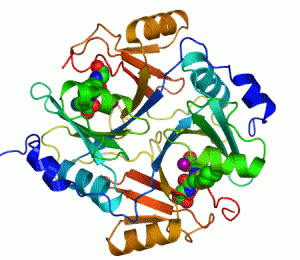
**Enzyme**

From Wikipedia, the free encyclopedia

[](http://en.wikipedia.org/wiki/File:GLO1_Homo_sapiens_small_fast.gif)

Human [glyoxalase I](http://en.wikipedia.org/wiki/Glyoxalase_I). Two [zinc](http://en.wikipedia.org/wiki/Zinc) ions that are needed for the enzyme to catalyze its reaction are shown as purple spheres, and an [enzyme inhibitor](http://en.wikipedia.org/wiki/Enzyme_inhibitor) called *S*-hexylglutathione is shown as a [space-filling model](http://en.wikipedia.org/wiki/Space-filling_model), filling the two active sites.

**Enzymes** [/](http://en.wikipedia.org/wiki/Help:IPA_for_English)[ˈɛnzaɪmz](http://en.wikipedia.org/wiki/Help:IPA_for_English#Key)[/](http://en.wikipedia.org/wiki/Help:IPA_for_English) are large biological [molecules](http://en.wikipedia.org/wiki/Molecule) responsible for the thousands of [metabolic processes](http://en.wikipedia.org/wiki/Metabolism) that sustain life.[[1]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-1)[[2]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-2) They are highly selective [catalysts](http://en.wikipedia.org/wiki/Catalysis), greatly accelerating both the rate and specificity of metabolic reactions, from the digestion of food to the synthesis of [DNA](http://en.wikipedia.org/wiki/DNA). Most enzymes are [proteins](http://en.wikipedia.org/wiki/Proteins), although some [catalytic RNA molecules](http://en.wikipedia.org/wiki/Ribozyme) have been identified. Enzymes adopt a specific [three-dimensional structure](http://en.wikipedia.org/wiki/Protein_structure), and may employ organic (e.g. [biotin](http://en.wikipedia.org/wiki/Biotin)) and inorganic (e.g.[magnesium](http://en.wikipedia.org/wiki/Magnesium) [ion](http://en.wikipedia.org/wiki/Ion)) [cofactors](http://en.wikipedia.org/wiki/Cofactor_(biochemistry)) to assist in catalysis.

In enzymatic reactions, the molecules at the beginning of the process, called [substrates](http://en.wikipedia.org/wiki/Substrate_(biochemistry)), are converted into different molecules, called [products](http://en.wikipedia.org/wiki/Product_(biology)). Almost all chemical reactions in a [biological cell](http://en.wikipedia.org/wiki/Cell_(biology)) need enzymes in order to occur at rates sufficient for life. Since enzymes are selective for their substrates and speed up only a few reactions from among many possibilities, the set of enzymes made in a cell determines which [metabolic pathways](http://en.wikipedia.org/wiki/Metabolic_pathway) occur in that cell.

Like all catalysts, enzymes work by lowering the [activation energy](http://en.wikipedia.org/wiki/Activation_energy) (*E*a‡) for a reaction, thus dramatically increasing the [rate of the reaction](http://en.wikipedia.org/wiki/Reaction_rate). As a result, products are formed faster and reactions reach their equilibrium state more rapidly. Most enzyme reaction rates are millions of times faster than those of comparable un-catalyzed reactions. As with all catalysts, enzymes are not consumed by the reactions they catalyze, nor do they alter the [equilibrium](http://en.wikipedia.org/wiki/Chemical_equilibrium) of these reactions. However, enzymes do differ from most other catalysts in that they are highly specific for their substrates. Enzymes are known to catalyze about 4,000 biochemical reactions.[[3]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-3) A few [RNA](http://en.wikipedia.org/wiki/RNA) molecules called [ribozymes](http://en.wikipedia.org/wiki/Ribozyme) also catalyze reactions, with an important example being some parts of the [ribosome](http://en.wikipedia.org/wiki/Ribosome).[[4]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-4)[[5]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-5) Synthetic molecules called [artificial enzymes](http://en.wikipedia.org/wiki/Artificial_enzyme) also display enzyme-like catalysis.[[6]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-6)

Enzyme activity can be affected by other molecules. [Inhibitors](http://en.wikipedia.org/wiki/Enzyme_inhibitor) are molecules that decrease enzyme activity; [activators](http://en.wikipedia.org/wiki/Enzyme_activator) are molecules that increase activity. Many [drugs](http://en.wikipedia.org/wiki/Drug) and[poisons](http://en.wikipedia.org/wiki/Poison) are enzyme inhibitors. Activity is also affected by [temperature](http://en.wikipedia.org/wiki/Temperature), [pressure](http://en.wikipedia.org/wiki/Pressure), chemical environment (e.g., [pH](http://en.wikipedia.org/wiki/PH)), and the [concentration](http://en.wikipedia.org/wiki/Concentration) of substrate. Some enzymes are used commercially, for example, in the synthesis of [antibiotics](http://en.wikipedia.org/wiki/Antibiotic). In addition, some household products use enzymes to speed up biochemical reactions (e.g., enzymes in biological[washing powders](http://en.wikipedia.org/wiki/Washing_powder) break down protein or [fat](http://en.wikipedia.org/wiki/Fat) stains on clothes; enzymes in [meat tenderizers](http://en.wikipedia.org/wiki/Papain) break down proteins into smaller molecules, making the meat easier to chew).

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**Etymology and history**

[](http://en.wikipedia.org/wiki/File:Eduardbuchner.jpg)

[Eduard Buchner](http://en.wikipedia.org/wiki/Eduard_Buchner)

As early as the late 17th and early 18th centuries, the digestion of [meat](http://en.wikipedia.org/wiki/Meat) by stomach secretions[[7]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-Reaumur1752-7) and the conversion of [starch](http://en.wikipedia.org/wiki/Starch) to [sugars](http://en.wikipedia.org/wiki/Sugar) by plant extracts and [saliva](http://en.wikipedia.org/wiki/Saliva) were known. However, the mechanism by which this occurred had not been identified.[[8]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-8)

In 1833, French chemist [Anselme Payen](http://en.wikipedia.org/wiki/Anselme_Payen) discovered the first enzyme, [diastase](http://en.wikipedia.org/wiki/Diastase).[[9]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-9) A few decades later, when studying the [fermentation](http://en.wikipedia.org/wiki/Fermentation_(food)) of sugar to [alcohol](http://en.wikipedia.org/wiki/Alcohol) by [yeast](http://en.wikipedia.org/wiki/Yeast), [Louis Pasteur](http://en.wikipedia.org/wiki/Louis_Pasteur) came to the conclusion that this fermentation was catalyzed by a vital force contained within the yeast cells called "[ferments](http://en.wikipedia.org/wiki/Vitalism)", which were thought to function only within living organisms. He wrote that "alcoholic fermentation is an act correlated with the life and organization of the yeast cells, not with the death or putrefaction of the cells."[[10]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-10)

In 1877, [German](http://en.wikipedia.org/wiki/Germany) physiologist [Wilhelm Kühne](http://en.wikipedia.org/wiki/Wilhelm_K%C3%BChne) (1837–1900) first used the term [*enzyme*](http://en.wiktionary.org/wiki/enzyme), which comes from [Greek](http://en.wikipedia.org/wiki/Ancient_Greek) ἔνζυμον, "leavened", to describe this process.[[11]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-11) The word *enzyme* was used later to refer to nonliving substances such as [pepsin](http://en.wikipedia.org/wiki/Pepsin), and the word *ferment* was used to refer to chemical activity produced by living organisms.

In 1897, [Eduard Buchner](http://en.wikipedia.org/wiki/Eduard_Buchner) submitted his first paper on the ability of yeast extracts that lacked any living yeast cells to ferment sugar. In a series of experiments at the [University of Berlin](http://en.wikipedia.org/wiki/Humboldt_University_of_Berlin), he found that the sugar was fermented even when there were no living yeast cells in the mixture.[[12]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-12)He named the enzyme that brought about the fermentation of sucrose "[zymase](http://en.wikipedia.org/wiki/Zymase)".[[13]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-13) In 1907, he received the [Nobel Prize in Chemistry](http://en.wikipedia.org/wiki/Nobel_Prize_in_Chemistry) "for his biochemical research and his discovery of cell-free fermentation". Following Buchner's example, enzymes are usually named according to the reaction they carry out. Typically, to generate the name of an enzyme, the suffix [*-ase*](http://en.wikipedia.org/wiki/-ase) is added to the name of its [substrate](http://en.wikipedia.org/wiki/Substrate_(biochemistry)) (e.g., [lactase](http://en.wikipedia.org/wiki/Lactase) is the enzyme that cleaves [lactose](http://en.wikipedia.org/wiki/Lactose)) or the type of reaction (e.g.,[DNA polymerase](http://en.wikipedia.org/wiki/DNA_polymerase) forms DNA polymers).[[14]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-14)

Having shown that enzymes could function outside a living cell, the next step was to determine their biochemical nature. Many early workers noted that enzymatic activity was associated with proteins, but several scientists (such as Nobel laureate [Richard Willstätter](http://en.wikipedia.org/wiki/Richard_Willst%C3%A4tter)) argued that proteins were merely carriers for the true enzymes and that proteins *per se* were incapable of catalysis.[[15]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-15) However, in 1926, [James B. Sumner](http://en.wikipedia.org/wiki/James_B._Sumner) showed that the enzyme [urease](http://en.wikipedia.org/wiki/Urease) was a pure protein and crystallized it; Sumner did likewise for the enzyme [catalase](http://en.wikipedia.org/wiki/Catalase) in 1937. The conclusion that pure proteins can be enzymes was definitively proved by [Northrop](http://en.wikipedia.org/wiki/John_Howard_Northrop) and [Stanley](http://en.wikipedia.org/wiki/Wendell_Meredith_Stanley), who worked on the digestive enzymes pepsin (1930), trypsin and chymotrypsin. These three scientists were awarded the 1946 Nobel Prize in Chemistry.[[16]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-16)

This discovery that enzymes could be crystallized eventually allowed their structures to be solved by [x-ray crystallography](http://en.wikipedia.org/wiki/X-ray_crystallography). This was first done for [lysozyme](http://en.wikipedia.org/wiki/Lysozyme), an enzyme found in tears, saliva and [egg whites](http://en.wikipedia.org/wiki/Egg_white) that digests the coating of some bacteria; the structure was solved by a group led by [David Chilton Phillips](http://en.wikipedia.org/wiki/David_Chilton_Phillips) and published in 1965.[[17]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-17) This high-resolution structure of lysozyme marked the beginning of the field of [structural biology](http://en.wikipedia.org/wiki/Structural_biology) and the effort to understand how enzymes work at an atomic level of detail.

**Structures and mechanisms**

[](http://en.wikipedia.org/wiki/File:Carbonic_anhydrase.png)

[Ribbon diagram](http://en.wikipedia.org/wiki/Ribbon_diagram) showing [human carbonic anhydrase II](http://en.wikipedia.org/wiki/Carbonic_anhydrase). The grey sphere is the [zinc](http://en.wikipedia.org/wiki/Zinc) cofactor in the active site. Diagram drawn from [PDB 1MOO](http://www.rcsb.org/pdb/explore.do?structureId=1MOO).

