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EFFECT OF INHIBITORS ON CHLORIDE-DEPENDENT TRANSMURAL POTENTIAL IN THE RECTAL WALL OF *SCHISTOCERCA GREGARIA*

L. HERRERA, R. JORDANA, AND F. PONZ
Department of Zoology and Department of Physiology,
University of Navarra, Pamplona, Spain

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Abstract—Previous experiments *in vitro* revealed a transmural potential difference (PD) and a short-circuit current (Isc) across the rectal wall of *Schistocerca gregaria*, which were dependent on chloride ions in lumen. The present report shows that anoxia, dinitrophenol and cyanide inhibit DP and Isc, proving that the required energy derives from oxidative metabolism. Acetazolamide also inhibits DP and Isc. Ouabain, when in haemocoele, has also an inhibitory effect, not ascribable to a Na^+–K^+ pump blocking action. It is suggested that HCO_3^- plays an important rôle in the active transport of Cl^- from lumen to haemocoele and that ouabain may in some way inhibit chloride pumping.

INTRODUCTION

THE IMPORTANCE of the rectal wall in insects as a regulator system of body fluids has been shown in many studies (SHAW and STOBBART, 1970; PHILLIPS, 1964a, b; STOBBART, 1969). The primary excretion produced in the Malpighian tubules concentrates in the posterior part of the intestine through an ions and water resorption.

A transmural potential difference (PD) of approximately 35 mV and a short-circuit current (Isc) of approximately 300 μA cm^{-2} h^{-1} have been measured *in vitro* in the rectum of *Schistocerca gregaria* (HERRERA, 1975; HERRERA *et al.*, 1976). They were interpreted as the result of a net chloride transport from lumen to haemocoele, suggesting the possible existence of a chloride pump in the luminal membrane, which would transport this anion from lumen to haemolymph, and another Na^+–K^+ pump in the haemocoele membrane that would expel Na^+ from the epithelial cells, accepting K^+.

As active transport mechanisms require an energy source, they are subjected to inhibitions from various substances, like DNP and cyanide, and from anaerobiosis. Since transport depends on the presence of specific enzymes (GLYNN, 1964) they in turn can be susceptible to other inhibitors such as cardiac glycosides, acetazolamide, sulfonamides, etc. HASKELL *et al.* (1965) observed in the isolated middle intestine from *Hyalophora cecropia* larvae, an inhibition of the Isc in anaerobiosis as well as in the presence of dinitrophenol on the haemocoelic compartment. Ouabain did not produce such effects.

IRVINE and PHILLIPS (1971) found that rectal water transport in *S. gregaria*, is totally inhibited by a mixture of potassium cyanide (KCN) and iodoacetate (IAA) 10^{-2} M; this effect was explained as a sodium absorption inhibition and a chloride ion movement increase towards lumen. A 10-times lower concentration of the inhibitors diminished Na^+ transport, but not that of water. HERRERA *et al.* (1976) proposed that the rectal wall potential is primarily dependent on chloride transport, responsible in turn for Na^+, K^+, and H_2O flux.

The effect of different inhibitors on PD and Isc has been studied in the present work, in order to clarify the Cl^- pump function and its dependence on cellular metabolism.

MATERIALS AND METHODS

Adult male and female specimens of the desert locust (*Schistocerca gregaria*) were used for the *in vitro* experiments. The way to obtain the everted rectal preparations, the procedure for measuring PD and Isc, as well as the composition of standard solution were described in a former paper (HERRERA *et al.*, 1976). Conditions for anaerobiosis were obtained by bubbling N_2 through the preparation instead of O_2.

The effects of potassium cyanide, 2,4-dinitrophenol (DNP), acetazolamide, and ouabain added to the medium were tested.

After a control incubation period of the preparations in the standard medium during approximately 13 min the PD and the Isc were measured. The medium was immediately changed using another one with the inhibitor, either in the lumen or in the haemocoele side, and the PD and the Isc were again measured. The standard medium was restored after 10 min and the variations produced in PD and Isc were once more registered.

