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Oscillatory behavior of a water/oil interface system in response to current-clamp and voltage-clamp stimulation

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Oscillatory behavior in response to current-clamp and voltage-clamp stimulation was examined on a water/oil/water system consisting of an aqueous solution of sodium oleate as surfactant, a solution of 2,2′-bipyridine in nitrobenzene and an aqueous solution of sodium chloride. Stable oscillation was observed only when the strength of the stimulation lay within a specific range of values.

1. Introduction

Self-sustained oscillations in biological membranes have been extensively investigated by many authors. Matsumoto and Stuhmer [1] observed the onset of self-sustained oscillation in squid giant axons when the Na^+ concentration in the external solution exceeded threshold value and interpreted their experimental results in terms of the Hodgkin-Huxley equations. Furthermore, by carrying out a simulation based on the Hodgkin-Huxley equations, they showed that a pulse potential oscillation was stimulated by a d.c. current above the threshold value. In an experimental study of d.c. current stimulation, however, only a few pulses appeared during the initial stages, and subsequently a depolarization of the resting potential was found to occur [2].

On the other hand, several investigations of great interest have been carried out on self-sustained potential oscillations across water/oil interface systems. Dupeyrat and Nakache [3] and Nakache et al. [4] observed quasi-periodic variations in interfacial tension and electric potential in an oil/water interface system composed of solutions of hexadecyltrimethylammonium chloride in water and picric acid in nitroethane or nitrobenzene. Yoshikawa and Matsubara [5] reported self-sustained oscillations in a two-phase system comprising a solution of picric acid in 2-nitropropane and an aqueous solution of the surfactant hexadecyltrimethylammonium bromide (CTAB) [5], and also in a three-phase (water/oil/water) system composed of an oil phase of nitrobenzene and two aqueous phases, one containing CTAB and alcohol, the other containing sucrose [6]. Subsequently, Yoshikawa and co-workers carried out extensive experimental studies on these kinds of water/oil interfaces and observed self-sustained oscillations in many systems [7–10], one of which was a three-phase system consisting of an aqueous solution of sodium oleate as surfactant, a solution of 2,2′-bipyridine in nitrobenzene and an aqueous solution of NaCl [9]. We examined the effect of

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surfactant concentration on the oscillatory behavior of this system and observed stable oscillation only when the concentration of surfactant fell within a particular range of values. In a previous study [11], we attempted to interpret the mechanism of self-sustained oscillation as well as its stability in terms of the diffusion of surfactant ions to the water/oil interface and the process of their absorption into the oil phase via the formation of inverted micelles.

In the present work, we have studied the effect of stimulation by d.c. current or d.c. voltage on a water/oil interface system, in relation to the oscillatory behavior of biological membranes induced by electrical stimulation. The material used was a three-phase system consisting of an aqueous solution of surfactant, nitrobenzene and an aqueous solution of NaCl.

2. Experimental and results

The experimental setup employed for measurements of electrical oscillations is shown in fig. 1. A solution of dried 2,2′-bipyridine in distilled nitrobenzene was placed at the bottom of the measuring cell, a U-shaped glass tube (12.5 mm diameter). An aqueous solution of NaCl (0.5 M) was poured into one arm of the cell and a mixture comprising an aqueous solution of sodium oleate (0.25 mM) and propanol (9 : 1, v/v) was added to the other arm. The temperature of the cell was

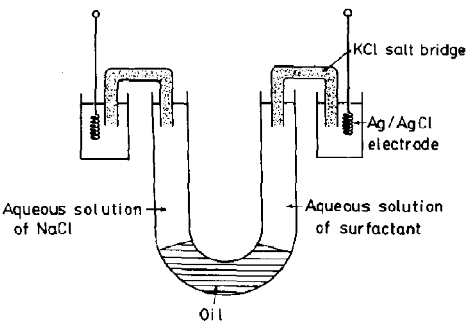

Fig. 1. Experimental setup for measurements of electrical oscillations in a water/oil/water system.