Enzymes are in general [globular proteins](http://en.wikipedia.org/wiki/Globular_protein) and range from just 62 amino acid residues in size, for the [monomer](http://en.wikipedia.org/wiki/Monomer) of [4-oxalocrotonate tautomerase](http://en.wikipedia.org/wiki/4-Oxalocrotonate_tautomerase),[[18]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-18) to over 2,500 residues in the animal [fatty acid synthase](http://en.wikipedia.org/wiki/Fatty_acid_synthase).[[19]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-19) A small number of RNA-based biological catalysts exist, with the most common being the [ribosome](http://en.wikipedia.org/wiki/Ribosome); these are referred to as either RNA-enzymes or[ribozymes](http://en.wikipedia.org/wiki/Ribozyme). The activities of enzymes are determined by their [three-dimensional structure](http://en.wikipedia.org/wiki/Quaternary_structure).[[20]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-20) However, although structure does determine function, predicting a novel enzyme's activity just from its structure is a very difficult problem that has not yet been solved.[[21]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-21)

Most enzymes are much larger than the substrates they act on, and only a small portion of the enzyme (around 2–4 [amino acids](http://en.wikipedia.org/wiki/Amino_acid)) is directly involved in catalysis.[[22]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-22) The region that contains these catalytic residues, binds the substrate, and then carries out the reaction is known as the [active site](http://en.wikipedia.org/wiki/Active_site). Enzymes can also contain sites that bind [cofactors](http://en.wikipedia.org/wiki/Cofactor_(biochemistry)), which are needed for catalysis. Some enzymes also have binding sites for small molecules, which are often direct or [indirect](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#Metabolic_pathways) products or substrates of the reaction catalyzed. This binding can serve to increase or decrease the enzyme's activity, providing a means for[feedback](http://en.wikipedia.org/wiki/Feedback) regulation.

Like all proteins, enzymes are long, linear chains of amino acids that [fold](http://en.wikipedia.org/wiki/Protein_folding) to produce a [three-dimensional product](http://en.wikipedia.org/wiki/Tertiary_structure). Each unique amino acid sequence produces a specific structure, which has unique properties. Individual protein chains may sometimes group together to form a [protein complex](http://en.wikipedia.org/wiki/Protein_complex). Most enzymes can be [denatured](http://en.wikipedia.org/wiki/Denaturation_(biochemistry))—that is, unfolded and inactivated—by heating or chemical denaturants, which disrupt the [three-dimensional structure](http://en.wikipedia.org/wiki/Tertiary_structure) of the protein. Depending on the enzyme, denaturation may be reversible or irreversible.

Structures of enzymes with substrates or substrate analogs during a reaction may be obtained using [Time resolved crystallography](http://en.wikipedia.org/wiki/Time_resolved_crystallography) methods.

**Specificity**

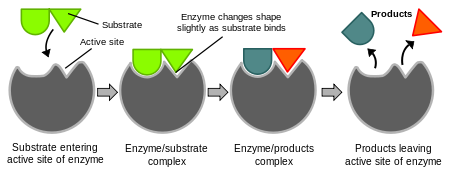
Enzymes are usually very specific as to which reactions they catalyze and the [substrates](http://en.wikipedia.org/wiki/Substrate_(biochemistry)) that are involved in these reactions. Complementary shape, charge and[hydrophilic](http://en.wikipedia.org/wiki/Hydrophilic)/[hydrophobic](http://en.wikipedia.org/wiki/Hydrophobic) characteristics of enzymes and substrates are responsible for this specificity. Enzymes can also show impressive levels of [stereospecificity](http://en.wikipedia.org/wiki/Stereospecificity),[regioselectivity](http://en.wikipedia.org/wiki/Regioselectivity) and [chemoselectivity](http://en.wikipedia.org/wiki/Chemoselectivity).[[23]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-23)

Some of the enzymes showing the highest specificity and accuracy are involved in the copying and [expression](http://en.wikipedia.org/wiki/Gene_expression) of the [genome](http://en.wikipedia.org/wiki/Genome). These enzymes have "proof-reading" mechanisms. Here, an enzyme such as [DNA polymerase](http://en.wikipedia.org/wiki/DNA_polymerase) catalyzes a reaction in a first step and then checks that the product is correct in a second step.[[24]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-24) This two-step process results in average error rates of less than 1 error in 100 million reactions in high-fidelity [mammalian](http://en.wikipedia.org/wiki/Mammal) polymerases.[[25]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-25) Similar proofreading mechanisms are also found in[RNA polymerase](http://en.wikipedia.org/wiki/RNA_polymerase),[[26]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-26) [aminoacyl tRNA synthetases](http://en.wikipedia.org/wiki/Aminoacyl_tRNA_synthetase)[[27]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-27) and [ribosomes](http://en.wikipedia.org/wiki/Ribosome).[[28]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-28)

Whereas some enzymes have broad-specificity, as they can act on a relatively broad range of different physiologically relevant substrates, many enzymes possess small side activities which arose fortuitously (i.e. [neutrally](http://en.wikipedia.org/wiki/Neutral_evolution)), which may be the starting point for the evolutionary selection of a new function; this phenomenon is known as [enzyme promiscuity](http://en.wikipedia.org/wiki/Enzyme_promiscuity).[[29]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-Tawfik10-29)

**"Lock and key" model**

Enzymes are very specific, and it was suggested by [Emil Fischer](http://en.wikipedia.org/wiki/Hermann_Emil_Fischer) in 1894 that this was because both the enzyme and the substrate possess specific complementary geometric shapes that fit exactly into one another.[[30]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-30) This is often referred to as "the lock and key" model. However, while this model explains enzyme specificity, it fails to explain the stabilization of the transition state that enzymes achieve.

[](http://en.wikipedia.org/wiki/File:Induced_fit_diagram.svg)

Diagrams to show the induced fit hypothesis of enzyme action

In 1958, [Daniel Koshland](http://en.wikipedia.org/wiki/Daniel_E._Koshland,_Jr.) suggested a modification to the lock and key model: since enzymes are rather flexible structures, the active site is continuously reshaped by interactions with the substrate as the substrate interacts with the enzyme.[[31]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-31) As a result, the substrate does not simply bind to a rigid active site; the amino acid [side-chains](http://en.wikipedia.org/wiki/Side_chain) that make up the active site are molded into the precise positions that enable the enzyme to perform its catalytic function. In some cases, such as glycosidases, the substrate [molecule](http://en.wikipedia.org/wiki/Molecule) also changes shape slightly as it enters the active site.[[32]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-32) The active site continues to change until the substrate is completely bound, at which point the final shape and charge is determined.[[33]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-33) Induced fit may enhance the fidelity of molecular recognition in the presence of competition and noise via the [conformational proofreading](http://en.wikipedia.org/wiki/Conformational_proofreading) mechanism.[[34]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-34)

Based on Fischer's lock-and-key model and Koshland’s induced fit theory, the [Chou’s distorted key theory for peptide drugs](http://en.wikipedia.org/wiki/Chou%E2%80%99s_distorted_key_theory_for_peptide_drugs) was proposed [[35]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-Chou01-35) to develop peptide drugs against [HIV/AIDS](http://en.wikipedia.org/wiki/HIV/AIDS) and [SARS](http://en.wikipedia.org/wiki/SARS).[[36]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-Gan01-36) [[37]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-Du01-37) [[38]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-Du02-38)

**Mechanisms**

Enzymes can act in several ways, all of which lower ΔG‡ (Gibbs energy):[[39]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-39)

* Lowering the [activation energy](http://en.wikipedia.org/wiki/Activation_energy) by creating an environment in which the transition state is stabilized (e.g. straining the shape of a substrate—by binding the transition-state conformation of the substrate/product molecules, the enzyme distorts the bound substrate(s) into their transition state form, thereby reducing the amount of energy required to complete the transition).
* Lowering the energy of the transition state, but without distorting the substrate, by creating an environment with the opposite charge distribution to that of the transition state.
* Providing an alternative pathway. For example, temporarily reacting with the substrate to form an intermediate ES complex, which would be impossible in the absence of the enzyme.
* Reducing the reaction entropy change by bringing substrates together in the correct orientation to react. Considering ΔH‡ alone overlooks this effect.
* Increases in temperatures speed up reactions. Thus, temperature increases help the enzyme function and develop the end product even faster. However, if heated too much, the enzyme's shape deteriorates and the enzyme becomes denatured. Some enzymes like thermolabile enzymes work best at low temperatures.
* The function of a protein is dependent on its structure so that if the structure is disrupted, so is its function.

It is interesting that this [entropic](http://en.wikipedia.org/wiki/Entropic) effect involves destabilization of the ground state,[[40]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-40) and its contribution to catalysis is relatively small.[[41]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-41)

**Transition state stabilization**

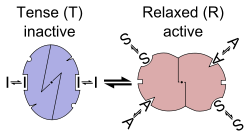
The understanding of the origin of the reduction of ΔG‡ requires one to find out how the enzymes can stabilize its transition state more than the transition state of the uncatalyzed reaction. It seems that the most effective way for reaching large stabilization is the use of electrostatic effects, in particular, when having a relatively fixed polar environment that is oriented toward the charge distribution of the transition state.[[42]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-42) Such an environment does not exist in the uncatalyzed reaction in water.

**Dynamics and function**

The internal dynamics of enzymes has been suggested to be linked with their mechanism of catalysis.[[43]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-43)[[44]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-44)[[45]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-45) Internal dynamics are the movement of parts of the enzyme's structure, such as individual amino acid residues, a group of amino acids, or even an entire [protein domain](http://en.wikipedia.org/wiki/Protein_domain). These movements occur at various time-scales ranging from[femtoseconds](http://en.wikipedia.org/wiki/Femtoseconds) to seconds. Networks of protein residues throughout an enzyme's structure can contribute to catalysis through dynamic motions.[[46]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-46)[[47]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-47)[[48]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-48)[[49]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-49) This is simply seen in the [kinetic scheme](http://en.wikipedia.org/wiki/Kinetic_scheme) of the combined process, enzymatic activity and dynamics; this scheme can have several independent [Michaelis-Menten](http://en.wikipedia.org/wiki/Michaelis-Menten_kinetics)-like reaction pathways that are connected through fluctuation rates.[[50]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-OF_2005-50)[[51]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-English_2006-51)[[52]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-Lu_1998-52)

Protein motions are vital to many enzymes, but whether small and fast vibrations, or larger and slower conformational movements are more important depends on the type of reaction involved. However, although these movements are important in binding and releasing substrates and products, it is not clear if protein movements help to accelerate the chemical steps in enzymatic reactions.[[53]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-53) These new insights also have implications in understanding allosteric effects and developing new medicines.

