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A Computer Model for the Movement of Electrically Stimulated Paramecium

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Abstract: In this paper, I will study some parameters that affect the motion behavior of a *Paramecium* which is exposed to stimulation by electrical pulses. This study is conducted by simulation using a two – segment electrophysiological model computer program. The goal of the simulation program is to find the relation between the intraciliary calcium concentration, $[Ca^{2+}]_i$ and the electric pulses' amplitude applied to a free swimming *Paramecium,* as well as to explore the relationship between the electric pulse amplitude and the ciliary reversal time. I have found that when the anterior segment of the model lies toward the anode before application of the electric pulses across the cell, the membrane potential of the cell will be depolarized at some electric pulses of different amplitude and duration. This depolarization causes the cilia to reverse their beating direction which makes the cell swim backward. The longest time for this reversal, about 2s, is found at the pulse of 80 mV and 0.6 ms. In contrast, the model shows that there are very small depolarization and no depolarization when the anterior segment lies toward the cathode before the electric pulses are applied.

Keywords: Computer model; Two–segment; Intraciliary calcium concentration $[Ca^{2+}]_I$.

Introduction

Paramecium is a unicellular micro-organism with a slipper – like shape. Its membranes are covered with tiny hair – like projections called cilia. This organism swims in a spiral path on its long axis due to beating the cilia. It swims forward when the cilia beat at angle backwards in unison, while it swims backward when the cilia reverse their beat (i.e., beating forward).

Many computer models were constructed for studying motile responses of cilia and flagella due to different stimulations [5–15]. A computer model was designed for simulation to study the responses of swimming *Paramecium* due to electric field (galvanotaxis) [16, 17]. Chemotactic behavior (Chemotaxis) of the *Paramecium* was also simulated by a computer model [18]. The effect of gravity on the *Paramecium* movement (gravitaxis) [19] and ciliate cell responses such as *Fabra salina* to light (Phototactic-behavior or Phototaxis-) had been studied by a computer model [20]. Other models simulated *Paramecium's* swimming orientation due to magnetic field (magnetotaxis) [21]. A considerable amount of information is now available on ionic relations and gating processes in *Paramecium*. Hook and Hildebrand's physiological model [2, 3] accounts well for available electrophysiological data on clamped cells and for variable ciliary reversing time which is observed when ionic concentrations in the medium are changed. A theoretical electrophysiological two – segment model for *Paramecium* based on Hook and Hildebrand's model is constructed to give an explanation to experimental results of freely – swimming *Paramecia* behavior when they are excited by electric pulses [1, 4]. Analysis of the experimental results [4] shows that the reverse swimming (backward swimming) due to external

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electric field pulses applied across a trough containing a free swimming *Paramecia* occurs among those cells which are swimming forward toward the anode (i.e., cell's anterior toward the anode) before the electric pulses are applied. In contrast, those cells swimming toward the cathode before the application of pulses generally increase their forward swimming velocity afterwards. It is found that there is a direct proportional relationship between the percentage increase or decrease in forward swimming velocity of the cells after the pulse and the initial (pre-pulse) swimming velocity [4]. In this paper, the simulation of a two-segment model is done to see if there is an effect of intraciliary calcium concentration and the membrane potential on the swimming of the *Paramecium.*

Computer Simulation

The two-segment model computer program was run on a computer for an extended period, sometimes for two days, to enable the steady-state (unexcited) parameters to be determined. In the steady-state, the intraciliary calcium concentration for both cell segments (interior and posterior of the cell) and the cytoplasmic calcium concentration are both about 26 n.mol. dm^{-3}. The intraciliary calcium concentration required to initiate ciliary reversal in the two-segment model is chosen to be 500 n.mol.dm^{-3}. Table 1 shows some parameters which are used in the two – segment model. Other models' parameters are the same as shown in previous work [1].

