Chapter 1

Terminology for physiological transport, exchange, and reaction

1-1. Summary

Virtually all fields of physiological research now encompass various aspects of solute transport by convection, diffusion, and permeation across membranes. Accordingly, this set of terms, symbols, definitions, and units is proposed as a means of clear communication among workers in the physiological, engineering, and physical sciences. The goal is to provide a setting for quantitative descriptions of physiological transport phenomena.

1-2. Introduction

This terminology provides a self-consistent set of terms for transport physiology. It is an extension of those proposed by Wood (1962), Gonzalez-Fernandez (1962), Zierler (1965), Kedem and Katchalsky (1958) and Bassingthwaighte et al. (1970, 1986). The extensions provide a set of symbols common to studies of transcapillary and cellular exchange and indicator-dilution studies. The rationale is to provide a self-consistent set of symbols covering broad aspects of circulatory flows, hydrodynamics, transcapillary and membrane transport. As the various previously rather separate aspects of these fields become intermeshed, the size of the required sets of symbols has enlarged to a point where the “standard” symbol for one group of users has a quite different “natural” meaning to another. This problem has necessitated some arbitrariness, but we have attempted to subscribe to the dominant usage so as to minimize changes in habits.

Care has been taken to provide each term with 1) a name, 2) a definition in words (and sometimes equations), 3) a unique symbol whenever possible, and 4) units mainly in centimeter-gram-second system but with some translation to approved International System of units (SI). Physical constants are listed separately.

$$C_{out}(t) = C_{in}(t) * h(t) = \int_0^t C_{in}(\tau) \cdot h(t-\tau)\,d\tau$$

Figure 1-1: Block diagram of a linear stationary system. Response to ideal impulse input $\delta(t)$ at the entrance is $h(t)$, the transport function. When input is of another form, $C_{in}(t)$, then outflow response $C_{out}(t)$ is the convolution of $C_{in}(t)$ and $h(t)$.

An important feature of this list is the provision of operational terminology for the general description of the behavior of linear stationary systems. The use of the time-domain impulse response or transport function, $h(t)$, etc., follows from the work of Stephenson (1948), Meier and Zierler (1954), and Zierler (1965), and is reviewed by Bassingthwaighte and Goresky (1984).

A system is diagrammed in Fig. 1-1. Most analysis is based on two fundamental assumptions, that the system is both linear and stationary. When both hold, superposition is applicable. In general, we also consider the system to be mass conservative; that is, indicator and solvent are neither formed nor consumed.

A linear system is one in which inputs and outputs are additive. Defining $C_{in}(t)$ as concentration-time curve at the input to a segment of the circulation and $C_{out}(t)$ as the concentration-time curve occurring in response to it at the outlet, the relationship is denoted by

$$C_{in}(t) \rightarrow C_{out}(t).$$

Given a second pair with the same relationship, $C'_{in}(t) \rightarrow C'_{out}(t)$, then in a linear system these can be summed or multiplied by a scalar

$$\begin{aligned} &C_{in}(t) + C'_{in}(t) \rightarrow C_{out}(t) + C'_{out}(t), \text{ or} \\ &kC_{in}(t) \rightarrow kC_{out}(t) \qquad \textit{linearity.} \end{aligned}$$

A stationary system is one in which the distribution of transit times through the system is constant from moment to moment; that is, flows and volumes are constant everywhere in the system. Stationarity implies that the response to a given input is independent of a shift in the timing of the input by an arbitrary time, t_0.

$$\text{If} \quad C_{in}(t) \rightarrow C_{out}(t)$$

$$\text{then} \quad C_{in}(t_0 + t) \rightarrow C_{out}(t_0 + t) \qquad \textit{stationarity.}$$

When the input system is an ideal unit impulse, the Dirac delta function, $\delta(t)$, then the output is the transport function, $h(t)$. When the input is of general form, $C_{in}(t)$, and $h(t)$ is known, then the form of the output, $C_{out}(t)$, can be calculated using the convolution integral given in Fig. 1-1.

A probability density function $h(x)$ or $w(x)$ is a weighting function or a frequency function that gives the probability of occurrence of an observation or measure as a linear function of the quantitative measure, x. The sum of probabilities of all the observations is unity; therefore the units of the density function are fraction per unit of the measure [e.g., the transport function $h(t)$]. A typical form of $h(t)$ for transport through an organ is given in Fig. 1-2, accompanied by closely related general functions.

1-2.1. Subscripts

A	Arterial.
B	Blood.
C or cap	Capillary, or the region of blood–tissue exchange.
cell	Cell.
D	Diffusive, or indicating a permeant tracer.
ECF	Extracellular fluid.
F	Flow or filtration.
i, j	Indices in series or summations or elements of arrays.
in or i	Into or inside or inflow.

