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Chapter 1

Mathematical prelude

> For more than two thousand years some familiarity with mathematics has been regarded as an indispensable part of the intellectual equipment of every cultured person.
>
> *(Richard Courant, 1941)*

1.1 Introduction

In biological research there is a steadily increasing trend to describe functions and mechanisms *quantitatively* by applying ideas and concepts from physics and physical chemistry. This tendency is found in large areas of biology, extending from ecology over the function of the integrated organism to processes taking place at the cellular and molecular level. This development will doubtless continue.

However, a quantitative treatment of any phenomenon in physics or physical chemistry requires an adequate command of the mathematical tools that are needed to formulate and solve the particular problem that is subject to such close scrutiny. For that reason, mastery of certain elements of mathematical analysis is an indispensable element in the arsenal of tools that are loaded into the knapsack of the serious student of general physiology or cell biology.

The sections that follow in this chapter are not presented as a self-contained mathematical text. The intention is to present a summary – short in some places, more detailed in others – of the mathematical concepts and techniques that are used in this book. It is presumed that the reader is already familiar with these concepts. Thus, a cursory reading of this chapter may have the effect of acting as a reminder of items that are known but perhaps not immediately recalled from memory.

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1.2 Basic concepts of differential calculus

1.2.1 Limits

A collection of numbers

$$a_1; a_2; a_3; a_4; \ldots a_n;$$

that follow each other according to a given law is called a *sequence* of numbers. If the number of elements n increases without bound the sequence is an *infinite* sequence. The elements of the sequence are said to *converge* to a *limit* L if the elements beyond that of a_μ behave in such a way that the difference

$$|L - a_n| \quad \text{for } n > \mu$$

is smaller than any arbitrarily small positive number ε. If the elements a_n do not pile up in this manner, the sequence is made up of elements that *diverge*. When the elements of a sequence are added they constitute a *series*

$$S_n = a_1 + a_2 + a_3 + a_4 + \cdots a_n,$$

which may be *finite* or *infinite* according to whether the number of elements n is bounded or not. An infinite series may converge to a definite value S_n when n increases beyond the boundary. This value $S_\infty = L$ is called the *limit* of the series. This is generally written as

$$S_n \to L, \quad \text{for } n \to \infty, \quad \text{or} \quad \lim_{n\to\infty} S_n = L.$$

1.2.2 Functions

Let x and y represent two arbitrary quantities that are coupled together in such a way that to each value of x there exists a definite value of y. We say then that the quantity y is a *function* of the quantity x. Usually this is represented as

$$y = f(x), \tag{1.2.1}$$

where x is called the *independent variable* and y is called the *dependent variable**. Of course one could equally well have considered the *inverse function*

$$x = g(y), \tag{1.2.2}$$

where y is now the independent variable and x is the dependent variable. The condition that the inverse function $x = g(y)$ is so well-behaved that there exists in the interval $a \leq x \leq b$ one and only one value of x for a given value of y, is

* To facilitate the readability of this text, mathematical and physical variable quantities are printed in *italics*. Similarly, mathematical operators are printed in Roman type.

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that the function $y = f(x)$ is increasing or decreasing *monotonically* in the same domain. Thus, the function $y = x^2$ is monotonically decreasing in the region $-a \le x \le 0$, and to every value of y there corresponds only one value $x = -\sqrt{y}$. In the region $0 \le x \le a$ the function $y = x^2$ increases monotonically, and to every value of y there corresponds likewise only one value $x = \sqrt{y}$. With increasing values for x in the region $-a \le x \le a$ the function $y = x^2$ both decreases monotonically as well as increasing, and for a given value of y we have the corresponding values $x = -\sqrt{y}$ and $x = \sqrt{y}$. A function that suddenly *jumps* from one value to another is said to be a *discontinuous function*. Thus, the function