TABLE 1. Some of the parameters used in the two – segments model

Parameter	Symbol	Value
Ca^{2+} - conductivity per cilium	g_{Ca}	3.75×10^{5} 1 / mV. s
K^{+} - conductivity per cilium	g_{K}	2.5×10^{8} 1 / mV. s
Intracellular Ca^{2+} - concentration	$[Ca^{2+}]_i$	10 nmol. dm^{-3}
Intracellular K^{+} - concentration	$[K^{+}]_i$	20×10^{6} nmol. dm^{-3}
Extracellular Ca^{2+} - concentration	$[Ca^{2+}]_o$	10 nmol. dm^{-3}
Extracellular K^{+} - concentration	$[K^{+}]_o$	2×10^{6} nmol. dm^{-3}
Steady – state membrane potential	V_m	- 30 mV
Overall membrane capacitance of the cell body	C	10.4×10^{-13} C / mV
Number of cilia	N	10^{4}
Volume of cilia	Δ_i	3×10^{-13} cm^{-3}
Effective volume of the cell body	Δ_c	10^{-5} cm^{-3}

Anterior Segment toward Anode before the Application of Electric Pulses

The two-segment asymmetric model predicts a reverse in cell swimming (backward swimming) after applying an electric pulse when the anterior segment faces the anode before the pulse. For pulses of a duration of 0.6 ms and varying amplitude, the simulation of the two – segment model shows that the membrane potential is depolarized (above 0mV) within 20-250 ms according to the amplitude of the pulse (FIG.1); then the membrane potential sharply drops around - 30 mV; i.e., the steady – state value.

The maximum value of membrane potential depolarization for each pulse increases as the pulse amplitude increases until it reaches a maximum peak at a pulse of 80 mV, then decreases for further increases in pulse amplitude (FIG.2).

The average intraciliary calcium concentration, $[Ca^{2+}]_{i.ave.}$, of both segments following a pulse amplitude of 80 mV and duration of 0.6 ms, remains on the plateau of about $6x10^{-5}$ mol. dm^{-3} for about 1.5s, then drops to around $6x10^{-6}$ mol. dm^{-6} and remains at this level for more than 20s without showing any indication of returning to the original steady level, while at 65 mV and 100 mV for 0.6 ms $[Ca^{2+}]_I$ shoos within a very short time to peak, then drops sharply to steady state level (FIG.3).

The maximum value of $[Ca^{2+}]_{i.ave}$ for different pulse amplitudes increases with increasing amplitude until it reaches maximum, then decreases with further increase in pulse amplitude (FIG.4). These findings suggest that the pulse of 80 mV and 0.6 ms has strong effects on the depolarization of the membrane potential and increase in intraciliary calcium concentration; hence, the cell will undergo a

longer ciliary reversal time than for other pulses. Cytoplasmic calcium concentration, $[Ca^{2+}]_c$, builds up to a maximum plateau due to a pulse (FIG.5) and remains at this level for a long time before returning to the steady – state level. This may be caused by slow diffusion process of Ca^{2+} ions from cytoplasm to cilia. The peak of $[Ca^{2+}]$ increases as the strength of the pulse increases until it reaches a maximum (peak) value of about $6x10^{-6}$ mol.dm^{-3} at a pulse of 80 mV and 0.6 ms and then decreases with further increase in pulse strength until reaching 0 mV (FIG.6).

