Relating microscopic charge movement to macroscopic currents: the Ramo-Shockley theorem applied to ion channels

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ABSTRACT

Since the discovery of gating current, electrophysiologists have studied the movement of charged groups within channel proteins by changing potential and measuring the resulting capacitive current. The relation of atomic-scale movements of charged groups to the gating current measured in an external circuit, however, is not obvious. We report here that a general solution to this problem exists in the form of the Ramo-Shockley theorem. For systems with different amounts of atomic detail, we use the theorem to calculate the gating charge produced by movements of protein charges. Even without calculation or simulation, the Ramo-Shockley theorem eliminates a class of interpretations of experimental results. The theorem may also be used at each time step of simulations to compute external current.

INTRODUCTION

Since Schneider and Chandler (1973), the internal movements of channel proteins have been estimated by measuring gating current (reviewed by Armstrong, 1975, 1981; Almers, 1978; Sigworth, 1994; Bezanilla, 2000; Hille, 2001). Gating current is the capacitive current (recorded as electron flow between macroscopic electrodes) produced by the movement of charged atoms in a channel protein, when the voltage between the electrodes is changed. It is distinct from the conduction current produced by the flow of ions through the open channel and can be separated from total measured current in a variety of ways, which give quite consistent results. Experiments using site-directed mutagenesis have since identified charged amino acid residues of channels that contribute to voltage-dependent gating (Stühmer et al., 1989) and gating current (Aggarwal and MacKinnon, 1996; Seoh et al., 1996).

To interpret these measurements quantitatively, one must know the relationship between the atomic-scale charge movements and the externally recorded current. Such a relation has recently been derived using a particular equilibrium model of statistical mechanics (linearized Poisson-Boltzmann theory) to describe the charges in the bathing solutions (Roux, 1997). Here, we present a general solution, one that has been known for some time in computational electronics. An extension of Kirchoff's current law, the Ramo-Shockley theorem, links current flowing in the external circuit to charge movement inside the system (Shockley, 1938; Ramo, 1939). Recent generalizations of the original theorem directly relate microscopic charge movements and macroscopic current in complex systems. We apply the Ramo-Shockley theorem to gating current experiments and show how it can be used to calculate measured charged movements

from atomic models. We use the theorem to rule out certain interpretations of experimental results and to compute external currents in simulated systems with high efficiency. The generalized theorem provides a concise formula and model-independent results that are applicable to many biophysical problems.

THE RAMO-SHOCKLEY THEOREM

In voltage clamp experiments used to study currents through a biological membrane, two electrodes impose a controlled voltage across a domain that contains different dielectrics and charged particles (ions in the baths and channels, and charged groups in the protein) (Hodgkin *et al.,* 1952). The charged particles move because of thermal agitation (heat) and the local electric field. The current measured by the external circuit has two components: the particle current carried by ions entering or leaving the electrodes and the displacement current. The displacement current is the movement of charge (electrons) in the electrodes induced by changes in the electric field caused by the movement of all the charged particles that do *not* reach the electrode (Jackson, 1999; Purcell, 1985, p. 371; Feynman *et al.*, 1964, for example, Ch. 23, p. 2). The Ramo-Shockley theorem equates the total current (particle plus displacement) measured in the external circuit with the microscopic motion of the charged particles in the domain between the electrodes.

Voltage-clamp experiments measure the total current I flowing into an electrode held at voltage E_m with respect to a grounded electrode. The Ramo-Shockley theorem (references given below) states that this current is

$$I = \frac{1}{1\,\mathrm{volt}} \sum_j q_j \mathbf{W}\left(\mathbf{r}_j\right) \cdot \mathbf{v}_j \ . \tag{1}$$

