

Memristive model of amoeba's learning

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Recently, it was shown that the amoeba-like cell *Physarum polycephalum* when exposed to a pattern of periodic environmental changes learns and adapts its behavior in anticipation of the next stimulus to come. Here we show that such behavior can be mapped into the response of a simple electronic circuit consisting of an *LC* contour and a memory-resistor (a memristor) to a train of voltage pulses that mimic environment changes. We also identify a possible biological origin of the memristive behavior in the cell. These biological memory features are likely to occur in other unicellular as well as multicellular organisms, albeit in different forms. Therefore, the above memristive circuit model, which has learning properties, is useful to better understand the origins of primitive intelligence.

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I. INTRODUCTION

Although it is a unicellular organism, *Physarum polycephalum* displays remarkably intelligent abilities: it is able to solve mazes¹ and geometrical puzzles², control robots³, and may even be able to learn and recall past events⁴. According to Ref. 4, when exposed to three spikes of cold temperature and low humidity, set at specific lengths of time and given at regular intervals, the *Physarum* decreased its movement speed at the same time as the shocks. However, after the spikes had stopped, the *Physarum* still decreased its speed at the times when the spikes would have occurred, effectively predicting the time of the spikes from the pattern it had been given. These "memory patterns" dissipate over time, but a single spike in temperature can trigger the oscillations again, provided it is within a certain time frame. This shows the amoeba "learned" that a single temperature spike can be followed by others at the given period.

At this point, the question may arise as to whether it is at all appropriate to use the term "learning" to describe the amoeba's response. Usually, when we discuss about learning in the animal world, that term refers to a more complex behavior (for example, classical conditioning and associative memory^{5,6}) which is observed in higher developed species such as mammals. In amoebas, this type of classical conditioning has not been observed yet, and their "learning" is rather primitive. Irrespective, the adaptive behavior of amoebas is astonishing, with direct experimental evidence that amoebas can memorize sequences of periodic environmental changes and recall past events. Therefore, in this paper we will use the term "learning" only in the context of recent experiments on this system⁴.

A partial model to describe this behavior has been advanced in Ref. 4 in terms of the ubiquitous biological oscillators. According to this model, these internal oscillators have a natural frequency, and may possibly deviate from that frequency so that multiple oscillators can

respond to the same frequency. The frequency of natural shocks excites one or more of these oscillators, which could be the source of *Physarum's* ability to recognize patterns and predict events. The model, however, does not fully explain the memory response of the amoeba and does not take into account the fact that, at a mi-

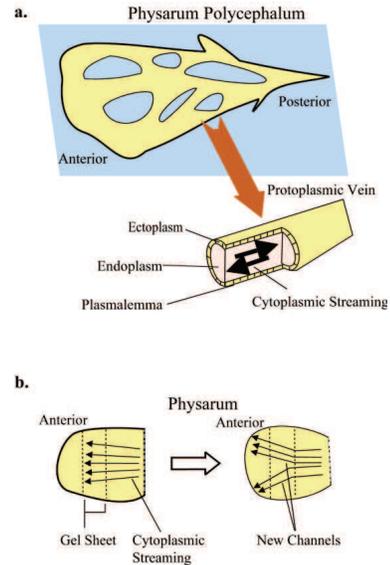


FIG. 1: (Color online) View of *Physarum* during movement. (a) *Physarum* moves via shuttle streaming, a process of periodic flow of the ectoplasm and endoplasm, with a greater net flow towards the direction of movement, or the anterior end. The ectoplasm contains radial and longitudinal actin-myosin fibers whose oscillating contractions help produce the pressure gradient which drives shuttle streaming⁷. (b) During movement, the anterior of *Physarum* may develop a sheet of gel that inhibits streaming. However, when the pressure gradient builds to a certain threshold, the gel can break down allowing for the formation of new channels of flow. These channels may become new permanent veins for streaming.