Table 1. Electric potential differences and short-circuit current strength across the rectal wall of locusts. Effects of anoxia, dinitrophenol and cyanide

Experimental condition	Parameters	Time (min) and condition: Standard 0	Standard 13	Experimental condition 15	Experimental condition 25	Standard 27	Changes %** Addition of inhibitor	Changes %** Omission of inhibitor
Anoxia N_2 in L (10)	PD	29.3 ± 2.3	19.3 ± 3.0	14.8 ± 2.3	4.4 ± 1.0	6.1 ± 0.9	−22.5 ± 2.9*	+48.7 ± 18.0§
	Isc	305.3 ± 15.0	160.8 ± 11.2	150.8 ± 10.0	33.9 ± 11.3	95.7 ± 18.0	−17.0 ± 2.6*	+79.9 ± 28.1‡
DNP 10^{-3} M in L (4)	PD	26.1 ± 1.7	15.9 ± 2.3	13.5 ± 1.9	7.4 ± 1.5	7.5 ± 1.0	−14.3 ± 3.2‡	+3.6 ± 13.9§
	Isc	258.2 ± 16.6	183.3 ± 27.8	131.3 ± 24.7	88.8 ± 17.9	71.1 ± 12.6	−30.7 ± 5.0†	−21.8 ± 11.6¶
DNP 10^{-3} M in H (6)	PD	27.8 ± 3.5	16.6 ± 2.5	12.5 ± 2.0	6.2 ± 1.0	7.7 ± 1.2	−24.6 ± 4.4†	+21.2 ± 2.2*
	Isc	265.4 ± 26.7	132.5 ± 18.9	109.6 ± 13.6	63.7 ± 8.4	88.9 ± 12.9	−15.6 ± 3.2†	+26.9 ± 3.4*
DNP 10^{-4} M in L (7)	PD	24.6 ± 3.8	18.1 ± 3.8	17.0 ± 4.0	12.5 ± 3.1	12.4 ± 2.1	−8.1 ± 2.8†	+8.4 ± 9.6¶
	Isc	299.5 ± 17.7	173.8 ± 33.2	154.3 ± 29.7	116.0 ± 23.1	126.1 ± 22.4	−11.8 ± 2.6†	+5.2 ± 9.6¶
DNP 10^{-4} M in H (10)	PD	26.1 ± 3.4	13.7 ± 2.7	12.5 ± 3.1	7.5 ± 2.6	7.9 ± 2.9	−18.7 ± 2.2*	+4.7 ± 9.4¶
	Isc	257.5 ± 15.6	123.6 ± 12.1	105.6 ± 9.2	70.3 ± 10.7	65.6 ± 11.0	−22.4 ± 2.3*	−11.9 ± 7.9¶
KCN 10^{-2} M in L (6)	PD	20.7 ± 3.9	10.7 ± 3.7	3.6 ± 1.4	0.6 ± 0.3	1.9 ± 0.6	−71.1 ± 5.1*	+70.3 ± 12.1†
	Isc	304.7 ± 32.2	163.5 ± 30.4	73.4 ± 21.1	14.8 ± 7.3	57.0 ± 14.7	−57.2 ± 8.8†	+79.4 ± 7.3*
KCN 10^{-2} M in H (5)	PD	30.3 ± 3.7	17.7 ± 3.2	13.2 ± 2.7	5.2 ± 2.0	7.3 ± 2.3	−28.3 ± 5.5†	+47.7 ± 12.3‡
	Isc	312.5 ± 13.1	238.1 ± 23.9	186.9 ± 32.6	76.5 ± 24.5	118.7 ± 23.1	−24.4 ± 7.3§	+41.4 ± 8.6†
KCN 10^{-3} M in L (9)	PD	25.7 ± 3.6	18.4 ± 4.9	15.1 ± 4.0	8.1 ± 2.2	8.4 ± 2.3	−17.6 ± 2.3*	+5.3 ± 12.1¶
	Isc	255.4 ± 17.4	173.2 ± 24.1	142.7 ± 29.0	82.1 ± 18.9	111.6 ± 21.8	−25.3 ± 8.9§	+25.8 ± 9.1¶
KCN 10^{-3} M in H (6)	PD	25.7 ± 6.6	16.2 ± 4.6	13.2 ± 3.6	6.6 ± 1.9	5.8 ± 1.3	−17.7 ± 2.1*	+0.7 ± 15.0¶
	Isc	271.7 ± 27.4	178.3 ± 33.6	152.7 ± 31.8	100.5 ± 22.2	95.5 ± 16.6	−16.6 ± 5.4§	+3.2 ± 12.7¶

