2 Exponential Growth and Decay

The exponential function is one of the most important and widely occurring functions in physics and biology. In biology it may describe the growth of bacteria or animal populations, the decrease of the number of bacteria in response to a sterilization process, the growth of a tumor, or the absorption or excretion of a drug. (Exponential growth cannot continue forever because of limitations of nutrients, etc.) Knowledge of the exponential function makes it easier to understand birth and death rates, even when they are not constant. In physics, the exponential function describes the decay of radioactive nuclei, the emission of light by atoms, the absorption of light as it passes through matter, the change of voltage or current in some electrical circuits, the variation of temperature with time as a warm object cools, and the rate of some chemical reactions.

In this book, the exponential function will be needed to describe certain probability distributions, the concentration ratio of ions across a cell membrane, the flow of solute particles through membranes, the decay of a signal traveling along a nerve axon, and the return of some physiologic variables to their equilibrium values after they have been disturbed.

Because the exponential function is so important, and because we have seen many students who did not understand it even after having been exposed to it, the chapter starts with a gentle introduction to exponential growth (Sect. 2.1) and decay (Sect. 2.2). Section 2.3 shows how to analyze exponential data using semilogarithmic graph paper. The next section shows how to use semilogarithmic graph paper to find instantaneous growth or decay rates when the rate varies. Some would argue that the availability of computer programs that automatically produce logarithmic scales for plots makes these sections unnecessary. We feel that intelligent use of semilogarithmic and logarithmic (log–log) plots requires an understanding of the basic principles.

Variable rates are described in Sect. 2.4. Clearance, discussed in Sect. 2.5, is an exponential decay process that is important in physiology. Microbiologists often grow cells in a chemostat, described in Sect. 2.6. Sometimes there are competing paths for exponential removal of a substance: multiple decay paths are introduced in Sect. 2.7. A very basic and simple model for many processes is the combination of input at a fixed rate accompanied by exponential decay, described in Sect. 2.8. Sometimes a substance exists in two forms, each with its own decay rate. One then must fit two or more exponentials to the set of data, as shown in Sect. 2.9.

Section 2.10 discusses the logistic equation, one possible model for a situation in which the growth rate decreases as the amount of substance increases. The chapter closes with a section on power–law relationships. While not exponential, they are included because data analysis can be done with log–log graph paper, a technique similar to that for semilog paper. If you feel mathematically secure, you may wish to skim the first four sections, but you will probably find the rest of the chapter worth reading.

2.1 Exponential Growth

An exponential growth process is one in which the rate of increase of a quantity is proportional to the present value of that quantity. The simplest example is a savings account. If the interest rate is 5 % and if the interest is credited to the account once a year, the account increases in value by 5 % of its present value each year. If the account starts out with \$ 100, then at the end of the first year, \$ 5 is credited to the account and the value becomes \$ 105. At the end of the second year, 5 % of \$ 105 is credited to the account and the value grows by \$ 5.25 to 110.25. The growth of such an account is shown in Table 2.1 and Fig. 2.1. These amounts can be calculated as follows: At the end of the first year, the original amount, y_0, has been augmented by $(0.05)y_0$:

$$y_1 = y_0(1 + 0.05).$$

During the second year, the amount y_1 increases by 5 %, so

$$y_2 = y_1(1.05) = y_0(1.05)(1.05) = y_0(1.05)^2.$$

R. K. Hobbie, B. J. Roth, *Intermediate Physics for Medicine and Biology*,
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Table 2.1 Growth of a savings account earning 5 % interest compounded annually, when the initial investment is \$ 100

Year	Amount (\$)	Year	Amount (\$)	Year	Amount (\$)
1	105.00	10	162.88	100	1.31×10^{4}
2	110.25	20	265.33	200	1.73×10^{6}
3	115.76	30	432.19	300	2.27×10^{8}
4	121.55	40	704.00	400	2.99×10^{10}
5	127.63	50	1146.74	500	3.93×10^{12}
6	134.01	60	1867.92	600	5.17×10^{14}
7	140.71	70	3042.64	700	6.80×10^{16}
8	147.75	80	4956.14	800	8.94×10^{18}
9	155.13	90	8073.04	900	1.18×10^{21}

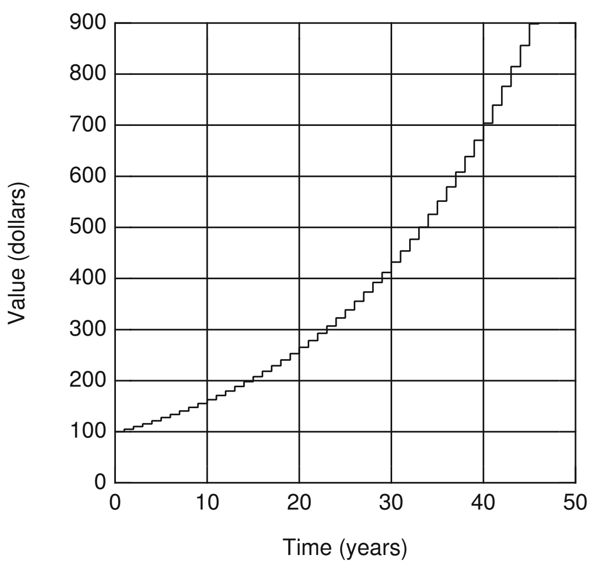

Fig. 2.1 The amount in a savings account after t years, when the amount is compounded annually at 5 % interest

After t years, the amount in the account is

$$y_t = y_0(1.05)^t.$$

In general, if the growth rate is b per compounding period, the amount after t periods is

$$y_t = y_0(1 + b)^t. \tag{2.1}$$

It is possible to keep the same annual growth (interest) rate, but to compound more often than once a year. Table 2.2 shows the effect of different compounding intervals on the amount, when the interest rate is 5 %. The last two columns, for monthly compounding and for "instant interest," are listed to the nearest tenth of a cent to show the slight difference between them.