$$y = f(x) = \begin{cases} 2 & \text{for } x \ge 1 \\ 1 & \text{for } x < 1 \end{cases}$$

is a discontinuous function for $x = 1$, since

$$f(1+\varepsilon) - f(1-\varepsilon) = 1$$

no matter how small we make the positive quantity ε. A *continuous function* is, roughly speaking, a function that does not do such things. Thus, the function

$$y = f(x) = \begin{cases} x^2 & \text{for } x \ge 1 \\ x & \text{for } x \le 1 \end{cases}$$

in continuous at the point $x = 1$ since

$$f(1+\varepsilon) - f(1-\varepsilon) = (1+\varepsilon)^2 - (1-\varepsilon) = 3\varepsilon + \varepsilon^2 \to 0 \quad \text{for } \varepsilon \to 0,$$

although the formula displays changes for $x = 1$.

1.2.3 The derivative

Consider the function $y = f(x)$ that is continuous in the range $a < x < b$. If the quantity, denoted the *difference quotient*, for the function $y = f(x)$ at the point x

$$\frac{f(x+h) - f(x)}{h}, \tag{1.2.3}$$

converges towards a *definite limit* as h approaches zero in an arbitrary manner 0, the value of this limit

$$\lim_{h\to 0}\left[\frac{f(x+h) - f(x)}{h}\right] \stackrel{\text{def}}{\equiv} f'(x), \tag{1.2.4}$$

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is called the *first derivative* of the function $y = f(x)$*. Another name for $f'(x)$ is the *differential quotient* of $f(x)$. We can illustrate this limiting process geometrically as follows: Eq. (1.2.3) represents the value of the slope of a straight line that is anchored at the curve point P_0 with coordinates $(x, f(x))$ and makes another section with the curve at the point P_1 at $(x+h, f(x+h))$. This line is called a *secant* to the curve. When we let h decrease in an arbitrary manner, the point P_1 approaches the point P_0 from either side according to the sign of h, and when $h \to 0$ the slope of the secant attains a limiting value that is equal to the slope of the line that, at the point P_0, has only one point in common with the curve $y = f(x)$, namely the *tangent* of the curve at P_0, or

$$\lim_{P_1 \to P_0} (\text{Slope of secant anchored at } P_0) = (\text{Slope of tangent at } P_0)$$

always provided there is a tangent with a well-defined direction at the point P_0 on the curve. This occurs if the limit of the ratio $(f(x+h) - f(x))/h$ in Eq. (1.2.4) converges to the definite value $f'(x)$ when $h \to 0$. In many physical applications involving the derivative it may useful to keep in mind this geometrical representation of $f'(x)$.

The expression $y' = f'(x)$ goes back to the work of J.-L. Lagrange†. Another way of writing the derivative $f'(x)$ is

$$f'(x) \stackrel{\text{def}}{\equiv} \frac{dy}{dx}, \tag{1.2.5}$$

which was introduced by G.W. Leibniz (1646–1716)‡, has many practical advantages, and is almost always used in applied mathematics.

The quantity (dy/dx) is not a fraction in the usual sense but a compact *symbol* meaning that the function $y = f(x)$ has been subjected to the operation that is defined by Eq. (1.2.4). To emphasize the character of dy/dx as a mathematical operation many people prefer to use the typographical convention

$$\frac{dy}{dx} \stackrel{\text{def}}{\equiv} \frac{\mathrm{d}y}{\mathrm{d}x}, \tag{1.2.6}$$

to distract one's thoughts from a fraction. This notation will be used in this book.