Component	Amoeba	Electronic circuit
Control parameter	Temperature and humidity	Applied voltage
Output signal	Velocity	Voltage
Oscillator	Biochemical oscillators	LC contour
Memory element	Gel/sol interactions	Memristor
Parameter containing information	Veins and low-viscosity channels	Resistance of memristor

TABLE I: Possible correspondence between learning of an amoeba and an electronic circuit.

crossopic level, other changes in the physiology of the organism may occur in addition to the biological oscillators. These changes also occur over a finite period of time and must be dependent on the state of the system at previous times.

This last point is particularly important: it is in fact this state-dependent feature which is likely to produce memory effects rather than the excitation of biological oscillators. Instead, the latter ones seem to control the rhythmical flow of the endoplasm through protoplasmic veins⁷ shown schematically in Fig. 1(a). As of now, it is not yet known how the memory in amoebas is actually realized. However, we identify a possible mechanism of amoeba’s memory as described below. Irrespective of whether this is the only mechanism leading to the observed response, our model is in excellent agreement with the recent experimental observations⁴ and can be used, in the form of differential equations, to describe the amoeba’s response to a changing environment.

Let us then consider mechanisms existing in amoebas which depend on the state of the system and on its dynamical history thus potentially giving rise to the observed memory response. These mechanisms are as follows. The *Physarum* contains in its interior a gel-sol solution. The gel, present in the ectoplasm, is more gelatinous than the less viscous sol, present in the endoplasm, and the sol flows through the gel almost in the same way as water through a sponge. Now, the gel-sol solution is thixotropic, meaning that the viscosity can change as a function of pressure. When the amoeba is moving, the actin-myosin fibers present in the ectoplasm contract radially and longitudinally, creating a pressure gradient pushing the endoplasm in the direction of motion. This gradient can increase to the point in which it causes the gel to break down into sol so that new low-viscosity channels form, which may even become permanent pathways (see Fig. 1(b))^{8,9}. Therefore, if the external temperature and humidity of the environment are changed, the sol flow changes in a non-linear way. A restoration of initial conditions upon change of the environment thus requires time, and depends on the number and shape of the formed low-viscosity channels. This mechanism is similar to the one underlying the memory-resistance (memristor) behaviour^{10,11,13,14,15,16,17} of cer-

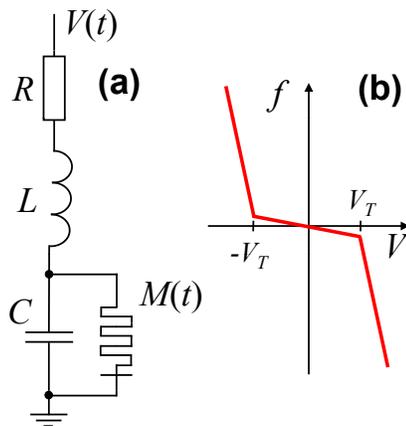


FIG. 2: (Color online) Electronic circuit that models amoeba’s learning. (a) Schematic representation of the learning circuit made of four fundamental two-terminal circuit elements: resistor R , inductor L , capacitor C and memristor M . (b) Sketch of the selected memristor function f which depends on the voltage applied to the memristor (more details are given in the text). It is defined as $f(V) = -\beta V + 0.5(\beta - \alpha)(|V + V_T| - |V - V_T|)$, where α and β are positive constants and V_T is a threshold voltage.

tain electronic devices^{13,14}. In these, the variation of an external parameter (e.g., the voltage) creates new, or modifies existing conducting channels thus altering the resistance in a non-linear way. Therefore, it is natural to argue that in the very same way that a memristor has its inherent memory, the *Physarum* acquires a memory through the interactions of the gel-sol solution, specifically through the formation of new, low-viscosity channels, and perhaps by other related complex interactions.

We now show this possible connection more clearly by presenting a juxtaposition of the mechanisms behind the movement process of *Physarum* with the operation of an equivalent electrical circuit made of just the four basic passive electrical elements: the resistor (R), capacitor (C), inductor (L), and memristor^{10,18} (M). Indeed, we show that, like the amoeba, this circuit can learn and predict subsequent signals. Due to the complexity of biological systems, the present analogy will be a simplification of what specifically happens during the learning process. Nevertheless, it may be very useful in understanding the origin of primitive intelligence in other organisms as well.