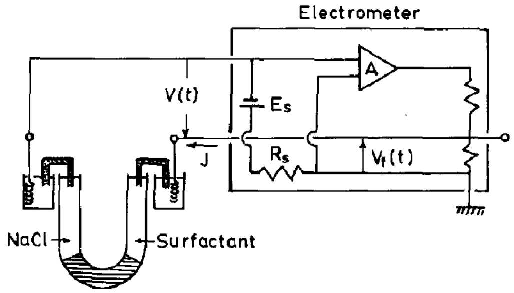

Fig. 2. Block diagram of the circuit used for measurements of the potential oscillation $V(t)$ in response to current-clamp stimulation J.

maintained constant at 25 °C within an accuracy of 0.1°C.

The above conditions were chosen, since a stable self-sustained oscillation was observed in the previous experiment [11] even when no current was passed through the system. Although the wave form and amplitude of the oscillation in the absence of electric stimulation are not exactly the same as those in the previous experiment, qualitative reproducibility of the data was observed. We have investigated the effect on electrical oscillation evoked by the application of an electric current or voltage.

2.1. Response to current-clamp stimulation

The dynamic potential across the oil phase was determined using a high-impedance electrometer through KCl salt bridges and Ag/AgCl electrodes. The experimental setup for the electrometer involves a constant current source and is illustrated by a block diagram of the circuit in fig. 2. The d.c. current flowing through the sample, J, is controlled by adjusting the resistance, R_s. The open-loop gain of the amplifier A is very large, such that both of the input terminals are at an equal potential, therefore, the potential across the sample V is equal to the feedback potential V_f.

Fig. 3 shows a series of traces representing the potential oscillations observed between the two aqueous solutions on varying the d.c. current flowing through the water/oil/water phases. For all of the runs shown in fig. 3a–d, all samples of the three phases were replaced by fresh samples pre-

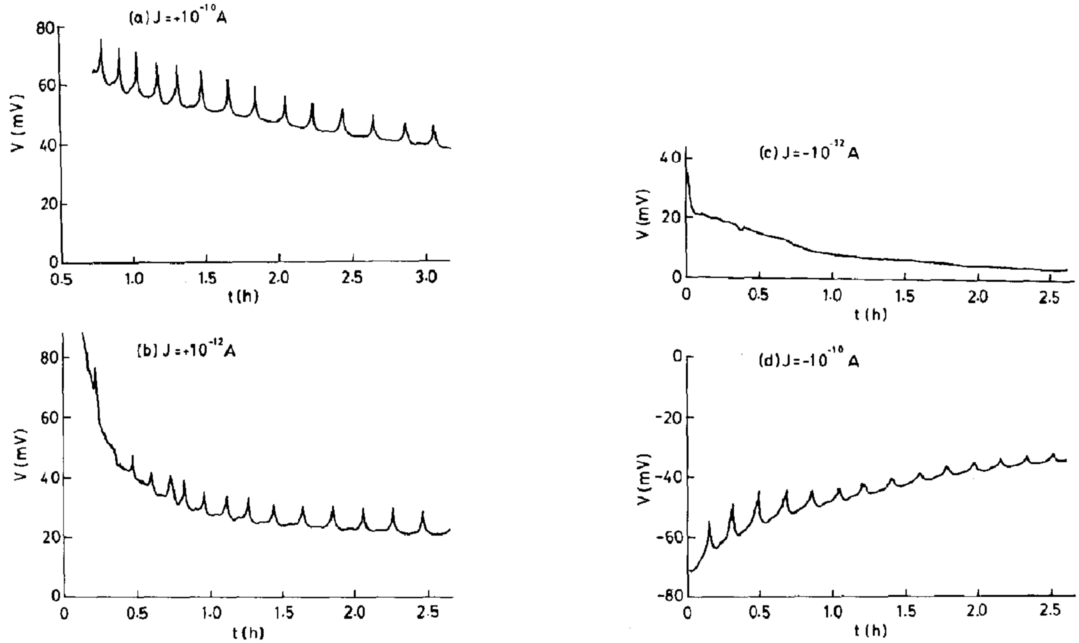

Fig. 3. Potential oscillations in response to current-clamp stimulation. A positive value of the current J signifies flow in the direction from the solution in the right arm to that in the left. A positive value of the voltage (ordinate) represents the potential of the solution in the right arm relative to that in the left.