* The symbol $\stackrel{\text{def}}{\equiv}$ is used in this text to emphasize that it is a definition.
† J.-L. Lagrange (1736–1813) was a Professor at École Polytechnique. He was one of the greatest mathematicians of the eighteenth century, who made fundamental contributions to the development of differential and integral calculus, calculus of variation, theory of numbers and to mechanics (Mécanique analytique) and astronomy.
‡ This is a remainder of the derivative being obtained from the difference quotient which he wrote as

$$\frac{f(x+\Delta x) - f(x)}{\Delta x} = \frac{\Delta y}{\Delta x}, \quad \text{for } \Delta x \to 0.$$

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As an illustration we consider the function $y = f(x) = x^2$. We have

$$\frac{(x+h)^2 - x^2}{h} = \frac{(x^2 + 2hx + h^2) - x^2}{h} = \frac{2hx + h^2}{h} = 2x + h.$$

Hence

$$\lim_{h \to 0} \frac{(x+h)^2 - x^2}{h} = 2x.$$

Thus, the limit exists, giving

$$f'(x) = \frac{\mathrm{d}y}{\mathrm{d}x} = 2x.$$

Continuing this argument to $y = f(x) = x^n$, where n is any real number, one gets

$$\frac{\mathrm{d}}{\mathrm{d}x}(x^n) = n\,x^{n-1}.$$

Naturally the operations of Eq. (1.2.3) and Eq. (1.2.4) can be applied to the function $f'(x)$. If the limit exists it is called the *second derivative* of the function $f(x)$. The notation for this limit is

$$f''(x) \overset{\text{def}}{\equiv} \frac{\mathrm{d}}{\mathrm{d}x}\left(\frac{\mathrm{d}y}{\mathrm{d}x}\right) \overset{\text{def}}{\equiv} \frac{\mathrm{d}^2 y}{\mathrm{d}x^2}. \tag{1.2.7}$$

Some mathematicians have never become reconciled to Leibniz's notation and have instead replaced the operator d( )/dx by the symbol D to denote the operation*

$$\mathrm{D}\,f(x) \overset{\text{def}}{\equiv} \lim_{h \to 0}\left[\frac{f(x+h) - f(x)}{h}\right] \overset{\text{def}}{\equiv} f'(x).$$

The D notation will not be used in this text.

The requirement for the limit of Eq. (1.2.4) to exist is that the function $f(x)$ is *continuous*. However, this condition is not sufficient, because a continuous function may exhibit a sudden break at a point x_0. In this case $f'(x_0 - \varepsilon)$ and $f'(x_0 + \varepsilon)$ both exist no matter how small we make ε, but they may differ drastically from each other in value, leaving $f'(x)$ to have a discontinuity at the point x_0.

* This was introduced in 1808 by Brisson and gained a footing owing to the extensive use of the operator D made by A.L. Cauchy (1789–1857).

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1.2.3.1 A few derived functions

Using the operations that are defined by Eq. (1.2.4) on the elementary mathematical functions one obtains explicit expressions for the derivatives of the functions in question. Below are a few important elementary examples*

(a) If $f(x) = A$, where A is a constant, $f'(x) = 0$.
(b) If $f(x) = Au(x)$, $f'(x) = Au'(x)$.
(c) If $f(x) = u(x) + v(x)$, $f'(x) = u'(x) + v'(x)$.
(d) If $f(x) = u(x)\,v(x)$, $f'(x) = u'(x)\,v(x) + u(x)\,v'(x)$.
(e) If $f(x) = \dfrac{u(x)}{v(x)}$, $f'(x) = \dfrac{u'(x)\,v(x) - u(x)\,v'(x)}{v(x)^2}$.
(f) If $f(x) = x$, $f'(x) = 1$.
(g) If $f(x) = x^n$, $f'(x) = nx^{n-1}$.
(h) If $f(x) = \sin x$, $f'(x) = \cos x$.
(i) If $f(x) = \cos x$, $f'(x) = -\sin x$.
(j) If $f(x) = \tan x$, $f'(x) = 1/\cos^2 x$.