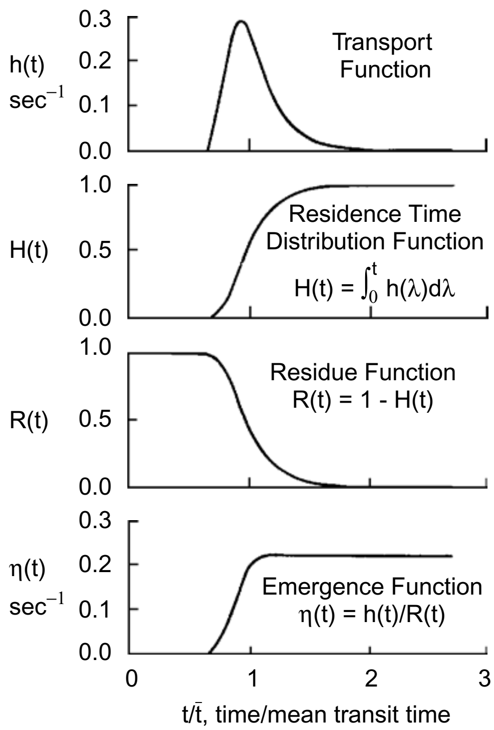

Figure 1-2: . Relationships between $h(t)$, $H(t)$, $R(t)$, and $\eta(t)$. Curve of $h(t)$ is in this instance given by a unimodal density function having a relative dispersion of 0.33 and a skewness of 1.5. However, the theory is general and applies to $h(t)$s of all shapes. Tail of this $h(t)$ curve becomes monoexponential and hence $\eta(t)$ becomes constant.

ISF or I	Interstitial fluid space, the extravascular, extracellular fluid.
m	Membrane.
out or o	Out of or outside or outflow.
p	Plasma.
RBC	Red blood cell.
R	Reference, nonpermeant tracer.
S	Solute.
T	Total.
V	Venous.
W	Water.

1-2.2. Principal Symbols

a	Activity, molar; $a = \varphi C$, an activity coefficient times a concentration.
A	Area of indicator concentration-time curve excluding recirculation equals $\int_0^\infty C(t)\,dt$, mol · s · l^{-1}.
C	Concentration, mol/l; $C_C(x, t)$ concentration in the capillary plasma at position x at time t (mol · l^{-1}). Also [Na^+] = sodium concentration. The relationship between an outflow concentration-time curve $C_{out}(t)$ and the inflow curve $C_{in}(t)$ in a stationary system is given by the convolution integral: $C_{out}(t) = \int_0^t h(t-\tau)C_{in}(\tau)d\tau = C_{in}(t) * h(t)$ where τ is a variable used in the integration. The asterisk denotes convolution.

$\overline{C}_S$ Concentration of solute, the average of the concentrations on the two sides of a membrane, molal, used in irreversible thermodynamic equations. Note that this average does not represent the mean concentration within the membrane when both convection and diffusion occur through a channel of finite length.

CV Coefficient of variation, dimensionless. See also RD; both are the standard deviation divided by the mean of a density function.

D Diffusion coefficient, $cm^2 \cdot s^{-1}$; D_o in free (aqueous) solution; D_b for observed bulk diffusion coefficient through tissue; D_{cell} for intracellular; D_I for interstitial.

E Electrical potential, volts; E_m, membrane potential; E_N, "Nernst" potential, occurring with a difference in concentration of an ion on the two sides of a membrane, $E_N = (RT/zF) \log_e(C_o/C_i)$.

$E(t)$ Extraction, dimensionless, is the fraction of a specific substance removed during transit through an organ. The calculation may be made relative to a reference substance that remains in the blood or relative to the inflow concentration. $E(t) = [h_R(t) - h_D(t)]/h_R(t)$ and is the instantaneous apparent fractional extraction of a permeating species, subscripted D, relative to a nonpermeating reference substance, subscripted R, at each time t, calculated from paired outflow dilution curves. This differs from a steady-state extraction, E, calculated from the arteriovenous difference, $E = (C_A - C_V)/C_A$, for a substance that is consumed during transorgan passage. $E(t_{peak})$ is the value of $E(t)$ obtained at the time of the peak of the curve for the nonpermeating reference tracer, $h_R(t)$.

E_{max} The maximum value of the instantaneous extraction, $E(t)$ estimated by smoothing through the values of $E(t)$ from the upslope and toward the peak of $h_R(t)$.

$E_{net}(t)$ An integral extraction, $\int_0^t (h_R - h_D)d\tau \,/\, \int_0^t h_R d\tau = (R_D - R_R)/(1 - R_R)$; when the reference tracer has all emerged, then $E_{net}(t) = R_D(t)$, the retained fraction of a permeant solute.

ECF Extracellular fluid, interstitial fluid + plasma.

f Frictional coefficient, $g \cdot cm$ equals $(g \cdot cm^2 \cdot s^{-1})/(cm \cdot s^{-1})$, following Spiegler (1958).

f_{excl} Excluded volume fraction, the fraction of solvent in a defined space that is not available to a particular solute, dimensionless.

f_i Relative regional flow in the i^{th} region of an organ divided by the mean flow for the organ per gram of tissue, dimensionless.

F Flow, $cm^3 \cdot s^{-1}$ or $cm^3 \cdot min^{-1}$.

F_B Blood flow to an organ, $cm^3 \cdot g^{-1} \cdot min^{-1}$ (= F/W, where W = organ weight).

