Appendix
Models of Chemical Kinetics and the Law of Mass Action

The law of mass action is taught early and often in the education of chemists and biologists. The law is taught as a commandment without derivation or discussion, as a glance at the textbook literature will show. Commandments taught early in one's education have a particular continuing impact on thought processes, as seen in the history of human behavior, religious, political, and social. They tend to be forever unquestioned. Commandments have their uses, but in the scientific tradition it is important that they be questioned just like everything else.

The law of mass action says that the flux of a species over a potential barrier into a solution of zero concentration (i.e., into an absorbing boundary) is proportional to the number density of that species. This 'law' is certainly a reasonable initial working hypothesis. It in fact can be proven to be true—as a matter of mathematics, not science—for systems of stochastic trajectories of uncharged particles satisfying Langevin equations with high friction[294,513].

$$m\frac{d^2}{dt^2} = \text{force on particle } \mathbf{X} = \bar{\beta}\,\frac{d\mathbf{X}(t)}{dt} + ze\Phi'(x) - \sqrt{2\bar{\beta}k_BT}\;\dot{w} \tag{1}$$

Here $\bar{\beta} = \text{friction} = m\left(k_BT/D\right)$; $m = \text{mass}$; $D = \text{Diffusion coefficient}$; $ze\Phi'(x)$ is the electrical force produced by the electric potential field $\Phi(x)$; $\sqrt{2\bar{\beta}k_BT}\;\dot{w}$ is the Gaussian white noise process that makes the Langevin equation a stochastic differential equation, with weighting chosen to satisfy the fluctuation dissipation theorem. Details are in[294,513] and explanations in [340,794,795].

The derivation of eq. (10) must use the properties of doubly conditioned trajectories if it is to deal with different concentrations in different locations. It must use the version of the Langevin equation with a second derivative. The version used by Einstein with one derivative does not allow two boundary conditions. Two boundary conditions are needed to account for the diffusion process addressed by Fick's law.

The theory[234,413] needs revision to avoid (misleading if not artifactual) boundary layers near electrodes[828,830] that fortunately have only small effects. The theory can easily be revised to describe the four electrode method widely used in experiments [38,660,790] because it avoids boundary layers altogether.

A careful derivation of the law of mass action leads to beautifully simple expressions. The solutions of the Langevin equation eq. (10) theory can be rewritten in an appealingly simple way[271,288] when concentrations are specified on either side of the channel, in the high friction limit, but without further approximation. J_k is the flux of species *k*. The unidirectional flux is defined precisely in operational terms in appendix[148] and in mathematics in[294]. Roughly speaking it is the flux of a tracer into a region with negligible tracer concentration (in the language of tracer experiments) or the flux into an absorbing boundary (in the language of stochastic processes).

$$J_k = \overbrace{\underbrace{C_k(L)}_{\substack{\text{Source}\\ \text{Concentration}}} \underbrace{\left(\frac{D_k}{l}\right)}_{\substack{\text{Diffusion}\\ \text{Velocity}}} \underbrace{\text{Prob}\{R|L\}}_{\substack{\text{Conditional}\\ \text{Probability}}}}^{\text{Unidirectional Efflux}} - \overbrace{C_k(R)\left(\frac{D_k}{l}\right)}^{\text{Unidirectional Infflux}} \text{Prob}\{L|R\} \qquad (2)$$

(Channel Length)

or

$$J_k = \overbrace{l \cdot k_f C_k(L_{eft})}^{\substack{\text{Unidirectional Efflux}\\ J_{out}}} - \overbrace{l \cdot k_b C_k(R_{ight})}^{\substack{\text{Unidirectional Infflux}\\ J_{in}}} \qquad (3)$$

Here

$$k_f \equiv \frac{J_{out}}{C_k(L_{eft})} = k\{R_{ight}|L_{eft}\} = \frac{D_k}{l^2}\text{Prob}\{R_{ight}|L_{eft}\} = \frac{D_k}{l^2}\frac{\exp(z_k F V_{trans}/RT)}{\frac{1}{l}\int_0^l \exp(z_k F\phi(\zeta)/RT)d\zeta};$$
$$k_b \equiv \frac{J_{in}}{C_k(R_{ight})} = k\{L_{eft}|R_{ight}\} = \frac{D_k}{l^2}\text{Prob}\{L_{eft}|R_{ight}\}\frac{D_k}{l^2}\frac{1}{\frac{1}{l}\int_0^l \exp(z_k F\phi(\zeta)/RT)d\zeta}. \qquad (4)$$

R is the gas constant, F is Faraday's constant, T is the absolute temperature, V_{trans} is the electrical potential across the channel, left minus right. Note the typo in eq. 14 of ref[202,], corrected here.