**Allosteric modulation**

[](http://en.wikipedia.org/wiki/File:Enzyme_allostery_en.svg)

Allosteric transition of an enzyme between R and T states, stabilized by an agonist, an inhibitor and a substrate (the [MWC model](http://en.wikipedia.org/wiki/MWC_model))

Allosteric sites are sites on the enzyme that bind to molecules in the cellular environment. The sites form weak, noncovalent bonds with these molecules, causing a change in the conformation of the enzyme. This change in conformation translates to the active site, which then affects the reaction rate of the enzyme.[[54]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-54) Allosteric interactions can both inhibit and activate enzymes and are a common way that enzymes are controlled in the body.[[55]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-55)

**Cofactors and coenzymes**

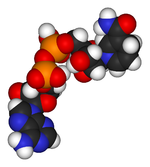
**Cofactors**

Some enzymes do not need any additional components to show full activity. However, others require non-protein molecules called cofactors to be bound for activity.[[56]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-56) Cofactors can be either [inorganic](http://en.wikipedia.org/wiki/Inorganic) (e.g., [metal ions](http://en.wikipedia.org/wiki/Metal_Ions_in_Life_Sciences) and [iron-sulfur clusters](http://en.wikipedia.org/wiki/Iron-sulfur_cluster)) or [organic compounds](http://en.wikipedia.org/wiki/Organic_molecules) (e.g., [flavin](http://en.wikipedia.org/wiki/Flavin_group) and [heme](http://en.wikipedia.org/wiki/Heme)). Organic cofactors can be either [prosthetic groups](http://en.wikipedia.org/wiki/Prosthetic_groups), which are tightly bound to an enzyme, or [coenzymes](http://en.wikipedia.org/wiki/Coenzyme), which are released from the enzyme's active site during the reaction. Coenzymes include [NADH](http://en.wikipedia.org/wiki/Nicotinamide_adenine_dinucleotide), [NADPH](http://en.wikipedia.org/wiki/Nicotinamide_adenine_dinucleotide_phosphate) and [adenosine triphosphate](http://en.wikipedia.org/wiki/Adenosine_triphosphate). These molecules transfer chemical groups between enzymes.[[57]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-57)

An example of an enzyme that contains a cofactor is [carbonic anhydrase](http://en.wikipedia.org/wiki/Carbonic_anhydrase), and is shown in the [ribbon diagram](http://en.wikipedia.org/wiki/Ribbon_diagram) above with a zinc cofactor bound as part of its active site.[[58]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-58)These tightly bound molecules are usually found in the active site and are involved in catalysis. For example, flavin and heme cofactors are often involved in [redox](http://en.wikipedia.org/wiki/Redox) reactions.

Enzymes that require a cofactor but do not have one bound are called *apoenzymes* or *apoproteins*. An apoenzyme together with its cofactor(s) is called a *holoenzyme* (this is the active form). Most cofactors are not covalently attached to an enzyme, but are very tightly bound. However, organic prosthetic groups can be covalently bound (e.g., [biotin](http://en.wikipedia.org/wiki/Biotin)in the enzyme [pyruvate carboxylase](http://en.wikipedia.org/wiki/Pyruvate_carboxylase)). The term "holoenzyme" can also be applied to enzymes that contain multiple protein subunits, such as the [DNA polymerases](http://en.wikipedia.org/wiki/DNA_polymerase); here the holoenzyme is the complete complex containing all the subunits needed for activity.

**Coenzymes**

[](http://en.wikipedia.org/wiki/File:NADH-3D-vdW.png)

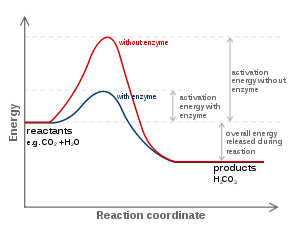
[Space-filling model](http://en.wikipedia.org/wiki/Molecular_graphics#Space-filling_models) of the coenzyme NADH

Coenzymes are small organic molecules that can be loosely or tightly bound to an enzyme. Tightly bound coenzymes can be called prosthetic groups. Coenzymes transport chemical groups from one enzyme to another.[[59]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-59) Some of these chemicals such as [riboflavin](http://en.wikipedia.org/wiki/Riboflavin), [thiamine](http://en.wikipedia.org/wiki/Thiamine) and [folic acid](http://en.wikipedia.org/wiki/Folic_acid)are [vitamins](http://en.wikipedia.org/wiki/Vitamins) (compounds that cannot be synthesized by the body and must be acquired from the diet). The chemical groups carried include the[hydride](http://en.wikipedia.org/wiki/Hydride) ion (H-) carried by [NAD or NADP+](http://en.wikipedia.org/wiki/Nicotinamide_adenine_dinucleotide), the phosphate group carried by [adenosine triphosphate](http://en.wikipedia.org/wiki/Adenosine_triphosphate), the acetyl group carried by [coenzyme A](http://en.wikipedia.org/wiki/Coenzyme_A), formyl, methenyl or methyl groups carried by [folic acid](http://en.wikipedia.org/wiki/Folic_acid) and the methyl group carried by [S-adenosylmethionine](http://en.wikipedia.org/wiki/S-adenosylmethionine).

Since coenzymes are chemically changed as a consequence of enzyme action, it is useful to consider coenzymes to be a special class of substrates, or second substrates, which are common to many different enzymes. For example, about 700 enzymes are known to use the coenzyme NADH.[[60]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-60)

Coenzymes are usually continuously regenerated and their concentrations maintained at a steady level inside the cell: for example, NADPH is regenerated through the [pentose phosphate pathway](http://en.wikipedia.org/wiki/Pentose_phosphate_pathway) and *S*-adenosylmethionine by [methionine adenosyltransferase](http://en.wikipedia.org/wiki/Methionine_adenosyltransferase). This continuous regeneration means that even small amounts of coenzymes are used very intensively. For example, the human body turns over its own weight in ATP each day.[[61]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-61)

**Thermodynamics**

[](http://en.wikipedia.org/wiki/File:Carbonic_anhydrase_reaction_in_tissue.svg)

The energies of the stages of a [chemical reaction](http://en.wikipedia.org/wiki/Chemical_reaction). Substrates need a lot of potential energy to reach a[transition state](http://en.wikipedia.org/wiki/Transition_state), which then decays into products. The enzyme stabilizes the transition state, reducing the energy needed to form products.

As all catalysts, enzymes do not alter the position of the chemical equilibrium of the reaction. Usually, in the presence of an enzyme, the reaction runs in the same direction as it would without the enzyme, just more quickly. However, in the absence of the enzyme, other possible uncatalyzed, "spontaneous" reactions might lead to different products, because in those conditions this different product is formed faster.

Furthermore, enzymes can couple two or more reactions, so that a thermodynamically favorable reaction can be used to "drive" a thermodynamically unfavorable one. For example, the hydrolysis of [ATP](http://en.wikipedia.org/wiki/Adenosine_triphosphate) is often used to drive other chemical reactions.[[62]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-Nicholls-62)

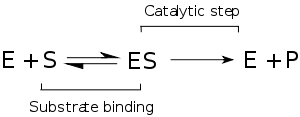
Enzymes catalyze the forward and backward reactions equally. They do not alter the equilibrium itself, but only the speed at which it is reached. For example, [carbonic anhydrase](http://en.wikipedia.org/wiki/Carbonic_anhydrase) catalyzes its reaction in either direction depending on the concentration of its reactants.

\mathrm{CO_2 + H_2O \xrightarrow{Carbonic\ anhydrase}
H_2CO_3} (in [tissues](http://en.wikipedia.org/wiki/Biological_tissue); high CO2 concentration)

\mathrm{H_2CO_3 \xrightarrow{Carbonic\ anhydrase}
CO_2 + H_2O} (in [lungs](http://en.wikipedia.org/wiki/Lung); low CO2 concentration)

Nevertheless, if the equilibrium is greatly displaced in one direction, that is, in a very [exergonic](http://en.wikipedia.org/wiki/Exergonic) reaction, the reaction is in effect irreversible. Under these conditions, the enzyme will, in fact, catalyze the reaction only in the thermodynamically allowed direction.

**Kinetics**

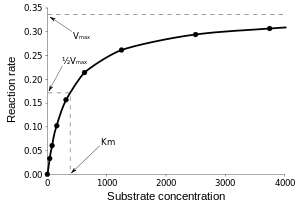
[](http://en.wikipedia.org/wiki/File:Simple_mechanism.svg)

Mechanism for a single substrate enzyme catalyzed reaction. The enzyme (E) binds a substrate (S) and produces a product (P).

Enzyme kinetics is the investigation of how enzymes bind substrates and turn them into products. The rate data used in kinetic analyses are commonly obtained from [enzyme assays](http://en.wikipedia.org/wiki/Enzyme_assay), where since the 90s, the dynamics of many enzymes are studied on the level of [individual molecules](http://en.wikipedia.org/wiki/Single-molecule_experiment).

In 1902 [Victor Henri](http://en.wikipedia.org/wiki/Victor_Henri) proposed a quantitative theory of enzyme kinetics,[[63]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-63) but his experimental data were not useful because the significance of the hydrogen ion concentration was not yet appreciated. After [Peter Lauritz Sørensen](http://en.wikipedia.org/wiki/S._P._L._S%C3%B8rensen) had defined the logarithmic pH-scale and introduced the concept of buffering in 1909[[64]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-64) the German chemist [Leonor Michaelis](http://en.wikipedia.org/wiki/Leonor_Michaelis)and his Canadian postdoc [Maud Leonora Menten](http://en.wikipedia.org/wiki/Maud_Leonora_Menten) repeated Henri's experiments and confirmed his equation, which is referred to as [Henri-Michaelis-Menten kinetics](http://en.wikipedia.org/wiki/Henri-Michaelis-Menten_kinetics) (termed also [Michaelis-Menten kinetics](http://en.wikipedia.org/wiki/Michaelis-Menten_kinetics)).[[65]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-65) Their work was further developed by [G. E. Briggs](http://en.wikipedia.org/wiki/George_Edward_Briggs) and [J. B. S. Haldane](http://en.wikipedia.org/wiki/J._B._S._Haldane), who derived kinetic equations that are still widely considered today a starting point in solving enzymatic activity.[[66]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-66)

The major contribution of Henri was to think of enzyme reactions in two stages. In the first, the substrate binds reversibly to the enzyme, forming the enzyme-substrate complex. This is sometimes called the Michaelis complex. The enzyme then catalyzes the chemical step in the reaction and releases the product. Note that the simple [Michaelis Menten mechanism](http://en.wikipedia.org/wiki/Michaelis-Menten_kinetics) for the enzymatic activity is considered today a basic idea, where many examples show that the enzymatic activity involves structural dynamics. This is incorporated in the enzymatic mechanism while introducing several Michaelis Menten pathways that are connected with fluctuating rates.[[50]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-OF_2005-50)[[51]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-English_2006-51)[[52]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-Lu_1998-52) Nevertheless, there is a mathematical relation connecting the behavior obtained from the basic Michaelis Menten mechanism (that was indeed proved correct in many experiments) with the generalized Michaelis Menten mechanisms involving dynamics and activity; [[67]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-XX_2006-67) this means that the measured activity of enzymes on the level of many enzymes may be explained with the simple Michaelis-Menten equation, yet, the actual activity of enzymes is richer and involves structural dynamics.