1.2.4 Approximate value of the increment Δy

In physics many relations are described in terms of the *rate* of change of a quantity. This change may depend upon time, position in space, or both. With hardly a single exception it is sufficient initially to express this change with an approximate accuracy that may be improved later as occasion requires. In this context, differential calculus is a very useful tool. One proceeds as follows. The curve in Fig. 1.1 shows an arbitrary differentiable function $y = f(x)$. The line AB denotes the tangent to the curve on the point (x, y) having a slope that is equal to the value of the derivative $f'(x)$ taken at the point (x, y). Let $x + h$ be a neighboring point to x that corresponds to assigning a finite increment $h = \Delta x$ to the value x of the independent variable. We denote the value of the function at the neighboring point $x + h$ as $f(x + h) = y + \Delta y$, where Δy is the increment in $y = f(x)$ due to the change h in the argument. According to Eq. (1.2.3) and Eq. (1.2.4), that defines the derivative $f'(x)$, the increment can be written as

$$\Delta y = f(x + h) - f(x) = f'(x)\,h + \varepsilon\Delta x, \tag{1.2.8}$$

or

$$y + \Delta y = f(x + \Delta x) = f(x) + f'(x)\Delta x + \varepsilon\Delta x, \tag{1.2.9}$$

* For more about hyperbolic functions, see Appendix I.

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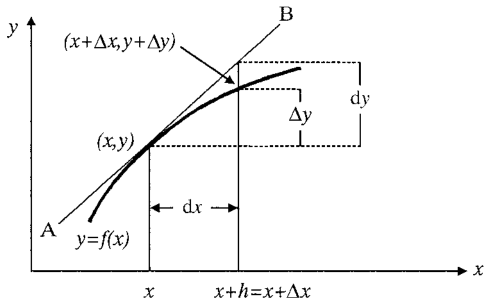

Fig. 1.1. Approximation of the increment Δy of a function $y = f(x)$ by a linear function. The figure also illustrates the geometrical meaning of the differentials $\mathrm{d}y$ and $\mathrm{d}x$.

where $\varepsilon = \varepsilon(\Delta x)$ depends on the magnitude of Δx and approaches zero when $h = \Delta x \to 0$.

We now regard the variable x as fixed and let the increment $h = \Delta x$ vary in an arbitrary manner. Equation (1.2.9) now states that the increment Δy to the value y of $f(x)$ at a given value of x is made up of two terms:

(i) a term $f'(x)h = f'(x)\Delta x$ that is proportional to the increment $h = \Delta x$ with $f'(x)$ as the proportionality coefficient that is a constant at a fixed value of x, and

(ii) a correction term $\varepsilon h = \varepsilon \Delta x$, which can be made as small as we wish relative to h by making the increment $h = \Delta x$ sufficiently small. Thus, the smaller we make the interval in question $h = \Delta x$ around x the more precisely will the function $f(x + h)$, being a function of h, be represented by its linear part

$$f(x + h) \approx f(x) + f'(x)h, \tag{1.2.10}$$

where both $f(x)$ and $f'(x)$ are two fixed numbers for a given value of x. From a geometrical viewpoint this approximate description of the value $f(x + h)$ of the function $y = f(x)$ at the point (x, y) means that the curve of $f(x)$ is *replaced* by the tangent and that the expression for the increment of the function

$$\Delta y = \Delta f = f(x + h) - f(x),$$

corresponding to the increment Δx of the independent variable, can be written approximately as

$$\Delta y = \Delta f \approx f'(x)\Delta x, \tag{1.2.11}$$

provided Δx is sufficiently small to make the term $\varepsilon \Delta x$ negligible relative to the term $f'(x)\Delta x$.