These equations can be written exactly as a chemical reaction in the usual mass action form, without further approximation,

$$L_{eft} \underset{k_b}{\overset{k_f}{\rightleftharpoons}} R_{ight} \qquad (5)$$

where

$$J_k = \overbrace{l \cdot k_f \cdot C_k(L_{eft})}^{\substack{\text{Unidirectional Efflux}\\ J_{out}}} - \overbrace{l \cdot k_b \cdot C_k(R_{ight})}^{\substack{\text{Unidirectional Infflux}\\ J_{in}}} \qquad (6)$$

This looks like a beautiful and clear result. A diffusion model can be written (nearly) exactly as a chemical reaction. But it is highly misleading.

Rate constants vary. The difficulty is in the properties of the rate constant. The rate constant is nearly always treated as a constant independent of concentration, for example, for admirable reasons. Experimentalists, or young scientists learning the law for the first time, fear that allowing the rate constant to vary will introduce a 'fudge factor' that "lets them fit anything". They wish to avoid such arbitrary behavior and so in the name of good science, they make the rate constant constant, as the name implies.

What is rarely realized, however, is that making a rate constant constant directly

contradicts physical facts of great importance. Consider the situation of interest in this paper, concentrated solutions of ions, flowing through channels, from one mixed solution to another.

The rate constant in such a system obviously must depend on the concentrations of each species**. Any property of the solutions on either side of the channel depends on the concentration of each and every species of ions.** This is the fundamental property of nonideal solutions described in many textbooks of physical chemistry for many years.[38,47,75,93,183,256,257,262,309,328,390,530,547,548,660,700,701,735,790,854] Only in ideal solutions of uncharged particles at infinite dilution are properties independent of concentration. Only in ideal solutions does the free energy of one ion depend only on the concentration of that type of ion. In real solutions and mixtures, everything interacts with everything else and all rate constants are variables depending on all concentrations. In particular, the conditional probabilities that appear in the law of mass action depend on the concentration of every ion. If those concentrations are changed, the rate constant must vary.

Indeed, even in dilute (say 1 mM) solutions of Na^+Cl^-, rate constants are variable. The properties of such solutions are described decently by the Debye-Hückel model of shielding and screening. In that model, ions are not ideal. Their electrochemical potential has a crucial term that varies as the square root of ionic strength. Indeed, in any system of mobile charge, screening of this sort is a crucial, if not dominant determinant of physical behavior.[135] Thus, whenever mobile charges are present, rate constants will vary with ionic strength, and with all the variables that determine ionic strength. The rate constant will not be constant.

As is discussed several times in the text, most ionic solutions do not follow the Debye-Hückel theory and have much more complex behavior. Their behavior deviates from the law of mass action in a profound way.

Rate Constants are not Constant in Crowded Conditions. Experimental conditions can be found, of course, in which the rate constant is constant, and those are just the conditions established in experiments designed to test the law of mass action or to use it to describe classical enzyme kinetics. But those conditions are remarkably far from the conditions in which the kinetic models are used, at least in ion channels, and probably in enzymes, and other applications in physical chemistry I am not familiar with. In ion channels, ions flow from mixed solutions, with nonideal properties, through regions of enormous concentration in which everything interacts with everything else, under the influence of large densities of charge and enormous electric fields, in systems so crowded that everything competes for the same tiny volume. Conditions of this sort are present not just to make our theories and simulations difficult. These special conditions are present in channels so a tiny valve can control macroscopic flows. One can expect crowded conditions whenever ions in small structures are used to control large flows.

Crowded conditions of this sort characterize any valve. Any valve uses small forces in small regions to control large flows in big regions. The nanovalves of life are no exception. Extreme conditions of crowding are present in ion channels because they are the conditions that allow a few atoms to control macroscopic flows of current. Extreme conditions allow robust and sensitive control of macroscopic biology by a few atoms of a

protein.