[](http://en.wikipedia.org/wiki/File:Michaelis-Menten_saturation_curve_of_an_enzyme_reaction.svg)

Saturation curve for an enzyme reaction showing the relation between the substrate concentration (S) and rate (*v*)

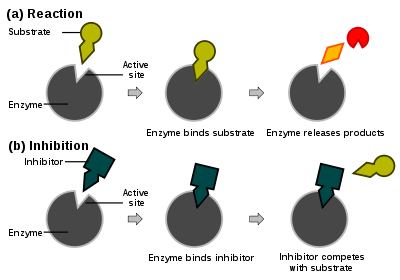
Enzymes can catalyze up to several million reactions per second. For example, the uncatalyzed decarboxylation of [orotidine 5'-monophosphate](http://en.wikipedia.org/wiki/Orotidine_5%27-monophosphate) has a half life of 78 million years. However, when the enzyme [orotidine 5'-phosphate decarboxylase](http://en.wikipedia.org/wiki/Orotidine_5%27-phosphate_decarboxylase) is added, the same process takes just 25 milliseconds.[[68]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-68) Enzyme rates depend on solution conditions and substrate concentration. Conditions that denature the protein abolish enzyme activity, such as high temperatures, extremes of pH or high salt concentrations, while raising substrate concentration tends to increase activity when [S] is low. To find the maximum speed of an enzymatic reaction, the substrate concentration is increased until a constant rate of product formation is seen. This is shown in the saturation curve on the right. Saturation happens because, as substrate concentration increases, more and more of the free enzyme is converted into the substrate-bound ES form. At the maximum reaction rate (*V*max) of the enzyme, all the enzyme active sites are bound to substrate, and the amount of ES complex is the same as the total amount of enzyme. However, *V*max is only one kinetic constant of enzymes. The amount of substrate needed to achieve a given rate of reaction is also important. This is given by the [Michaelis-Menten constant](http://en.wikipedia.org/wiki/Michaelis-Menten_constant) (*K*m), which is the substrate concentration required for an enzyme to reach one-half its maximum reaction rate; generally, each enzyme has a characteristic *K*m for a given substrate. Another useful constant is *k*cat, which is the rate of product formation handled by one active site and is generally given in units of inverse seconds.

The efficiency of an enzyme can be expressed in terms of *k*cat/*K*m. This is also called the specificity constant and incorporates the [rate constants](http://en.wikipedia.org/wiki/Rate_constant) for all steps in the reaction. Because the specificity constant reflects both affinity and catalytic ability, it is useful for comparing different enzymes against each other, or the same enzyme with different substrates. The theoretical maximum for the specificity constant is called the diffusion limit and is about 108 to 109 (M−1 s−1). At this point every collision of the enzyme with its substrate will result in catalysis, and the rate of product formation is not limited by the reaction rate but by the diffusion rate. Enzymes with this property are called[*catalytically perfect*](http://en.wikipedia.org/wiki/Catalytically_perfect_enzyme) or *kinetically perfect*. Example of such enzymes are [triose-phosphate isomerase](http://en.wikipedia.org/wiki/Triosephosphateisomerase), [carbonic anhydrase](http://en.wikipedia.org/wiki/Carbonic_anhydrase), [acetylcholinesterase](http://en.wikipedia.org/wiki/Acetylcholinesterase), [catalase](http://en.wikipedia.org/wiki/Catalase), fumarase, β-lactamase, and [superoxide dismutase](http://en.wikipedia.org/wiki/Superoxide_dismutase).

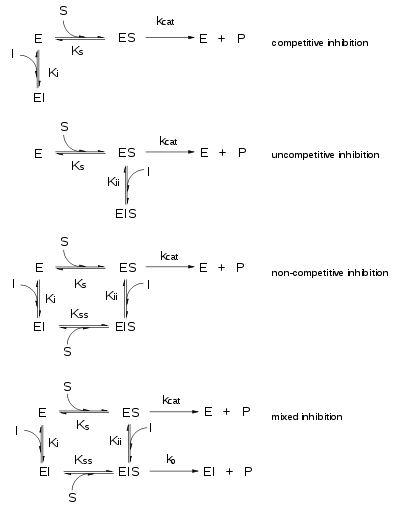
Michaelis-Menten kinetics relies on the [law of mass action](http://en.wikipedia.org/wiki/Law_of_mass_action), which is derived from the assumptions of free [diffusion](http://en.wikipedia.org/wiki/Diffusion) and thermodynamically driven random collision. However, many biochemical or cellular processes deviate significantly from these conditions, because of [macromolecular crowding](http://en.wikipedia.org/wiki/Macromolecular_crowding), phase-separation of the enzyme/substrate/product, or one or two-dimensional molecular movement.[[69]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-69) In these situations, a [fractal](http://en.wikipedia.org/wiki/Fractal) [Michaelis-Menten kinetics](http://en.wikipedia.org/wiki/Michaelis-Menten_kinetics) may be applied.[[70]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-70)[[71]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-71)[[72]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-72)[[73]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-73)

Some enzymes operate with kinetics, which are faster than diffusion rates, which would seem to be impossible. Several mechanisms have been invoked to explain this phenomenon. Some proteins are believed to accelerate catalysis by drawing their substrate in and pre-orienting them by using dipolar electric fields. Other models invoke a quantum-mechanical [tunneling](http://en.wikipedia.org/wiki/Quantum_tunneling) explanation, whereby a proton or an electron can tunnel through activation barriers, although for proton tunneling this model remains somewhat controversial.[[74]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-74)[[75]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-75) Quantum tunneling for protons has been observed in [tryptamine](http://en.wikipedia.org/wiki/Tryptamine).[[76]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-76) This suggests that enzyme catalysis may be more accurately characterized as "through the barrier" rather than the traditional model, which requires substrates to go "over" a lowered energy barrier.

**Inhibition**

[](http://en.wikipedia.org/wiki/File:Competitive_inhibition.svg)

Competitive inhibitors bind reversibly to the enzyme, preventing the binding of substrate. On the other hand, binding of substrate prevents binding of the inhibitor. Substrate and inhibitor compete for the enzyme.

[](http://en.wikipedia.org/wiki/File:Types_of_inhibition_en.svg)

Types of inhibition. This classification was introduced by [W.W. Cleland](http://en.wikipedia.org/wiki/W.W._Cleland).[[77]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-77)

Enzyme reaction rates can be decreased by various types of [enzyme inhibitors](http://en.wikipedia.org/wiki/Enzyme_inhibitor).

**Competitive inhibition**

In competitive inhibition, the inhibitor and substrate compete for the enzyme (i.e., they can not bind at the same time).[[78]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-78) Often competitive inhibitors strongly resemble the real substrate of the enzyme. For example,[methotrexate](http://en.wikipedia.org/wiki/Methotrexate) is a competitive inhibitor of the enzyme [dihydrofolate reductase](http://en.wikipedia.org/wiki/Dihydrofolate_reductase), which catalyzes the reduction of [dihydrofolate](http://en.wikipedia.org/wiki/Folic_acid) to [tetrahydrofolate](http://en.wikipedia.org/wiki/Folic_acid). The similarity between the structures of folic acid and this drug are shown in the figure to the *right* bottom. In some cases, the inhibitor can bind to a site other than the binding-site of the usual substrate and exert an [allosteric effect](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#Allosteric_modulation) to change the shape of the usual binding-site. For example, [strychnine](http://en.wikipedia.org/wiki/Strychnine) acts as an allosteric inhibitor of the glycine receptor in the mammalian spinal cord and brain stem. Glycine is a major post-synaptic inhibitory neurotransmitter with a specific receptor site. Strychnine binds to an alternate site that reduces the affinity of the glycine receptor for glycine, resulting in convulsions due to lessened inhibition by the glycine.[[79]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-79) In competitive inhibition the maximal rate of the reaction is not changed, but higher substrate concentrations are required to reach a given maximum rate, increasing the apparent Km.

**Uncompetitive inhibition**

In uncompetitive inhibition, the inhibitor cannot bind to the free enzyme, only to the ES-complex. The EIS-complex thus formed is enzymatically inactive. This type of inhibition is rare, but may occur in multimeric enzymes.

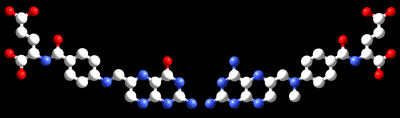
**Non-competitive inhibition**

Non-competitive inhibitors can bind to the enzyme at the binding site at the same time as the substrate,but not to the active site. Both the EI and EIS complexes are enzymatically inactive. Because the inhibitor can not be driven from the enzyme by higher substrate concentration (in contrast to competitive inhibition), the apparent Vmax changes. But because the substrate can still bind to the enzyme, the Km stays the same.

**Mixed inhibition**

This type of inhibition resembles the non-competitive, except that the EIS-complex has residual enzymatic activity.This type of inhibitor does not follow Michaelis-Menten equation.

In many organisms, inhibitors may act as part of a [feedback](http://en.wikipedia.org/wiki/Feedback) mechanism. If an enzyme produces too much of one substance in the organism, that substance may act as an inhibitor for the enzyme at the beginning of the pathway that produces it, causing production of the substance to slow down or stop when there is sufficient amount. This is a form of [negative feedback](http://en.wikipedia.org/wiki/Negative_feedback). Enzymes that are subject to this form of regulation are often multimeric and have allosteric binding sites for regulatory substances. Their substrate/velocity plots are not hyperbolar, but sigmoidal (S-shaped).

[](http://en.wikipedia.org/wiki/File:Methotrexate_and_folic_acid_compared.png)

The coenzyme folic acid (left) and the anti-cancer drug methotrexate (right) are very similar in structure. As a result, methotrexate is a competitive inhibitor of many enzymes that use folates.

[Irreversible inhibitors](http://en.wikipedia.org/wiki/Irreversible_inhibition) react with the enzyme and form a [covalent](http://en.wikipedia.org/wiki/Covalent_bond) adduct with the protein. The inactivation is irreversible. These compounds include [eflornithine](http://en.wikipedia.org/wiki/Eflornithine) a drug used to treat the parasitic disease [sleeping sickness](http://en.wikipedia.org/wiki/African_trypanosomiasis).[[80]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-Poulin-80) [Penicillin](http://en.wikipedia.org/wiki/Penicillin) and [Aspirin](http://en.wikipedia.org/wiki/Aspirin) also act in this manner. With these drugs, the compound is bound in the active site and the enzyme then converts the inhibitor into an activated form that reacts irreversibly with one or more amino acid residues.