The table entries were calculated in the following way: Suppose that compounding is done N times a year. In t years, the number of compoundings is Nt. If the annual fractional rate of increase is b, the increase per compounding is b/N. For 6 months at 5 % ($b = 0.05$), the increase is 2.5, for 3 months it is 1.25, etc. The amount after t units of time (years) is, in analogy with Eq. 2.1,

$$y = y_0 (1 + b/N)^{Nt}. \tag{2.2}$$

Recall (refer to Appendix C) that $(a)^{bc} = (a^b)^c$. The expression for y can be written as

$$y = y_0 \left[(1 + b/N)^N \right]^t. \tag{2.3}$$

Most calculus textbooks show that the quantity

$$(1 + b/N)^N \to e^b$$

as N becomes very large. (Rather than proving this fact here, we give numerical examples in Table 2.3 for two different values of b.) Therefore, Eq. 2.3 can be rewritten as

$$y = y_0 e^{bt} = y_0 \exp(bt). \tag{2.4}$$

(The exp notation is used when the argument is complicated.) To calculate the amount for instant interest, it is necessary only to multiply the fractional growth rate per unit time b by the length of the time interval and then look up the exponential function of this amount in a table or evaluate it with a computer or calculator. The number e is approximately equal to 2.71828 . . . and is called the *base of the natural logarithms*. Like π (3.14159 . . .), e has a long history (Maor 1994).

Table 2.2 Amount of an initial investment of \$ 100 at 5 % annual interest, with different methods of compounding

Month	Annual (\$)	Semiannual (\$)	Quarterly (\$)	Monthly (\$)	Instant (\$)
0	100.00	100.00	100.00	100.000	100.000
1	100.00	100.00	100.00	100.417	100.418
2	100.00	100.00	100.00	100.835	100.837
3	100.00	100.00	101.25	101.255	101.258
4	100.00	100.00	101.25	101.677	101.681
5	100.00	100.00	101.25	102.101	102.105
6	100.00	102.50	102.52	102.526	102.532
7	100.00	102.50	102.52	102.953	102.960
8	100.00	102.50	102.52	103.382	103.390
9	100.00	102.50	103.80	103.813	103.821
10	100.00	102.50	103.80	104.246	104.255
11	100.00	102.50	103.80	104.680	104.690
12	105.00	105.06	105.09	105.116	105.127

Table 2.3 Numerical examples of the convergence of $(1 + b/N)^N$ to e^b as N becomes large

N	$b = 1$	$b = 0.05$
10	2.594	1.0511
100	2.705	1.0513
1000	2.717	1.0513
e^b	2.718	1.0513

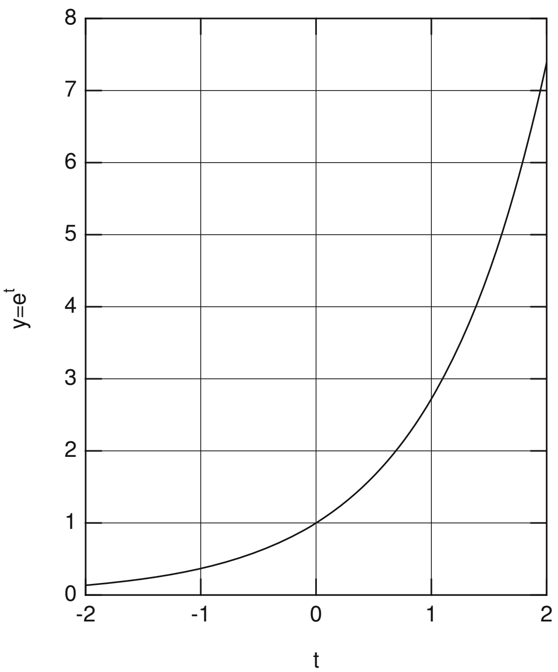

Fig. 2.2 A graph of the exponential function $y = e^t$

The exponential function is plotted in Fig. 2.2. (The meaning of negative values of t will be considered in the next section.) This function increases more and more rapidly as t increases. This is expected, since the rate of growth is always proportional to the present amount. This is also reflected in the following property of the exponential function:

$$\frac{d}{dt}\left(e^{bt}\right) = be^{bt}. \tag{2.5}$$

This means that the function $y = y_0 e^{bt}$ has the property that

$$\frac{dy}{dt} = by. \tag{2.6}$$

Any constant multiple of the exponential function e^{bt} has the property that its rate of growth is b times the function itself. Whenever we see the exponential function, we know that it satisfies Eq. 2.6. Equation 2.6 is an example of a *differential equation*. If you learn how to solve only one differential equation, let it be Eq. 2.6. Whenever we have a problem in which the growth rate of something is proportional to the present amount, we can expect to have an exponential solution. Notice that for time intervals t that are not too large, Eq. 2.6 implies that $\Delta y = (b\Delta t)y$. This again says that the increase in y is proportional to y itself.

The independent variable in this discussion has been t. It can represent time, in which case b is the fractional growth rate per unit time; distance, in which case b is the fractional growth per unit distance; or something else. We could, of course, use another symbol such as x for the independent variable, in which case we would have $dy/dx = by$, $y = y_0 e^{bx}$.

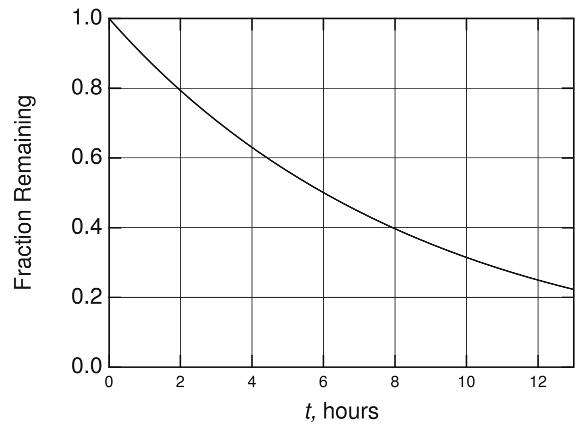

Fig. 2.3 A plot of the fraction of nuclei of ^{99m}Tc surviving at time t

2.2 Exponential Decay

Figure 2.2 shows the exponential function for negative values of t as well as positive ones. (Remember that $e^{-t} = 1/e^t$.) To see what this means, consider a bank account in which no interest is credited, but from which 5 % of what remains is taken each year. If the initial balance is \$ 100, \$ 5 is removed the first year to leave \$ 95.00. In the second year, 5 % of \$ 95 or \$ 4.75 is removed. In the third year, 5 % of \$ 90.25 or \$ 4.51 is removed. The annual decrease in y becomes less and less as y becomes less and less. The equations developed in the preceding section also describe this situation. It is only necessary to call b the fractional decay and allow it to have a negative value, $-|b|$. Equation 2.1 then has the form $y = y_0(1-|b|)^t$ and Eq. 2.4 is

$$y = y_0 e^{-|b|t}. \tag{2.7}$$

Often b is regarded as being intrinsically positive, and Eq. 2.7 is written as

$$y = y_0 e^{-bt}. \tag{2.8}$$

One could equally well write $y = y_0 e^{bt}$ and regard b as being negative, but this can cause confusion, for example with Eq. 2.10 below.

