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# Potential difference responses to nutrient $K^+$, $Na^+$ and $Cl^-$ changes with varying nutrient $HCO_3^-$ in resting frog stomach

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**The effects of changes in nutrient concentrations of $K^+$, $Na^+$ and $Cl^-$ on the transmucosal potential difference (PD) and resistance were compared for 25 and 5 mM nutrient $HCO_3^-$ in resting fundus. With 25 mM $HCO_3^-$, increase of $K^+$ from 4 to 40 mM, decrease of $Na^+$ from 100 to 10 mM and decrease of $Cl^-$ from 81 to 8.1 mM gave, 10 min after the change, $\Delta$PD values of $-23.2$, $-15.1$ and $-21.3$ mV, respectively. With 5 mM $HCO_3^-$, the same changes in nutrient ion concentration gave $\Delta$PD values of $-11.9$, $-9.4$ and $-10.0$ mV, respectively. From these results, in going from 25 to 5 mM $HCO_3^-$, it follows that the resistances of the ionic pathways for $K^+$, $Na^+$ and $Cl^-$ increased. The anomalous PD response following the increase in nutrient $K^+$ from 4 to 40 mM with 5 mM nutrient $HCO_3^-$ gave further evidence that the resistance of the simple $K^+$ conductance pathway increased prior to the increase to 40 mM $K^+$. The fact that 2 mM $Ba^{2+}$ in the 25 mM $HCO_3^-$ nutrient gave a smaller increase in resistance, compared to the decrease in nutrient $HCO_3^-$ from 25 to 5 mM, supported the inference that resistances of ion pathways other than that of the $K^+$ pathway increased.**

## Introduction

Using ion substitution, in which an ion is replaced by a relatively impermeant ion, we found that there were conductance pathways for $HCO_3^-$ in the nutrient membrane of the bullfrog antrum [1] and of the resting (or inhibited) fundus of *Rana pipiens* [2]. In contrast to the resting fundus, Sanders et al. [3] found in the secreting fundus no significant change in potential difference (PD) with a change in nutrient $HCO_3^-$ concentration and hence had no evidence of $HCO_3^-$ conductance pathways in the nutrient membrane. We note further that, previously, Flemstrom and Sachs [4] reported a change in PD resulting from a change in $HCO_3^-$ concentration both in the nutrient and secretory sides of the antrum. They did not determine, however, whether a linear relationship existed between $|\Delta PD|$ and the log of the $HCO_3^-$ concentration. We reported such a relationship for both the antrum [1] and the resting fundus [2].

Moreover, with a decrease in $HCO_3^-$ concentration in the nutrient solution, there was an increase in transmucosal resistance. It is difficult to explain the linear relationship when the resistance increases with a decrease in $HCO_3^-$ concentration. An explanation which we gave assumed that not only did the resistance of the $HCO_3^-$ pathway vary, but also the resistances of other ionic pathways varied inversely with the $HCO_3^-$ concentration (see Refs. 1,2 and Discussion).

The purpose of the present paper was to determine which of the known conductance pathways (e.g., $K^+$, $Na^+$, $Cl^-$) other than the $HCO_3^-$ pathway were involved in the increase in resistance.

## Methods

Experiments were performed on fundi of stomachs of *R. pipiens* by an in vitro method in which the stomachs were mounted between a pair of cylindrical chambers [5]. All experiments began with standard $Cl^-$ solutions on both sides of the mucosa. The $Cl^-$ nutrient (serosal) solution contained (in mM): $Na^+$, 102; $K^+$, 4; $Ca^{2+}$, 1; $Mg^{2+}$, 0.8; $Cl^-$, 81; $SO_4^{2-}$, 0.8; $HCO_3^-$, 25; phosphate, 1; and glucose, 10; and the $Cl^-$ secretory (mucosal) solution, which is hypertonic [6], contained $Na^+$, 156; $K^+$, 4; and $Cl^-$, 160. In the decrease in nutrient $HCO_3^-$ from 25 to 5 mM, standard nutrient solutions which were phosphate-free were used for both $HCO_3^-$ concentrations. In the decrease from 25 to 5 mM $HCO_3^-$, $SO_4^{2-}$ replaced $HCO_3^-$ and sucrose was added to main-