pared beforehand in a large quantity, since the ion concentration in each arm appeared to change due to chemical reactions and diffusion after several hours of current flowing. The experiment was carried out three times for each value of the current stimulation and qualitatively identical results were obtained. In fig. 3, a positive value of the current signifies that the current flows from the aqueous solution of surfactant (right arm) to the aqueous solution of NaCl (left) and a negative value indicates flow in the opposite direction. The voltage on the ordinate denotes the potential of the solution in the right arm relative to that in the left. For very high values of the current, no oscillation was observed, while for a current of $J = 10^{-10}$ A, a stable oscillation appeared. The period of oscillation is between 7 and 12 min in duration. The tendency of the period to increase with time appears to be due to a decrease in surfactant concentration in the left arm, which is the result of the transfer of surfactant to the right arm through the oil phase. With decreasing current ($J = 10^{-12}$ A) the amplitude of oscillations was found to diminish and the period displayed a rather random pattern of variation. On reversing the current ($J = -10^{-12}$ A), the oscillation disappeared; however, with increasing reverse current ($J = -10^{-10}$ A), the oscillation reappeared and a drastic change in the background voltage to negative values was observed. It is clearly evident that a specific range of values of current stimulation are required for a stable voltage oscillation to persist and that the spikes of oscillation are polarized in the direction of positive potentials, irrespective of the direction of current stimulation.

2.2. Response to voltage-clamp stimulation

The voltage-clamp experiment was carried out by applying a controlled voltage across the sample and measuring the current flowing through it using the electrometer. The circuit employed is depicted by the block diagram in fig. 4. Fig. 5 shows a series of traces recorded for current oscillations

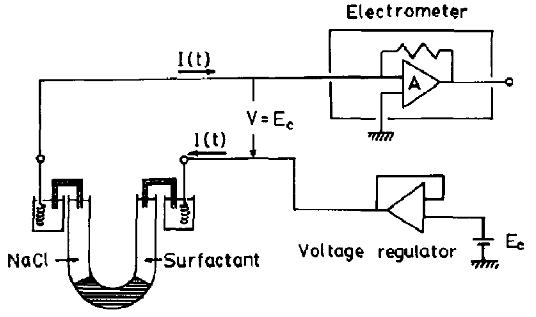

Fig. 4. Block diagram of the circuit used for measurements of the current oscillation $I(t)$ in response to voltage-clamp stimulation V.

occurring in the external circuit when various fixed values of the voltage were applied across the sample. In fig. 5, a positive value for the applied voltage denotes the potential of the solution in right arm relative to that in the left and a positive value of the current on the ordinate indicates the direction of current as flowing from the electric source to the right arm. For a high voltage ($V = 100$ mV), no stable oscillation was observed, while for decreasing voltage ($V = 50$ mV), a rather stable oscillatory current appeared. In contrast to the response to current-clamp stimulation, the spikes of the oscillation in this case point downward. This can be accounted for as being the result of the corrective action of voltage control by the electric source, i.e., the voltage pulse due to firing occurs in such a way that the potential of the right arm rises while the voltage regulator cancels this increase in potential by passing a reverse current pulse. Under these conditions of zero applied voltage and small reverse voltage ($V = -5$ mV), the current oscillation became very unstable, while for large reverse voltages ($V = -50$ mV) stable oscillation reappeared. Finally, for a larger reverse voltage ($V = -100$ mV) the oscillation vanishes again. Thus, the polarity of the applied voltage does not affect the form of current oscillation; however, a specific range of absolute values of the voltage seems to be required for a stable current oscillation to persist.