The radioactive isotope $^{99\mathrm{m}}$Tc (read as technetium-99) has a fractional decay rate $b = 0.1155\,\mathrm{h}^{-1}$. If the number of atoms at $t = 0$ is y_0, the fraction $f = y/y_0$ remaining at later times decreases as shown in Fig. 2.3. The equation that describes this curve is

$$f = \frac{y}{y_0} = e^{-bt}, \tag{2.9}$$

where t is the elapsed time in hours and $b = 0.1155\,\mathrm{h}^{-1}$. The product bt must be dimensionless, since it is in the exponent.

People often talk about the *half-life* $T_{1/2}$, which is the length of time required for f to decrease to one-half. From inspection of Fig. 2.3, the half-life is 6 h. This can also be determined from Eq. 2.9:

$$0.5 = e^{-bT_{1/2}}.$$

From a table of exponentials, one finds that $e^{-x} = 0.5$ when $x = 0.69315$. This leads to the very useful relationship $bT_{1/2} = 0.693$ or

$$T_{1/2} = \frac{0.693}{b}. \tag{2.10}$$

For the case of ^{99m}Tc, the half-life is $T_{1/2} = 0.693/0.1155 = 6$ h.

One can also speak of a *doubling time* if the exponent is positive. In that case, $2 = e^{bT_2}$, from which

$$T_2 = \frac{0.693}{b}. \tag{2.11}$$

2.3 Semilog Paper

A special kind of graph paper, called *semilog paper*, makes the analysis of exponential growth and decay problems much simpler. If one takes logarithms (to any base) of Eq. 2.4, one has

$$\log y = \log y_0 + bt \log e. \tag{2.12}$$

If the dependent variable is considered to be $u = \log y$, and since $\log y_0$ and $\log e$ are constants, this equation is of the form

$$u = c_1 + c_2 t. \tag{2.13}$$

The graph of u vs t is a straight line with positive slope if b is positive and negative slope if b is negative.

On semilog paper the vertical axis is marked in a logarithmic fashion. The graph can be plotted without having to calculate any logarithms. Figure 2.4 shows a plot of the exponential function of Fig. 2.2, for both positive and negative values of t. First, note how to read the vertical axis. A given distance along the axis always corresponds to the same multiplicative factor. Each cycle represents a factor of ten. To use the paper, it is necessary first to mark off the decades with the desired values. In Fig. 2.4, the decades have been marked 0.1, 1, 10, and 100. The 6 that lies between 0.1 and 1 is 0.6; the 6 between 1 and 10 is 6.0; the 6 between 10 and 100 represents 60; and so forth. The paper can be imagined to go vertically forever in either direction; one never reaches zero. Figure 2.4 has two examples marked on it with dashed lines. The first shows that for $t = -1.0$, $y = 0.36$; the second shows that for $t = +1.5$, $y = 4.5$.

Semilog paper is most useful for plotting data that you suspect may have an exponential relationship. If the data plot as a straight line, your suspicions are confirmed. From the

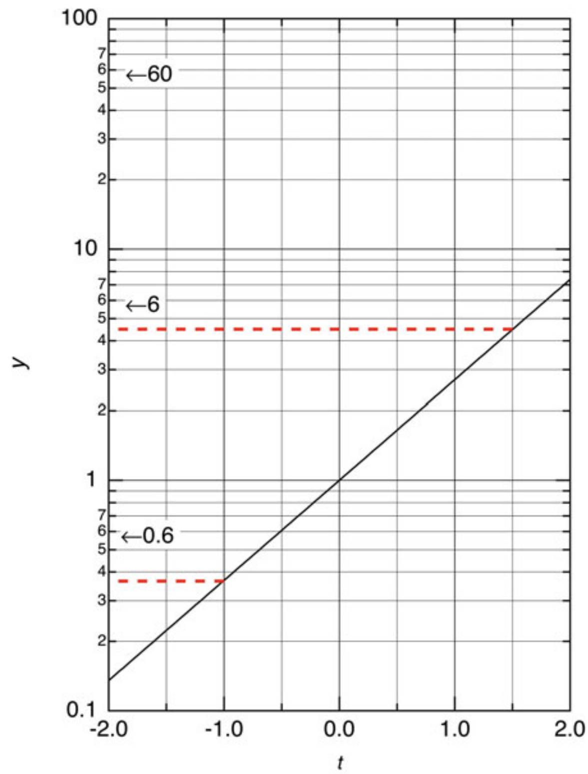

Fig. 2.4 A plot of the exponential function on semilog paper

straight line, you can determine the value of b. Figure 2.5 is a plot of the intensity of light that passed through an absorber in a hypothetical example. The independent variable is absorber thickness x. The decay is exponential, except for the last few points, which may be high because of experimental error. (As the intensity of the light decreases, it becomes harder to measure accurately.) We wish to determine the decay constant in $y = y_0 e^{-bx}$. One way to do it would be to note (dashed line A in Fig. 2.5) that the half-distance is 0.145 cm, so that, from Eq. 2.10,

$$b = \frac{0.693}{0.145} = 4.8 \text{ cm}^{-1}.$$

This technique can be inaccurate because it is difficult to read the graph accurately. It is more accurate to use a portion of the curve for which y changes by a factor of 10 or 100. The general relationship is $y = y_0 e^{bx}$, where the value of b can be positive or negative. If two different values of x are selected, one can write

$$\frac{y_2}{y_1} = \frac{y_0 e^{bx_2}}{y_0 e^{bx_1}} = e^{b(x_2 - x_1)}.$$

If $y_2/y_1 = 10$, then this equation has the form $10 = e^{bX_{10}}$ where $X_{10} = x_2 - x_1$ when $y_2/y_1 = 10$. From a table of

