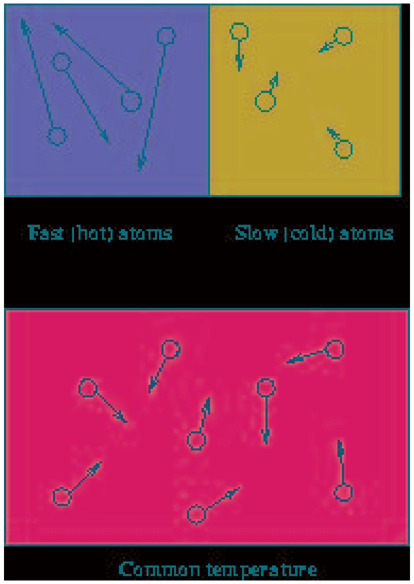
Diffusion is the spontaneous spreading of matter (particles or molecules), heat, momentum, or light. Diffusion is one type of transport phenomenon. Diffusion is the movement of particles from higher chemical potential to lower chemical potential (chemical potential can in most cases of diffusion be represented by a change in concentration). It is readily observed, for example, when dried food like spaghetti is cooked; water molecules diffuse into the spaghetti strings, making them thicker and more flexible. It is a physical process rather than a chemical reaction, which requires no net energy expenditure. In cell biology, diffusion is often described as a form of passive transport, by which substances cross membranes.

`http://video.google.com/videoplay?docid=5336575425429921218&q=diffusion`

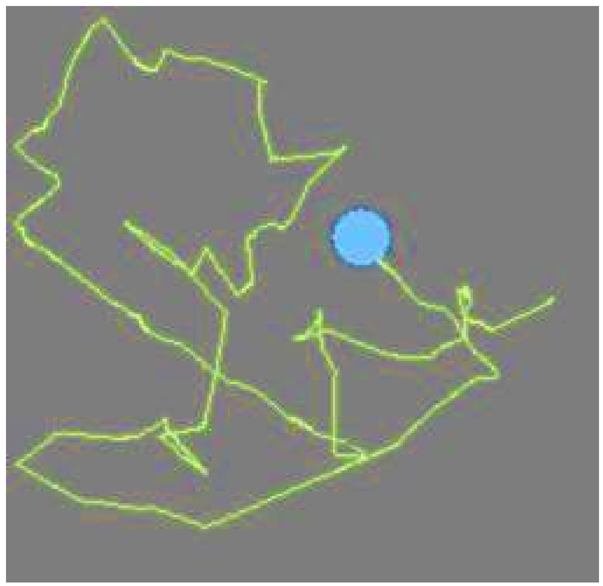
Diffusion as physics: heat transfer (air condition, heater)

The flow of heat by conduction occurs via collisions between atoms and molecules in the substance and the subsequent transfer of kinetic energy. Let us consider two substances at different temperatures separated by a barrier which is subsequently removed, as in the following figure.

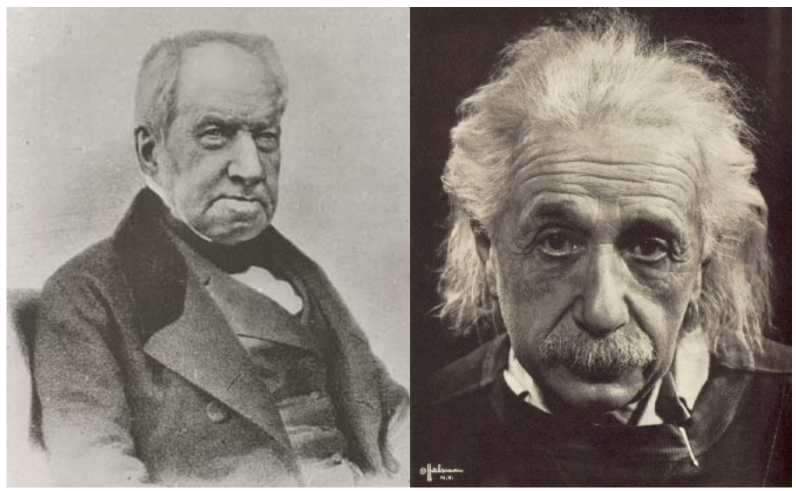


`http://www.biologycorner.com/resources/diffusion-animated.gif`

The concept of **Brownian motion** is closely related diffusion. Brownian motion is the random movements of microscopic particles in a gas or liquid. This motion is caused by the collision of the microparticle with the moving atoms of the surrounding medium. The first complete theory of Brownian motion was formulated by Albert Einstein in 1905 but still diffusion and Brownian motion are active research areas.



Brownian motion is generally regarded as having been discovered by the botanist Robert Brown in 1827. It is believed that Brown was studying pollen particles floating in water under the microscope. He then observed minute particles within the vacuoles of the pollen grains executing a jittery motion. By repeating the experiment with particles of dust, he was able to rule out that the motion was due to pollen particles being "alive," although the origin of the motion was yet to be explained.



R. Brown (1827) `http://sciweb.nybg.org/science2/pdfs/dws/Brownian.pdf`

A. Einstein (1905) `http://www.wiley-vch.de/berlin/journals/adp/549_560.pdf`

Mathematical formulation of diffusion

Random walk (a simpler version of Brownian motion)

Considers a walker that takes steps of length Δx to the left or right along a line, and after each Δt time units, the walker will take one step. If the walker is at location x_0 at the time t_0, then at time $t = t_0 + \Delta t$, the walker will either be at $x_0 - \Delta x$ or $x_0 + \Delta x$. Normally the chances or going left or right should be equal, thus the probability of the walker going left or right is 1/2. Now we assume that many walkers are walking with the same time frame simultaneously, with the same step size and on the same lattice on the line. We define $P(t, x)$ as the number of walkers at time t and location x. Then after one time step Δt, everyone who is at x_0 is gone now (go to $x_0 - \Delta x$ or $x_0 + \Delta x$), and half of those who are at $x_0 - \Delta x$ and half of those who are at $x_0 + \Delta x$ move to $x = x_0$ now.