We use the nomenclature of Yoder *et al.* (1997) where $\mathbf{v}_j$ and $\mathbf{r}_j$ are the instantaneous velocity and position vectors, respectively, of the particle j with charge q_j when the clamped voltage E_m is applied. **W** is the electric field that would be generated by removing *all* particle charges (mobile and fixed) from the domain and setting the clamped voltage to 1 volt. The only charges contributing to **W** are the charges needed to impose ground potential and 1 volt at the electrodes and charges induced by the electrode charges on and in the dielectrics of the domain. **W** is *not* the field that is present when the clamped voltage E_m is applied and the current is observed. The field resulting from the clamped voltage E_m enters the equation indirectly, through the positions $\mathbf{r}_j$ and velocities $\mathbf{v}_j$ that it imparts to mobile charged particles. The sum in Eq. 1 is over all mobile particle charges q_j in the domain; that is, it is the sum of all charges q_j moving with velocity $\mathbf{v}_j$ at the time the sum is taken, including both those that belong to the channel protein and all ions in the bath solutions and the pore of the channel.

The measured current I of Eq. 1 is converted to charge by integrating over arbitrary trajectories that connect known starting locations $\mathbf{r}_j'$ of the particles to known ending locations $\mathbf{r}_j''$. This integration yields the externally measured gating charge:

$$Q = -\frac{1}{1\,\text{volt}} \sum_j q_j \left[U\left(\mathbf{r}_j''\right) - U\left(\mathbf{r}_j'\right) \right] \tag{2}$$

where $U\left(\mathbf{r}\right)$ is the potential at location **r** that would be generated by removing *all* particle charges (mobile and fixed) from the domain and setting the clamped voltage to 1 volt.

Again, the potential field present while the clamped voltage is held at E_m enters the equation only indirectly; it determines the locations of the charged particles.

The theorem was derived independently by Shockley (1938) and Ramo (1939) and is commonly used in computational electronics as a generalization of Kirchoff's current law that includes displacement current. The original derivations assumed negligible magnetic and radiation effects (that is, they assumed quasi-electrostatics) to describe electron transport in vacuum tubes. The theorem has subsequently been generalized to systems containing inhomogeneous linear dielectrics (Pellegrini, 1986; Kim *et al.*, 1991). An extended version for the full electrodynamic regime has been derived (Yoder *et al.*, 1996, 1997). We use the generalized quasi-electrostatic version of the theorem.

To illustrate the theorem, we give a simple derivation for a capacitive linear circuit that applies to a voltage-clamped system. Imagine that a vanishingly small conductive sphere *j* is placed at location $\mathbf{r}_j$, where it forms capacitors C_{jR} and C_{jG} (Fig. 1). The surfaces of capacitor C_{jR} are the conductive sphere and the recording electrode *R* (the electrode where E_m is applied in a voltage clamp experiment). The surfaces of capacitor C_{jG} are the conductive sphere and the second (grounded) voltage clamp electrode *G* and any other grounded surfaces.

We consider two experiments. In the first experiment, labeled (1), a single, mobile, charged particle with charge q_j is placed in the small conductive sphere located at $\mathbf{r}_j$ and the electrode *R* is set to zero potential. The charge induced on *R* (the charge that the voltage clamp applies to maintain *R* at zero potential) will be

$$q_R^{(1)} = -q_j \frac{C_{jR}}{C_{jR} + C_{jG}}. \tag{3}$$

The charge induced on the electrode can be computed by Eq. 3 for any q_j if the calibration factor $C_{jR} \big/ \left(C_{jR} + C_{jG} \right)$ is known. We determine this factor in a separate, second experiment, labeled (2).

In the second experiment, the charge of all charged particles is removed (that is, $q_j^{(2)} = 0$), and a voltage of 1 volt is imposed on *R*. The capacitors C_{jR} and C_{jG} now form a voltage divider, and the resulting voltage at $\mathbf{r}_j$ is

$$U^{(2)}\left(\mathbf{r}_j\right) = \frac{C_{jR}}{C_{jR} + C_{jG}} \times \left(1 \text{ volt}\right) \tag{4}$$

Combining the results of the two experiments, we have

$$q_R^{(1)} = -\frac{1}{1 \text{ volt}} q_j U^{(2)}\left(\mathbf{r}_j\right) \tag{5}$$