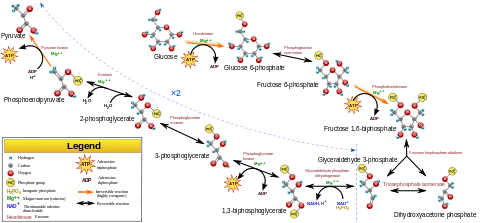
**Uses of inhibitors**

Since inhibitors modulate the function of enzymes they are often used as drugs. A common example of an inhibitor that is used as a drug is [aspirin](http://en.wikipedia.org/wiki/Aspirin), which inhibits the [COX-1](http://en.wikipedia.org/wiki/Cyclooxygenase) and [COX-2](http://en.wikipedia.org/wiki/Cyclooxygenase) enzymes that produce the[inflammation](http://en.wikipedia.org/wiki/Inflammation) messenger [prostaglandin](http://en.wikipedia.org/wiki/Prostaglandin), thus suppressing pain and inflammation. However, other enzyme inhibitors are poisons. For example, the poison [cyanide](http://en.wikipedia.org/wiki/Cyanide) is an irreversible enzyme inhibitor that combines with the copper and iron in the active site of the enzyme [cytochrome c oxidase](http://en.wikipedia.org/wiki/Cytochrome_c_oxidase) and blocks [cellular respiration](http://en.wikipedia.org/wiki/Cellular_respiration).[[81]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-81)

**Biological function**

Enzymes serve a wide variety of [functions](http://en.wikipedia.org/wiki/Function_(biology)) inside living organisms. They are indispensable for [signal transduction](http://en.wikipedia.org/wiki/Signal_transduction) and cell regulation, often via [kinases](http://en.wikipedia.org/wiki/Kinase) and [phosphatases](http://en.wikipedia.org/wiki/Phosphatase).[[82]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-82) They also generate movement, with[myosin](http://en.wikipedia.org/wiki/Myosin) hydrolyzing ATP to generate [muscle contraction](http://en.wikipedia.org/wiki/Muscle_contraction) and also moving cargo around the cell as part of the[cytoskeleton](http://en.wikipedia.org/wiki/Cytoskeleton).[[83]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-83) Other ATPases in the cell membrane are [ion pumps](http://en.wikipedia.org/wiki/Ion_pump_(biology)) involved in [active transport](http://en.wikipedia.org/wiki/Active_transport). Enzymes are also involved in more exotic functions, such as [luciferase](http://en.wikipedia.org/wiki/Luciferase) generating light in [fireflies](http://en.wikipedia.org/wiki/Firefly).[[84]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-84) [Viruses](http://en.wikipedia.org/wiki/Virus) can also contain enzymes for infecting cells, such as the [HIV integrase](http://en.wikipedia.org/wiki/HIV_integrase) and[reverse transcriptase](http://en.wikipedia.org/wiki/Reverse_transcriptase), or for viral release from cells, like the [influenza](http://en.wikipedia.org/wiki/Influenza) virus [neuraminidase](http://en.wikipedia.org/wiki/Neuraminidase).

An important function of enzymes is in the [digestive systems](http://en.wikipedia.org/wiki/Digestive_systems) of animals. Enzymes such as [amylases](http://en.wikipedia.org/wiki/Amylases) and [proteases](http://en.wikipedia.org/wiki/Proteases) break down large molecules ([starch](http://en.wikipedia.org/wiki/Starch) or [proteins](http://en.wikipedia.org/wiki/Protein), respectively) into smaller ones, so they can be absorbed by the intestines. Starch molecules, for example, are too large to be absorbed from the intestine, but enzymes hydrolyze the starch chains into smaller molecules such as [maltose](http://en.wikipedia.org/wiki/Maltose) and eventually [glucose](http://en.wikipedia.org/wiki/Glucose), which can then be absorbed. Different enzymes digest different food substances. In[ruminants](http://en.wikipedia.org/wiki/Ruminants), which have [herbivorous](http://en.wikipedia.org/wiki/Herbivorous) diets, microorganisms in the gut produce another enzyme, [cellulase](http://en.wikipedia.org/wiki/Cellulase), to break down the cellulose cell walls of plant fiber.[[85]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-85)

[](http://en.wikipedia.org/wiki/File:Glycolysis.svg)

Glycolytic enzymes and their functions in the [metabolic pathway](http://en.wikipedia.org/wiki/Metabolic_pathway) of [glycolysis](http://en.wikipedia.org/wiki/Glycolysis)

Several enzymes can work together in a specific order, creating [metabolic pathways](http://en.wikipedia.org/wiki/Metabolic_pathway). In a metabolic pathway, one enzyme takes the product of another enzyme as a substrate. After the catalytic reaction, the product is then passed on to another enzyme. Sometimes more than one enzyme can catalyze the same reaction in parallel; this can allow more complex regulation: with, for example, a low constant activity provided by one enzyme but an inducible high activity from a second enzyme.

Enzymes determine what steps occur in these pathways. Without enzymes, metabolism would neither progress through the same steps nor be fast enough to serve the needs of the cell. Indeed, a metabolic pathway such as [glycolysis](http://en.wikipedia.org/wiki/Glycolysis) could not exist independently of enzymes. Glucose, for example, can react directly with ATP to become [phosphorylated](http://en.wikipedia.org/wiki/Phosphorylation) at one or more of its carbons. In the absence of enzymes, this occurs so slowly as to be insignificant. However, if [hexokinase](http://en.wikipedia.org/wiki/Hexokinase) is added, these slow reactions continue to take place except that phosphorylation at carbon 6 occurs so rapidly that, if the mixture is tested a short time later, [glucose-6-phosphate](http://en.wikipedia.org/wiki/Glucose-6-phosphate) is found to be the only significant product. As a consequence, the network of metabolic pathways within each cell depends on the set of functional enzymes that are present.

**Control of activity**

There are five main ways that enzyme activity is controlled in the cell.

1. **Enzyme production** ([transcription](http://en.wikipedia.org/wiki/Transcription_(genetics)) and [translation](http://en.wikipedia.org/wiki/Translation_(genetics)) of enzyme [genes](http://en.wikipedia.org/wiki/Gene)) can be enhanced or diminished by a cell in response to changes in the cell's environment. This form of [gene regulation](http://en.wikipedia.org/wiki/Regulation_of_gene_expression) is called [enzyme induction and inhibition](http://en.wikipedia.org/wiki/Enzyme_induction_and_inhibition). For example, bacteria may become [resistant to antibiotics](http://en.wikipedia.org/wiki/Antibiotic_resistance) such as [penicillin](http://en.wikipedia.org/wiki/Penicillin) because enzymes called [beta-lactamases](http://en.wikipedia.org/wiki/Beta-lactamase) are induced that hydrolyze the crucial [beta-lactam ring](http://en.wikipedia.org/wiki/Beta-lactam) within the penicillin molecule. Another example are enzymes in the [liver](http://en.wikipedia.org/wiki/Liver) called [cytochrome P450 oxidases](http://en.wikipedia.org/wiki/Cytochrome_P450_oxidase), which are important in [drug metabolism](http://en.wikipedia.org/wiki/Drug_metabolism). Induction or inhibition of these enzymes can cause [drug interactions](http://en.wikipedia.org/wiki/Drug_interaction).
2. Enzymes can be **compartmentalized**, with different metabolic pathways occurring in different [cellular compartments](http://en.wikipedia.org/wiki/Cellular_compartment). For example, [fatty acids](http://en.wikipedia.org/wiki/Fatty_acids) are synthesized by one set of enzymes in the [cytosol](http://en.wikipedia.org/wiki/Cytosol), [endoplasmic reticulum](http://en.wikipedia.org/wiki/Endoplasmic_reticulum) and the [Golgi apparatus](http://en.wikipedia.org/wiki/Golgi_apparatus) and used by a different set of enzymes as a source of energy in the [mitochondrion](http://en.wikipedia.org/wiki/Mitochondrion), through[β-oxidation](http://en.wikipedia.org/wiki/%CE%92-oxidation).[[86]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-86)
3. Enzymes can be regulated by [**inhibitors**](http://en.wikipedia.org/wiki/Enzyme_inhibitor)**and activators**. For example, the end product(s) of a metabolic pathway are often inhibitors for one of the first enzymes of the pathway (usually the first irreversible step, called *committed step*), thus regulating the amount of end product made by the pathways. Such a regulatory mechanism is called a [negative feedback mechanism](http://en.wikipedia.org/wiki/Negative_feedback), because the amount of the end product produced is regulated by its own concentration. Negative feedback mechanisms can effectively adjust the rate of synthesis of intermediate metabolites according to the demands of the cells. This helps allocate materials and energy economically, and prevents the manufacture of excess end products. The control of enzymatic action helps to maintain a [stable internal environment](http://en.wikipedia.org/wiki/Homeostasis) in living organisms.
4. Enzymes can be regulated through [**covalent modulation**](http://en.wikipedia.org/wiki/Covalent_modulation). This can include [phosphorylation](http://en.wikipedia.org/wiki/Phosphorylation), [myristoylation](http://en.wikipedia.org/wiki/Myristic_acid) and [glycosylation](http://en.wikipedia.org/wiki/Glycosylation). For example, in the response to [insulin](http://en.wikipedia.org/wiki/Insulin), the [phosphorylation](http://en.wikipedia.org/wiki/Phosphorylation) of multiple enzymes, including [glycogen synthase](http://en.wikipedia.org/wiki/Glycogen_synthase), helps control the synthesis or degradation of [glycogen](http://en.wikipedia.org/wiki/Glycogen) and allows the cell to respond to changes in[blood sugar](http://en.wikipedia.org/wiki/Blood_sugar).[[87]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-87) Another example of post-translational modification is the cleavage of the polypeptide chain. [Chymotrypsin](http://en.wikipedia.org/wiki/Chymotrypsin), a digestive [protease](http://en.wikipedia.org/wiki/Protease), is produced in inactive form as [chymotrypsinogen](http://en.wikipedia.org/wiki/Chymotrypsinogen) in the [pancreas](http://en.wikipedia.org/wiki/Pancreas) and transported in this form to the [duodenum](http://en.wikipedia.org/wiki/Duodenum) where it is activated. This stops the enzyme from digesting the pancreas or other tissues before it enters the gut. This type of inactive precursor to an enzyme is known as a [zymogen](http://en.wikipedia.org/wiki/Zymogen).
5. Some enzymes may become **activated when localized to a different environment** (e.g., from a reducing ([cytoplasm](http://en.wikipedia.org/wiki/Cytoplasm)) to an oxidizing ([periplasm](http://en.wikipedia.org/wiki/Periplasm)) environment, high pH to low pH, etc.). For example, [hemagglutinin](http://en.wikipedia.org/wiki/Hemagglutinin) in the [influenza](http://en.wikipedia.org/wiki/Influenza) virus is activated by a conformational change caused by the acidic conditions, these occur when it is taken up inside its host cell and enters the [lysosome](http://en.wikipedia.org/wiki/Lysosome).[[88]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-88)

**Involvement in disease**

[](http://en.wikipedia.org/wiki/File:Phenylalanine_hydroxylase_brighter.jpg)

[Phenylalanine hydroxylase](http://en.wikipedia.org/wiki/Phenylalanine_hydroxylase). Created from [PDB 1KW0](http://www.rcsb.org/pdb/explore.do?structureId=1KW0)

Since the tight control of enzyme activity is essential for [homeostasis](http://en.wikipedia.org/wiki/Homeostasis), any malfunction (mutation, overproduction, underproduction or deletion) of a single critical enzyme can lead to a [genetic disease](http://en.wikipedia.org/wiki/Genetic_disease). The importance of enzymes is shown by the fact that a lethal illness can be caused by the malfunction of just one type of enzyme out of the thousands of types present in our bodies.