F_S, F_p Flow of solute-containing mother fluid, $cm^3 \cdot g^{-1} \cdot min^{-1}$. When solute is excluded from red blood cells, $F_S = F_B(1 - \text{Hct}) = F_p$, the plasma flow. (In modeling analysis, this is the flow of fluid containing solute available for exchange.).

FER(t) Fractional escape rate at time t for indicator contained in a system regardless of time of entry, s^{-1}. With an impulse input, $\delta(t)$, then $\text{FER}(t) = \eta(t)$, the emergence function. In general, $\text{FER} = (dq/dt)/q = d \log_e q/dt$, where q is the system's content of a substance and $dq/dt = F[C_{in}(t) - C_{out}(t)]$.

G Gulosity coefficient or first-order rate constant for substrate consumption or clearance within a region, $cm^3\ g^{-1}\ min^{-1}$ or $cm^3\ g^{-1} \cdot s^{-1}$. Gulosity means 'greediness', therefore avidity, of consumption. It is analogous to a PS and is normally considered unidirectional.

$h(t)$ Transport function, fraction/unit time (s^{-1}), is the fraction of indicator injected at the inflow at $t = 0$, arriving at the outflow at time t. It is the unit impulse response, the frequency function of transit times, or the probability density function of transit times. The transport function, $h(t)$, has the shape of the concentration-time curve that would be obtained by flow-proportional sampling at the output if indicator were injected in ideal fashion into the inflow, i.e., across a cross section with indicator amount at each point in proportion to local flow, as defined by Gonzalez-Fernandez (1962), and recirculation absent. Under such conditions $h(t) = F \cdot C(t)/q_0$, where q_0 is the mass injected at $t = 0$. Subscripting denotes region (e.g., A, V, or cap) or solute characteristic (R for intravascular or D for permeant).

$H(t)$ Cumulative residence time distribution function (dimensionless) of a system; it represents the fraction of an ideally injected tracer that has exited from the system since $t = 0$. It is also the response to a step input. Formally, $H(t) = \int_0^t h(\tau)d\tau = 1 - R(t)$, where $R(t)$ is the residue function.

Hct Hematocrit, the fraction of the blood volume that is erythrocytes, dimensionless.

ISF Interstitial fluid, the extravascular extracellular fluid.

J Flux, usually moles per unit surface area of membrane per second, $\text{mol} \cdot \text{s}^{-1} \cdot \text{cm}^{-2}$. $J_{\text{net } 1\to 2}$ is net flux from *side 1* to *side 2*. In the notation of irreversible thermodynamics the equations of Kedem and Katchalsky (1958) and Katchalsky and Curran (1965) for water and solute transport across an ideal membrane composed of infinitely thin impermeant material pierced by aqueous channels (the K and K membrane) are

$$J_V = L_p \Delta p + L_{pD} \Delta \pi$$

$$J_D = L_{Dp} \Delta p + L_D \Delta \pi,$$

where J_D is a solute velocity relative to the solvent velocity, J_V, which is in turn relative to the membrane. [Although these expressions are incomplete in that the forces on the membrane, in effect a second solute, should also be considered (Silberberg, 1982), they provide an elementary conceptual approach to an idealized system.] J_V and J_D may be properly regarded as flows rather than mass fluxes.

J_V Solvent velocity or volume flux per unit membrane surface area relative to a membrane, $\text{cm} \cdot \text{s}^{-1}$ or $\text{cm}^3 \cdot \text{s}^{-1}$ per cm^2 area. $J_V = L_p(\Delta p - \sigma\Delta\pi)$, and when J_D is small,

$$J_V = J_W \tilde{V}_W + J_S \tilde{V}_S \simeq J_W \tilde{V}_W.$$

J_D Solute movement relative to solvent, $\text{cm}^3 \cdot \text{s}^{-1}$ per cm^2 surface area or $\text{cm} \cdot \text{s}^{-1}$. For the Kedem-Katchalsky (K-K) ideal membrane $J_D = J_S/\overline{C}_S - \tilde{V}_W J_W$. See J_S.

J_W Water flux across a membrane, $\text{mol} \cdot \text{s}^{-1} \cdot \text{cm}^{-2}$. For the K-K membrane $J_W = -\tilde{V}_S J_S / \tilde{V}_W$.

J_S Solute flux across a membrane, $\text{mol} \cdot \text{s}^{-1} \cdot \text{cm}^{-2}$. For the K-K membrane $J_S = \overline{C}_S(1 - \sigma)J_V$. Also

$$J_S/\overline{C}_S = (L_p + L_{Dp})\Delta p + (L_{pD} + L_D)\Delta\pi, \quad \text{or}$$

$$J_S = \overline{C}_S(1 - \sigma)J_V + \omega\Delta\pi.$$

k Rate constant for an exchange process, usually s^{-1}; $k(C)$ is concentration-dependent rate.

k_F Filtration coefficient, $cm^3 \cdot s^{-1} \cdot cm^{-2}$ $(mmHg)^{-1}$; $k_F = L_p$. See L_p and also P_F.