II. MEMRISTIVE CIRCUIT

Let us then start by identifying the relation between the basic circuit elements and the biological processes in the cell (see Table I). In this respect the biological oscillators can be simulated with the oscillations of an LC contour. The resistance R describes the fact that there must be some signal impedance and dissipation inside the amoeba, or else signals would travel instantaneously and

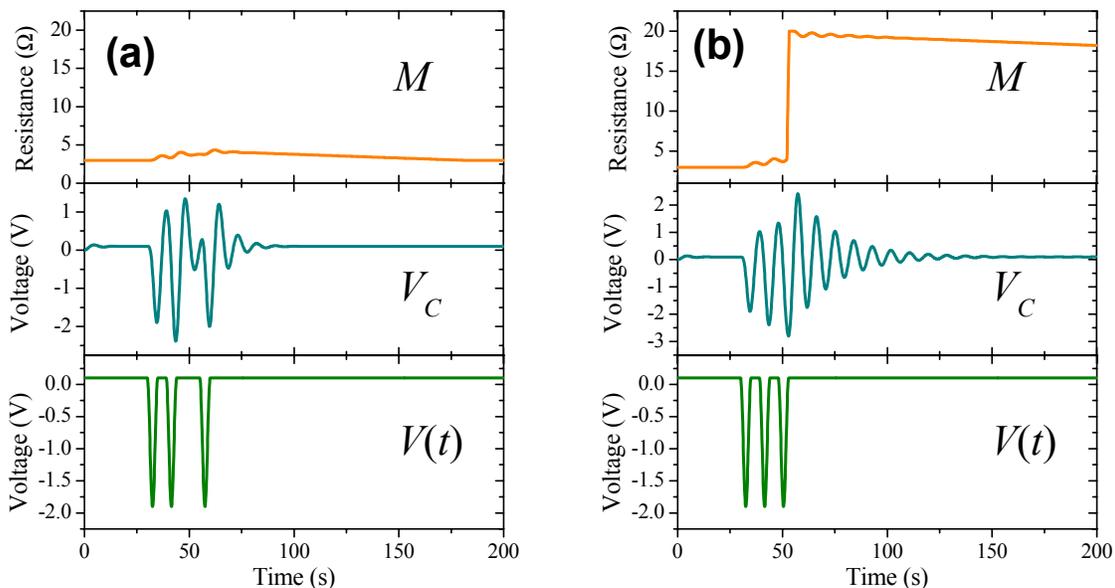


FIG. 3: (Color online) Simulations of the circuit response to applied pulse sequences. (a) Arbitrary pulse sequence. (b) Learning pulse sequence. The calculations were made using the following system parameters: $R = 1\Omega$, $L = 2\text{H}$, $C = 1\text{F}$, $M_1 = 3\Omega$, $M_2 = 20\Omega$, $\alpha = 0.1\Omega/(\text{Vs})$, $\beta = 100\Omega/(\text{Vs})$, and $V_T = 2.5\text{V}$. The applied pulse sequence was selected in the form $V(t) = V_F - V_p \sum_i (\cos(2\pi(t - t_i)/W_p) - 1) \theta(t - t_i) \theta(t_i + W_p - t) / 2$, where V_F is the voltage corresponding to the standard (favourable) conditions, V_p is the pulse amplitude, t_i is the time of start and W_p is the pulse width. In the calculations, we used $V_F = 0.1\text{V}$, $V_p = 2\text{V}$, and $W_p = 5\text{s}$. The t_i 's can be identified from the figure.

indefinitely. Finally the memristor M summarizes the memory mechanisms we have described above, or any other possible mechanism for memory. The temperature and humidity that control the motion of the amoeba correspond to the external voltage that controls the circuit. The response, namely the amoeba's velocity, is nothing other than the voltage at the memristor.

The electronic scheme that accomplishes the learning process in response to a train of voltage pulses is shown in Fig. 2(a). The capacitor and memristor are connected in parallel. The main idea behind functioning of this scheme is to use the internal state of memristor in order to store information about the past and control oscillations in the LC contour. In particular, we use the model of a voltage-controlled memristor, inspired by recent experiments¹⁴, in which the resistance of memristor M can be changed between two limiting values M_1 and M_2 , $M_1 < M_2$. In our scheme, M increases as a result of increased number of periodic stimuli and thus as a result of learning.