One example is the most common type of [phenylketonuria](http://en.wikipedia.org/wiki/Phenylketonuria). A mutation of a single amino acid in the enzyme [phenylalanine hydroxylase](http://en.wikipedia.org/wiki/Phenylalanine_hydroxylase), which catalyzes the first step in the degradation of [phenylalanine](http://en.wikipedia.org/wiki/Phenylalanine), results in build-up of phenylalanine and related products. This can lead to[intellectual disability](http://en.wikipedia.org/wiki/Intellectual_disability) if the disease is untreated.[[89]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-89) Another example of enzyme deficiency is [pseudocholinesterase](http://en.wikipedia.org/wiki/Pseudocholinesterase), in which the body's ability to break down choline ester drugs is impaired.[[90]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-90)

A further example is when [germline mutations](http://en.wikipedia.org/wiki/Germline_mutation) in genes coding for [DNA repair](http://en.wikipedia.org/wiki/DNA_repair) enzymes cause hereditary [cancer syndromes](http://en.wikipedia.org/wiki/Cancer_syndrome) such as[xeroderma pigmentosum](http://en.wikipedia.org/wiki/Xeroderma_pigmentosum). Defects in these enzymes cause cancer since the body is less able to repair mutations in the genome. This causes a slow accumulation of mutations and results in the development of many types of cancer in the sufferer.

Oral administration of enzymes can be used to treat several diseases (e.g. pancreatic insufficiency and lactose intolerance). Since enzymes are proteins themselves they are potentially subject to inactivation and digestion in the gastrointestinal environment. Therefore a non-invasive imaging assay was developed to monitor gastrointestinal activity of exogenous [enzymes](http://en.wikipedia.org/wiki/Enzymes) ([prolyl endopeptidase](http://en.wikipedia.org/wiki/Prolyl_endopeptidase) as potential adjuvant therapy for [celiac disease](http://en.wikipedia.org/wiki/Celiac_disease)) in vivo.[[91]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-91)

**Naming conventions**

An enzyme's name is often derived from its substrate or the chemical reaction it catalyzes, with the word ending in ***-ase***. Examples are [lactase](http://en.wikipedia.org/wiki/Lactase), [alcohol dehydrogenase](http://en.wikipedia.org/wiki/Alcohol_dehydrogenase) and[DNA polymerase](http://en.wikipedia.org/wiki/DNA_polymerase). This may result in different enzymes, called [isozymes](http://en.wikipedia.org/wiki/Isozymes), with the same function having the same basic name. Isoenzymes have a different amino acid sequence and might be distinguished by their optimal [pH](http://en.wikipedia.org/wiki/PH), kinetic properties or immunologically. Isoenzyme and isozyme are homologous proteins. Furthermore, the normal physiological reaction an enzyme catalyzes may not be the same as under artificial conditions. This can result in the same enzyme being identified with two different names. For example, [glucose isomerase](http://en.wikipedia.org/wiki/Glucose_isomerase), which is used industrially to convert [glucose](http://en.wikipedia.org/wiki/Glucose) into the sweetener [fructose](http://en.wikipedia.org/wiki/Fructose), is a xylose isomerase *in vivo* (within the body).

The [International Union of Biochemistry and Molecular Biology](http://en.wikipedia.org/wiki/International_Union_of_Biochemistry_and_Molecular_Biology) have developed a [nomenclature](http://en.wikipedia.org/wiki/Nomenclature) for enzymes, the [**EC numbers**](http://en.wikipedia.org/wiki/Enzyme_Commission_number); each enzyme is described by a sequence of four numbers preceded by "EC". The first number broadly classifies the enzyme based on its mechanism.

The top-level classification is[[92]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-92)

* EC 1 [*Oxidoreductases*](http://en.wikipedia.org/wiki/Oxidoreductase): catalyze [oxidation](http://en.wikipedia.org/wiki/Oxidation)/reduction reactions
* EC 2 [*Transferases*](http://en.wikipedia.org/wiki/Transferase): transfer a [functional group](http://en.wikipedia.org/wiki/Functional_group) (*e.g.* a methyl or phosphate group)
* EC 3 [*Hydrolases*](http://en.wikipedia.org/wiki/Hydrolase): catalyze the [hydrolysis](http://en.wikipedia.org/wiki/Hydrolysis) of various bonds
* EC 4 [*Lyases*](http://en.wikipedia.org/wiki/Lyase): cleave various bonds by means other than hydrolysis and oxidation
* EC 5 [*Isomerases*](http://en.wikipedia.org/wiki/Isomerase): catalyze [isomerization](http://en.wikipedia.org/wiki/Isomer) changes within a single molecule
* EC 6 [*Ligases*](http://en.wikipedia.org/wiki/Ligase): join two molecules with [covalent bonds](http://en.wikipedia.org/wiki/Covalent_bond).

According to the naming conventions, enzymes are generally classified into six main family classes and many sub-family classes. Some web-servers, e.g., [EzyPred](http://www.csbio.sjtu.edu.cn/bioinf/EzyPred/) [[93]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-93) and bioinformatics tools have been developed to predict which main family class [[94]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-94) and sub-family class [[95]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-95) [[96]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-96) an enzyme molecule belongs to according to its sequence information alone via the [pseudo amino acid composition](http://en.wikipedia.org/wiki/Pseudo_amino_acid_composition).

**Industrial applications**

Enzymes are used in the [chemical industry](http://en.wikipedia.org/wiki/Chemical_industry) and other industrial applications when extremely specific catalysts are required. However, enzymes in general are limited in the number of reactions they have evolved to catalyze and also by their lack of stability in [organic solvents](http://en.wikipedia.org/wiki/Organic_solvent) and at high temperatures. As a consequence, [protein engineering](http://en.wikipedia.org/wiki/Protein_engineering) is an active area of research and involves attempts to create new enzymes with novel properties, either through rational design or *in vitro* evolution.[[97]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-97)[[98]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-98) These efforts have begun to be successful, and a few enzymes have now been designed "from scratch" to catalyze reactions that do not occur in nature.[[99]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-99)