K_m Michaelis constant, molar. For an enzymatic reaction

$$E + S \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} \text{ES} \xrightarrow{k_2} E + P$$

with E, free enzyme; S, substrate; and P, product. Then $K_m = (k_{-1} + k_2)/k_1$, which in the limit where $k_2 \ll k_{-1}$ becomes the original apparent dissociation constant, k_{-1}/k_1, which at equilibrium = [E] · [S]/[ES]. K_1, molar^{-1} s^{-1}, is the association rate; K_{-1}, s^{-1}, is the dissociation rate; K_2, s^{-1}, is the forward reaction rate.

l, L Length, cm.

L Conductance (general) per unit area as in $J = LX$; flux = conductance times driving force.

L_p Pressure filtration coefficient or hydraulic conductance; the flow of pure solvent across a membrane per unit area per unit pressure difference, e.g., cm · s^{-1}(mmHg)$^{-1}$; also, $L_p = \tilde{V}_w P_F / RT = k_F$.

L_{pD} Osmotic coefficient; the flow of solution across a membrane per unit area per unit osmotic pressure difference. Same units as L_p; also, $L_{pD} = - \sigma L_p$.

L_{Dp} Ultrafiltration coefficient; the conductance for the hydrostatically driven flow of solute relative to that of solvent, per unit area per unit hydrostatic pressure difference. Same units as L_p. By Onsager reciprocity, $L_{Dp} = L_{pD}$. (For an ideal semipermeable membrane, $\sigma = 1$, $\omega = 0$, and $-L_{pD} = L_p = L_D = -L_{Dp}$).

L_D Coefficient for diffusional mobility per unit osmotic pressure. Same units as L_p. See ω and P.

M Molarity, moles of solute per liter of solution. Also mM, 10^{-3} M and µM, 10^{-6} M. (Molality is moles of solute per kilogram of solvent. The use of molal units gives consistency in transient states; for example, the molal concentration of solute 1 is not changed by the removal of solute 2, but the molar concentration may be raised or lowered).

Mean $\overline{X}$, the mean of a density function, $w(x)$, is calculated by

$$\bar{x} = \int_0^\infty x \cdot w(x) dx \Big/ \int_0^\infty w(x) dx, \quad \text{or}$$

$$= \sum_i x_i \cdot w(x_i) \Delta x_i \Big/ \sum_i w(x_i) \Delta x_i.$$

Same as α_1.

n_i Moles of substance i in a solution. See mole fraction x_i.

N Number of observations or number of elements in a series, $i = 1$ to N.

p Pressure, mmHg or Pa (1 Torr = 1 mmHg). See osmotic pressure, π.

P Permeability coefficient for a solute traversing a membrane, cm · s^{-1}; equivalent to a diffusion coefficient for a solute in a membrane divided by the thickness. $P = \omega RT$. P_0, P_L, permeabilities at the arterial and venous end of a capillary of length L, respectively. $P(x)$ for $0 < x < L$ for permeability at position x. (Usually observed as a product, PS, with the membrane surface area, S).

Pe Peclet number, ratio of a convective to a diffusive velocity, dimensionless.

P_F Filtration permeability, $L_p RT/\tilde{V}_w$, cm · s^{-1}. [The conversion factor $RT/\tilde{V}_w$ at 20˚C, from the experimental units for L_p or k_F, is (18.36 mmHg · cm^3 · mol^{-1})/(18 cm^3 · mol^{-1}) equals 1.02 mmHg].

PS Permeability-surface area product of a barrier, cm^3 · g^{-1} · s^{-1} or cm^3 · g^{-1} · min^{-1}. PS_{cap} for capillary (the same as capillary diffusion capacity), PS_{cell} for parenchymal cell.

PS_{max} Maximum membrane conductance for a saturable transporter occurring in the absence of competition, cm^3 · g^{-1} · s^{-1}. The P_{max} for a symmetrical Michaelis-Menten type transporter is the concentration of total transporter in the membrane, T_T moles/cm^2 membrane times 1/2 times P_{TS} cm · s^{-1}, the rate of transfer of the transporter-bound substrate to the opposite side of the membrane divided by K_d, the dissociation constant, molar, for the transporter-substrate complex. (The 1/2 occurs because the [symmetrical] transporter has the same likelihood of facing either of the two sides.) $PS_{max} = 1/2\ (T_T\ P_{TS}/k_d)S$, cm^3 · g^{-1} · s^{-1}, where S is surface area of membrane, cm^2/g.

q Mass, g or mol. $q(t)$ is mass (or content of tracer) in region or organ (at time t). q_0, mass of indicator injected at $t = 0$.

r, R Radius or radial distance, cm. R_C, capillary radius.

RD Relative dispersion (dimensionless) = SD/mean = $\sqrt{\mu_2/\alpha_1}$. Same as coefficient of variation.

$R(t)$ Residue function (dimensionless) is the complement of $H(t)$, i.e., $R(t) = 1 - H(t)$. It represents the fraction of injectate in the system at time t after an impulse input at *time zero*, i.e., the probability of a tracer residing in the system for time t or greater.

S Surface area. S_C and S_{cell} for capillary and cell surface areas, cm^2 · (g tissue)$^{-1}$.

SD Standard deviation = square root of the variance of a density function, $\mu_2^{1/2}$. Also SD = $\sqrt{\alpha_2 - \alpha_1^2}$ (units are those of the independent variable).