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1.2.5 Differential

The approximate description of the increment Δy by the linear part $f'(x)h = f'(x)\Delta x$ can also be used to put the term *differential* on a firmer logical basis. The original meaning of differentials as infinitely small quantities – different from zero – very soon turned out to have no precise meaning. One of the founders of differential calculus G.W. Leibniz (1646–1716) tried, without success, around 1680 to define the differential quotient as the ratio between two infinitely small increments $\mathrm{d}y$ and $\mathrm{d}x$ that were considered just before both quantities assumed the value zero. More than 100 years passed before the Bohemian priest B. Bolzano (in 1817) sharpened the definitions of such concepts as limits, continuity, etc., and then described the derivative by the limiting process in Eq. (1.2.4). However, Leibniz's notation has turned out to be the most suitable for handling calculations in physics and chemistry. For that reason, it is of value to attempt to give an unambiguous description of the identity

$$f'(x) \stackrel{\text{def}}{\equiv} \frac{\mathrm{d}y}{\mathrm{d}x},$$

in such a way that the expression $\mathrm{d}y/\mathrm{d}x$ need not be regarded only as a symbol for the limiting process

$$\frac{\mathrm{d}y}{\mathrm{d}x} = \lim_{h\to 0} \frac{f(x+h) - f(x)}{h},$$

but can also be considered as a quotient between two actual, well-defined, quantities.

Starting from the definition of the derivative $f'(x)$ as a limiting process, as in Eq. (1.2.4), we then assign a fixed value to the independent variable x and consider the increment $h = \Delta x$ as the variable (see Fig. 1.1). The quantity $h = \Delta x$ is then called the *differential* of x, and is designated as $\mathrm{d}x$. We then *define* the quantity

$$\mathrm{d}y \stackrel{\text{def}}{\equiv} f'(x)\,\mathrm{d}x, \tag{1.2.12}$$

as the *differential* $\mathrm{d}y$ of the function $y = f(x)$ corresponding to the differential $\mathrm{d}x$ of the independent variable. Thus, by means of this definition the derivative $f'(x)$ is regarded as the ratio between two quantities $\mathrm{d}y$ and $\mathrm{d}x$, which can have any value provided their ratio is constant and equal to $f'(x)$. Comparing Eq. (1.2.9) with Eq. (1.2.10) shows that the differential $\mathrm{d}y$ is equal to the linear portion of the increment Δy that corresponds to the increment $\mathrm{d}x$ of the independent variable x (compare Fig. 1.1).

The introduction of the differentials $\mathrm{d}y$ and $\mathrm{d}x$ due to S.-F. Lacroix (1765–1843) and A.L. Cauchy (1789–1857) does not represent a new idea. But their

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merit is to make more precise the wording of "infinitesimal quantity": these quantities are now of finite magnitude, and not quantities "just differing from zero". Hence, when considering a particular problem, they may be chosen to be small enough so that one can, with confidence, replace the increment Δy of the function with its differential $\mathrm{d}y$ and write

$$\Delta y \approx \mathrm{d}y = f'(x)\,\mathrm{d}x = \left(\frac{\mathrm{d}y}{\mathrm{d}x}\right)\mathrm{d}x, \tag{1.2.13}$$

and

$$f(x+\mathrm{d}x) \approx f(x) + f'(x)\,\mathrm{d}x = f(x) + \left(\frac{\mathrm{d}y}{\mathrm{d}x}\right)\mathrm{d}x. \tag{1.2.14}$$

The validity of the above approximation depends on the special character of the physical situation in question. In general, the error introduced will be insignificant for the solution of the physical problem as long the infinitesimal quantities introduced are smaller than the actual error of measurement that are related to the physical situation.

1.2.5.1 The chain rule

One often finds that the dependent variable y is a function of the independent variable u that again is a function of the independent variable x, e.g.