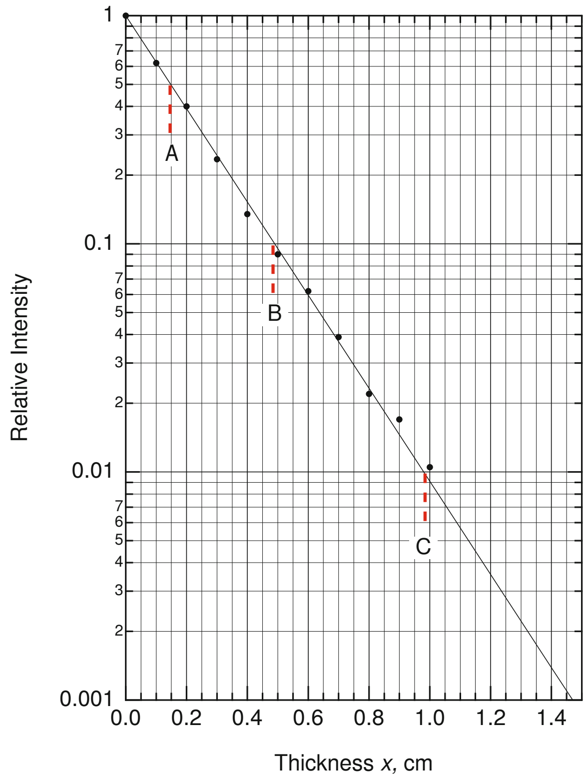

Fig. 2.5 A semilogarithmic plot of the intensity of light after it has passed through an absorber of thickness x

exponentials, $bX_{10} = 2.303$, so that

$$b = \frac{2.303}{X_{10}}. \tag{2.14}$$

The same procedure can be used to find b using a factor of 100 change in y:

$$b = \frac{4.605}{X_{100}}. \tag{2.15}$$

If the curve represents a decaying exponential, then $y_2/y_1 = 10$ when $x_2 < x_1$, so that $X_{10} = x_2 - x_1$ is negative. Equation 2.14 then gives a negative value for b. It is customary to state separately that we are dealing with decay and regard b as positive.

As an example, consider the exponential decay in Fig. 2.5. Using points B and C, we have $x_1 = 0.97$, $y_1 = 10^{-2}$, $x_2 = 0.48$, $y_2 = 10^{-1}$, $X_{10} = 0.480 - 0.97 = -0.49$. Therefore, $b = 2.303/(0.49) = 4.7\ \text{cm}^{-1}$, which is a more accurate determination than the one we made using the half-life.

When we are dealing with real data, we must consider the fact that each measurement has an experimental error associated with it. If we make several measurements of y for a particular value of the independent variable x, the values of y will be scattered. We indicate this by the error bars in

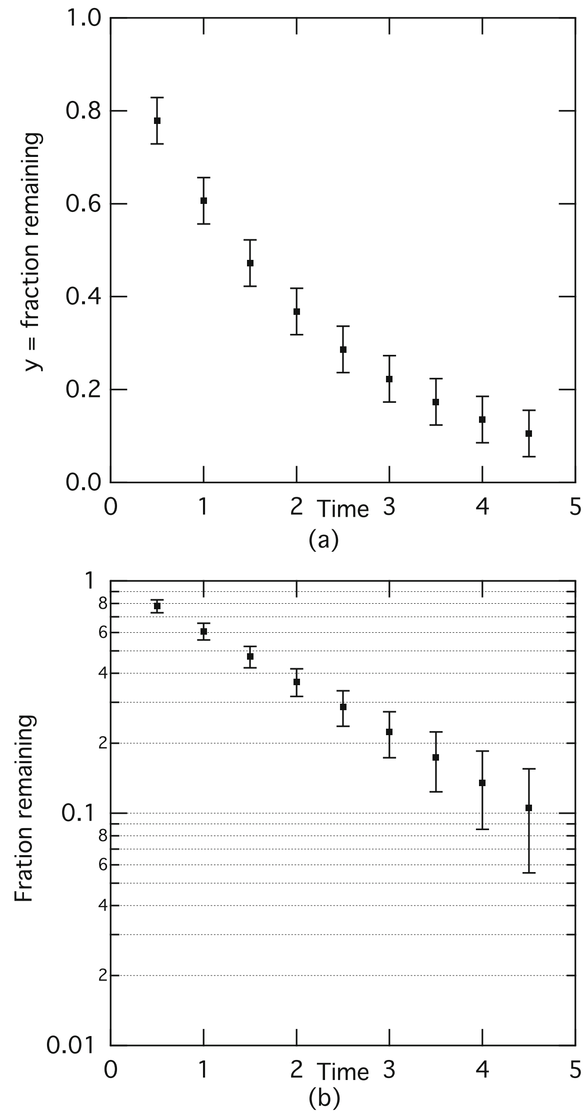

Fig. 2.6 Plot of $y = e^{-0.5t}$ with error bars ± 0.05 on linear (**a**) and semilog paper (**b**)

Fig. 2.6. (Determining the size of these error bars is discussed in Chap. 11.) The data points in Fig. 2.6 are given exactly by $y = e^{-0.5x}$, where y is the fraction remaining at time x. There is no data point for $x = 0$, but we must make sure that our fitting line passes through the point (0,1). The error bars show an error of ± 0.09. The error bars on the semilog plot are not all the same length, being much larger for long times (small values of y). If we do not plot the error bars before drawing our line, we will give too much emphasis to the data points for small y.

Equal error bars for all the points on a semilog plot correspond to the same percentage error for each point, as shown in Fig. 2.7.