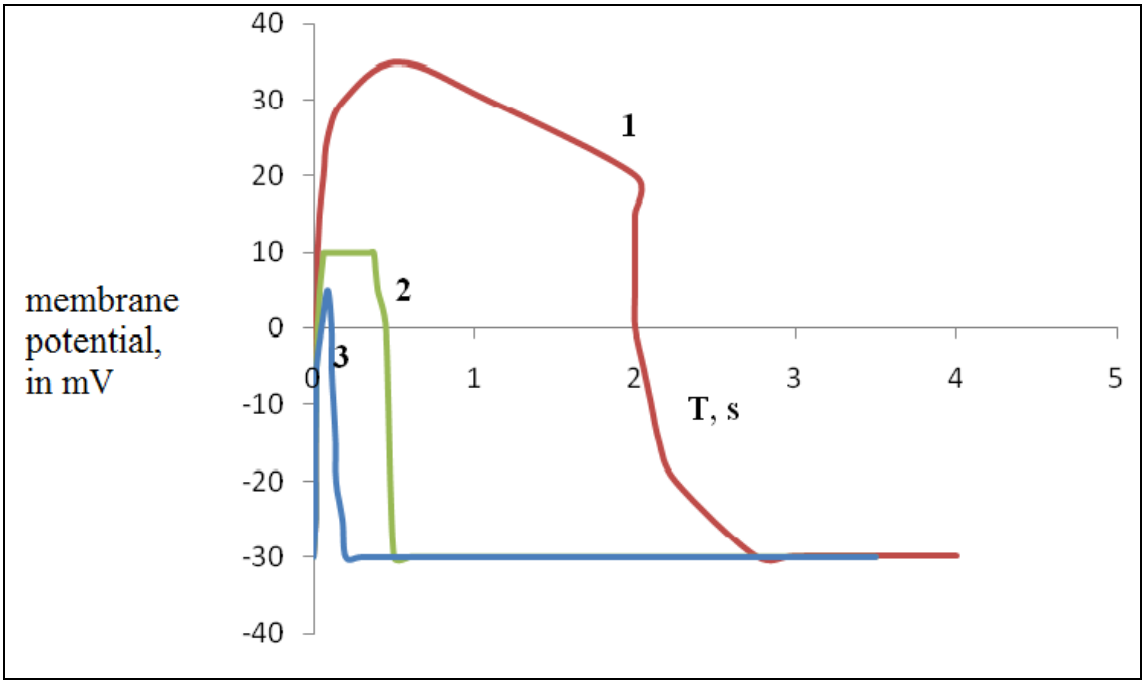

FIG. 1. Computed change in membrane potential in response to electric pulses. T is the time in seconds for depolarization of membrane potential (i.e., above 0 mV) and returning to steady – state level – 30 mV. a- Curve 1 is for a pulse of 80 mV and 0.6 ms. b – Curve 2 is for a pulse of 100 mV and 0.6 ms. c- Curve 3 is for a pulse of 65 mv and 0.6 ms

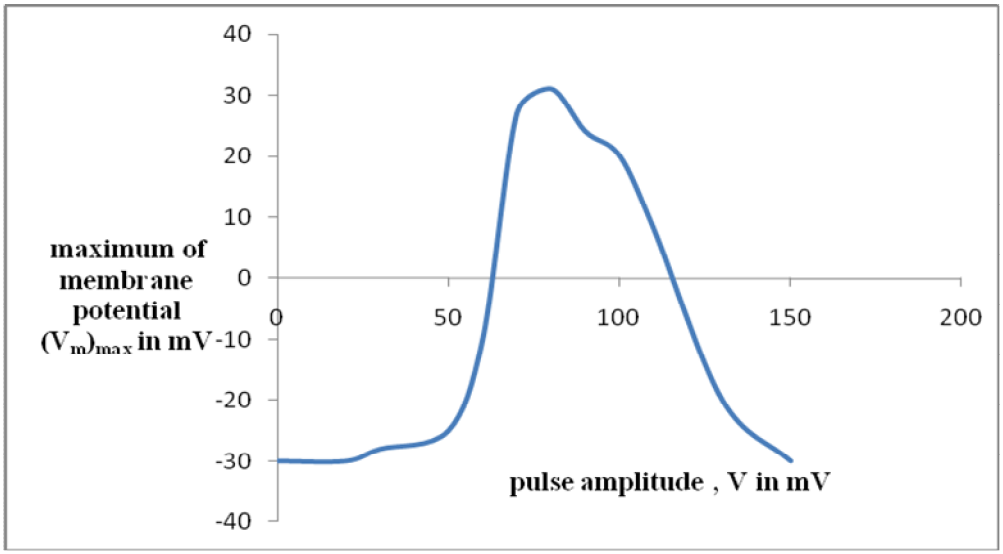

FIG. 2. Computed relationship between maximum membrane potential, $(V_m)_{max}$, in mV and pulse amplitude, V, in mV