Random walker

Diffusion equation: a partial differential equation

$$\frac{\partial P}{\partial t}(t,x) = D\frac{\partial^2 P}{\partial x^2}(t,x)$$
(The time-derivative equals to a constant times the second spatial-derivative)
the rate of change w.r.t. time is caused by the the spatial movement, and it is the second derivative since the average of the first derivative is zero.

It was first derived by Joseph Fourier in his treatise *Thorie analytique de la chaleur*, published in 1822, to describe the heat conduction; The particle diffusion equation was originally derived by Albert Einstein in 1905. Einstein used it in order to model Brownian motion.

Diffusion constant D: dimension m^2/sec

Example: oxygen (depends on temperature and media)

Temperature ($^{\circ}C$)	Media	D (cm^2/sec)
0	air	1.78×10^{-1}
20	air	2.01×10^{-1}
18	water	2.41×10^{-5}
25	water	4.58×10^{-5}

One solution of diffusion equation: normal distribution

$$\frac{\partial P}{\partial t}(t,x) = D\frac{\partial^2 P}{\partial x^2}(t,x)$$

solution: $P(t,x) = \frac{1}{(4\pi Dt)^{1/2}}e^{-\frac{x^2}{4Dt}}$

It is a normal distribution of mean 0 and of variance $2Dt$.

Biological meaning: if a fixed amount of organism is released from a point ($x = 0$), then the dispersal of the organism follows the diffusion equation, and the distribution of the organism is a normal one with mean 0 and variance $2Dt$.

Random walk (discrete diffusion): binomial distribution

Reaction-diffusion equation: combining reaction (growth, genetic evolution, action potential) and diffusion

Example 1 Genetics drifting model (Lecture 20)
$\frac{dp}{dt} = p(1-p)\frac{(w_x - w_y)p + (w_y - w_z)(1-p)}{w_x p^2 + 2w_y p(1-p) + w_z(1-p)^2}$ where $p(t)$ is the fraction of one Allele at generation t, and w_x, w_y and w_z are fitness constants.
A simpler version: $\frac{dp}{dt} = sp(1-p)$
Now consider a species randomly dispersing in an unbounded habitat, and we look for one particular gene. Let $p(x,t)$ be the density of the species which possesses an advantageous allele. Then (Fisher equation or diffusive logistic equation, 1937)

$$\frac{\partial p}{dt} = D\frac{\partial^2 p}{\partial x^2} + sp(1-p)$$

Example 2 Population growth (Lecture 16-17) Competition, predator-prey

$$\frac{\partial u}{\partial t} = D_u \frac{\partial^2 u}{\partial x^2} + u(1 - mu) - \frac{uv}{u+1},$$
$$\frac{\partial v}{\partial t} = D_v \frac{\partial^2 v}{\partial x^2} - cv + \frac{puv}{u+1}.$$

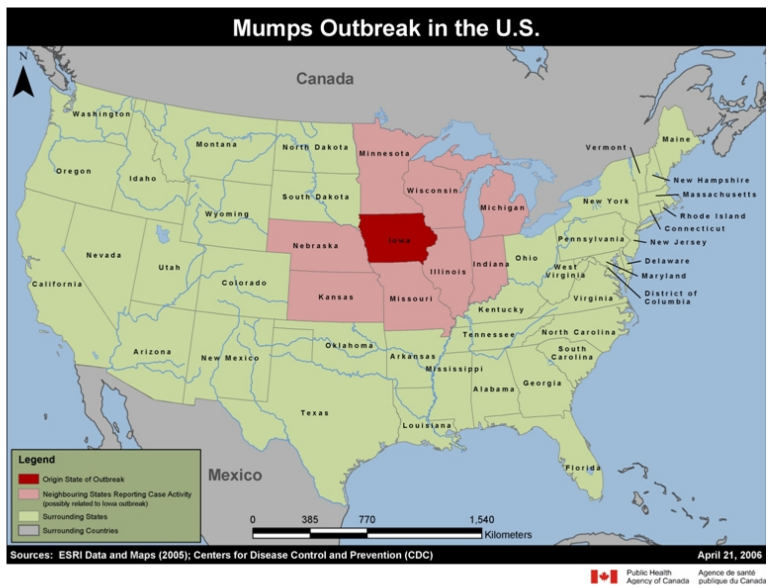
where $u(t,x)$ and $v(t,x)$ are the density functions of prey and predator.

This is a reaction-diffusion system, which is one of main tools to model pattern formation in biology.

`http://www.math.wm.edu/~shij/reu.html`

Example 3 Epidemic model (Lecture 18-19)

$$S_t = D_S S_{xx} - \beta SI$$
$$I_t = D_I I_{xx} + \beta SI - \alpha I$$
$$R_t = D_R R_{xx} + \alpha I$$



Example 4 FitzHugh-Nagumo equation (Lecture 22)

$$\epsilon \frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} + v(v-a)(1-v) - w, \quad \frac{\partial w}{\partial t} = v - bw - c.$$

$v(t,x)$ is the excitability of the system (voltage),
$w(t,x)$ is recovery variable representing the force that tends to return the resting state