The change of M is described by the following equation

$$\frac{dM}{dt} = f(V_C) [\theta(V_C) \theta(M - M_1) + \theta(-V_C) \theta(M_2 - M)], \quad (1)$$

where $f(V_C)$ is a function describing the change of the memristor state, V_C is the voltage applied to the memris-

tor (equal to the voltage drop on the capacitor) and $\theta(\dots)$ is a step function. The expression in square brackets guarantees that M changes between M_1 and M_2 . Here, we assume that $f(V_C)$ consists of several linear segments as shown in Fig. 2(b). This is the simplest memristor model which takes into account the activation change of the memristor state¹⁹. In other words, the memristor learns faster when $|V_C| > V_T$ and slower when $|V_C| < V_T$, where V_T is a threshold voltage.

The response of the circuit shown in Fig. 2(a) is described by the following equations:

$$V_C + L\dot{I} + IR = V(t), \quad (2)$$

$$C\dot{V}_C + \frac{V_C}{M} = I, \quad (3)$$

where V_C is the voltage on the capacitor, I is the total current and $V(t)$ is the applied voltage. Eq. (2) simply states that the applied voltage is equal to the sum of voltage drops on each element of the circuit, and Eq. (3) is the Kirchhoff's current law at the point of connection of capacitor, inductor and memristor. We solve Eqs. (2) and (3) together with Eq. (1) numerically using initial conditions close to a steady state and different $V(t)$.

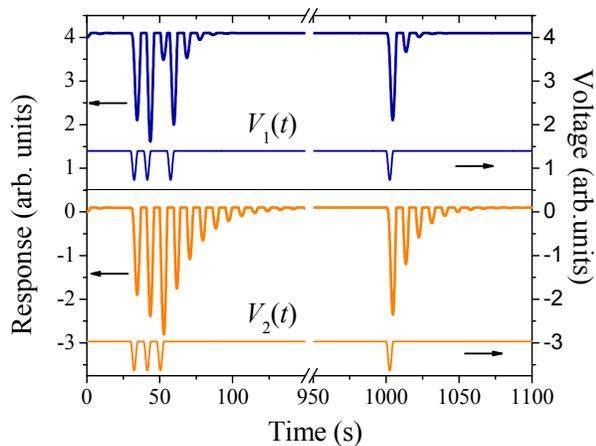


FIG. 4: (Color online) Modeling of the spontaneous in-phase slowdown responses. This plot demonstrates that stronger and longer lasting responses for both spontaneous in-phase slowdown and spontaneous in-phase slowdown after one disappearance of the stimulus are observed only when the circuit was previously “trained” by a periodic sequence of three equally spaced pulses as present in $V_2(t)$. The applied voltage $V_1(t)$ is irregular and thus three first pulses do not “train” the circuit to learn. The simulation parameters are as in Fig. 3. The lines were displaced vertically for clarity. The arrows are used to define the correct vertical axis for each line.

III. RESULTS AND DISCUSSION

In our circuit scheme, a favorable (standard) environmental condition corresponds to a positive applied voltage and unfavorable condition to a negative applied voltage. If the favorable condition is applied for a long period of time, then, during this period of time, a positive voltage is applied to the memristor. According to Eq. (1) and $f(V_C)$ as in Fig. 2(b), the latter switches into the low resistance state M_1 . In this case, the LC contour is damped and excited oscillations decay fast. Fig. 3(a) demonstrates that when a non-periodic sequence of pulses is applied to the scheme, the circuit learning ability (or change of M) is small and oscillations in the contour are strongly damped. In the opposite case, when we apply periodic pulses with a frequency close to the LC contour’s resonant frequency, the change of M is much more pronounced, the memristor switches into its higher resistance state and, since the LC contour becomes less damped, oscillations in the contour survive for a longer time. Such behavior is related to the fact that during the application of resonant pulses the amplitude of voltage oscillations on the capacitor increases with each pulse and at some point exceeds V_T in amplitude. As a consequence, the memristor learns fast and its state changes significantly.