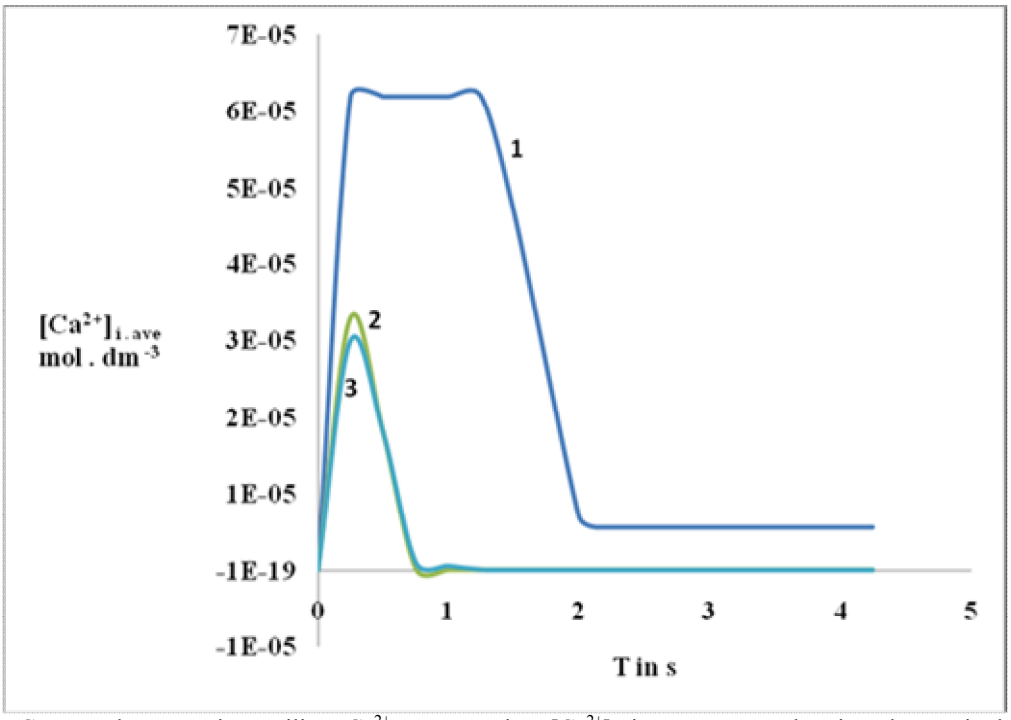

FIG. 3. Computed average interaciliary Ca^{2+} concentration, $[Ca^{2+}]_i$, in response to electric pulses. T is the time lasting for increasing Ca^{2+} within cilia and then returning to steady – state level. a – Curve 1 is for a pulse of 80 mV and 0.6 ms, b – Curve 2 is for a pulse of 100 mV and 0.6 ms, and c – Curve 3 is for a pulse of 65 mV and 0.6 ms

