

Figure 3. Plot of PD as a function of pH for 4 fish. Points recorded every 10 minutes from histamine administration to the time at which pH started to increase again. Line drawn by least squares.

For the four fish in which both parameters were measured, Figure 3 shows a plot of PD vs. pH. Less scatter is seen than in vitro, and the line has a slope of -12 mV/pH and an extrapolated PD at pH 0.57 of +11.0, very close to the in vitro value, and much different from zero.

I conclude that: 1) while diffusion of H^+ from primary secretion to lumen probably contributes to the measured PD, some other process gives rise to the serosal-positive PD at pH 0.57. 2) the inverted (serosal-negative) PD observed in elasmobranchs alone may be due to H^+ diffusion. 3) the consistency of the observations between in vivo and in vitro (hyperbaric) conditions gives some assurance that the latter are a good model for the former.

ACID SECRETION BY THE GASTRIC MUCOSA OF *Squalus acanthias* IN CHLORIDE-FREE SOLUTIONS

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The isolated gastric mucosa of the dogfish transports both H^+ and Cl^- from serosal to mucosal solutions, producing a small potential difference (PD) compared to other species. Some have inferred that in this tissue the coupling between H^+ and Cl^- active transport is especially strong, leading to the electroneutral secretion of HCl. It was therefore of interest to study the acid secretory rates (J_H) in the presence and absence of Cl^- , both under the hypoxic conditions used for much of the previous work and under O_2 -sufficient conditions, which require a hyperbaric chamber.

Tissues were dissected and mounted in Cl^- -free solutions, produced by substituting SO_4^{--} for the Cl^- in the solutions reported by Hogben (Science 129:1224, 1959), restoring osmolality with glucose. Carbachol

(0.25 mM) was added to stimulate maximum secretion, and the tissue was monitored for PD, J_H and trans-epithelial resistance (R) in the hyperbaric system as previously described (Kidder, AJP 231:1240, 1976). In four sequential periods of 1.5 hours each, the tissues were treated as shown in Figure 1. Compared to the corresponding SO_4^{--} period, the addition of Cl^- increases J_H , decreases R, and shifts PD from serosal negative to serosal positive. Much of this latter effect is probably diffusional in origin, as the mucosal solution remained Cl^- -free throughout.

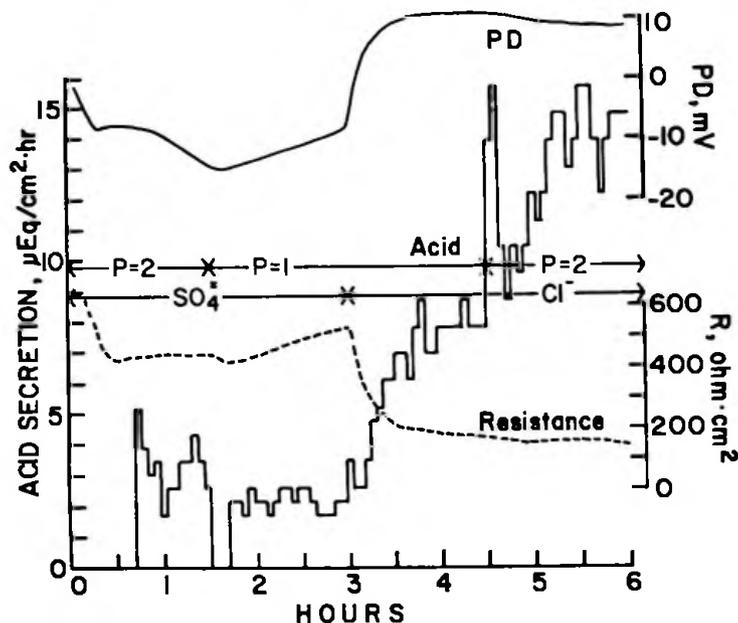


Figure 1

For each of the 5 tissues examined, J_H over the last 15 minutes and PD and R at 7.5 minutes from the period's end have been presented as Table 1. The average J_H in SO_4^{--} solutions is more than 20% of that

TABLE I
Anion and pO_2/pCO_2 changes on acid secretion

Conditions	pO_2/pCO_2 (atm)	J_H ($\mu Eq/cm^2 \cdot hr$)	PD (mV)	R ($ohm \cdot cm^2$)
Serosal SO_4^{--}	1.9/0.1	1.47 ± 0.19	-9.4 ± 2.2	433 ± 99
SO_4^{--}	0.9/0.05	0.79 ± 0.09	-6.8 ± 2.8	477 ± 88
Cl^-	0.9/0.05	3.26 ± 0.29	$+8.9 \pm 1.5$	251 ± 35
Cl^-	1.9/0.1	6.70 ± 0.33	$+6.4 \pm 1.0$	215 ± 34