|  |  |  |
| --- | --- | --- |
| **Application** | **Enzymes used** | **Uses** |
| [**Food processing**](http://en.wikipedia.org/wiki/Food_processing)  [http://upload.wikimedia.org/wikipedia/commons/thumb/4/45/Amylose.svg/180px-Amylose.svg.png](http://en.wikipedia.org/wiki/File:Amylose.svg)  Amylases catalyze the release of simple sugars from starch. | [Amylases](http://en.wikipedia.org/wiki/Amylase) from [fungi](http://en.wikipedia.org/wiki/Fungus) and plants | Production of sugars from [starch](http://en.wikipedia.org/wiki/Starch), such as in making [high-fructose corn syrup](http://en.wikipedia.org/wiki/High-fructose_corn_syrup).[[100]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-100) In baking, catalyze breakdown of starch in the [flour](http://en.wikipedia.org/wiki/Flour) to sugar. Yeast fermentation of sugar produces the carbon dioxide that raises the dough. |
| Proteases | Biscuit manufacturers use them to lower the protein level of flour. |
| [**Baby foods**](http://en.wikipedia.org/wiki/Baby_food) | [Trypsin](http://en.wikipedia.org/wiki/Trypsin) | To predigest baby foods |
| [**Brewing industry**](http://en.wikipedia.org/wiki/Brewing)  [http://upload.wikimedia.org/wikipedia/commons/thumb/3/32/Sjb_whiskey_malt.jpg/180px-Sjb_whiskey_malt.jpg](http://en.wikipedia.org/wiki/File:Sjb_whiskey_malt.jpg)  Germinating [barley](http://en.wikipedia.org/wiki/Barley) used for malt | Enzymes from barley are released during the mashing stage of beer production. | They degrade starch and proteins to produce simple sugar, amino acids and peptides that are used by yeast for fermentation. |
| Industrially produced barley enzymes | Widely used in the brewing process to substitute for the natural enzymes found in barley. |
| Amylase, glucanases, proteases | Split polysaccharides and proteins in the [malt](http://en.wikipedia.org/wiki/Malt). |
| Betaglucanases and arabinoxylanases | Improve the wort and beer filtration characteristics. |
| Amyloglucosidase and pullulanases | Low-calorie [beer](http://en.wikipedia.org/wiki/Beer) and adjustment of fermentability. |
| Proteases | Remove cloudiness produced during storage of beers. |
|  | Acetolactatedecarboxylase (ALDC) | Increases fermentation efficiency by reducing [diacetyl](http://en.wikipedia.org/wiki/Diacetyl)formation.[[101]](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_note-101) |
| [**Fruit juices**](http://en.wikipedia.org/wiki/Juice) | Cellulases, pectinases | Clarify fruit juices. |
| [**Dairy industry**](http://en.wikipedia.org/wiki/Dairy)  [http://upload.wikimedia.org/wikipedia/commons/thumb/9/92/Roquefort_cheese.jpg/180px-Roquefort_cheese.jpg](http://en.wikipedia.org/wiki/File:Roquefort_cheese.jpg)  Roquefort cheese | [Rennin](http://en.wikipedia.org/wiki/Rennin), derived from the stomachs of young [ruminant animals](http://en.wikipedia.org/wiki/Ruminant)(like calves and lambs) | Manufacture of cheese, used to [hydrolyze](http://en.wikipedia.org/wiki/Hydrolyze) protein |
| Microbially produced enzyme | Now finding increasing use in the dairy industry |
| [Lipases](http://en.wikipedia.org/wiki/Lipase) | Is implemented during the production of [Roquefort cheese](http://en.wikipedia.org/wiki/Roquefort_cheese) to enhance the ripening of the [blue-mold cheese](http://en.wikipedia.org/wiki/Danish_Blue_cheese). |
| Lactases | Break down [lactose](http://en.wikipedia.org/wiki/Lactose) to [glucose](http://en.wikipedia.org/wiki/Glucose) and galactose. |
| [**Meat tenderizers**](http://en.wikipedia.org/wiki/Tenderizing) | [Papain](http://en.wikipedia.org/wiki/Papain) | To soften meat for cooking |
| [**Starch industry**](http://en.wikipedia.org/wiki/Starch)  [http://upload.wikimedia.org/wikipedia/commons/thumb/c/c6/Alpha-D-Glucopyranose.svg/90px-Alpha-D-Glucopyranose.svg.png](http://en.wikipedia.org/wiki/File:Alpha-D-Glucopyranose.svg)  Glucose  [http://upload.wikimedia.org/wikipedia/commons/thumb/4/4a/Alpha-D-Fructofuranose.svg/110px-Alpha-D-Fructofuranose.svg.png](http://en.wikipedia.org/wiki/File:Alpha-D-Fructofuranose.svg)  Fructose | Amylases, amyloglucosideases and glucoamylases | Converts [starch](http://en.wikipedia.org/wiki/Starch) into [glucose](http://en.wikipedia.org/wiki/Glucose) and various [syrups](http://en.wikipedia.org/wiki/Inverted_sugar_syrup). |
| Glucose isomerase | Converts [glucose](http://en.wikipedia.org/wiki/Glucose) into [fructose](http://en.wikipedia.org/wiki/Fructose) in production of [high-fructose syrups](http://en.wikipedia.org/wiki/High-fructose_corn_syrup) from starchy materials. These syrups have enhanced sweetening properties and lower [calorific values](http://en.wikipedia.org/wiki/Calorie) than sucrose for the same level of sweetness. |
| [**Paper industry**](http://en.wikipedia.org/wiki/Paper)  [http://upload.wikimedia.org/wikipedia/commons/thumb/c/c5/InternationalPaper6413.jpg/160px-InternationalPaper6413.jpg](http://en.wikipedia.org/wiki/File:InternationalPaper6413.jpg)  A paper mill in [South Carolina](http://en.wikipedia.org/wiki/South_Carolina) | [Amylases](http://en.wikipedia.org/wiki/Amylase), [Xylanases](http://en.wikipedia.org/wiki/Xylanase), [Cellulases](http://en.wikipedia.org/wiki/Cellulase) and [ligninases](http://en.wikipedia.org/wiki/Ligninase) | Degrade starch to lower [viscosity](http://en.wikipedia.org/wiki/Viscosity), aiding [sizing](http://en.wikipedia.org/wiki/Sizing) and coating paper. Xylanases reduce bleach required for decolorizing; cellulases smooth fibers, enhance water drainage, and promote ink removal; lipases reduce pitch and lignin-degrading enzymes remove [lignin](http://en.wikipedia.org/wiki/Lignin) to soften paper. |
| [**Biofuel**](http://en.wikipedia.org/wiki/Biofuel)**industry**  [http://upload.wikimedia.org/wikipedia/commons/thumb/f/f9/Cellulose-Ibeta-from-xtal-2002-3D-balls.png/220px-Cellulose-Ibeta-from-xtal-2002-3D-balls.png](http://en.wikipedia.org/wiki/File:Cellulose-Ibeta-from-xtal-2002-3D-balls.png)  Cellulose in 3D | [Cellulases](http://en.wikipedia.org/wiki/Cellulase) | Used to break down cellulose into sugars that can be fermented (see [cellulosic ethanol](http://en.wikipedia.org/wiki/Cellulosic_ethanol)) |
| [Ligninases](http://en.wikipedia.org/wiki/Ligninase) | Use of [lignin](http://en.wikipedia.org/wiki/Lignin) waste |
| [**Biological detergent**](http://en.wikipedia.org/wiki/Biological_detergent) | Primarily [proteases](http://en.wikipedia.org/wiki/Protease), produced in an [extracellular](http://en.wikipedia.org/wiki/Extracellular) form from[bacteria](http://en.wikipedia.org/wiki/Bacteria) | Used for presoak conditions and direct liquid applications helping with removal of protein stains from clothes |
| [Amylases](http://en.wikipedia.org/wiki/Amylase) | [Detergents](http://en.wikipedia.org/wiki/Detergents) for machine dish washing to remove resistant starch residues |
| [Lipases](http://en.wikipedia.org/wiki/Lipase) | Used to assist in the removal of fatty and oily stains |
| [Cellulases](http://en.wikipedia.org/wiki/Cellulase) | Used in biological [fabric conditioners](http://en.wikipedia.org/wiki/Fabric_conditioner) |
| [**Contact lens cleaners**](http://en.wikipedia.org/wiki/Contact_lens) | [Proteases](http://en.wikipedia.org/wiki/Proteases) | To remove [proteins](http://en.wikipedia.org/wiki/Proteins) on [contact lens](http://en.wikipedia.org/wiki/Contact_lens) to prevent infections |
| [**Rubber industry**](http://en.wikipedia.org/wiki/Rubber) | [Catalase](http://en.wikipedia.org/wiki/Catalase) | To generate [oxygen](http://en.wikipedia.org/wiki/Oxygen) from [peroxide](http://en.wikipedia.org/wiki/Peroxide) to convert [latex](http://en.wikipedia.org/wiki/Latex) into foam rubber |
| [**Photographic industry**](http://en.wikipedia.org/wiki/Photography) | [Protease](http://en.wikipedia.org/wiki/Protease) (ficin) | Dissolve [gelatin](http://en.wikipedia.org/wiki/Gelatin) off scrap [film](http://en.wikipedia.org/wiki/Photographic_film), allowing recovery of its [silver](http://en.wikipedia.org/wiki/Silver)content. |
| [**Molecular biology**](http://en.wikipedia.org/wiki/Molecular_biology)  [http://upload.wikimedia.org/wikipedia/commons/thumb/d/d9/DNA123_rotated.png/180px-DNA123_rotated.png](http://en.wikipedia.org/wiki/File:DNA123_rotated.png)  Part of the DNA [double helix](http://en.wikipedia.org/wiki/Double_helix) | [Restriction enzymes](http://en.wikipedia.org/wiki/Restriction_enzyme), [DNA ligase](http://en.wikipedia.org/wiki/DNA_ligase) and [polymerases](http://en.wikipedia.org/wiki/Polymerases) | Used to manipulate DNA in [genetic engineering](http://en.wikipedia.org/wiki/Genetic_engineering), important in[pharmacology](http://en.wikipedia.org/wiki/Pharmacology), [agriculture](http://en.wikipedia.org/wiki/Agriculture) and [medicine](http://en.wikipedia.org/wiki/Medicine). Essential for [restriction digestion](http://en.wikipedia.org/wiki/Restriction_enzyme) and the [polymerase chain reaction](http://en.wikipedia.org/wiki/Polymerase_chain_reaction). Molecular biology is also important in [forensic science](http://en.wikipedia.org/wiki/Forensic_science). |

**See also**

* [Catalytic triad](http://en.wikipedia.org/wiki/Catalytic_triad)
* [Diffusion limited enzyme](http://en.wikipedia.org/wiki/Diffusion_limited_enzyme)
* [Enzyme substrate (biology)](http://en.wikipedia.org/wiki/Enzyme_substrate_(biology))
* [Immobilized enzyme](http://en.wikipedia.org/wiki/Immobilized_enzyme)
* [Ki Database](http://en.wikipedia.org/wiki/Ki_Database)
* [List of enzymes](http://en.wikipedia.org/wiki/List_of_enzymes)
* [Proteomics](http://en.wikipedia.org/wiki/Proteomics)
* [Protein family](http://en.wikipedia.org/wiki/Protein_family)
* [Protein superfamily](http://en.wikipedia.org/wiki/Protein_superfamily)
* [SUMO enzymes](http://en.wikipedia.org/wiki/SUMO_enzymes)
* [The Proteolysis Map](http://en.wikipedia.org/wiki/The_Proteolysis_Map)