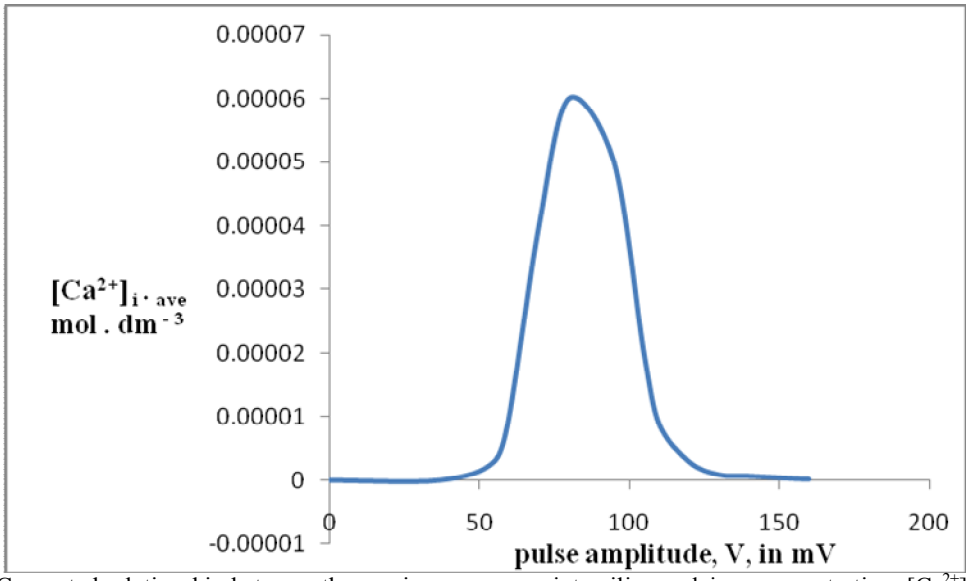

FIG. 4. Computed relationship between the maximum average intraciliray calcium concentration, $[Ca^{2+}]_{i.ave.}$, and the pulse amplitude,V

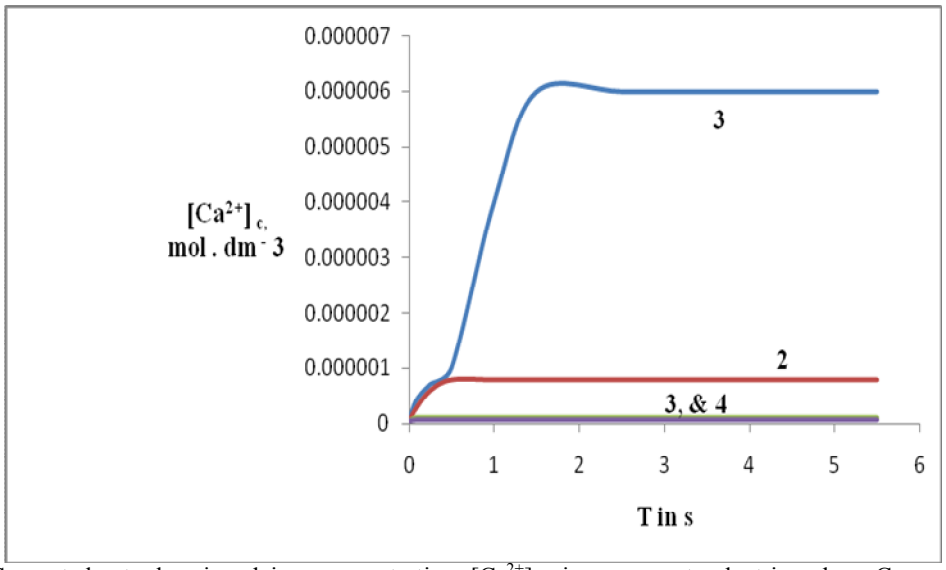

FIG. 5. Computed cytoplasmic calcium concentration, $[Ca^{2+}]_c$, in response to electric pulses. Curve 1 is for a pulse of 80 mV and 0.6 ms, Curve 2 is for a pulse of 100 mV and 0.6 ms, and Curves 3and4 coincide with each other because there are very little differences between their values. Curve 3 is for a pulse of 65 mV and 0.6 ms, and curve 4 is for a pulse of 130 mV and 0.6 ms. T is the time for $[Ca^{2+}]_c$ level in the cell due to a different pulses