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tain osmolality. Various phosphate-free modifications were also used in which the $HCO_3^-$ concentrations were reduced from 25 mM $HCO_3^-$. In all these solutions, the $Ca^{2+}$, $Mg^{2+}$, $K^+$ and $Cl^-$ concentrations were unaltered unless a specific experiment demanded a change in $K^+$ or $Cl^-$ concentration. For increases in $K^+$ concentration on the nutrient side, $K^+$ replaced $Na^+$ and, for decreases in $Na^+$ concentration on the nutrient side, choline replaced $Na^+$ or $Mg^{2+}$ replaced $Na^+$. For a decrease in $Cl^-$ concentration, $SO_4^{2-}$ replaced $Cl^-$ and sucrose was added to make up any osmotic deficit.

In these studies, the transmucosal resistance, the transmucosal PD and the $H^+$ secretory rate were measured. Two pairs of electrodes were used, one for sending current across the mucosa and the other for measuring the PD. The PD is considered positive when the nutrient side is positive relative to the secretory side of the stomach. The resistance was determined as the change in PD per unit of applied current. Current (20 $\mu$A per 1.3 $cm^2$ of tissue area) was applied for 1 or 2 s, first in one direction and 2 or 3 s later, in other direction. The $H^+$ secretory rate was determined by the pH-stat method of Durbin and Heinz [7]. The pH of the secretory solution was generally maintained between 4.7 and 5.0. Moreover, both sides of the gastric mucosa were gassed with 95% $O_2$/5% $CO_2$ throughout these experiments and 0.1 mM histamine in the nutrient solution was used to stimulate secretion. For inhibition, 20 mM $SCN^-$ in the secretory solution decreased the $H^+$ secretory rate to zero.

In previous studies on the nutrient side, due to the existence of a diffusion barrier between the nutrient solution and the nutrient membrane, it took about 10 min (approx. 5 time constants) for the concentration of the ion at the cell membrane to attain the new concentration in the nutrient solution [8]. Hence the PD and resistance were generally read at the 10 min mark following the change to the new solution.

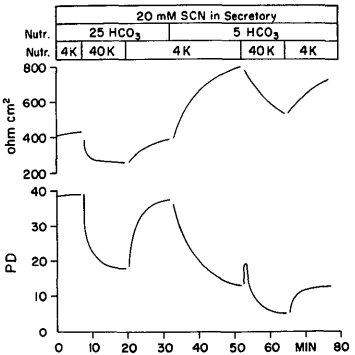


Fig. 1. Effect of changes in $K^+$ concentration on the nutrient side from 4 to 40 mM and back to 4 mM with 25 and 5 mM nutrient $HCO_3^-$ and with 20 mM $SCN^-$ in the secretory side. Resistance and PD are plotted vs. time. Concentrations are in mM.

## Results

### *PD responses and resistance changes of the resting fundus due to changes in $K^+$ concentration in nutrient solutions with 25 and with 5 mM $HCO_3^-$*

Fig. 1 is a plot of transmucosal resistance and PD versus time for the change from 4 to 40 mM $K^+$ and back to 4 mM $K^+$ for resting fundus in the presence of

TABLE I

*Effect on PD and resistance of changes in $K^+$ concentrations in the nutrient solution containing varying concentrations of $HCO_3^-$*

Values are means ± S.D. Student's *t*-test using paired observations was used to determine the level of significance. Columns labelled PD and *R* refer to the control values of transmucosal potential difference and corresponding resistance and columns labelled $\Delta PD_M$, $\Delta PD$ and $\Delta R$ refer respectively to changes of the PD at the maximum and at 10 min and the change in *R* at 10 min following the change to the final concentration of the ion. Number of experiments, 6.

| $[K^+]$ (mM) | | PD (mV) | $\Delta PD_M$ (mV) | $\Delta PD$ (mV) | *R* ($\Omega \cdot cm^2$) | $\Delta R$ ($\Omega \cdot cm^2$) |
|---|---|---|---|---|---|---|
| orig. soln. | final soln. | | | | | |
| Resting state: 25 mM nutrient $HCO_3^-$ | | | | | | |
| 4 | 40 | 42.9 ± 9.2 | – | −23.2 ± 5.9 [a] | 335 ± 63 | −119 ± 35 [a] |
| 40 | 4 | 18.1 ± 4.3 | – | 20.6 ± 3.6 [a] | 205 ± 30 | 53 ± 39 [b] |
| Resting state: 5 mM nutrient $HCO_3^-$ | | | | | | |
| 4 | 40 | 20.6 ± 8.2 | 4.9 ± 2.9 [a*] | −11.9 ± 4.3 [a] | 680 ± 200 | −192 ± 29 [a] |
| 40 | 4 | 7.0 ± 3.5 | – | 9.4 ± 4.5 [a] | 478 ± 123 | 188 ± 110 [a] |