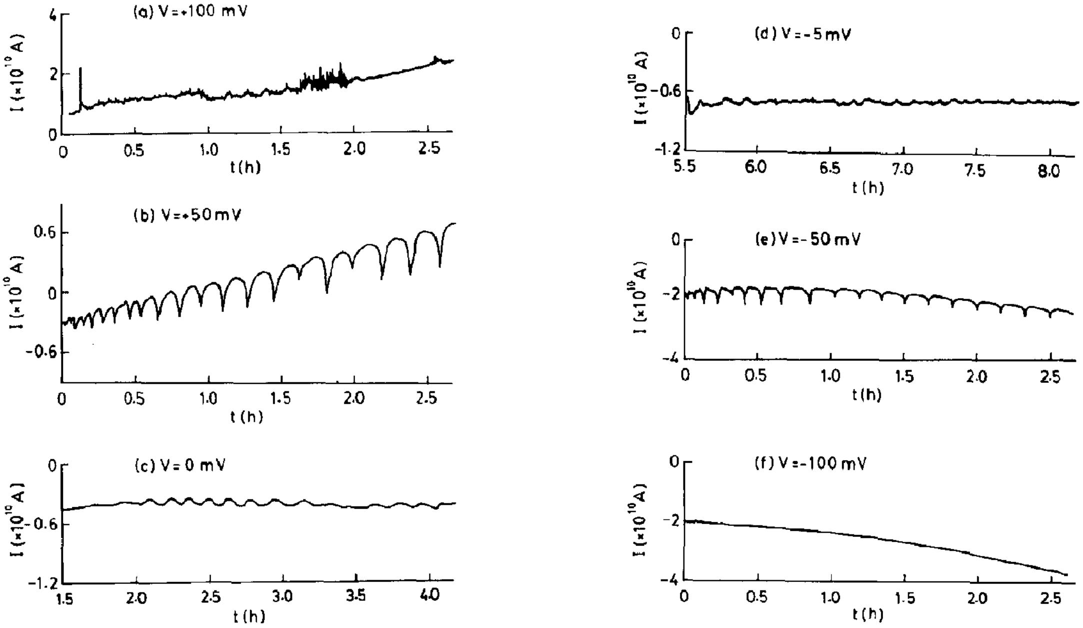

Fig. 5. Current oscillations occurring in the external circuit in response to voltage-clamp stimulation. A positive value of the applied voltage V corresponds to the potential of the solution in the right arm relative to that in the left. A positive value of the current (ordinate) indicates the direction of current flow to be from the voltage regulator to the right arm.

3. Discussion

Oscillatory behavior observed in an interface system composed of an aqueous solution of surfactant and oil was found to become more stable on application of current- or voltage-clamp stimulation of sufficient strength. Here, 'stable' implies large amplitude and regular periodicity. The direction of the spikes in response to current stimulation was upward, irrespective of the direction of the current, while that in the case of voltage stimulation was downward and independent of the direction of the voltage. The oppositely polarized responses to stimulation by current and voltage appear to result from the difference between the functions of the current and voltage regulators. Let us assume that electrical stimulation induces oscillatory absorption of surfactant into the oil and gives rise to a series of upward voltage responses as shown in the case of current-clamp stimulation. If this assumption holds true, then the same oscillatory absorption of surfactant will also occur in the case of voltage-clamp stimulation; however, the voltage regulator maintains a constant bias potential by controlling the current in the circuit via passing a pulse of current at the moment of firing and thereby counterbalancing the voltage pulse produced by the absorption of surfactant.

This water/oil interface is a nonlinear active system which displays spontaneous oscillation even when no electrical stimulation is applied and thus far the problem of dealing with the behavior of such active systems under conditions of a constant current or constant voltage remains to be resolved. In order to elucidate the mechanism of oscillatory behavior, direct determination of the changes in concentration of ions in the oil and aqueous phases would be desirable.

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