** These values represent the mean of per cent changes for each independent experiment. Statistical significance (Student's t test for no independent values): *, $P < 0.001$; †, $P < 0.01$; ‡, $P = 0.02$; §, $P < 0.05$; ¶, not significant.

Mean values ± S.E. PD, in mV (Lumen always positive). Isc in $\mu A\,cm^{-2}$. Number of experiments in parentheses. Changes per cent: + = increase; − = decrease.

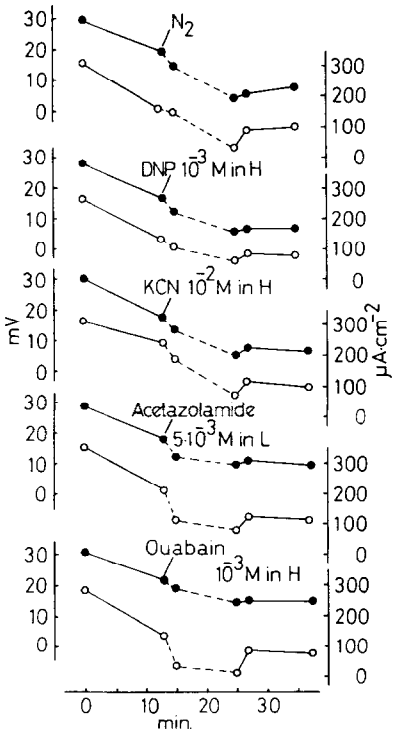

Fig. 1. Electropotential difference (PD) and short-circuit current (Isc) across the rectal wall of locust. Effects of anoxia (N_2), DNP, KCN, acetazolamide and ouabain on the lumen (L) or haemocoel (H). PD (●). Isc (○). Control, ——; Inhibitor, – – –.

RESULTS

The statistical analysis of the observed changes in PD and Isc present, in most cases, a high significance. In the few cases which do not show enough statistical significance, changes have been considered valid only when the shifts were in the same direction in 100% of the experiments, in spite of individual quantitative differences. It should also be mentioned that the purpose of this paper was to verify whether PD and Isc were or not affected by the inhibitors tested. These differences may be due to small technical variations, such as the insulation degree in the saline bridges employed, handling of preparations, etc.

Anaerobiosis

The PD and the Isc declined after N_2 was substituted for O_2 in the gasification of the rectal wall preparations. Twelve minutes after the suppression of O_2, i.e. 25 min from the initiation of the experiment (Table 1, Fig. 1), both PD and Isc diminished considerably. A clear recovery of both parameters was observed when O_2 was restored to the medium. The total blocking of PD and Isc was not obtained, perhaps because of the presence of some O_2, since the bubbling takes place only in lumen and there might be an O_2 exchange at the free surfaces.

2,4-Dinitrophenol

This inhibitor, a well known uncoupler of oxidative phosphorylation, has been used at 10^{-4} M and 10^{-3} M concentrations, either in lumen or in haemocoele (Table 1, Fig. 1). A 10^{-4} M concentration in haemocoele produced a small Isc inhibition, without an appreciable PD change, but a 10^{-3} M concentration exerts a highly significant inhibitory effect on both PD and Isc, followed by their recovery upon the suppression of DNP. This latter concentration in lumen produced only a small Isc decline. An easier penetration of DNP through the haemocoelic membrane might account for this difference of effect. DNP inhibitions were inferior to those produced in the absence of O_2.

The required DNP concentrations to produce inhibitions were higher than those usually employed for the uncoupling of oxidative phosphorylation.