[a] $P < 0.01$;
[b] $P < 0.02$;
* $\Delta PD_M$ is the average of five experiments, since no maximum was obtained in one experiment.

TABLE II

*Effect on PD and resistance of changes in $Na^+$ concentrations in the nutrient solution containing varying concentrations of $HCO_3^-$*

See Table I for details. Number of experiments, 6.

| $[Na^+]$ (mM) orig. soln. | final soln. | PD (mV) | ΔPD (mV) | $R$ ($\Omega \cdot cm^2$) | $\Delta R$ ($\Omega \cdot cm^2$) |
|---|---|---|---|---|---|
| Resting state: 25 mM $HCO_3^-$ | | | | | |
| 100 | 10 | 41.7 ± 7.9 | −15.1 ± 3.1 [a] | 381 ± 70 | 180 ± 57 [a] |
| 10 | 100 | 25.2 ± 6.5 | 15.5 ± 4.4 [a] | 590 ± 132 | −156 ± 61 [a] |
| Resting state: 5 mM $HCO_3^-$ | | | | | |
| 100 | 10 | 21.4 ± 5.7 | −9.4 ± 2.0 [a] | 755 ± 93 | 132 ± 199 |
| 10 | 100 | 8.0 ± 2.9 | 5.9 ± 2.3 [a] | 839 ± 283 | −51 ± 91 |

[a] $P < 0.01$.

25 mM $HCO_3^-$ and later in the presence of 5 mM $HCO_3^-$. With 25 mM $HCO_3^-$, the increase in $K^+$ from 4 to 40 mM in the nutrient solution decreased the resistance and decreased the PD. With the change to 5 mM $HCO_3^-$, the resistance increased substantially. Then, in the change from 4 to 40 mM $K^+$, there was a biphasic response: an initial increase in PD, an anomalous response, previously attributed to the existence of a $Na^+/K^+$-ATPase pump [9–11], followed by a decrease in PD below the control level, a normal response but of lesser magnitude than with 25 mM $HCO_3^-$. Here also the resistance decreased with the change from 4 to 40 mM $K^+$. These results may be explained by an increase in resistance of the simple $K^+$ resistance pathway with 4 mM $K^+$ in the nutrient solution due to the decrease in the concentration of nutrient $HCO_3^-$ (see Discussion). The return to 4 mM $K^+$ brought the PD and resistance back toward control levels at 25 and 5 mM nutrient $HCO_3^-$.

In Table I, in going from 4 to 40 mM $K^+$, ΔPD at 10 min was −23.2 mV with 25 mM nutrient $HCO_3^-$ and −11.9 mV with 5 mM nutrient $HCO_3^-$. In five of the six experiments, the PD response was biphasic in that a maximum PD occurred generally within 1 min after the $K^+$ increase from 4 to 40 mM was made and the maximum was followed by a decrease in PD below the control level. The maximum ΔPD did not occur in one of the six experiments and the average value of the maximum ΔPD for the five experiments was 4.9 mV. In the case of the antrum, the maximum ΔPD was about 8 mV [11]. The respective decreases in resistance for 25 and 5 mM nutrient $HCO_3^-$ were 119 and 192 $\Omega \cdot cm^2$. In percentages, the decreases were respectively 36 and 28%. Upon return to 4 mM $K^+$, only a normal response was observed, that is, the PD and resistance both increased towards control values.

