Chemosensory transduction in Paramecium: role of membrane potential

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ABSTRACT.

Paramecia are unicells that swim by means of beating cilia. Cells accumulate in or disperse from soluble chemicals by modulating the components of swimming (frequency of turning by transient ciliary reversal and speed of swimming). Mutants were useful in differentiating the two mechanisms of attraction and repulsion: one requiring and one not requiring the cells' ability to change direction by transient ciliary reversal.

Since ciliary beating direction, frequency and angle are under membrane electrical control, a membrane potential hypothesis for the control of chemokinesis behavior was developed. Measurement of membrane potential are in good agreement with this hypothesis.

INTRODUCTION

Paramecia are unicells that swim by means of beating cilia. These cells can detect soluble chemicals in their environment and populations accumulate in or disperse from them.[1] The cells accomplish this population behavior by changing components of swimming of the individual cells. The two most important components are frequency of turning and speed of swimming. There are two mechanisms of attraction and replusion that depend to different extents upon these components.[2] Type I requires the ability to the cells to make turns and to modulate the frequency of turning. Type II apparently requires only the ability of the cells to modulate speed of swimming.

Both components of swimming are controlled by membrane electrical properties. Speed of swimming is determined by frequency and angle of ciliary beating, which are functions of membrane potential;[3] sharp turns correlate with transient reversals of cilia of beating and calcium action potentials.[4] Therefore, chemical cues are somehow transduced into electrical signals that affect ciliary movement and, hence, population behavior.

Through the use of mutants, we discerned the second mechanisms of attraction and repulsion described above, and, consequently, developed a hypothesis for membrane potential control of chemoaccumulation[2] to account for both mechanisms. Two mutants were particularly useful: Pawn[5] (isolated by C. Kung) is a mutant with membrane electrical defects that make it unable to reverse its cilia and, hence, unable to turn and to be attracted or repelled by Mechanism I. Mutant d4-530[6] is repelled by NaOAc by Mechanism II while normal cells are attracted by Mechanism I.

We have subsequently used mutants of chemoaccumulation and swimming behavior to study chemosensory transduction at the level of the receptor, individual cells, and populations and to

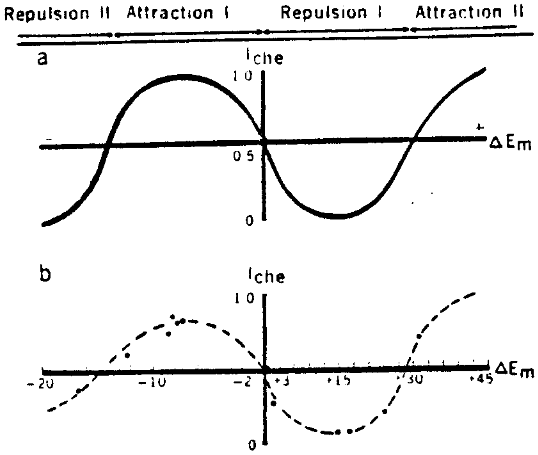

Figure 1. A graphical description of membrane potential control of chemokinesis. Change of membrane potential (ΔE_m) from control (at origin) is plotted vs the index of chemokinesis (I_{che}). $I_{che} > 0.5$ indicates attraction; $I_{che} < 0.5$ indicates repulsion[8]. As chemical stimuli change E_m relative to control, the animals will be attracted or repelled, depending on the magnitude and direction of the E_m change.

B. Data from Vm recordings are plotted as ΔE_m produced by the attractant or repellents vs I_{che}. Scale of ΔE_m is different for depolarizing and hyperpolarizing stimuli. With permission of American Association for the Advancement of Science, copyright 1979.

test the membrane potential hypothesis. The results of these latter tests are reported and are in good agreement with the predicted[7] (Fig. 1). Briefly, the hypothesis predicts that a solution inducing a small hyperpolarizing shift in membrane potential relative to control will cause attraction (type I); a large hyperpolarization will cause repulsion (II); a small depolarization will cause repulsion (I); a large depolarization will cause attraction (II). Note qualitatively similar changes in membrane potential causes opposite population behaviors. For example, hyperpolarization from rest (Fig. 1 Attractants Type I) will temporarily decrease frequency of turns and increase speed probably by decreasing frequency of calcium action potentials and increasing ciliary frequency, resulting in population attraction. A larger hyperpolarization (Fig.1 Repellents Type II) will likewise decrease turning and increase speed but the result is repulsion and the mechanism is apparently different. Pawns are not attracted by agents causing small hyperpolarizations but are repelled by agents causing large hyperpolarizations[2].

Table I. Normal and Pawn Membrane Potentials and Indices of Chemokinesis in Attractants (Type I Requiring the Ability to Turn Sharply by Ciliary Reversal)

Strain	Control Solution 5 mM	Test Solution 5 mM	Vm in Control Vm ± SEM		Vm in Test Vm ± SEM		I_{che}	
Wild Type	KCl	K-acetate	-31.1	0.8	-38.8	1.6	0.84	± 0.07
	KCl	K-lactate	-31.1	0.8	-37.4	1.4	0.83	0.06
	NaCl	Na-acetate	-27.0	0.8	-37.7	1.1	0.75	0.11
Pawn-B	KCl	K-acetate	-29.1	1.0	-33.7*	1.6	0.55	0.05
	KCl	K-lactate	-29.1	1.0	-35.6*	1.6	0.46	0.13

Membrane Potentials (Vm) of cells in test and control solutions. Cells were bathed in control or test buffer at pH 7. The vm are averages of 5 - 50 measurements ± one Standard error. The response of the cells to the attractants was measured by a Tmaze assay designed to preset a test and control solution to a population of animals[8]. The index of chemokinesis $I_{che} > 0.5$ indicate attraction; I_{che} 0.5 indicates repulsion. I_{che} data are averages of four or more experiments + one standard deviation.

*These Vm appear slightly low compared to wild type, but measurements of Vm when solution is changed from test to control solution and back (Δ Vm) are not significantly different from wild type.

Pawns slightly hyperpolarize normally in attractants of the first type (Table I) but apparently their inability to make sharp turns prevents their accumulation by this type of attraction. Other mutants defective in turning by ciliary reversal support this idea[2].

Mutant 4-530 is repelled by fast smooth swimming in NaOAc (relative to NaCl) an attractant (type I) to normal cells[6]. Membrane potential measurements of d4-530 in attractants and repellents indicate that this mutant has abnormal resting membrane potential and abnormal responses to sodium solutions, in particular. For example, membrane potentials of normal cells are generally more negative in KCl than in NaCl (-31.1 ± 0.8 and -27.0 ± 0.8 mV respectively Table I) while d4-530 cells' membrane potentials are more negative than wild types' and potentials in KCl and NaCl are not significantly different (-35.7 ± 0.09 and -36.8 ± 0.9 respectively.) The ionic bases of this defect are being investigated.

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