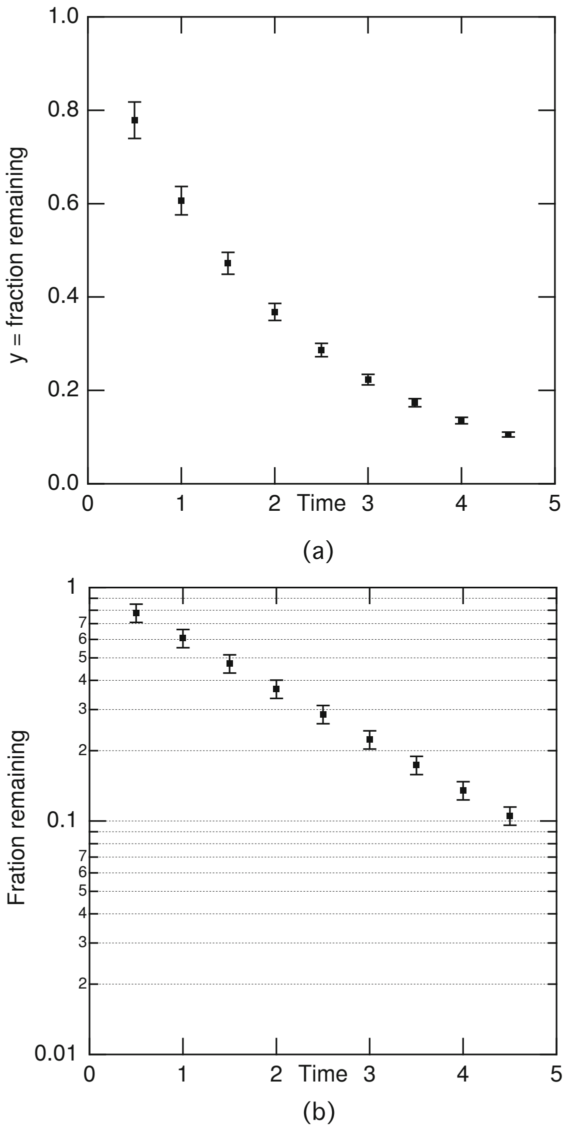

Fig. 2.7 Plot of $y = e^{-0.5t}$ with 5 % error bars in linear (**a**) and semilog paper (**b**)

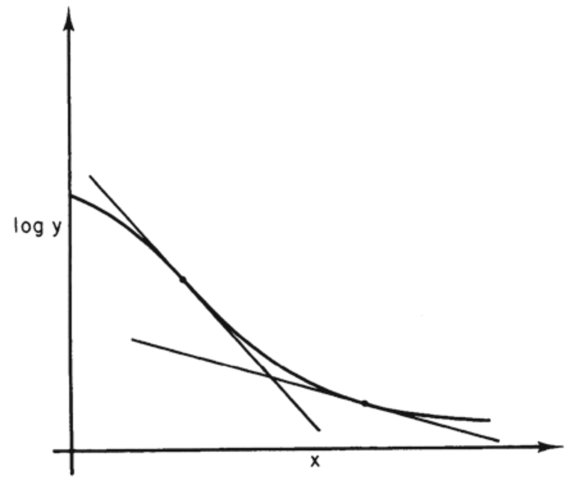

Fig. 2.8 A semilogarithmic plot of y vs x when the decay rate is not constant. Each *tangent line* represents the instantaneous decay rate for that value of x

2.4 Variable Rates

The equation $dy/dx = by$ (or $dy/dt = by$) says that y grows or decays at a rate that is proportional to y. The constant b is the *fractional rate of growth or decay*. It is possible to define the fractional rate of growth or decay even if it is not constant but is a function of x:

$$b(x) = \frac{1}{y}\frac{dy}{dx}. \tag{2.16}$$

Semilogarithmic graph paper can be used to analyze the curve even if b is not constant. Since $d(\ln y)/dy = 1/y$, the chain rule for evaluating derivatives gives

$$\frac{d}{dx}(\ln y) = \frac{1}{y}\frac{dy}{dx} = b.$$

This means that $b(x)$ is the slope of a plot of $\ln y$ vs x. A semilogarithmic plot of y vs x is shown in Fig. 2.8. The straight lines are tangent to the curve and decay with a constant rate equal to $b(x)$ at the point of tangency. The ordinate in Fig. 2.8 can be the log of y to any base; the value of b for the tangent line is determined using the methods in the previous section.

If finite changes Δx and Δy have been measured, they may be used to estimate $b(x)$ directly from Eq. 2.16. For example, suppose that y=100,000 people and that in $\Delta x =$ 1 year there is a change $\Delta y = -37$. In this case, Δy is very small compared to y, so we can say that $b = (1/y)(\Delta y/\Delta x) = -37 \times 10^{-5}\,\mathrm{y}^{-1}$. If the only cause of change in this population is deaths, the absolute value of b is called the *death rate*.

A plot of the number of people surviving in a population, all of whom have the same disease, can provide information about the prognosis for that disease. The death rate is equivalent to the decay constant. An example of such a plot is shown in Fig. 2.9. Curve A shows a disease for which the death rate is constant. Curve B shows a disease with an initially high death rate that decreases with time; if the patient survives the initial period, the prognosis is much better. Curve C shows a disease for which the death rate increases with time.

Surprisingly, there are a few diseases that have death rates independent of the duration of the disease (Zumoff et al. 1966). Any discussion of mortality should be made in terms

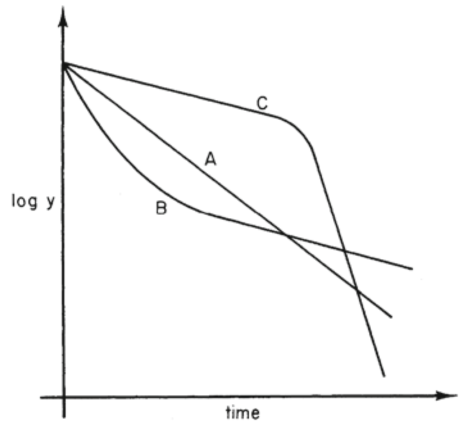

Fig. 2.9 Semilogarithmic plots of the fraction of a population surviving in three different diseases. The death rates (decay constants) depend on the duration of the disease