*PD responses and resistance changes of the resting fundus due to changes in the $Na^+$ concentration in nutrient solutions with 25 and with 5 mM $HCO_3^-$*

Table II shows results for changes in $Na^+$ concentration in resting fundus similar to that obtained above for changes in $K^+$ concentration. For decreases in nutrient $Na^+$ concentration from 100 to 10 mM for 25 and 5 mM $HCO_3^-$, the respective decreases in PD were 15.1 and 9.4 mV. Since the PD decreases with a decrease in nutrient $Na^+$ concentration, this result was previously considered as an anomalous response and was attributed to the existence of an electrogenic NaCl symport in the nutrient membrane [12,13]. The increase in resistance was significant only with 25 mM $HCO_3^-$ and was in this case 180 $\Omega \cdot cm^2$. Upon the return to 100 mM

TABLE III

*Effect on PD and resistance of changes in $Cl^-$ concentrations in the nutrient solution containing varying concentrations of $HCO_3^-$*

See Table I for details. Number of experiments, 6.

| $[Cl^-]$ (mM) orig. soln. | final soln. | PD (mV) | ΔPD (mV) | $R$ ($\Omega \cdot cm^2$) | $\Delta R$ ($\Omega \cdot cm^2$) |
|---|---|---|---|---|---|
| Resting state: 25 mM $HCO_3^-$ | | | | | |
| 81 | 8.1 | 45.2 ± 3.0 | −21.3 ± 2.6 [a] | 309 ± 90 | 71 ± 97 |
| 8.1 | 81 | 23.1 ± 2.7 | 21.4 ± 2.5 [a] | 381 ± 154 | −18 ± 57 |
| Resting state: 5 mM $HCO_3^-$ | | | | | |
| 81 | 8.1 | 25.2 ± 7.8 | −10.0 ± 2.7 [a] | 688 ± 196 | −4 ± 62 |
| 8.1 | 81 | 9.8 ± 8.8 | 8.5 ± 3.7 [a] | 713 ± 199 | 69 ± 67 |

[a] $P < 0.01$.

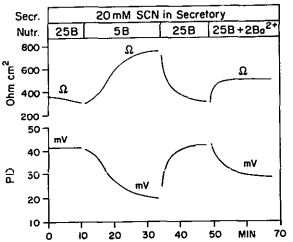


Fig. 2. Effect of change in nutrient $HCO_3^-$ from 25 to 5 mM and back to 25 mM followed by effect of addition of 2 mM $Ba^{2+}$ to the 25 mM nutrient solution. Throughout 20 mM $SCN^-$ was present in the secretory side. Resistance and PD are plotted vs. time. Concentrations are in mM and B refers to $HCO_3^-$.

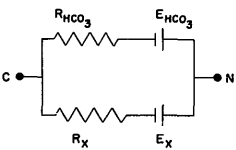


Fig. 3. Equivalent circuit for nutrient membrane consisting of a $HCO_3^-$ limb and an X limb representing all other ionic pathways. C and N refer respectively to cell and nutrient.

$Na^+$, the results returned to control values for 25 mM $HCO_3^-$ but only partly for 5 mM $HCO_3^-$.

*PD responses and resistance changes of the resting fundus due to changes in the $Cl^-$ concentration in nutrient solutions with 25 and with 5 mM $HCO_3^-$*

Table III shows the results for decreases in $Cl^-$ concentration in the nutrient solution from 81 to 8.1 mM for 25 and for 5 mM nutrient $HCO_3^-$. The respective decreases in PD were 21.3 and 10.0 mV. The changes in resistance were, however, not significant. Upon return to 8.1 mM $Cl^-$, the PD returned to control or near control values.

*Effect on PD and resistance due to a decrease in nutrient $HCO_3^-$ from 25 to 5 mM $HCO_3^-$ compared to the addition of 2 mM $Ba^{2+}$ to the 25 mM nutrient $HCO_3^-$ solution*

It has long been established that $Ba^{2+}$ in the nutrient solution of frog gastric mucosa blocks the $K^+$ conductance pathway [14,15] (see Discussion). It was therefore thought that, if the resistance increase due to $Ba^{2+}$ was about the same as the resistance increase due to the decrease in $HCO_3^-$, then only the resistance of the $K^+$ pathway increased due to a decrease in $HCO_3^-$. In reality, as described below, the decrease in $HCO_3^-$ gave a greater increase in resistance than the addition of $Ba^{2+}$ to a 25 mM $HCO_3^-$ nutrient solution. Hence this result gave further evidence that other pathways like $Na^+$ and $Cl^-$ also increased in resistance with a decrease in $HCO_3^-$.