SEM Standard error of the mean = SD/$\sqrt{N}$, where N = number of observations.

t, Δt Time, s; Δt is a finite time interval.

$\bar{t}$ Mean transit time, s. The first moment of the impulse response, $\bar{t} = \int_0^\infty t \cdot h(t)dt = \int_0^\infty R(t)dt.$

t_a Appearance (a) time; the time at which the first detectable indicator (or a concentration of, for example, 1% of the peak) passed through the system.

t_0 Zero time; midpoint of pulse injection for indicator-dilution studies or beginning of constant-rate injection.

t_{peak} Time from injection to peak of indicator-dilution curve (modal time).

V Volume, cm^3 or ml; in a solution, $V = \Sigma n_i \tilde{V}_i$, the sum of the products of the mole fraction times the partial molar volume for each contained species.

V_{max} Maximum flux via a Michaelis-Menten enzymatic reaction, molar · s^{-1} or moles s^{-1} L^{-1}. When the enzyme is fully saturated the flux is $k_2 E_{Tot}$ where k_2 is the rate constant (s^{-1}) for product formation ES $\xrightarrow{k_2} E + P$ and E_{Tot} is the total enzyme concentration, molar. See K_m.

V_{region} Anatomic volumes within regions of an organ, i.e., V_C, capillary; V_I, interstitial fluid; V_{cell}, parenchymal cells, cm^3 · (g tissue of the organ)$^{-1}$.

V_m Transmembrane potential, volts. V_{Na}, Nernst transmembrane potential, e.g., for sodium, $V_{Na} = (RT/zF)\log_e([Na]_o/[Na]_i) = 61.3\ \log_{10}([Na]_o/[Na]_i)$.

v_{region} Fractional regional volumes of distribution available to a particular solute, i.e., v_C, within the capillary; v_I, interstitial fluid space; v_{cell}, parenchymal cells. At equilibrium, for a substance passively exchanging between plasma and ISF, v_I is the ratio of the concentration in V_I to that in the plasma and is equal to the partition coefficient $\lambda = C_I / C_p$. For steady-state processes producing transmembrane fluxes, the effective volume of distribution is not the same as the equilibrium ratio, i.e., $v_I \neq \lambda$.

v_F Velocity of fluid flow, $cm \cdot s^{-1}$.

V' Volumes of distribution, $cm^3 \cdot g^{-1} \cdot V'_C$, in capillary; V'_I, in ISF; and V'_{cell}, in parenchymal cell. These are the anatomic volumes times the fractional volume of distribution, e.g., $V'_I = v_I V_I$. Commonly used ratios are $\gamma = V'_I / V'_c$ and $\Theta = V'_{cell} / V'_C$.

$\tilde{V}_i$ Partial molar volume of solute i, cm^3/mol; the increment in the volume of a solution per mole of added solute, e.g., $\tilde{V}_W \simeq 18\ cm^3 \cdot mol^{-1}$. ($RT/V_W \simeq 1.02$ mmHg at 20C.)

W Mass, g ("weight," mass times gravitational acceleration).

$w(x)$ Weighting function or probability density function of variable x.

w_i or $w_i(f)$ Weighting or fraction of total in the i^{th} group. Units are fraction per unit of f. Given a density function of regional flows, $w(f)$, in its finite histogram representation $w_i \Delta f_i$, is the fraction of the mass of the organ having a flow f_i, the average of the flows grouped as the i^{th} class. The fraction of the total flow going to the regions falling into the i^{th} class is $w_i f_i \Delta f_i$.

x Distance, cm; e.g., distance along the capillary from inflow, $x = 0$, to outflow, $x = L$.

$\bar{x}$ Mean of a density function, $w(x)$; see mean and moments, α.

X Generalized driving force, as in $J = LX$.

x_i Mole fraction of component i; i.e., moles of the i^{th} component divided by the total moles in the system, $= n_i/n$, where n is the total.

z Valence of an ionic solute, number of unpaired electrons (or missing electrons) per molecule.

1-2.3. Greek Symbols

$\alpha_0, \alpha_1, \alpha_n$ Alpha: Moments about zero for a probability density function. (Units are t^n when t is the independent variable.) [α_0 = area; α_1 = mean; for the density function $h(t)$, $\alpha_n = \int_0^{+\infty} t^n h(t) dt$]. See central moments, μ.

β_{n-2} Beta: Dimensionless parameters of shape of density function calculated from the central moments, $\beta_{n-2} = \mu_n / SD^n = \mu_n / \mu_2^{n/2}$. β_1 is skewness (or asymmetry); it is zero for all symmetrical functions, positive for right skewness. β_2 is kurtosis (or flatness). $\beta_2 > 3$ for leptokurtosis (highpeakedness), and < 3 for platykurtosis (flat-topped).

γ Gamma: Ratio of interstitial volume of distribution to intracapillary volume of distribution, V'_I / V'_{cap}.

Δ Capital delta: Difference.

$\delta(t)$ Delta: Unit impulse function, or Dirac delta function, has unity area, an infinite amplitude at $t = 0$, and is zero at all other times. It is the limit of any symmetrical unimodal density function of unity area as its width approaches zero. For delta function occurring at a nonzero time t_0, it is written $\delta(t - t_0)$.