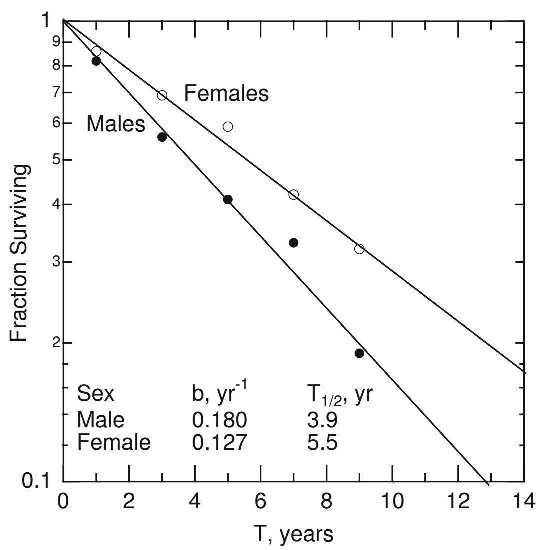

Fig. 2.10 Survival of patients with congestive heart failure. (Data are from McKee et al. 1971)

of the surviving population, since any further deaths must come from that group. Nonetheless, one often finds results in the literature reported in terms of the cumulative fraction of patients who have died. Figure 2.10 shows the survival of patients with congestive heart failure for a period of 9 years. The data are taken from the Framingham study (McKee et al. 1971; Levy and Brink 2005); the death rate is constant during this period. For a more detailed discussion of various possible survival distributions, see Clark (1975).

As long as b has a constant value, it makes no difference what time is selected to be $t = 0$. To see this, suppose that the value of y decays exponentially with constant rate: $y = y_0 e^{-bt}$. Consider two different time scales, shifted with respect to each other so that $t' = t_0 + t$. In terms of the shifted

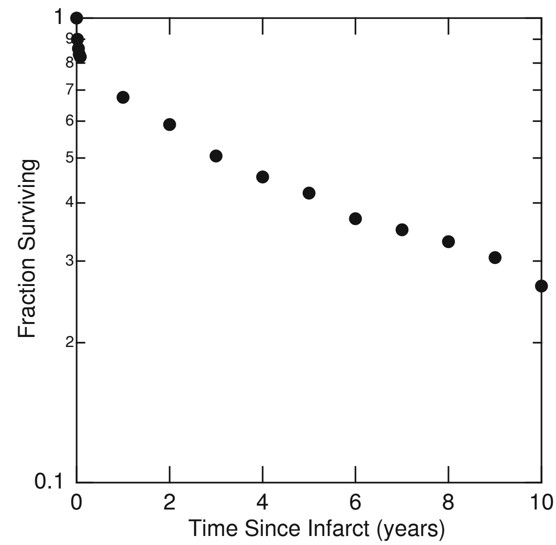

Fig. 2.11 The fraction of patients surviving after a myocardial infarction (heart attack) at $t = 0$. The mortality rate decreases with time. (From data in Bland and White 1941)

time t', the value of y is

$$y = y_0 e^{-bt} = y_0 e^{-b(t'-t_0)} = \left(y_0 e^{bt_0}\right) e^{-bt'}.$$

This has the same form as the original expression for $y(t)$. The value of y_0' is $y_0 e^{bt_0}$, which reflects the fact that $t' = 0$ occurs at an earlier time than $t = 0$, so $y_0' > y_0$.

If the decay rate is not constant, then the origin of time becomes quite important. Usually there is something about the problem that allows $t = 0$ to be determined. Figure 2.11 shows survival after a heart attack (myocardial infarct). The time of the initial infarct defines $t = 0$; if the origin had been started 2 or 3 years after the infarct, the large initial death rate would not have been seen.

As long as the rate of increase can be written as a function of the independent variable, Eq. 2.16 can be rewritten as $dy/y = b(x)dx$. This can be integrated:

$$\int_{y_1}^{y_2} \frac{dy}{y} = \int_{x_1}^{x_2} b(x)\,dx,$$
$$\ln(y_2/y_1) = \int_{x_1}^{x_2} b(x)\,dx,$$
$$\frac{y_2}{y_1} = \exp\left(\int_{x_1}^{x_2} b(x)\,dx\right). \tag{2.17}$$

If we can integrate the right-hand side analytically, numerically, or graphically, we can determine the ratio y_2/y_1.

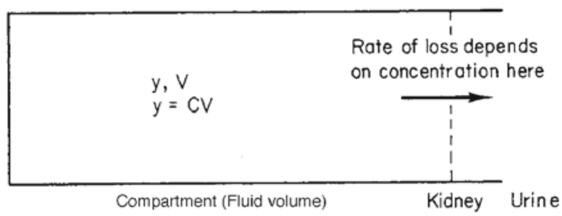

Fig. 2.12 A case in which the rate of removal of a substance from the a fluid compartment depends on the concentration, not on the total amount of substance in the compartment. Increasing the compartment volume with the same concentration of the substance would not change the rate of removal

2.5 Clearance

In some cases in physiology, the amount of a substance may decay exponentially because the rate of removal is proportional to the concentration of the substance (amount per unit volume) instead of to the total amount. For example, the rate at which the kidneys excrete a substance may be proportional to the concentration in the blood that passes through the kidneys, while the total amount depends on the total fluid volume in which the substance is distributed. This is shown schematically in Fig. 2.12. The large box on the left represents the total fluid volume V. It contains a total amount of some substance, y. If the fluid is well mixed, the concentration is $C = y/V$. The removal process takes place only at the dashed line, at a rate proportional to C. The equation describing the change of y is

$$\frac{dy}{dt} = -KC = -K\left(\frac{y}{V}\right). \tag{2.18}$$

The proportionality constant K is called the *clearance*. Its units are $\mathrm{m^3\,s^{-1}}$. The equation is the same as Eq. 2.6 if K/V is substituted for b. The solution is

$$y = y_0 e^{-(K/V)t}. \tag{2.19}$$

The basic concept of clearance is best remembered in terms of Fig. 2.12. Other definitions are found in the literature. It sometimes takes considerable thought to show that the definitions are equivalent. A common definition in physiology books is "*clearance is the volume of plasma from which y is completely removed per unit time*." To see that this definition is equivalent, imagine that y is removed from the body by removing a volume V of the plasma in which the concentration of y is C. The rate of loss of y is the concentration times the rate of volume removal:

$$\frac{dy}{dt} = -\left|\frac{dV}{dt}\right| C. \tag{2.20}$$

(dV/dt is negative for removal.) Comparison with Eq. 2.18 shows that $|dV/dt| = K$.