Ion channels are an extreme system. They are as small as they can be, given the particulate nature of matter. Ion channels are atomic valves that allow a handful of atoms to control macroscopic flows of current, and thus macroscopic properties of cells, tissues, animals and life. They do this by working at the extremes of forces as well as sizes. They have enormous densities of ions crowded into tiny spaces with huge electric and chemical fields and forces of excluded volume. I believe ion channels will prove to be extraordinarily strong and often rigid proteins (although I hasten to say this is an idea unproven and even untested as of now, as far as I know).

Traditional chemical theories are designed for the opposite extreme, for the case of dilute noninteracting solutions that are hardly ionic. Traditional chemical theories fail altogether when used with rate constants that are constants to describe systems that are wildly nonideal.

Mathematics must deal with interactions. In my view, many proteins, like channels, must be analyzed with a mathematics that deals naturally with the real properties of ions, that allows everything to interact with everything else. The mathematics should deal with interactions in a natural way. Interactions should be at the core of the mathematics. They should not require *ad hominem* (or worse *ad hominiculum*) arguments that are different for each type of interaction. The mathematics should not start with ideal fluids. It cannot use the law of mass action with constant constants. Of course, not all interactions occur everywhere. Interactions that are not important in a particular system can be ignored, as PNP-DFT ignores some interactions and yet succeeds magnificently with the ryanodine receptor. Of course, it is much safer for the mathematics to include insignificant interactions than it is to ignore them a priori, if the numerical and computational complexities can be handled.

I suspect that most enzymes will use crowded ions to control flows of substrates to products, as channels use crowded ions to control flows from ‘substrates’ (i.e., ions outside the cell) to ‘products’ (i.e., ions inside the cell).

The analogy between channels and enzymes[285] has deep evolutionary origins, I suspect, since life before membranes must have used electrostatics to ‘confine’ its crucial molecules.

It is clear that life existed for millions or billions of years before cells were invented. Pre-cellular life was probably an RNA universe. That RNA cell free universe was devoured and encompassed by today’s cellular based organisms. Today, cells use their membranes to confine the ‘expensive’ macromolecules that allow life to reproduce. These macromolecules of nucleic acids—RNA and DNA—and proteins are for that very real reason the essential components of life.

The crucial macromolecules of life must be confined close together if they are to function. Membranes of cells and organelles provide that confinement today. The question is what provided that confinement in life before cells existed?

I propose that the electric charge of nucleic acids and their surrounding electric field was the main confining agent before membranes took on that role. The density of mobile charge within a Debye length of RNA is ~10 molar.

I propose that the confinement motif of pre-cellular life was then used inside proteins in their active sites. The same motif would be repeated in binding proteins, enzymes, and channels inside and on the boundaries of cells, and so on and so forth, in my fanciful view of life's evolution.

In this view, enzymes, like channels and proteins, use confined ions to force everything to interact with everything else. Those interactions are central to the functioning of some channels, as we have seen. I suspect those interactions of crowded charges will prove to be central to the function of binding proteins, and enzymes as well.

If everything interacts with everything else in a way important for function, the mathematics used to describe everything must deal naturally with interactions. In that case, a variational approach like *EnVarA* becomes the natural mathematics of physiological function, as it is the natural mathematics of interaction. The mathematics should deal with interactions. It should not start with noninteracting particles of perfect fluids. It should not start with perfect fluids and perturb them because interactions dominate. They are not perturbations. The mathematics cannot use the law of mass action with constant constants.

On a larger scale, we know that most biological systems (of organelles, cells, and tissues, even organs) involve water flows, mechanical forces, membrane and cellular movements,[110] along with the ionic flows discussed in this paper. I suspect all these flows interact with each other. If they do, I know they must be analyzed with a mathematics built for interactions, like a variational approach.[642] In that case, a variational approach like *EnVarA* becomes the natural mathematics of organ function, as it is the natural mathematics of channel function, and perhaps enzyme function as well. A variational approach is needed when interactions dominate.

In electrochemistry it is clear that ions near electrodes determine many of the characteristic properties of electrochemical systems. These crowded environments are crucial to the function of electrochemical systems and to many other properties of ionic systems used in chemical engineering, I suspect. The crowded environment guarantees that everything talks to everything else. In that case, a variational approach like *EnVarA* is the natural mathematics of electrochemical function, as it is the natural mathematics of many biological functions. Wherever in physical science or engineering ions are concentrated, ions interact and a variational approach is needed, in my view. A variational approach unites physical and biological science whenever ions are concentrated and often that is where they are most important.

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