Cyanide

A 10^{-2} M concentration of potassium cyanide in lumen produced after 2 min a strong PD and Isc inhibition, 71 and 57%, respectively, and it practically nullified them after 10 min. After removing the KCN through washing and restoring the standard medium, both parameters recovered quickly (Table 1, Fig. 1). The same concentration in the haemocoele caused a similar effect, but less intense, perhaps because of a lower KCN diffusion from this side. Lower concentrations of cyanide produced smaller inhibitions.

Acetazolamide

In mammals, acetazolamide, a well known diuretic, (SPRAGUE, 1958), acts as a specific inhibitor of carbonic anhydrase, reducing the HCO_3^- intracellular concentration and, therefore, the possibility of a HCO_3^- exchange with Cl^- and the resorption of H_2O in the renal tubules (ROBSON and STACEY, 1962). It has been observed that in other tissues it affects the ionic exchange across membranes (GOODING, 1975). This inhibitor has been used to observe the effect of HCO_3^- on Cl^- transport, since the PD and Isc in the rectal wall of *Schistocerca gregaria* is dependent on chloride.

Acetazolamide was only added in lumen (Table 2, Fig. 1), where the anion exchange could take place, and an inhibitory action on PD and Isc was observed. The inhibition was of nearly the same magnitude at 10^{-3} M than at 5×10^{-3} M concentrations.

Ouabain

Ouabain was tested either in lumen or in haemocoele. No effect of ouabain on transmural PD was found (Table 2, Fig. 1), but it exerts an inhibitory effect on the Isc, when present in haemocoele. At 10^{-3} M concentration, ouabain produced very high inhibition and practically nullified the Isc, as if the net flux of ions from lumen to haemolymph, was stopped.

Table 2. Electric potential differences and short-circuit current strength across the rectal wall of locusts. Effects of acetazolamine and ouabain

Experimental condition	Parameters	Time (min) and condition: Standard 0	Standard 13	Experimental condition 15	Experimental condition 25	Standard 27	Changes °/°** Addition of inhibitor	Changes °/°** Omission of inhibitor
Acetazolamide	PD	29.0 ± 4.3	18.1 ± 2.9	12.8 ± 3.0	9.8 ± 2.0	10.6 ± 2.1	−33.4 ± 7.6†	+2.0 ± 12.0¶
5.10^{-3} M in L (9)	Isc	354.6 ± 35.5	215.4 ± 24.2	115.1 ± 13.1	81.6 ± 13.2	121.1 ± 20.7	−47.8 ± 11.1†	+30.9 ± 7.9†
Acetazolamide	PD	24.1 ± 3.8	17.3 ± 2.9	11.7 ± 2.6	9.0 ± 2.4	8.3 ± 2.5	−33.0 ± 10.1‡	−11.7 + 6.8¶
10^{-3} M in L (6)	Isc	337.7 ± 37.2	262.0 ± 39.4	153.0 ± 24.1	113.8 ± 23.7	144.2 ± 26.8	−37.8 ± 9.3†	+22.1 ± 3.4†
Ouabain 10^{-3} M	PD	31.0 ± 1.6	21.5 ± 2.5	19.0 ± 2.3	14.4 ± 2.2	14.5 ± 2.1	−10.6 ± 3.2†	+0.6 ± 5.0¶
in H (8)	Isc	283.6 + 23.9	138.7 + 29.5	35.7 ± 10.2	13.0 ± 3.2	87.2 ± 14.2	−78.2 + 4.8*	+85.6 ± 3.1*
Ouabain 10^{-3} M	PD	48.7 ± 2.1	33.2 ± 3.4	30.0 ± 3.5	22.0 ± 2.6	19.6 ± 2.6	−10.5 ± 3.9†	−13.8 ± 4.7‡
in L (7)	Isc	376.4 ± 9.3	249.6 ± 20.0	258.0 ± 20.8	231.7 ± 25.2	213.3 ± 23.5	+3.4 ± 0.5*	−8.9 ± 4.8¶
Ouabain 10^{-4} M	PD	42.7 + 2.3	33.0 + 1.7	27.7 + 2.3	22.3 ± 2.4	22.5 ± 2.6	−16.6 ± 3.6*	−0.3 ± 4.1¶
in H (9)	Isc	354.0 ± 11.7	236.4 ± 13.1	159.7 ± 10.4	141.4 ± 8.8	181.5 ± 14.3	−31.3 ± 4.4*	+20.8 ± 2.9*
Ouabain 10^{-4} M	PD	42.2 ± 3.0	25.9 ± 2.6	21.5 ± 2.0	14.1 ± 2.6	15.2 ± 1.6	−15.9 ± 2.6*	−14.3 ± 5.4‡
in L (7)	Isc	309.0 ± 8.7	226.1 + 22.4	197.1 + 20.0	178.0 + 20.6	163.7 + 17.7	−5.4 ± 3.9¶	−8.7 ± 4.8¶
Ouabain 5.10^{-5} M	PD	35.6 ± 4.9	20.8 ± 3.8	17.1 ± 3.1	12.6 ± 2.1	12.2 ± 2.0	−18.2 ± 3.2*	−6.9 ± 10.3¶
in H (8)	Isc	339.6 ± 29.2	187.6 ± 23.8	173.3 ± 21.0	148.4 ± 22.0	143.8 ± 22.5	−7.0 ± 1.6*	−3.8 ± 2.3¶
Ouabain 5.10^{-5} M	PD	38.3 ± 4.1	25.2 ± 4.4	22.5 ± 4.2	17.5 ± 3.3	15.9 ± 3.0	−12.1 ± 4.3‡	−9.1 ± 4.7¶
in L (7)	Isc	391.8 ± 21.7	219.2 ± 24.1	205.1 ± 22.8	178.2 ± 22.6	164.3 ± 19.5	−6.3 ± 1.2*	−8.2 ± 6.5¶