Fig. 4 shows simulations of spontaneous in-phase slowdown (SPS) and SPS after one disappearance (SPSD) events as in the experiments with the amoeba⁴ (a de-

scription of these experiments is given below). In these simulations we use the scheme described above with the only restriction that the response signal can not exceed a certain value, which in our particular calculations is selected to be equal to the voltage corresponding to standard (favorable) conditions V_F . This signal is selected to be equal to V_C if $V_C < V_F$ and to V_F if $V_C > V_F$.²⁰

In SPS experiments, the amoeba was exposed to three intervals of unfavorable conditions (namely, low temperature and humidity). Each time, the locomotion speed decreased. After that, standard (favorable) conditions were applied. However, the movement of the amoeba has been found to slow spontaneously when the next intervals of unfavorable conditions would have occurred. Exactly the same behavior is found in our circuit model. This is shown in Fig. 4, where a regular pulse sequence $V_2(t)$ is applied. It is clearly seen that in response to the application of three regular pulses, the response signal decreases each time these pulses are applied as well as at subsequent times when following pulses would have occurred. The opposite behavior is demonstrated when the three training pulses are not periodic as shown in Fig. 4 with an irregular pulse sequence $V_1(t)$. In this case, the anticipated response is significantly smaller.

Application of the fourth pulse in Fig. 4 corresponds to conditions of SPSD experiments⁴ in which the anticipated slowdown after a single unfavorable condition was observed only among previously trained organisms. Again, we can see a striking similarity with the experimental results on amoeba’s learning: in the case of a pulse sequence with the first three non-periodic pulses ($V_1(t)$), the subsequent application of a single pulse does not result in a significant anticipated slow-down after the pulse. On the other hand, a “trained” circuit (by applying the $V_2(t)$ pulse sequence) manifests several well-defined slowdown events after the fourth pulse.

Finally, we plot in Fig. 5 the final state of the memristor just after the application of three learning pulses as a function of time interval between the pulses. It can be noticed that learning occurs in the interval $8s < \tau < 10s$, which is close to the LC contour time sequence. Also, the larger the rate at which the memristor learns (as exemplified by the parameter β in the function $f(V_C)$) the more defined is the time interval for learning. To some extent, this plot resembles Fig. 3 in Ref. [4] for amoeba’s learning. A qualitative description of the dependence shown in Fig. 5 is the following. It is well known that the amplitude of oscillations excited in a LC contour decreases when the applied voltage frequency moves away from the resonant frequency. In particular, if we consider just a simple LC contour (as in Fig. 2(a) but without R and M) driven by $V(t) = V_0 \cos(\omega t)$, then the amplitude of steady-state voltage oscillations on the capacitor is

$$V_C^0 = \left| \frac{V_0}{1 - LC\omega^2} \right|. \quad (4)$$

If we now assume a memristor connected in parallel with the capacitor in such a contour, to first approximation,

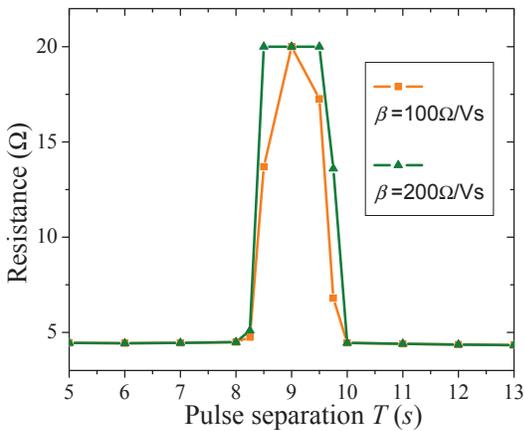


FIG. 5: (Color online) Resistance of memristor calculated at two different values of the parameter β in the function $f(V_C)$ as a function of time interval τ between the pulses. Here, we plot the value of the memristance M right after the last (third) pulse in the learning sequence. The memristor state significantly changes when pulse period is close to the LC contour frequency. The simulation parameters are as in Fig. 3.