This treatment can be extended to a system of many small spheres *j* that contain charges q_j ; by superposition, we then have

$$q_R^{(1)} = -\frac{1}{1 \text{ volt}} \sum_j q_j U^{(2)}\left(\mathbf{r}_j\right) \tag{6}$$

If we move the charges *j* from locations $\mathbf{r}_j'$ to locations $\mathbf{r}_j''$, the electrode charge will change by

$$Q = -\frac{1}{1 \text{ volt}} \sum_j q_j \left[U^{(2)}\left(\mathbf{r}_j''\right) - U^{(2)}\left(\mathbf{r}_j'\right) \right] \tag{7}$$

which is the Ramo-Shockley theorem in the form of Eq. 2.

APPLICATIONS TO ION CHANNELS

Defining electrical coordinate and electrical travel

For a given dielectric geometry of the baths, membrane, and channel, Eq. 2 relates induced electrode charge with microscopic charge and the function $U(\mathbf{r})$. The geometric coordinate $\mathbf{r}$ is thereby mapped onto the "electrical coordinate" $U(\mathbf{r})/(1\text{ volt})$ and the geometric travel $\mathbf{r}_j'' - \mathbf{r}_j'$ onto the "electrical travel" of the charge *j*,

$$T_{el} \equiv \frac{1}{1\text{ volt}}\left[U\left(\mathbf{r}_j''\right) - U\left(\mathbf{r}_j'\right)\right]. \tag{8}$$

The potential U is found by solving the Poisson equation for the channel geometry with 1 volt of potential on the electrode R and all the linear dielectrics in place, but no charged particles of any kind (neither fixed or mobile structural charges, nor bath ions). The only charges present are the electrode charges that maintain boundary conditions like the potential of 1 volt and polarization charges induced by the electrodes on and in the dielectrics. The dielectrics that we include are linear and isotropic; their polarization settles much faster than the experimentally observable charge movements. The effects of these linear dielectrics are expressed in Eqs. 1 and 2 by the field $\mathbf{W}$ or the potential U. A voltage-gated channel will add what might be described as a nonlinear, time-dependent, and probably location-dependent anisotropic polarizability to the membrane; charge movements underlying such complex behavior reflect the interesting gating movements of the channel protein. They are included as explicit charge movements in the sums of Eqs. 1 and 2.

Figs. 2 and 3 show calculations of electrical coordinate maps, found by solving the Poisson equation numerically on a domain in which bath solutions, lipid, and protein

are represented as linear, isotropic dielectrics. The dielectric geometries shown are low-resolution representations of an open conduction pore (Fig. 2) and of a "gating pore" that allows an S4 segment to slide back and forth through the membrane (Fig. 3). The domain is cylindrical about the vertical axis and is represented in an axial cross-section. The points **r** of each contour line are each at the same potential U; they are plotted at increments of $\Delta U = 0.05$ volt (and some at $\Delta U = 0.025$ volt). Each "electrical coordinate" $U(\mathbf{r})/(1\text{ volt})$ is a surface and not a unique location **r**; all points of the surface represented by a contour line are at the same electrical coordinate from the external voltage clamp electrode.

A map of electrical coordinates can help predict the gating charge measured in a thought experiment, for example, if a charge q were moved between two locations. According to Eq. 2, the gating charge would be $Q = -qT_{el}$, where T_{el} can be read from the map. Note that manipulating one or many charges this way does not affect the map; the map changes only when the geometry of the linear dielectrics changes. If many charges are moved simultaneously, their contributions to the gating charge sum algebraically. This additivity itself may appear surprising because it holds in a domain of condensed matter. The invariance of the map and the additivity of individual readings make the "electrical travel" defined via the Ramo-Shockley theorem a useful concept.