ε Epsilon, vanishingly small difference.

ζ Zeta: tortuosity of diffusion pathway. ζ is ratio of apparent path length to measured length of diffusion pathway, dimensionless; thus the effective diffusion coefficient, $D = D_0 / \zeta^2$ where D is the free aqueous diffusion coefficient.

η Eta: Viscosity, poise (P) = $dyn/cm^2 = g \cdot s^{-1} \cdot cm^{-1}$. Water viscosity = 0.01002 P at 20°C. Plasma viscosity $\approx$ 0.011.

$\eta(t)$ Eta: $\eta(t) = h(t)/R(t)$ (fraction/s); it is the emergence function, the specific fractional escape rate following an impulse input. Of the particles residing in the system for t seconds after entering, $\eta(t)$ is the fraction that will depart or escape in the t^{th} second. In chemical engineering it is known as the intensity function (Shinnar and Naor, 1967), and in population statistics as the risk function, the death rate of those living at age t. Also, $\eta(t) = (dR/dt)/R(t) = -d \log_e R(t)/dt$. See FER($t$).

Θ_{cell} Capital theta: Ratio of intracellular volume of distribution to intracapillary volume of distribution, V'_{cell} / V'_{cap}, dimensionless.

λ, λ_{ij} Lambda: Partition coefficient, a dimensionless ratio of Bunsen solubility coefficients in two phases. λ_{ij} is the ratio of solubility in region or solvent i to the solubility in region j. The reference region j is usually the plasma. At equilibrium, λ_{ij} is the ratio of concentrations.

μ Mu: Chemical potential for a solute in a solution, $N \cdot m^{-2}$; $\mu = \mu^0 + RT \ln a$, where the activity a is a concentration times an activity coefficient and μ^0 is the potential at a reference state of temperature and pressure.

μ_n Mu: n^{th} central moment of a density function, $h(t)$, a moment around the mean, $\bar{t}$. $\mu_n = \int_{-\infty}^{\infty} (t - \bar{t})^n \, h(t)dt$. Units are those of t to the n^{th} power. See also α_n.

μ_2, μ_3, μ_4 Mu: μ_2 is variance, the second moment of a density function around the mean, $= \alpha_2 - \alpha_1^2$. Also $\mu_3 = \alpha_3 - 3\alpha_1\alpha_2 + 2\alpha_1^3$, and $\mu_4 = \alpha_4 - 4\alpha_1\alpha_3 + 6\alpha_1^2\,\alpha_2 - 3\alpha_1^4$. See also β_n.

π Pi: Osmotic pressure, Pa or $N \cdot m^{-2}$ or mmHg, is the pressure that would have to be exerted on a solution to prevent pure water from entering it from across an ideal semipermeable membrane, i.e., a membrane permeable to solvent only. $\pi = CRT$ is Van't Hoff's law for ideal dilute solutions, and across a membrane impermeable to solute. $\pi = \varphi CRT$ is preferred to account for activity coefficients less than unity. When the solute can permeate the membrane, the effective $\pi = \sigma\phi CRT$. Osmotic pressure, a colligative property of solutions, is related to actual pressure in the same fashion as a freezing point is to actual temperature. Oncotic pressure is a term, now obsolete although historically useful, for the osmotic pressure associated with the presence of large, relatively impermeant molecules such as plasma proteins. It should now be replaced by more exact terms, e.g., across some specific membrane the effective $\Delta\pi$ equals $RT \sum_{i=1}^{i=N} \sigma_i \phi \Delta C_i$, where the effects of concentration differences for a set of N solutes are summed.

ρ Rho: Density, $g \cdot cm^{-3}$. ("Specific gravity" is old terminology no longer to be used. Generally, it meant density relative to the density of water at a specified temperature, and has been replaced by the dimensionless density ratio, ρ/ρ_w.)

σ Sigma: Reflection coefficient, in notation of irreversible thermodynamics, dimensionless; $\sigma = -L_{pD}/L_p$ or, experimentally, $\sigma = -J_D/J_V$ for $\Delta C_s = 0$. The effective osmotic pressure across a membrane is $\sigma\Delta\pi$, mmHg; i.e., σ = (observed osmotic pressure)/CRT.

τ Tau: Time constant for an exponential process, as in $e^{-t/\tau}$, seconds. See Physical Constants for τ for shear stress.

τ_C Tau sub C: Capillary mean transit time, $\bar{t}_C$, used in Krogh cylinder capillary-tissue models with plug flow velocity profiles.

ϕ Phi: Activity coefficient, the ratio of apparent chemically effective concentration to the actual concentration in a solution, in the absence of chemical binding, dimensionless. The osmotic activity coefficient $\phi = \pi/CRT$.

Φ Capital phi: Dissipation function or rate of heat production, equals the sum of the products of fluxes times driving forces, joules or ergs.
Ψ Capital psi: Driving force, force per unit area, $g\ cm^{-1}\ s^{-2}$
ψ Psi: Electrical potential, V, volts.
ω Omega: Solute permeability coefficient, $\omega = P/RT$, $mol \cdot cm^{-2} \cdot s^{-1} \cdot (mmHg)^{-1}$. In the notation of irreversible thermodynamics $\omega = (L_D - \sigma^2 L_p)\overline{C}_s$, where $\overline{C}_s$ is the average solute concentration across the membrane.