M can be significantly changed only if V_C exceeds the memristor threshold V_T . This occurs when, according to Eq. (4), the frequency ω of the applied field is close to the resonance frequency $1/\sqrt{LC}$. Fig. 5 clearly demonstrates that the range of periods of applied oscillations leading to significant changes in M is distributed around the period of resonant oscillations in the contour, which in the present case is $T = 2\pi\sqrt{LC} = 8.9$ s.

We have demonstrated that a simple electronic circuit can be used to model the results found in Ref. 4, which show that an amoeba migrating across a narrow lane can learn the period of temperature shocks, and predict when future shocks would occur. As the amoeba migrates in normal conditions, new veins form in the amoeba as a natural process of movement, and old ones decay into the tail of the amoeba (see Fig 1). As a result, the amoeba’s internal structure dynamically changes with vein formation and degradation. The vein formation is pressure dependent, and the pressure is a result of the constriction of the sol by the actin fibers in the gel, with both radial and longitudinal contractions. This contraction is rhythmic and periodic with ATP and Ca^{2+} levels, and possibly with other biological compounds as well. Thus, in amoeba’s motility, it is the internal oscillations of actin fiber contractions that create the pressure gradients that control the formation of new veins and the decay of old ones; movement entails change in the vein structure, whether or not an outside periodic stimulus is present. The circuit in Fig. 2 can be seen as describing the process of vein formation, whereby LC oscillations generate the voltage threshold to change the state of the memristor. In the amoeba, the formation of veins means that sol can flow more easily; in our circuit, a high resis-

tance state in the memristor means that the input signal is more conserved, so that current can flow more easily.

Ref. 4 explains that a periodic stimulus may in fact link certain biological oscillators together, producing a strong rhythmic response to that stimulus. Qualitatively speaking, assuming these oscillators link together locally in the amoeba, a strong local response would aid vein formation in that local area so that the sol flow caused by those oscillators is less damped than sol flow in veins that resulted from a normal or weak oscillatory response. To reiterate, a periodic stimulus will produce a stronger periodic response, assuming that biological oscillators link together, resulting in stronger vein formation, as a consequence of which the oscillatory response can be more conserved than usual. We argue that therein lies the memory of the amoeba: the passive “decision” to conserve the strongest output signal produced by a given input signal. This is the effect illustrated by our circuit; a strong LC response is conserved by a high memristor value. Vein structures are changed over time by the movement of the amoeba in response to any given stimulus; however, it seems that a periodic stimulus produces the strongest response that leads to memory. Clearly, due to the complexity of the biological problem at hand, we cannot exclude that other mechanisms are at play in producing the observed amoeba’s memory.

IV. CONCLUSIONS

In conclusion, we have presented an electronic circuit model to describe the amoeba’s ability to recognize patterns and predict events. This model contains a memristive element and simulates the mechanisms of biological memory that possibly occur in the protoplasm of the *Physarum*, which produce a sol flow that depends on the history and state of the system. A collection of circuits as those presented here (but with different resonant frequencies), or, possibly, a single circuit with the replacement of the capacitor and/or inductor with the newly introduced memory-capacitor (memcapacitor) and memory-inductor (meminductor)¹², closely simulates the experimentally observed learning ability of the amoeba⁴ including the memory of period, and provides a dynamic picture of the memory mechanism in this unicellular organism. It is worth noting that the proposed electronic circuit is made only of passive elements and can be realized in the laboratory. It may thus find applications in electronic applications that require “circuit learning” or pattern recognition. Finally, this model may be extended to multiple learning elements and may thus find application in neural networks and guide us in understanding the origins of primitive intelligence and adaptive behavior.

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 - ¹⁸ In this paper we use the word memristor in a broad sense to include both perfect memristors¹⁰ and memristive systems¹¹.
 - ¹⁹ This model is inspired by a recent experimental paper (Ref. 13), where it is shown that the memristor state changes fast at high applied voltages, and varies little at low voltages.
 - ²⁰ Electronically, such a response signal can be obtained using a resistor connected from one side to the junction of the inductor, capacitor and memristor in Fig. 2(a) and a diode connected between another side of the resistor and a power source at V_F voltage.