Figs. 2 and 3A are computed in a small domain that is typical for a simulation. In actual experiments, electrodes are much farther away from the membrane, making the electrical travel across each bath much larger than the electrical travel across the membrane. This leads to an apparent paradox: in the experimental situation, movement of structural charge in the membrane itself contributes very little to the measured charge Q

in Eq. 2, since the structural charge is scaled by a small electrical travel. The paradox is due to the fact that the electrical coordinate is computed with all source charges removed from the interior of the system (including the ions in the bathing solutions), whereas the external charge movement Q is computed from the movements of all mobile charges of the system (including the ions in the bathing solutions). In a system with deep baths, Q is dominated by the contributions of the bath ions that move in response to the movement of charges in the membrane (and thus conduct the gating current towards the electrodes).

In principle, Eqs. 1 and 2 can be applied to any domain in a circuit that is bounded by surfaces where controlled potentials are applied, provided that the movements of *all* charges in the domain (for example, all ions in the bathing solutions) are included in the summation. If the domain is geometrically expanded the electrical travel of all charges is reduced, but charges newly included in the domain are appended to the summation. For a chosen domain (large or small), the Ramo-Shockley theorem *exactly* computes the current that would be measured in an experiment performed in that geometry.

Realistic simulations of an actual biological experiment are frustrating because most of the computational effort concerns ions in the baths, not charges in the pore or channel protein of biological interest. It is more efficient to use a multi-scale approach. At one level of multi-scale approach, one could treat the bathing solutions as ideal conductors. Such idealized baths extend the electrodes to the boundaries of the membrane and protein and reduce the summations in Eqs. 1 and 2 to the movements of only the charges within the channel/membrane. The summations then give an upper bound to the measured gating charge because each geometrical movement results in the maximal possible electrical travel. Such a map is shown in Fig. 3B; later we show how an upper

limit of the gating charge helps explain experimental results.

Comparison with a linear equilibrium analysis

An expression for the external charge similar to Eq. 2 has been previously derived by Roux (1997) and used by Islas and Sigworth (2001). Roux's derivation includes the effects of the bathing solutions on electrical coordinate and external charge movement, and he finds that the electrical coordinate in a system with bath ions is independent of the applied voltage. Whereas the simplicity of the latter result is appealing, it is a direct consequence of the linearized theory used to describe the bathing solutions. Boundary layers described by linearized Poisson-Boltzmann (PB) theory have capacitance that is independent of an applied electric field, whereas boundary layers of real solutions (or solutions described by nonlinear PB theory) have voltage-dependent capacitance. Roux's approximation for the bathing solutions is equivalent to applying Ramo-Shockley to a system without bath ions in which the electrodes are placed a Debye length away from the membrane and protein. (Placing the electrodes right on the membrane, as in Fig. 3B, is equivalent to having bathing solutions with infinite ionic strength.) The error in Roux's approximation could be evaluated by a simulation including explicit bath ions and Eq. 2 to evaluate the external charge movement. Roux's result is an exact consequence of his assumption of a linearized equilibrium bath. Eq. 2 is less restrictive: it is a consequence of Maxwell's Equations and is applicable (in the form of Eq. 1) to systems in which currents flow (for instance, through open channels); Roux's result implies that no currents flow in the baths.

Interpreting gating charges

When applied to gating charge experiments, the Ramo-Shockley theorem ex-

presses gating charge as the product of the physical charge and the well-defined electrical travel of the physical charge, summed over all mobile charges present in the domain. To apply Ramo-Shockley to a specific example, we consider an experiment by Seoh *et al.* (1996) that produced an unforeseen result. Seoh *et al.* created mutants in which a charged residue of a membrane-spanning segment in a K channel monomer was replaced by a neutral residue. They found that deleting a positive charge of the S4 segment eliminated up to $7e_0$ of measured gating charge. (e_0 is the proton charge.) Because of the tetrameric structure of the protein, one might expect that at most $4e_0$ of gating charge would be eliminated in such mutants. In the Seoh *et al.* experiment, upper bounds for the magnitude of the physical charges in the wild type and mutants are known. The movements of the charges in the protein are not known. It is not clear a priori if the movement of these atomic charges (in the native protein) could contribute a disproportionately large amount to the gating charge recorded by the external electrodes.