Units and abbreviations as in Table 1.

Table 3. Electric potential differences and short-circuit current strength across the rectal wall of locusts. Changes induced by different chloride concentrations in lumen

Chloride concentration	Parameters	Time (min) and condition: Standard 0	Standard 13	Chloride diminished 15	Chloride diminished 25	Standard 27	Changes °/°** Diminution	Changes °/°** Restitution
25°/° Cl^- in L (6)	PD	31.0 ± 4.8	16.4 ± 2.8	15.9 ± 2.9	10.2 ± 3.2	9.2 ± 2.7	−4.3 ± 5.0¶	−29.9 ± 16.1¶
	Isc	322.2 ± 23.2	158.2 ± 20.7	141.6 ± 16.8	67.1 ± 17.1	66.7 ± 18.3	−9.7 ± 2.5†	−5.7 ± 3.9¶
10°/° Cl^- in L (7)	PD	28.6 ± 5.2	21.6 ± 5.6	16.7 ± 3.8	9.2 ± 2.3	12.4 ± 2.6	−18.0 ± 6.5‡	+32.0 ± 10.3‡
	Isc	272.4 ± 21.7	179.4 ± 30.7	106.6 ± 24.5	57.6 ± 12.5	100.7 ± 15.6	−39.7 ± 8.4*	+45.2 ± 4.7*

Units and abbreviations as in Table 1.

DISCUSSION

Dependence of PD and Isc on aerobic metabolism

The results show that PD and Isc in the rectal wall of *S. gregaria* are dependent on aerobic metabolism.

Anoxia, provoked on substituting N_2 for O_2, produces a decline in PD and Isc, and quickly recovered on restoring O_2. A similar phenomenon was observed in the middle intestine of *Hyalophora cecropia* (HASKELL *et al.*, 1965), where an Isc inhibition of 83% was found. Similar results were obtained by WOOD *et al.* (1969) on the transluminal potential. The impossibility of nullifying the PD and Isc might be due, either to the experimental conditions that do not guarantee total absence of O_2 or to some energy production from anaerobic processes.