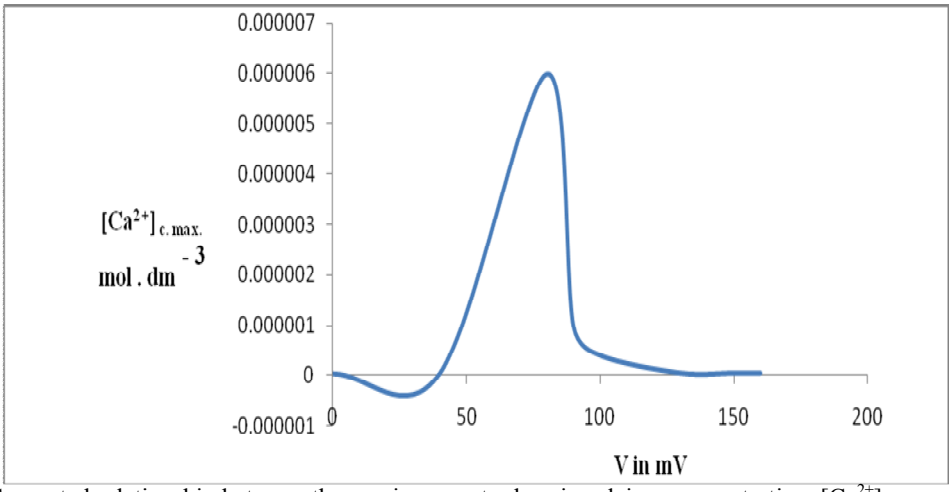

FIG. 6. Computed relationship between the maximum cytoplasmic calcium concentration, $[Ca^{2+}]_{c.\,max.}$, and pulse amplitude, V

Table 2 shows the relationship between pulses of varying amplitude and duration, and ciliary reversal time ($T_{s.r.;}$ i.e., the time during which the cilia beat forward opposite to normal backward beating).

The table was analyzed in the direction of fixed pulse duration (τ) and varying pulse amplitude (V). When τ is 0.2 and 0.4 ms, there is no reversal and very weak reversal, respectively.

H represents a ciliary reversal time, T_{cr}, greater than 20s, τ is the pulse duration in ms, and V is the pulse amplitude in mV.

At further increase in τ, the ciliary reversal time ($T_{cr.}$) reaches the maximum value immediately after the threshold where it remains on a plateau as long as the pulse amplitude increases. The plateau represents a long $T_{cr.}$of more than 20 s, as the cell needs more time to resume its forward swimming (i.e., the cilia return to normal beating) by pumping out the calcium to reach a level below $5x10^{-7}$ $mol.dm^{-3}$

(the suggested amount of $[Ca^{2+}]_i$ which causes a ciliary reversal). As the pulse amplitude (strength) increases further, the duration of ciliary reversal falls very sharply.

TABLE 2. Computed effects of varying duration and amplitude on the duration of ciliary reversal time, T_{cr}, in ms

V in mV	τ in ms 0.2	0.4	0.6	0.8	1.0	1.2
40	0	0	0	10	25	33
60	0	20	30	H	H	H
70	0	25	H	H	H	H
80	0	25	H	H	H	H
90	0	20	H	H	H	H
100	0	15	450	H	H	H
110	0	13	30	H	H	H
120	0	13	25	30	45	H
150	0	12	13	16	19	21

The Anterior Segment Facing the Cathode before the Application of Electric Pulses

We find that both the membrane potential, and the average intraciliary calcium concentration, $[Ca^{2+}]_{i.ave.}$, are responding very weakly to different pulses when the anterior segment lies toward the cathode before the electric pulses are applied. The overall membrane is depolarized very little and for a short time (about 20 ms) due to a pulse of 80 mV and 1.2 ms, whereas a pulse of 100 mV and 1.2 ms causes a slight hyperpolarization before returning to steady – state level of -30 mV (FIG. 7).

$[Ca^{2+}]_{i.ave.}$ increases above 5 x 10^{-7} mol. dm^{-3} for about the 20 ms following the pulse of 80 mV and 0.6 ms, and then drops sharply to the steady – state level of about 3.5 x 10^{-8} mol. dm^3, whereas a pulse of 100 mV and 0.6 ms causes no effect on the steady –state level of $[Ca^{2+}]_{i.ave.}$ (FIG. 8).