Eq. 2 allows one to narrow the interpretation of these results. For instance, one might think that even if the charges move between the same starting and ending points, the measured charge would depend on the local electric field in which the physical charges travel. If this were true, charges traveling across a region of high local field strength might contribute disproportionately to the measured gating charge, or their deletion might reduce gating charge disproportionately. Eq. 2 states, however, that neither structural charges nor their polarization charges can exert such an amplifying effect on the relation between atomic and measured charge movements; if the mobile charges move between the same points $\mathbf{r}_j'$ and $\mathbf{r}_j''$, the electrical travel $\left[U\left(\mathbf{r}_j''\right)-U\left(\mathbf{r}_j'\right)\right]\Big/\left[1\,\text{volt}\right]$ does not change because the particle charges and polarization

charges induced by particle charges do not contribute to $U(\mathbf{r})$.

The gating process is, of course, not independent of the local electric field present where and when the charges move. In particular, changes in the local electric field can change the electrical travel that the mobile charges actually undergo when perturbed by an applied voltage, although they do not change the map defining electrical coordinates. For example, deletion of some of the mobile structural charges of an S4 helix that moves as a solid body likely reduces the total electric force acting on the helix. Consequently, the geometric travel of the mutated helix, and of the undeleted S4 charges on it, might be reduced. The positions $\mathbf{r}_j'$ and/or $\mathbf{r}_j''$ would change, reducing the measured gating charge.

Within the constraints set by the Ramo-Shockley theorem, the experiment of Seoh *et al.* can be interpreted in two ways: (1) that deletion of charges q_k restricts in some way the electrical travel of the other mobile charges q_j (changing $\mathbf{r}_j'$ and/or $\mathbf{r}_j''$) or (2) that the mutant channels have a different dielectric geometry from the native channel, changing $U(\mathbf{r})$. Of course, the experiment might both restrict electric travel and change the dielectric geometry.

Ramo-Shockley and energy

Electrophysiologists have long used effective parameters to assign energy contributions to physical processes inferred from experiments. For example, Hodgkin and Huxley (1952) hypothesized that charged particles moving in the membrane electric field do the work $W = ze_0E_m$ on the membrane component that creates the voltage dependence of the Na^+ and K^+ conductances. Here, E_m is the membrane potential, z the effective valency of the particle, and e_0 the proton charge. Similarly, Woodhull (1973) described

the voltage-dependent block of Na^+ current by protons assuming that the "potential energy" of the blocking proton included a contribution $W = e_0 \delta E_m$, where δ is the "fraction of membrane potential acting at the site." Whereas the relationship between the moving microscopic charges and the externally recorded charge is given by the Maxwell Equations (which lead to the Ramo-Shockley theorem), the definition of effective charges is based on energetics. Energetics, however, are difficult to assess in an open system such as an ion channel because energy can flow in and out of the system in so many ways. Indeed, the phenomena of slow inactivation (Kuo *et al.*, 2004) suggest that energy can also be stored for long times in complex conformational changes important for channel function.

Effective charges characterize processes (gating, block) that modulate ionic flux through channels and are thereby coupled with a non-equilibrium process occurring in the same macromolecule. The conduction process is associated with a very large flow of energy. Consider an ion channel that opens for 1 ms to conduct a current of 1 pA driven by an electrochemical potential difference of $2\,kT$. The channel macromolecule will receive an energy of order $10^4 kT$ ($2\,kT \times 1\text{ ms} \times 1\text{ pA} / e_0$) in the open interval since most of the energy delivered by the external voltage source is dissipated in the conduction pore of the channel. (On a macroscopic scale, the energy flow for 1 g-mole of channels would be 30 GW!)