1-2.4. Physical Units, Constants

A Ampere, unit of electrical current, coulomb per second ($C \cdot s^{-1}$).
Å Ångstrom, 10^{-10} m or 0.1 nm.
C Charge, coulomb, ampere · second (A · s).
C Capacitance, farad, = $A \cdot s \cdot V^{-1}$. Membrane capacitance is approx. 1 $\mu F/cm^2$.
cal Thermochemical calorie,energy required to raise the temperature of 1 ml water from 14.5˚C to 15.5˚C at 101325 Pa pressure = 4.1855 joule.
˚K Degrees of temperature, Kelvin (absolute); ˚C for degrees Celsius = 273.15 + ˚K.
dyn Dyne, force, $g \cdot cm \cdot s^{-2} \equiv 10^{-5}$ N (newton).
eq Equivalent weight = molecular weight/valence. One equivalent carries 9.65×10^4 C of charge.
e or q_e Elementary charge, $1.6021892 \times 10^{-19}$ C.
erg Energy, $dyn \cdot cm = g \cdot cm^2 \cdot s^{-2} = 10^{-7}\ J = 2.3901 \times 10^{-8}$ cal.
E_a Energy of activation, $cal/mol = 4.1840\ J\ mol^{-1} = 4.1840 \times 10^7\ erg \cdot mol^{-1}$.
F Faraday constant, 9.648456×10^4 elementary charge $\cdot\ eq^{-1}$ = 96,484.6 $C \cdot mol^{-1} = N_A e$.
g Acceleration due to gravity = 980.665 $cm \cdot s^{-2}$.
h Planck’s constant (energy quantum) = $6.626176 \times 10^{-27}\ erg \cdot s = 6.626 \times 10^{-34}\ J \cdot s$.
η Viscosity; 1 poise (P) = $1\ cm^{-1} \cdot g \cdot s^{-1}$ = 0.1 pascal · second (Pa · s).
I Current, amperes.
J Joule, unit of energy ≡ Watt · second (W · s) ≡ ampere · volt · second (A · V · s) ≡ 10^7 erg = $10^7\ g \cdot cm^2 \cdot s^{-2} = 2.3901 \times 10^{-1}$ cal = 0.2389 cal (??which is right??)
k_B Boltzmann constant, $1.380662 \times 10^{-23}\ J \cdot {}^\circ K^{-1} = R/N_A$, the gas constant over Avogadro’s number = $1.37900 \times 10^{-16}\ g \cdot cm^2 \cdot s^{-2} \cdot {}^\circ K^{-1}$.
l, liter Liter = 1 dm^3 = 1,000 cm^3. Also milliliter (ml) and microliter (µl).
M Mol/l (molarity).
mol/kg Mol solute/kg solvent (molality).
N Newton, force, = 10^5 dyn = $10^5\ cm \cdot g \cdot s^{-2}$.
N_A Avogadro’s number, $6.022045 \times 10^{23}\ mol^{-1}$, the number of molecules contained in 1 mol.
n_S, n_w Number of moles of solute and water.
ν nu, kinematic viscosity, η/ρ, viscosity/density, $cm^2 \cdot s^{-1}$.
p Pressure (= force per unit area), $N \cdot m^{-2}$ or Pa (pascal). (1 Pa ≡ $1\ N \cdot m^{-2} \equiv 10\ g \cdot cm^{-1} \cdot s^{-2} \equiv 10^{-2}$ mbar ≡ 0.10197 $mmH_2O \equiv 7.5 \times 10^{-3}$ mmHg ≡ 9.869×10^{-6} atm; or 1 atm = 101325 Pa = 760 Torr= 760 mmHg; 1 cmH_2O (at density $1\ g \cdot cm^{-3}$) = 98.0665 Pa = 981 $g \cdot cm^{-1} \cdot s^{-2}$; 1 mmHg = 1.00000014 Torr = 133.322 Pa = 1,333.22 $g \cdot cm^{-1} \cdot s^{-2}$. 1 KPa = 7.5 mmHg.
ρ Density, $g \cdot cm^{-3}$. Water (3.98˚C, 1 atm) = 0.999972 $g \cdot cm^{-3}$. Mercury (0˚C, 1 atm) = 13.59508 $g \cdot cm^{-3}$.