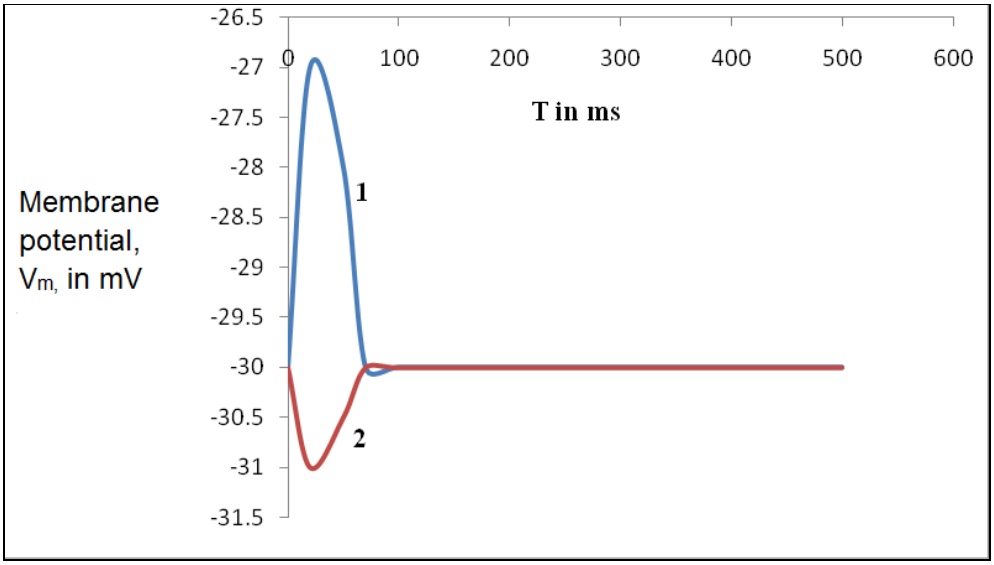

FIG. 7. Computed membrane potential responses to electric pulses when the anterior segment lies toward the cathode during the pulse. Curve 1 is for a pulse of 80 mV and 0.6 ms, and curve 2 is for a pulse of 100 mV and 0.6 ms. T is the time of membrane potential response in ms.

