyzed for the presence of period-one UPOs. As the following data demonstrate, the analysis method described here is suitable for examining the transient appearance and disappearance of UPOs in response to step and/or periodic variations in the temperature of as little as $\pm 1^\circ$C.

4. Results

Fig. 2 shows some example results from experiments on the catfish electroreceptor, though a more complete account has been made elsewhere [1]. The top panel shows four first return maps. The complete data files from which these maps were constructed are shown by the open diamonds. The selected encounters are shown by enlarged symbols: squares indicating the stable directions and circles the unstable direction. The middle panel shows the temporal record of all time intervals ID (small diamonds), together with the time interval sequences comprising the identified encounters in enlarged symbols (squares, stable; circles, unstable directions; large diamonds, the interval pair closest to the fixed point). The solid bars above show the file segments analyzed and the respective $K$-values. The bottom panel shows the temperature time course.

Note the response to the step temperature increase (30–35°C) at about 85 s. Prior to this change, the value $K = 1.6$ indicates no statistically significant concentration of UPOs. However, the larger $K$-values after the change as well as the histograms of identified encounters $E$, plotted above indicate the appearance of large concentrations of UPOs in response to the temperature change. These large concentrations ($K = 9.9$ and 10.2), however, accommodate after about 175 s to insignificant values. The return maps in the top panel echo these findings: only the center two for the largest $K$-values show two well-defined populations of encounter points. In this case, the appearance of UPOs is clearly a transient phenomenon. We note that the mean firing rate $F$, shown in a lower panel, indicates very little sensitivity to the temperature step.

Some results of our experiments with the rat facial cold receptor [2] are shown in Fig. 3. Here, we illustrate the response of the neuron to a sinusoidal temperature stimulus of only $\pm 1^\circ$C at an average temperature of 29°C. The temporal record of all time intervals ID, is shown with bars and $K$-values above. The identified encounters are again indicated by enlarged symbols. The histogram $E$, in the top panel shows that the encounter events indicating large concentrations of UPOs are
phase locked to the stimulus sine wave albeit with a phase shift of about $3\pi/4$, that is, the large concentrations appear on the downward phase of the temperature cycle. In this case the firing rate $F$, shows a similar behavior though it seems to lag the UPO concentration somewhat. The UPOs enter during the increasing phases of the firing rate cycle.

Fig. 4 shows some results obtained from a hypothalamic neuron in the PVN. In this case, a linearly increasing temperature ramp is applied. Note the bifurcation to bursting beginning at approximately 200 s. In this case the $K$-values and histogram show that a large concentration of UPOs enters the dynamics at about 110 s after the ramp begins prior to the bursting bifurcation. After the bifurcation the neuron accommodates and the UPOs disappear. The firing rate shows no indication of this behavior.

5. Summary

In summary, we have demonstrated the existence of period-one UPOs in three diverse types of temperature sensitive neurons. In response to step, periodic or ramp temperature stimuli, the UPOs enter and depart transiently.
Fig. 4. Paraventricular nucleus neuron of rat brain with data arranged as in Fig. 3.

References