DNP acts similarly to anaerobiosis, but less intensely. The blocking of the ATP oxidative production does not lead to the total nullification of PD or Isc, pointing also to a certain capacity in the tissues for obtaining energy from non-aerobic processes. HASKELL *et al.* (1965) found a similar phenomenon in *Hyalophora cecropia*. IRVINE and PHILLIPS (1971), however, observed that the 10^{-3} M DNP in *Schistocerca in vitro* completely abolished water transport in the rectal wall. This discrepancy might be due perhaps that their experiments were not carried out under strict aerobic condition, since the sacs were not everted and the oxygenation takes place at the haemocoelic side, rather than at the luminal surface.

A 10^{-2} M concentration of KCN, which produced an aerobic metabolism inhibition, completely nullified the PD and Isc. Ten times lower concentrations produced a lesser inhibition.

These results reveal that the transmural PD and the Isc, and consequently the net flux of Cl^-, mainly depend on the energy derived from aerobic processes, although the possibility that the cell obtains a certain amount of energy from anaerobic metabolic processes remains open.

Relation between PD and Isc, and HCO_3^-

The inhibitory effect of acetazolamide on PD and Isc in the rectum of *S. gregaria*, suggests an interesting relation between bicarbonate and the net flux of Cl^-. As acetazolamide inhibits carbonic anhydrase, (EDWARDS and PATTON, 1967), it will lessen HCO_3^- concentration in the cells. The net movement of Cl^- from lumen to haemocoele might be dependent on the level of intracellular HCO_3^-, due perhaps to an exchange of Cl^- and HCO_3^- at the luminal membrane. This exchange, however, would not be sufficient to explain the net flux of Cl^- to haemocoele since it takes place against a high electrochemical gradient. Moreover, if the net flux of Cl^- were a simple consequence of HCO_3^- outflux towards lumen, then the partial substitution of Cl^- by the nonpenetrating $SO_4^=$ anion a gradual effect on the potential should be expected, but this does not occur. In fact, Cl^- concentration in the luminal side can be considerably lessened without altering the PD or the Isc. Both parameters begin to decrease only with Cl^- concentrations as low as 18 mEq/l (Table 3). Such a behaviour conforms better with a Cl^- active transport system with high affinity for this anion.

Another possibility would be that the systems for active transport of chloride were sensitive to bicarbonate ions.

Effect of ouabain

Ouabain, a Na^+ K^+-dependent ATP-ase specific inhibitor, abolishes the activity of the Na^+ and K^+ pump.

Ouabain lessens mainly the Isc (flux of anions) in the rectal wall of the *Schistocerca*, only when the glucoside is in haemocoele at a 10^{-4} M or higher concentration. This effect cannot be attributed to an inhibition of the Na^+-pump, which on the contrary would provoke an increase in Isc and in haemocoele negativity, as it happens by omitting Na^+ and K^+ in the medium (HERRERA *et al.*, 1976). It has to be admitted, therefore, that the Cl^- active transport mechanism itself is sensitive to ouabain and that it is likely located at the basal side of the epithelial cells, since the inhibitor acts only from haemocoele.

The lesser sensitivity of PD to ouabain is not surprising, since a small flux of anions is sufficient to maintain the potential, and ouabain does not totally inhibit Cl^- transport. Furthermore the simultaneous inhibition of the Na^+ pump may account for the lesser quantity of negative charge transferred to haemocoele.

After a consideration of these results, the scheme suggested by HERRERA *et al.* (1976) to interpret the origin of PD and Isc in the rectal wall of *S. gregaria* remains valid, and can be expanded in the following points: (1) The PD and the Isc, directly dependent on the Cl^- active transport from lumen to haemocoele, require aerobic metabolism which appears as the main energy source for transport. (2) The PD and Isc inhibitions caused by acetazolamide manifest the importance of HCO_3 in the process, either, because it directly stimulates Cl^- pumping, or, because it aids Cl^- entrance in the cells through an exchange with the outflux of HCO_3^-. (3) It is very probable that ouabain, besides inhibiting the Na^+ pump, might also inhibit Cl^- pumping, and if so, this transport system would be located in the basal membrane of the epithelial cells, rather than in the lumen.

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