$$y = u^3 \quad \text{and} \quad u = \sin x.$$

This situation is described by saying that y is a *function of a function* or that y is a *compound function* of x. In general we write this as

$$y = f(x) = F(u) = F\{u(x)\}.$$

If both derivatives

$$\frac{\mathrm{d}F}{\mathrm{d}u} \quad \text{and} \quad \frac{\mathrm{d}u}{\mathrm{d}x}$$

exist it can be shown that

$$f'(x) = F'(u)\,u'(x),$$

or, in terms of Leibniz's notation,

$$\frac{\mathrm{d}y}{\mathrm{d}x} = \frac{\mathrm{d}F}{\mathrm{d}x} = \frac{\mathrm{d}F}{\mathrm{d}u}\,\frac{\mathrm{d}u}{\mathrm{d}x}, \tag{1.2.15}$$

which illustrates both the flexibility and suggestive strength of this notation. It appears as if the symbols $\mathrm{d}y$ and $\mathrm{d}x$ are quantities that can be considered

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and manipulated as if they were real numerical quantities. In fact, they can. According to Eq. (1.1.10) we have

$$\mathrm{d}F = \frac{\mathrm{d}F}{\mathrm{d}u}\mathrm{d}u, \quad \text{and} \quad \mathrm{d}u = \frac{\mathrm{d}u}{\mathrm{d}x}\mathrm{d}x,$$

so that

$$\mathrm{d}F = \frac{\mathrm{d}F}{\mathrm{d}u}\frac{\mathrm{d}u}{\mathrm{d}x}\,\mathrm{d}x,$$

which on division on both sides by $\mathrm{d}x$ becomes Eq. (1.2.15). In the above example we have $\mathrm{d}y/\mathrm{d}u = 3u^2$ and $\mathrm{d}u/\mathrm{d}x = \cos x$. Hence

$$\frac{\mathrm{d}y}{\mathrm{d}x} = \frac{\mathrm{d}y}{\mathrm{d}u}\frac{\mathrm{d}u}{\mathrm{d}x} = 3\sin^2 x\,\cos x.$$

For the function $y = \sin^3 \alpha x$ we obtain $\mathrm{d}y/\mathrm{d}x = 3\alpha \sin^2 \alpha x\,\cos\alpha x$, since

$$\frac{\mathrm{d}(\sin\alpha x)}{\mathrm{d}x} = \frac{\mathrm{d}(\sin\alpha x)}{\mathrm{d}(\alpha x)}\frac{\mathrm{d}(\alpha x)}{\mathrm{d}x} = \alpha\cos\alpha x.$$

If $y = \sin\sqrt{x} = \sin u$, where $u = \sqrt{x} = x^{1/2}$ we have

$$\frac{\mathrm{d}y}{\mathrm{d}x} = \frac{\mathrm{d}\sin u}{\mathrm{d}u}\frac{\mathrm{d}u}{\mathrm{d}x} = \cos\sqrt{x}\,\frac{\mathrm{d}}{\mathrm{d}x}(\sqrt{x}) = \cos\sqrt{x}\left(\frac{1}{2}\right)x^{-\frac{1}{2}} = \frac{1}{2}\frac{\cos\sqrt{x}}{\sqrt{x}}.$$

1.2.5.2 The derivative of the inverse function

It has previously been stated that if a continuous function $y = f(x)$ is either increasing or decreasing monotonically in an interval (say $a \le x \le b$) then the *inverse* function $x = g(y)$ also exists as a single-valued function that is continuous and monotonic in the same interval. If the function $y = f(x)$ is differentiable in the interval, the function increases monotonically if $f'(x) > 0$ in the interval and, correspondingly, can decrease monotonically if $f'(x) < 0$. Knowledge of the differentiability of a function in a given interval provides a tool for deciding whether the function also possesses an unambiguous inverse function as expressed in the following statement.

If the function $y = f(x)$ is differentiable in the interval $a < x < b$ and $f'(x) > 0$ everywhere or $f'(x) < 0$ everywhere, then the inverse function $x = g(y)$ also has a derivative $x' = g'(y)$ in the whole interval. The derivative of the original function $y = f(x)$ and that of the inverse function $x = g(y)$ are for the values of x and y belonging together connected by the following relation:

$$f'(x)\cdot g'(y) = 1, \tag{1.2.16}$$

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