As long as the compartment containing the substance is well mixed, the concentration will decrease uniformly throughout the compartment as y is removed. The concentration also decreases exponentially:

$$C = C_0 e^{-(K/V)t}. \tag{2.21}$$

An example may help to clarify the distinction between b and K. Suppose that the substance is distributed in a fluid volume $V = 18\,\mathrm{l}$. The substance has an initial concentration $C_0 = 3\,\mathrm{mg\,l^{-1}}$and the clearance is $K = 2\,\mathrm{l\,h^{-1}}$. The total amount is $y_0 = C_0 V = 3 \times 18 = 54\,\mathrm{mg}$. The fractional decay rate is $b = K/V = 1/9\,\mathrm{h^{-1}}$. The equations for C and y are $C = (3\,\mathrm{mg\,l^{-1}})e^{-t/9}$, $y = (54\,\mathrm{mg})e^{-t/9}$. At $t = 0$, the initial rate of removal is $-dy/dt = 54/9 = 6\,\mathrm{mg\,h^{-1}}$.

Now double the fluid volume to $V = 36\,\mathrm{l}$ without adding any more of the substance. The concentration falls to $1.5\,\mathrm{mg\,l^{-1}}$ although y_0 is unchanged. The rate of removal is also cut in half, since it is proportional to K/V and the clearance is unchanged. The concentration and amount are now $C = 1.5e^{-t/18}$, $y = 54e^{-t/18}$. The initial rate of removal is $dy/dt = 54/18 = 3\,\mathrm{mg\,h^{-1}}$. It is half as large as above, because C is now half as large.

If more of the substance were added along with the additional fluid, the initial concentration would be unchanged, but y_0 would be doubled. The fractional decay rate would still be $K/V = 1/18\,\mathrm{h^{-1}}$: $C = 3.0e^{-t/18}$, $y = 108e^{-t/18}$. The initial rate of disappearance would be $dy/dt = 108/18 = 6\,\mathrm{mg\,h^{-1}}$. It is the same as in the first case, because the initial concentration is the same.

2.6 The Chemostat

The *chemostat* is used by bacteriologists to study the growth of bacteria (Hagen 2010). It allows the rapid growth of bacteria to be observed over a longer time scale. Consider a container of bacterial nutrient of volume V. It is well stirred and contains y bacteria with concentration $C = y/V$. Some of the nutrient solution is removed at rate Q and replaced by fresh nutrient. The bacteria in the solution are reproducing at rate b. The rate of change of y is

$$\frac{dy}{dt} = by - QC = by - \frac{Qy}{V}. \tag{2.22}$$

Therefore the growth rate is slowed to

$$b - \frac{Q}{V}$$

and can be adjusted by varying Q.

2.7 Multiple Decay Paths

It is possible to have several independent paths by which y can disappear. For example, there may be several competing ways by which a radioactive nucleus can decay, a radioactive isotope given to a patient may decay radioactively and be excreted biologically at the same time, a substance in the body can be excreted in the urine and metabolized by the liver, or patients may die of several different diseases.

In such situations the total decay rate b is the sum of the individual rates for each process, as long as the processes act independently and the rate of each is proportional to the present amount (or concentration) of y:

$$\frac{dy}{dt} = -b_1 y - b_2 y - b_3 y - \cdots = -(b_1 + b_2 + b_3 + \cdots) y = -by. \tag{2.23}$$

The equation for the disappearance of y is the same as before, with the total decay rate being the sum of the individual rates. The rate of disappearance of y by the ith process *is not* dy/dt but is $-b_i y$. Instead of decay rates, one can use half-lives. Since $b = b_1 + b_2 + b_3 + \cdots$, the total half-life T is given by

$$\frac{0.693}{T} = \frac{0.693}{T_1} + \frac{0.693}{T_2} + \frac{0.693}{T_3} + \cdots$$

or

$$\frac{1}{T} = \frac{1}{T_1} + \frac{1}{T_2} + \frac{1}{T_3} + \cdots. \tag{2.24}$$

2.8 Decay Plus Input at a Constant Rate

Suppose that in addition to the removal of y from the system at a rate $-by$, y enters the system at a constant rate a, independent of y and t. The net rate of change of y is given by

$$\frac{dy}{dt} = a - by. \tag{2.25}$$

It is often easier to write down a differential equation describing a problem than it is to solve it. In this case the solution to the equation and the techniques for solving it are well known. However, a good deal can be learned about the solution by examining the equation itself. Suppose that $y(0) = 0$. Then the equation at $t = 0$ is $dy/dt = a$, and y initially grows at a constant rate a. As y builds up, the rate of growth decreases from this value because of the $-by$ term. Finally when $a - by = 0$, dy/dt is zero and y stops growing. This is enough information to make the sketch in Fig. 2.13.

The equation is solved in Appendix F. The solution is

$$y = \frac{a}{b}\left(1 - e^{-bt}\right). \tag{2.26}$$

The derivative of y is $dy/dt = \left(\frac{a}{b}\right)(-1)(-b)e^{-bt} = ae^{-bt}$.

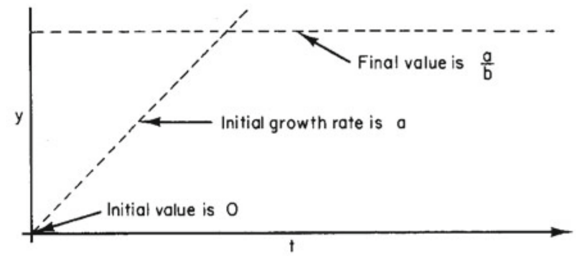

Fig. 2.13 Sketch of the initial slope a and final value a/b of y when $y(0) = 0$

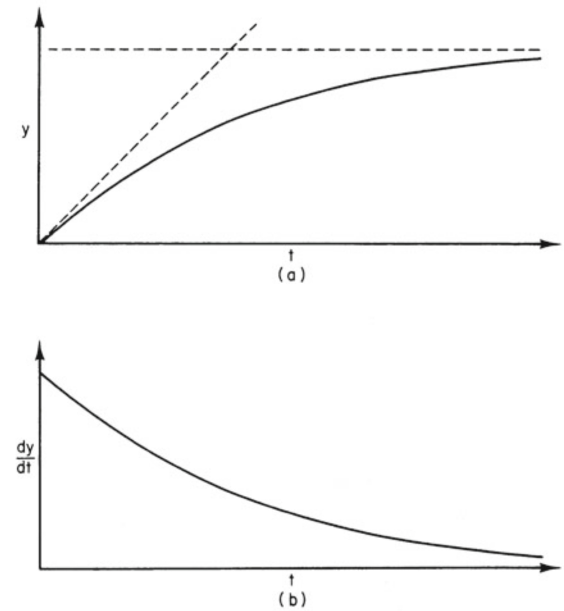

Fig. 2.14 **a** Plot of $y(t)$. **b** Plot of dy/dt

You can verify by substitution that Eq. 2.26 satisfies Eq. 2.25. The solution does have the properties sketched in Fig. 2.13, as you can see from Fig. 2.14. The initial value of dy/dt is a, and it decreases exponentially to zero. When t is large, the exponential term in y vanishes, leaving $y = a/b$.