Fig. 2 shows the results under the two circumstances, a decrease in nutrient $HCO_3^-$ and the addition of nutrient $Ba^{2+}$. In the first case, the resistance increased markedly and the PD decreased markedly. In the second case, similar changes occurred in resistance and PD but to a lesser extent.

In Table IV, the decrease in nutrient $HCO_3^-$ from 25 to 5 mM decreased the PD by 17.7 mV and increased the resistance by 284 $\Omega \cdot cm^2$, while the addition of $Ba^{2+}$ to 2 mM in the nutrient solution decreased the PD by 10.0 mV and increased the resistance by 112 $\Omega \cdot cm^2$. The respective increases in resistance were, in percentages, 72 and 28%. It is to be noted that the relatively low increase in resistance (112 ohm $\cdot cm^2$) due to the addition of $Ba^{2+}$ is to be expected in the resting fundus, whereas much larger increases in resistance (about 700 $\Omega \cdot cm^2$ [16]) occur for stomachs with high acid-secreting rates. As expected [14], the addition of $Ba^{2+}$ to 2 mM in the 25 mH $HCO_3^-$ nutrient solution gave essentially maximal increase in resistance. In the present experiments, with 5 mM $HCO_3^-$ in the nutrient solution, the addition of $Ba^{2+}$ in steps up to 6 or 8 mM

TABLE IV

*Effect on PD and resistance for a decrease in nutrient $HCO_3^-$ and for the addition of nutrient $Ba^{2+}$*

See Table I for details. Number of experiments, 6.

| $[HCO_3^-]$ (mM) | | PD (mV) | ΔPD (mV) | $R$ ($\Omega \cdot cm^2$) | $\Delta R$ ($\Omega \cdot cm^2$) |
|---|---|---|---|---|---|
| orig. soln. | final soln. | | | | |
| Case I: No $Ba^{2+}$ in original or final nutrient solution | | | | | |
| 25 | 5 | 36.5 ± 7.4 | −17.7 ± 2.8 [a] | 393 ± 145 | 284 ± 94 [a] |
| Case II: 2 mM $Ba^{2+}$ in final nutrient solution | | | | | |
| 25 | 25 | 36.8 ± 5.8 | −10.0 ± 1.5 [a] | 403 ± 161 | 112 ± 28 [a] |

[a] $P < 0.01$.

gave no further increase in resistance, and at higher concentrations a small decrease on occasion.

## Discussion

As mentioned in the Introduction, it is difficult to explain the linear relationship between ΔPD and the log of the $HCO_3^-$ concentration with an increase in transmucosal resistance. To see how this difficulty arises, let us refer to Fig. 3 in which is shown an electrical circuit consisting of a $HCO_3^-$ limb and an X limb for all other ion pathways. Each limb consists of a resistance, $R$, and an emf, $E$. Even though the transport system is complex in the gastric mucosa, one can use a simplified circuit for the purpose under discussion. For this circuit, it follows that the PD is given by

$$PD = (R_X E_{HCO_3} + R_{HCO_3} E_X)(R_{HCO_3} + R_X)^{-1}$$

If $R_X$ and $R_{HCO_3}$ were constant, then for a change in $HCO_3^-$ concentration, it would follow (since $\Delta E_X = 0$) that

$$\Delta PD = R_X (R_{HCO_3} + R_X)^{-1} \Delta E_{HCO_3}$$

and a linear relationship would exist between ΔPD and $\Delta E_{HCO_3}$ and hence between ΔPD and the log of the $HCO_3^-$ concentration. However, since changes in $HCO_3^-$ concentration gave rise to changes in transmucosal resistance, some hypothesis other than constancy of $R_X$ and $R_{HCO_3}$ was needed. As a possibility, it was assumed that, if $R_X$ and $R_{HCO_3}$ both varied inversely with the $HCO_3^-$ concentration, then $R_X (R_{HCO_3} + R_X)^{-1}$ would remain constant. In general, it would be very difficult to explain the linear relationship based on a model in which either resistance alone of the parallel pathways changed with variation in the $HCO_3^-$ concentration.