Irreversibility must also be considered in experiments where the conduction of the channel is abolished to study gating current. The channels can be subjected to many cycles of applied voltage, yet their gating charge movements are reversible within experimental accuracy. This might suggest that channels operating under such conditions

also have reversible energetics. It is easy to see that this is not true. For instance, when gating charge flows, external work is exchanged with the circuitry of the voltage clamp. The amount of work is simply computed because it is the work that moves the external charge between the constant potentials of the two electrodes. (In *Shaker* K channels, in which about $13\,e_0$ can be displaced by a step of 0.1 volt, the work would be approximately $52\,kT$.) None of this work is recovered from the channels when the change of voltage is reversed (even though all of the moved charge returns). This is evident if we start a cycle from the holding potential of 0 volt. A step to a different voltage V moving a charge Q does the external work $Q \times V$ on the system, whereas the external work recovered from the system upon return to 0 volt is $-Q \times 0$ volt – that is, nil. Generally, the channel protein completely dissipates the external work of the voltage cycles applied to electrodes to test gating kinetics.

Irreversible flows of matter, charge, and energy in a condensed system, which necessarily involve friction, are not included in the thermodynamic view that is commonly applied to ion channels. In this view, a channel is said to isomerize among well-defined equilibrium states, whose Gibbs energies depend in a simple way on an applied electric field and whose isomerization rates obey microscopic reversibility under all conditions. Typically, many closed and many open equilibrium states with distinct effective charges are postulated on kinetic grounds. Such states are assumed to be visited during relaxations evoked by jumps of applied voltage.

If the energetics of gating or block are outside the realm of equilibrium thermodynamics, then what kind of analysis could be used? Perhaps one should not analyze energies involved in the modulation of the ion flux, but instead focus on the

original physiological question: how does the channel (or blocking molecule) achieve the voltage dependence of the ionic flux? This approach has been applied in semiconductor device physics for decades, with obvious success (Sze, 1981). There, analysis is based on a hierarchy of physical models, not energy flow. In the case of the diode, results can be interpreted analytically (Laux and Hess, 1999), but most physical understanding comes from numerical simulations (for example, Hess, 1991).

These semiconductor devices are understood despite their complexity, which rivals that of channels (including gating). Physical generalizations concerning such devices are rarely made, probably because they seem impossible in such complex systems. Physiologists, however, have found a useful generalization, namely their definition of gating current (Hodgkin and Huxley, 1952; Schneider and Chandler, 1973; Armstrong, 1975, 1981; Almers, 1978; Sigworth, 1999; Bezanilla, 2000; Hille 2001). The Ramo-Shockley theorem shows that their definition has a sound general physical basis. The theorem gives a universal relation between microscopic charge movement and observed external charge, regardless of reversible or irreversible energetics of the charge movements under study. “Gating current” is a universal measure of the gating molecule, in just that sense.

Calculating current in simulations of ion channels

Eq. 1 allows calculation of currents in a simulation when charged particles move between positions, for instance in simulations of gating current or of ionic current flowing through the pore of an ion channel. Eq. 1 estimates current much more efficiently than counting ions crossing a surface (Chung *et al*., 1998), because it provides a sample

of the instantaneous current at each time step of the simulation, whereas counting of crossings produces relatively few current pulses and does not capture displacement current nor its essential contribution to the noise. Similarly, Eq. 2 allows one to track charge efficiently.

The sampling of current is an important application of the Ramo-Shockley theorem in electronic device simulations at the particle level (Gruzinskis *et al.,* 1991; Babiker *et al.,* 1998). This method is just now finding its way into simulations of ion channels (U. Ravaioli (University of Illinois, Urbana-Champaign), personal communication; M. Saraniti (Illinois Institute of Technology), personal communication).

CONCLUSION

The Ramo-Shockley theorem allows one to relate, in a general way, microscopic movements of physical charges in ion channels to macroscopic currents recorded in a voltage clamp.