2.9 Decay With Multiple Half-Lives and Fitting Exponentials

Sometimes y is a mixture of two or more quantities, each decaying at a constant rate. It might represent a mixture of radioactive isotopes, each decaying at its own rate. A biological example is the survival of patients after a myocardial infarct (Fig. 2.11). The death rate is not constant, and many models can be proposed to explain why. One possible model is that there are two distinct classes of patients immediately after the infarct. Each class has an associated death rate that

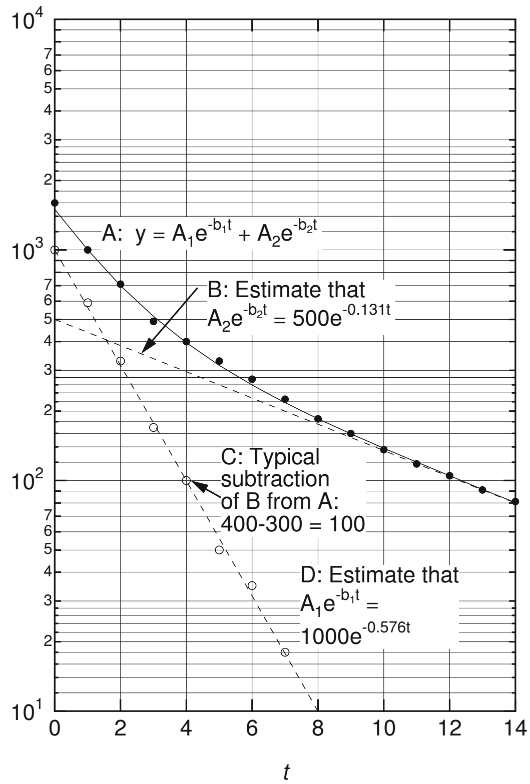

Fig. 2.15 Fitting a curve with two exponentials

is constant. After 3 years, virtually none of the subgroup with the higher death rate remains. Another model is that the death rate is higher right after the infarct for all patients. This higher death rate is due to causes associated with the myocardial injury: irritability of the muscle, arrhythmias in the heartbeat, the weakening of the heart wall at the site of the infarct, and so forth. After many months, the heart has healed, scar tissue has replaced the necrotic (dead) muscle, and deaths from these causes no longer occur.

Whatever the cause, it is sometimes useful to fit a set of experimental data with a sum of exponentials. It should be clear from the discussion of survival after myocardial infarction that simply fitting with an exponential or a sum of exponentials does not prove anything about the decay mechanism.

If y consists of two quantities, y_1 and y_2, each with its own decay rate, then

$$y = y_1 + y_2 = A_1 e^{-b_1 t} + A_2 e^{-b_2 t}. \tag{2.27}$$

Suppose that $b_1 > b_2$, so that y_1 decays more rapidly than y_2. After enough time has elapsed, y_1 will be much less than y_2, and its effect on a semilog plot will be negligible. A typical plot of y is curve A in Fig. 2.15. Line B can then be drawn through the data and used to determine A_2 and b_2. This line is extrapolated back to earlier times, so that y_2 can be subtracted from y to give an estimate for y_1. For example, at point C ($t = 4$), $y = 400$, $y_2 = 300$, and $y_1 = 100$. At $t = 0$, $y_1 = 1500 - 500 = 1000$. For times greater than 5 s, the curves for y and y_2 are close together, and error in reading the graph produces considerable scatter in y_1. Once several values of y_1 have been determined, line D is drawn, and parameters A_1 and b_1 are estimated.

This technique can be extended to several exponentials. However it becomes increasingly difficult to extract meaningful parameters as more exponentials are used, because the estimated parameters for the short-lived terms are very sensitive to the initial guess for the parameters of the longest-lived term. Fig. 2.6 suggests that estimating the parameters for the longest-lived term may be difficult because of the potentially large error bars associated with the data for small values of y. For a discussion of this problem, see Riggs (1970, pp. 146–163). A more modern and better way to fit multiple exponentials is the technique of nonlinear least squares. This is discussed in Sect. 11.2.

2.10 The Logistic Equation

Exponential growth cannot go on forever. This fact is often ignored by economists and politicians. Albert Bartlett has written extensively on this subject. You can find several references in *The American Journal of Physics* and *The Physics Teacher*. See the summary in Bartlett (2004).

Sometimes a growing population will level off at some constant value. Other times the population will grow and then crash. One model that exhibits leveling off is the *logistic model*, described by the differential equation

$$\frac{dy}{dt} = b_0 y \left(1 - \frac{y}{y_\infty}\right), \tag{2.28}$$

where b_0 and y_∞ are constants. This equation has constant solutions $y = 0$ and $y = y_\infty$. If $y \ll y_\infty$, then the equation is approximately $dy/dt = b_0 y$ and y grows exponentially. As y becomes larger, the term in parentheses reduces the rate of increase of y, until y reaches the saturation value y_∞. This might happen, for example, as the population begins to consume a significant fraction of the food supply, causing the birth rate to decrease or the mortality rate to increase.

If the initial value of y is y_0, the solution of Eq. 2.28 is

$$y(t) = \frac{1}{\dfrac{1}{y_\infty} + \left(\dfrac{1}{y_0} - \dfrac{1}{y_\infty}\right) e^{-b_0 t}} \tag{2.29}$$

$$= \frac{y_0 y_\infty}{y_0 + (y_\infty - y_0) e^{-b_0 t}}.$$

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