R	Resistance, electrical (Ω, ohm = V/A); or electrophysiological (Ω/cm^2) or vascular (a pressure divided by a flow, mmHg cm^{-3} s).
R	Universal gas constant = 8.31441 J · mol^{-1} · °K^{-1}= 8.31441 ×10^7 g · cm^2 · s^{-2} · mol^{-1} · °K^{-1}= 0.082 l · atm · mol^{-1} · °K^{-1}= 0.062363 mmHg · mM^{-1} · °K^{-1}= 8.31441×10^{-7} erg · mol^{-1} · °K^{-1} = 1.987 cal · mol^{-1} · °K^{-1}
RT	Energy/mol, gas constant × absolute temperature; e.g., at 37°C or 310.16°K, *RT* = 19.34 × 10^6 mmHg · cm^3 · mol^{-1}= 19.34 mmHg · mM^{-1}= 2578.8 J · mol^{-1} = 616.35 cal · mol^{-1}.
RT/F	24.83 mV at 15°C, 26.73 mV at 37°C. Values of $\log_e 10$ *RT/F* at 15, 20, 25, 30, and 37°C are 57.17, 58.17, 59.16, 60.15, and 61.54 mV.
Re	Reynolds number, = $2r_0\rho\bar{v}_F/\eta$, dimensionless, where r_0 is tube radius, $\bar{v}_F$ is mean fluid velocity, ρ is density, and η is viscosity. Critical Reynolds numbers near the transition from laminar to turbulent flows are about 2000 for aqueous solutions.
S	Siemens, unit of conductance, reciprocal of resistance: = A · V^{-1}. In electrophysiology, used as conductance per unit area of membrane, e.g. μS/mm^2, or conductance per unit membrane capacitance, e.g. μS/μF. Membrane capacitance is approx. 1 μF/cm^2.
STP	Standard temperature and pressure (ice point of water, 0°C = 273.16°K; 760 mmHg = 1 atm = 1.01325 × 10^6 dyn · cm^{-2} = 1.013 × 10^5 N · m^{-2}).
T	Temperature, absolute, in degrees Kelvin (°K); 0°C = 273.16 °K.
τ	tau, shear stress (force/unit area). g cm^{-1} s^{-2}. The mean shear stress for flow in a cylindrical tube is $4\pi\bar{v}_F/(\pi r^3)$.
V	Volt, electrical driving force; millivolt, mV; microvolt, μV. One volt = 1 watt per ampere = 1 joule per coulomb = [(10^7 g · cm^2 s^{-2})/(A · s)] = 9.484 g · cm^2 s^{-2} mol^{-1}.
$\tilde{V}_i$	Partial molar volume, ml/mol = $(\partial V/\partial n_i)_{T,p,n_j,j\neq i}$ = change of volume of total system per mole additional solute *i*, at *T*, p, and constant presence of other components *j*, and at the particular concentration n_i/V. ($\tilde{V}_W$ is the partial molar volume of water; close to 18 ml/mol for physiological solutions).
Watt	Unit of power, joules per second, J · s^{-1}.
Work	Work is energy × time or force × distance × time, erg · s or J · s or cm^{2}g · s^{-1}.
Ω	Ohm, unit of electrical resistance; 1 ohm = 1 V per ampere.

1-3. References

Bassingthwaighte, J. B., F. P. Chinard, C. Crone, N. A. Lassen, and W. Perl. Definitions and terminology for indicator dilution methods. In: *Capillary Permeability*, edited by C. Crone and N. A. Lassen. Copenhagen: Munksgaard, 1970, pp. 665-669.

Bassingthwaighte, J. B., and C. A. Goresky. Modeling in the analysis of solute and water exchange in the microvasculature. In: *Handbook of Physiology. Sect. 2, The Cardiovascular System. Vol IV, The Microcirculation*, edited by E. M. Renkin and C. C. Michel. Bethesda, MD: Am. Physiol. Soc., 1984, pp. 549-626.

Bassingthwaighte, J. B., F. P. Chinard, C. Crone, C. A. Goresky, N. A. Lassen, R. S. Reneman, and K. L. Zierler. Terminology for mass transport and exchange. *Am. J. Physiol.* (*Heart Circ. Physiol.*) 250: H539-H545, 1986.

Gonzalez-Fernandez, J. M. Theory of the measurement of the dispersion of an indicator in indicator-dilution studies. *Circ. Res.* 10:409-428, 1962.

Katchalsky, A., and P. F. Curran. *Nonequilibrium Thermodynamics in Biophysics*. Cambridge, MA: Harvard Univ. Press, 1965.

Kedem, O., and A. Katchalsky. Thermodynamic analysis of the permeability of biological membranes to non-electrolytes. *Biochim. Biophys. Acta* 27:229-246, 1958.

Meier, P., and K. L. Zierler. On the theory of the indicator-dilution method for measurement of blood flow and volume. *J. Appl. Physiol.* 6:731-744, 1954.

Shinnar, R., and P. Naor. Residence time distributions in systems with internal reflux. *Chem. Eng. Sci.* 22:1369-1381, 1967.

Silberberg, A. The mechanics and thermodynamics of separation flow through porous, molecularly disperse, solid media—the Poiseuille Lecture 1981. *Biorheology* 19:111-127, 1982.

Spiegler, K. S. Transport process in ionic membranes. *Trans. Faraday Soc.* 54:1408-1428, 1958.

Stephenson, J. L. Theory of the measurement of blood flow by the dilution of an indicator. *Bull. Math. Biophys.* 10:117-121, 1948.

Wood, E. H. Definitions and symbols for terms commonly used in relation to indicator-dilution curves. *Circ. Res.* 10:379-380, 1962.

Zierler, K. L. Equations for measuring blood flow by external monitoring of radioisotopes. *Circ. Res.* 16:309-321, 1965.