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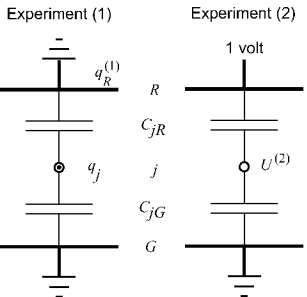
Figure Captions

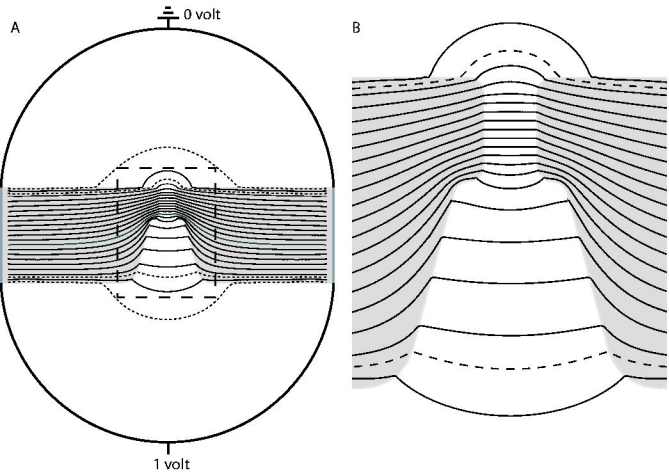
Figure 1. Equivalent circuits for the two thought experiments used to derive the Ramo-Shockley theorem (see text).

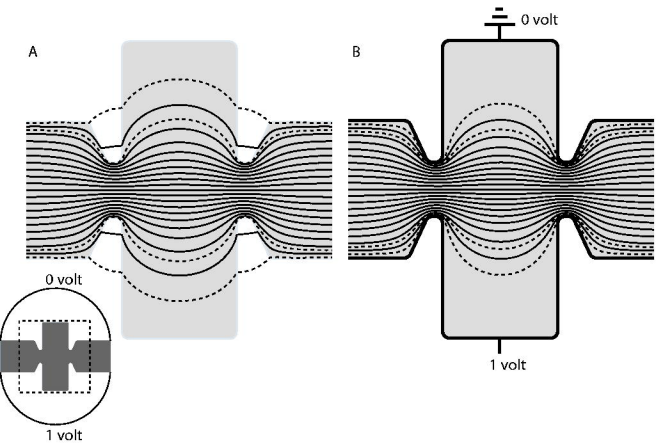
Figure 2. Mapping geometric coordinates to electrical coordinates. A conductive pore provides an aqueous bridge through the membrane (qualitatively similar to the open pore of a K channel (Jiang et al., 2003)). The domain (*panel A*, drawn to scale) is a generalized cylinder (maximal radius 5 nm, length 13 nm) and is shown in an axial cross-section; the highlighted part in A is shown at larger scale in *panel B*. Electrodes bound the two hemispherical baths. The top (external) electrode is grounded, whereas the bottom (internal) electrode is maintained at 1 volt. Isopotential lines are shown at 50 mV intervals (*solid lines*); some intermediate isopotentials corresponding to 25 mV intervals are also included (*dashed lines*). The isopotential lines also mark surfaces of constant "electrical coordinate" (with respect to the grounded electrode), corresponding to intervals of 0.05 (or 0.025). The dielectrics are described by dielectric coefficients of 80 (bath solutions and pore, *unshaded*) and 2 (lipid and channel, *shaded in gray*). A linearly varying potential is imposed at the lateral boundary of the membrane (*dark gray lines)*.

Figure 3. Mapping geometric coordinates to electrical coordinates. An S4 helix segment spans the membrane through a "gating pore" (as envisioned by Bezanilla (2002)). The domain either includes bath solutions between the membrane and electrodes (*panel A*, c.f.

Fig. 2), or the electrodes cover membrane and protein like a thin metal foil (*panel B*). Isopotential lines are shown at 50 mV intervals (*solid lines*); some intermediate isopotentials corresponding to 25 mV intervals are also included (*dashed lines*). The dielectrics are described by dielectric coefficients of 80 (bath solutions, *unshaded*) and 2 (lipid and channel, *shaded in gray*).


Experiment (1)
Experiment (2)
1 volt
$q_R^{(1)}$
R
C_{jR}
q_j
j
$U^{(2)}$
C_{jG}
G


A
0 volt
1 volt
B


A
0 volt
1 volt
B
0 volt
1 volt