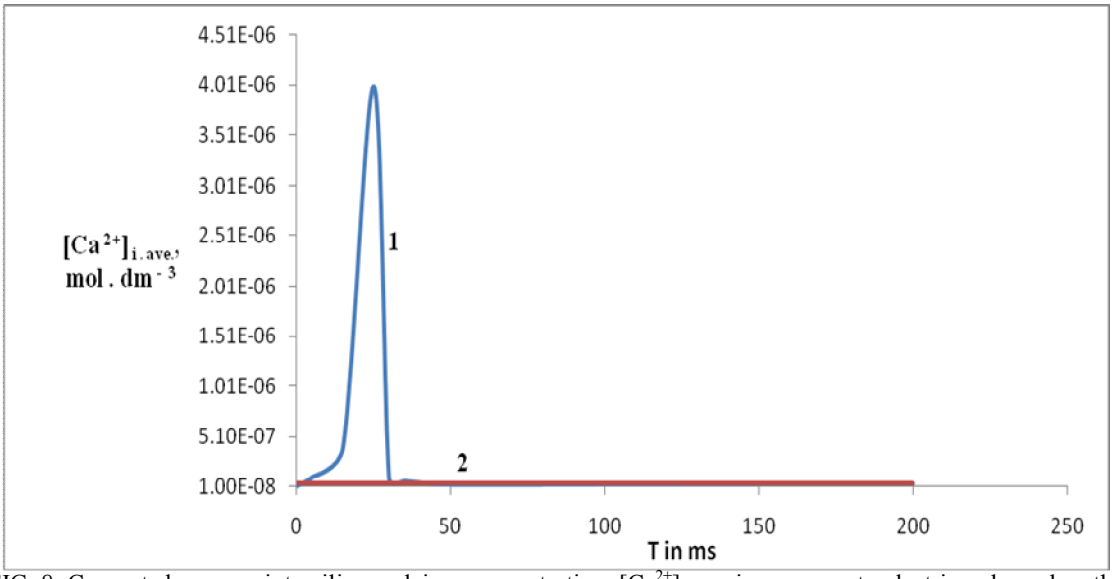

FIG. 8. Computed average intraciliray calcium concentration, $[Ca^{2+}]_{i\,ave.}$, in response to electric pulse, when the anterior segment lies toward the cathode during the pulse. Curve 1 is for a pulse of 80 mV and 0.6 ms, and curve 2 is for a pulse of 100 mv and 0.6 ms. T is the time of $[Ca^{2+}]_{i.ave.}$ after the application the electric pulses.

Discussion

The two – segment model is designed to simulate the reversal movement of the cilia on the anterior part of the *Paramecium* facing the anode before the application of electric pulses. This simulation is done by an uneven distribution for Ca^{2+} and K^{+} channels over the cell body. The ionic channel asymmetry (Ca^{2+} and K^{+} channels) implies that the posterior segment of the model plays the more important role in controlling ciliary reversal, because the majority of the Ca^{2+} - channels are assumed to be located there. According to the two – segment model, the cell is considered to be in a fully reversed state (i.e., the cilia beat toward the cell's anterior) as long as $[Ca^{2+}]_{i.\,ave.}$ – level in both segments is above 5×10^{2} n.ml. dm^{-3}.

The experimental observation that the *Paramecia* resume their forward swimming after a period of reverse swimming [4] is successfully interpreted by the two – segment model. The argument on this can be put as follows: As the level of the intraciliary calcium concentration, $[Ca^{2+}]_i$, falls below 5×10^{2} n.mol.dm^{-3} (the minimal level for initiating reversal), and the membrane potential repolarizes the steady – state level of -30 mV (FIG. 1 and FIG. 3), the cilia start beating in the normal direction (i.e., toward the posterior end), and cause the cell to swim forward. The cell reversal due to electric field pulses must be caused by perturbation of the membrane potential (depolarization) which then leads to an increase in calcium conductance, $g_{Ca,}$ and thereby allows more Ca^{2+} - ions rush into the cell. As a consequence, the intraciliary calcium concentration, $[Ca^{2+}]$, increases causing a ciliary reversal [22]. This sequence, leading to ciliary reversal, can be explained by comparing the membrane potential and $[Ca^{2+}]_{i.\,ave.}$ – level responses (FIG. 1 and FIG. 2). It is noticeable how these two responses have similarity in their shapes which implies that as the membrane depolarizes, $[Ca^{2+}]_i$ increases.

The two – segment model simulation shows that ciliary reversal time attains a plateau due to pulses of varying duration and amplitude (TABLE 2), which is in agreement with experimental results [4]. This may be interpreted as follows: For each pulse duration, there is an optimum pulse amplitude each one of which causes the same ciliary reversal time. This result can be used to explain the plateau which is formed by the percentage of cells reversing due to electric pulses of varying duration and amplitude [4].

The analysis of TABLE 2 in the direction of varying pulse in ciliary reversal time shows that there is no decrease in the ciliary reversal time following the plateau for further increase in pulse duration, because the intraciliary calcium

concentration, $[Ca^{2+}]_i$, in both segments remains above $5x10^2$ n.mol.dm^{-3} (FIG.5). In contrast, the experimental results show the existence of a decrease in ciliary reversal time as the pulse duration is increased further [4]. Analyzing TABLE 2 in the direction of varying amplitude and fixed duration of pulse shows the existence of a decrease in reversal time as the pulse amplitude increases, which agrees with experimental results.

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