Data for 5 tissues, \pm SEM. All J_H significantly (5%) different from each other. For PD and R, only differences between SO_4^{--} and Cl^- are significant.

the corresponding Cl^- solutions, and increasing the O_2 and CO_2 doubles the rate in either solution. A serosal-negative PD is observed in SO_4^{--} solutions, as expected. The rise in resistance upon changing from SO_4^{--} to Cl^- solutions under hypoxic conditions is significant; the other differences in R, while dramatic in individual cases, are not significant with this number of experiments.

The persistence of J_H with no exogenous Cl^- can be explained by an electrogenic H^+ pump, with no requirement for simultaneous Cl^- transport. Chloride might enhance pump activity without itself being transported, as seems to be true for the bullfrog gastric mucosa (Shanbour and Rehm, PSEBM 136:1236, 1971, Kidder and Montgomery, J. Balto. Col. Dent. Surg. 29:52, 1974). In this case, one would expect J_H to be measured by I_{SC} , which can be approximated by PD/R . For the 10 measurements in SO_4^{--} solutions, the relationship $I_{SC} = 6.46 + 0.46 J_H$ (in μA) provided the best fit, and the slope is thus far from unity. These experiments are not ideally suited to this analysis (the tissue was not actually short circuited, for instance), but to the extent that they are valid, they suggest active transport of some other ions than H^+ and Cl^- in this tissue, a conclusion likewise supported by other data (Kidder, Bull. MDIBL, This issue).

In any event, the demonstration of active H^+ transport in the absence of exogenous Cl^- is a result which is not expected from a tightly-coupled neutral HCl pump, but quite consistent with an electrogenic mechanism.

THE "REHM EFFECT" IN DOGFISH GASTRIC MUCOSA WITH SUFFICIENT OXYGEN

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The passage of electrical current through gastric mucosae has been found to affect the rate of H^+ secretion in dog (Rehm, AJP 144:115, 1945) and frog (Crane et al., Biochem. J. 43:21, 1948) in a manner consistent with an electrogenic H^+ secretory mechanism; this has been termed the Rehm effect. Hogben (Bull. MDIBL 15:45, 1975) has recently reported that this effect is absent in dogfish gastric mucosa. He also failed to find a long time-constant transient (LTCT) in the voltage response to current which is found in the frog. These observations are consistent with an explanation for the Rehm effect based on ion concentration changes in the cells during current passing (Hogben, in Sachs et al. "Gastric Secretion," Acad. P. 1972), since these concentration changes are the basis for one model for the LTCT (Kidder and Rehm, Biophys. J. 10:215, 1970).

However, Hogben's experiments were conducted using $p\text{O}_2 = 1$ atm, which is hypoxic for this tissue *in vitro* (Kidder, AJP 231:1240, 1976). It was therefore desirable to repeat these experiments with elevated $p\text{O}_2$. Mucosae from 6 dogfish were mounted under hyperbaric conditions (Kidder, op. cit.) at $p\text{O}_2 = 1.9$ atm, $p\text{CO}_2 = 0.1$ atm, and their secretory rate measured with the pH-stat apparatus during a 1.5 hour equilibration period. Sufficient current was then passed (via Ag/AgCl electrodes remote from the tissue) to bring the transepithelial potential difference (PD) to -60 mV (reference mucosal solution) for 1 hour. The current was then reversed to $+60$ mV for one hour, followed by an hour of open circuit control. A typical experiment is shown as Figure 1. Negative PD is seen to inhibit secretion, while positive PD slightly enhances secretion, and for all changes, the time course of the response is slow; i.e., this is not a current-induced artifact of the chamber and electrodes. In 2 cases, the order of current sending was reversed.

The secretory rate was noted for the last 20 minutes of each period, when the tissue has apparently reached a steady state, and the results used to construct Table 1. Acid secretion was always inhibited by -60 mV as compared to either control period (or their average), and this inhibition is significant. While $+60$ mV usually stimulated secretion, the increase is not statistically significant. It thus appears that the Rehm effect can be demonstrated in dogfish gastric mucosa which are not hypoxic.