The present study provided a means of determining whether ionic pathways besides the $HCO_3^-$ pathway underwent a change in resistance with a change in $HCO_3^-$ concentration. Such information is associated with the result that ΔPD due to a change in concentration of an ion (e.g., $K^+$, $Na^+$, $Cl^-$) in the nutrient is less with a low nutrient concentration of $HCO_3^-$ than with a high concentration of $HCO_3^-$. The decrease in ΔPD results generally from an increase in resistance of the ionic pathway under consideration. In addition, the 10-fold increase in $K^+$ in the nutrient solution containing 5 mM $HCO_3^-$ gave an initial transient increase in ΔPD with a maximum of 4.9 mV. Such transient increases in PD were not observed with 25 mM $HCO_3^-$.

As stated above, the PD responses provide some idea of the changes in conductance in going from 25 to 5 mM $HCO_3^-$ in the nutrient solution. The $K^+$ transport is associated with both a simple conductance pathway and a $Na^+/K^+$-ATPase pump pathway [8–11]. Since the resistance of the latter pathway is normally high, changes in ΔPD often reflect changes in the resistance of the simple $K^+$ conductance pathway. However, there are exceptions [9–11], as occurred with 5 mM $HCO_3^-$ in the 4 mM $K^+$ nutrient solution. In this case, the resistance of the simple $K^+$ conductance pathway increased so that the PD response from an increase in $K^+$ was due to the $Na^+/K^+$-ATPase pump, that is, the increase from 4 to 40 mM $K^+$ gave an anomalous PD response. The presence of 40 mM $K^+$ in the nutrient solution decreases the resistance of the simple $K^+$ conductance pathway. For this reason, the anomalous response was quickly followed by a normal response (for details, see Ref. 10).

As for other pathways, the $Na^+$ transport is associated mainly with the NaCl symport pathway [12,13]. Then for $Na^+$, a decrease in magnitude in ΔPD due to a decrease in $HCO_3^-$ concentration reflects essentially an increase in the resistance of the symport pathway. For $Cl^-$, there are two pathways: a simple conductance pathway and the NaCl symport pathway [8,12,13]. It would be difficult to determine which pathway or whether both pathways are affected by a decrease in nutrient $HCO_3^-$. The results with $Ba^{2+}$ support the increase in resistance in pathways besides the $K^+$ pathway.

Evidence that $Ba^{2+}$ in the nutrient solution blocks the nutrient $K^+$ pathway and increases markedly the resistance of this pathway is provided by the following information and experiment. In the absence of $Ba^{2+}$, we note that, in the secretory membrane, the resistance of the $K^+$ pathway is high and that of the $Cl^-$ pathway is low [5,17] while, in the nutrient membrane, the resistance of the $K^+$ pathway is low and that of the $Cl^-$ pathway(s) about twice that of the $K^+$ pathway [8]. As a consequence, the ratio of the $K^+$ resistance to the $Cl^-$ resistance in the secretory membrane is considerably greater than the ratio of the $K^+$ resistance to the $Cl^-$ resistance in the nutrient membrane. Then, if an external step current is sent through the frog gastric mucosa, the transient voltage response versus time has as one of its components an exponential curve with a very long time constant [17]. If, however, $Ba^{2+}$ is added to the nutrient solution, the above-mentioned ratios approach equality and the transient voltage-response versus time is immediate [17]. Thus this experiment, in addition to the one previously mentioned [15], proves that $Ba^{2+}$ in the nutrient solution increases the resistance of the $K^+$ pathway markedly. In the present study, it becomes evident from these considerations that any further increase in transmucosal resistance, such as that resulting from the decrease in nutrient $HCO_3^-$, must arise from the increase in resistance in pathways other than the $K^+$ pathway.

We wish now to comment briefly on intracellular pH regulation. Paradiso et al. [18] found evidence for neu-

tral $Na^+$–$H^+$ and $Cl^-$–$OH^-$ ($HCO_3^-$) exchange in gastric glands of rabbit stomach. These mechanisms were associated with internal pH regulation. In the intact frog gastric mucosa there is considerable evidence for conductance pathways. From the present study in the resting fundus we might infer that the decrease in nutrient $HCO_3^-$ decreases internal pH. It would appear then that, while ions like $Na^+$ and $Cl^-$ play a role in pH regulation, the pH in turn plays a role in controlling the resistance of ion pathways such as those for $K^+$, $Na^+$ and $Cl^-$ transport.

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