**References**

* 1. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-1) Smith AL (Ed) (1997). *Oxford dictionary of biochemistry and molecular biology*. Oxford [Oxfordshire]: Oxford University Press. [ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [0-19-854768-4](http://en.wikipedia.org/wiki/Special:BookSources/0-19-854768-4).
  2. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-2) Grisham, Charles M.; Reginald H. Garrett (1999). *Biochemistry*. Philadelphia: Saunders College Pub. pp. 426–7. [ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [0-03-022318-0](http://en.wikipedia.org/wiki/Special:BookSources/0-03-022318-0).
  3. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-3) Bairoch A. (2000). ["The ENZYME database in 2000"](http://web.archive.org/web/20110601003507/http:/www.expasy.org/NAR/enz00.pdf) (PDF).*Nucleic Acids Res* **28** (1): 304–5. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1093/nar/28.1.304](http://dx.doi.org/10.1093%2Fnar%2F28.1.304). [PMC](http://en.wikipedia.org/wiki/PubMed_Central) [102465](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC102465). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [10592255](http://www.ncbi.nlm.nih.gov/pubmed/10592255).
  4. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-4) Lilley D (2005). "Structure, folding and mechanisms of ribozymes". *Current Opinion in Structural Biology* **15** (3): 313–23. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/j.sbi.2005.05.002](http://dx.doi.org/10.1016%2Fj.sbi.2005.05.002). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [15919196](http://www.ncbi.nlm.nih.gov/pubmed/15919196).
  5. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-5) Cech T (2000). "Structural biology. The ribosome is a ribozyme". *Science* **289** (5481): 878–9. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1126/science.289.5481.878](http://dx.doi.org/10.1126%2Fscience.289.5481.878).[PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [10960319](http://www.ncbi.nlm.nih.gov/pubmed/10960319).
  6. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-6) Groves JT (1997). "Artificial enzymes. The importance of being selective". *Nature* **389**(6649): 329–30. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1038/38602](http://dx.doi.org/10.1038%2F38602). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [9311771](http://www.ncbi.nlm.nih.gov/pubmed/9311771).
  7. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-Reaumur1752_7-0) [de Réaumur, RAF](http://en.wikipedia.org/wiki/Ren%C3%A9_Antoine_Ferchault_de_R%C3%A9aumur) (1752). "Observations sur la digestion des oiseaux". *Histoire de l'academie royale des sciences* **1752**: 266, 461.
  8. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-8) Williams, H. S. (1904) [A History of Science: in Five Volumes. Volume IV: Modern Development of the Chemical and Biological Sciences](http://etext.lib.virginia.edu/toc/modeng/public/Wil4Sci.html) Harper and Brothers (New York) Accessed 4 April 2007
  9. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-9) Payen, A. et J.-F. Persoz (1833) ["Mémoire sur la diastase, les principaux produits de ses réactions et leurs applications aux arts industriels"](http://books.google.be/books?id=Q9I3AAAAMAAJ&pg=PA73#v=onepage&q&f=false) (Memoir on diastase, the principal products of its reactions and their applications to the industrial arts), *Annales de chimie et de physique*, 2nd series, **53** : 73–92.
  10. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-10) Dubos J. (1951). "Louis Pasteur: Free Lance of Science, Gollancz. Quoted in Manchester K. L. (1995) Louis Pasteur (1822–1895)—chance and the prepared mind". *Trends Biotechnol* **13**(12): 511–5. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/S0167-7799(00)89014-9](http://dx.doi.org/10.1016%2FS0167-7799%2800%2989014-9). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [8595136](http://www.ncbi.nlm.nih.gov/pubmed/8595136).
  11. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-11) Kühne coined the word "enzyme" in: W. Kühne (1877) "[Über das Verhalten verschiedener organisirter und sog. ungeformter Fermente](http://books.google.com/books?id=jzdMAAAAYAAJ&pg=PA190&ie=ISO-8859-1&output=html)" (On the behavior of various organized and so-called unformed ferments), *Verhandlungen des naturhistorisch-medicinischen Vereins zu Heidelberg*, new series, vol. 1, no. 3, pages 190–193. The relevant passage occurs on page 190: *"Um Missverständnissen vorzubeugen und lästige Umschreibungen zu vermeiden schlägt Vortragender vor, die ungeformten oder nicht organisirten Fermente, deren Wirkung ohne Anwesenheit von Organismen und ausserhalb derselben erfolgen kann, als* Enzyme *zu bezeichnen."* (Translation: In order to obviate misunderstandings and avoid cumbersome periphrases, [the author, a university lecturer] suggests designating as "enzymes" the unformed or not organized ferments, whose action can occur without the presence of organisms and outside of the same.)
  12. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-12) [Nobel Laureate Biography of Eduard Buchner at http://nobelprize.org](http://nobelprize.org/nobel_prizes/chemistry/laureates/1907/buchner-bio.html). Retrieved 4 April 2007.
  13. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-13) [Text of Eduard Buchner's 1907 Nobel lecture at http://nobelprize.org](http://nobelprize.org/nobel_prizes/chemistry/laureates/1907/buchner-lecture.html). Retrieved 4 April 2007.
  14. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-14) The naming of enzymes by adding the suffix "-ase" to the substrate on which the enzyme acts, has been traced to French scientist [Émile Duclaux](http://en.wikipedia.org/wiki/%C3%89mile_Duclaux) (1840–1904), who intended to honor the discoverers of [diastase](http://en.wikipedia.org/wiki/Diastase) – the first enzyme to be isolated – by introducing this practice in his book[*Traité de Microbiologie*](http://books.google.com/books?id=Kp9EAAAAQAAJ&printsec=frontcover), vol. 2 (Paris, France: Masson and Co., 1899). See Chapter 1, especially page 9.
  15. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-15) Willstätter, R. (1927). Problems and Methods in Enzyme Research. Cornell University Press, Ithaca. quoted in Blow, David (2000). ["So do we understand how enzymes work?"](http://cmgm3.stanford.edu/biochem/sb241/Herschlag_lectures/papers/Blow.pdf) (pdf).*Structure* **8** (4): R77–R81. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/S0969-2126(00)00125-8](http://dx.doi.org/10.1016%2FS0969-2126%2800%2900125-8). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [10801479](http://www.ncbi.nlm.nih.gov/pubmed/10801479).
  16. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-16) [1946 Nobel prize for Chemistry laureates at http://nobelprize.org](http://nobelprize.org/nobel_prizes/chemistry/laureates/1946/). Retrieved 4 April 2007.
  17. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-17) Blake CC, Koenig DF, Mair GA, North AC, Phillips DC, Sarma VR. (1965). "Structure of hen egg-white lysozyme. A three-dimensional Fourier synthesis at 2 Angstrom resolution".*Nature* **206** (4986): 757–61. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1038/206757a0](http://dx.doi.org/10.1038%2F206757a0). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [5891407](http://www.ncbi.nlm.nih.gov/pubmed/5891407).
  18. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-18) Chen LH, Kenyon GL, Curtin F, Harayama S, Bembenek ME, Hajipour G, Whitman CP (1992). "4-Oxalocrotonate tautomerase, an enzyme composed of 62 amino acid residues per monomer". *J. Biol. Chem.* **267** (25): 17716–21. [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [1339435](http://www.ncbi.nlm.nih.gov/pubmed/1339435).
  19. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-19) Smith S (1 December 1994). "The animal fatty acid synthase: one gene, one polypeptide, seven enzymes". *FASEB J.* **8** (15): 1248–59. [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [8001737](http://www.ncbi.nlm.nih.gov/pubmed/8001737).
  20. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-20) Anfinsen C.B. (1973). "Principles that Govern the Folding of Protein Chains". *Science* **181**(4096): 223–30. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1126/science.181.4096.223](http://dx.doi.org/10.1126%2Fscience.181.4096.223). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [4124164](http://www.ncbi.nlm.nih.gov/pubmed/4124164).
  21. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-21) Dunaway-Mariano D (2008). "Enzyme function discovery". *Structure* **16** (11): 1599–600.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/j.str.2008.10.001](http://dx.doi.org/10.1016%2Fj.str.2008.10.001).[PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [19000810](http://www.ncbi.nlm.nih.gov/pubmed/19000810).
  22. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-22) [The Catalytic Site Atlas at The European Bioinformatics Institute](http://www.ebi.ac.uk/thornton-srv/databases/CSA/). Retrieved 4 April 2007.
  23. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-23) Jaeger KE, Eggert T. (2004). "Enantioselective biocatalysis optimized by directed evolution".*Current Opinion in Biotechnology* **15** (4): 305–13. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/j.copbio.2004.06.007](http://dx.doi.org/10.1016%2Fj.copbio.2004.06.007). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [15358000](http://www.ncbi.nlm.nih.gov/pubmed/15358000).
  24. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-24) Shevelev IV, Hubscher U. (2002). "The 3' 5' exonucleases". *Nature Reviews Molecular Cell Biology* **3** (5): 364–76. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1038/nrm804](http://dx.doi.org/10.1038%2Fnrm804).[PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [11988770](http://www.ncbi.nlm.nih.gov/pubmed/11988770).
  25. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-25) Tymoczko, John L.; Stryer Berg Tymoczko; Stryer, Lubert; Berg, Jeremy Mark (2002).*Biochemistry*. San Francisco: W.H. Freeman. [ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [0-7167-4955-6](http://en.wikipedia.org/wiki/Special:BookSources/0-7167-4955-6).
  26. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-26) Zenkin N, Yuzenkova Y, Severinov K. (2006). "Transcript-assisted transcriptional proofreading". *Science.* **313** (5786): 518–20. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1126/science.1127422](http://dx.doi.org/10.1126%2Fscience.1127422). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [16873663](http://www.ncbi.nlm.nih.gov/pubmed/16873663).
  27. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-27) Ibba M, Soll D. (2000). "Aminoacyl-tRNA synthesis". *Annu Rev Biochem.* **69**: 617–50.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1146/annurev.biochem.69.1.617](http://dx.doi.org/10.1146%2Fannurev.biochem.69.1.617). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [10966471](http://www.ncbi.nlm.nih.gov/pubmed/10966471).
  28. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-28) Rodnina MV, Wintermeyer W. (2001). "Fidelity of aminoacyl-tRNA selection on the ribosome: kinetic and structural mechanisms". *Annu Rev Biochem.* **70**: 415–35.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1146/annurev.biochem.70.1.415](http://dx.doi.org/10.1146%2Fannurev.biochem.70.1.415). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [11395413](http://www.ncbi.nlm.nih.gov/pubmed/11395413).
  29. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-Tawfik10_29-0) Tawfik, O. K. A. D. S.; Tawfik, D. S. (2010). "Enzyme Promiscuity: A Mechanistic and Evolutionary Perspective". *Annual Review of Biochemistry* **79**: 471–505.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1146/annurev-biochem-030409-143718](http://dx.doi.org/10.1146%2Fannurev-biochem-030409-143718). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [20235827](http://www.ncbi.nlm.nih.gov/pubmed/20235827).
  30. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-30) Fischer E. (1894). ["Einfluss der Configuration auf die Wirkung der Enzyme" [Influence of configuration on the action of enzymes]](http://gallica.bnf.fr/ark:/12148/bpt6k90736r/f364.chemindefer). *Berichte der Deutschen chemischen Gesellschaft zu Berlin* **27** (3): 2985–93. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1002/cber.18940270364](http://dx.doi.org/10.1002%2Fcber.18940270364). From page 2992: *"Um ein Bild zu gebrauchen, will ich sagen, dass Enzym und Glucosid wie Schloss und Schlüssel zu einander passen müssen, um eine chemische Wirkung auf einander ausüben zu können."*(To use an image, I will say that an enzyme and a glucoside [i.e., glucose derivative] must fit like a lock and key, in order to be able to exert a chemical effect on each other.)
  31. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-31) Koshland D. E. (1958). ["Application of a Theory of Enzyme Specificity to Protein Synthesis"](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC335371). *Proc. Natl. Acad. Sci.* **44** (2): 98–104. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1073/pnas.44.2.98](http://dx.doi.org/10.1073%2Fpnas.44.2.98). [PMC](http://en.wikipedia.org/wiki/PubMed_Central) [335371](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC335371). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [16590179](http://www.ncbi.nlm.nih.gov/pubmed/16590179).
  32. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-32) Vasella A, Davies GJ, Bohm M. (2002). "Glycosidase mechanisms". *Current Opinion in Chemical Biology* **6** (5): 619–29. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/S1367-5931(02)00380-0](http://dx.doi.org/10.1016%2FS1367-5931%2802%2900380-0). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [12413546](http://www.ncbi.nlm.nih.gov/pubmed/12413546).
  33. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-33) Boyer, Rodney (2002) [2002]. "6". *Concepts in Biochemistry* (2nd ed.). New York, Chichester, Weinheim, Brisbane, Singapore, Toronto.: John Wiley & Sons, Inc. pp. 137–8.[ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [0-470-00379-0](http://en.wikipedia.org/wiki/Special:BookSources/0-470-00379-0). [OCLC](http://en.wikipedia.org/wiki/OCLC) [51720783](http://www.worldcat.org/oclc/51720783).
  34. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-34) Savir Y & Tlusty T (2007). ["Conformational proofreading: the impact of conformational changes on the specificity of molecular recognition"](http://www.weizmann.ac.il/complex/tlusty/papers/PLoSONE2007.pdf). In Scalas, Enrico.*PLoS ONE* **2** (5): e468. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1371/journal.pone.0000468](http://dx.doi.org/10.1371%2Fjournal.pone.0000468). [PMC](http://en.wikipedia.org/wiki/PubMed_Central) [1868595](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1868595). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [17520027](http://www.ncbi.nlm.nih.gov/pubmed/17520027).
  35. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-Chou01_35-0) Chou K.C. (1996). "Review: Prediction of human immunodeficiency virus protease cleavage sites in proteins". *Analytical Biochemistry* **233** (1): 1–14. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1006/abio.1996.0001](http://dx.doi.org/10.1006%2Fabio.1996.0001). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [8789141](http://www.ncbi.nlm.nih.gov/pubmed/8789141).
  36. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-Gan01_36-0) Gan, Y. R., Huang, H., Huang, Y. D., Rao, C. M., Zhao, Y., Liu, J. S., Wu, L. & Wei, D. Q. (April 2006). "Synthesis and activity of an octapeptide inhibitor designed for SARS coronavirus main proteinase". *Peptides* **27** (4): 622–625. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/j.peptides.2005.09.006](http://dx.doi.org/10.1016%2Fj.peptides.2005.09.006). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [16242214](http://www.ncbi.nlm.nih.gov/pubmed/16242214).
  37. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-Du01_37-0) Du, Q. S., Wang, S., Wei, D. Q., Sirois, S. & Chou, K. C. (2005). "Molecular modelling and chemical modification for finding peptide inhibitor against SARS CoV Mpro". *Analytical Biochemistry* **337** (2): 262–270. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/j.ab.2004.10.003](http://dx.doi.org/10.1016%2Fj.ab.2004.10.003). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [15691506](http://www.ncbi.nlm.nih.gov/pubmed/15691506).
  38. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-Du02_38-0) Du, Q. S., Sun, H. & Chou, K. C. (2007). "Inhibitor design for SARS coronavirus main protease based on "distorted key theory"". *Medicinal Chemistry* **3** (1): 1–6.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.2174/157340607779317616](http://dx.doi.org/10.2174%2F157340607779317616).[PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [17266617](http://www.ncbi.nlm.nih.gov/pubmed/17266617).
  39. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-39) Fersht, Alan (1985). *Enzyme structure and mechanism*. San Francisco: W.H. Freeman. pp. 50–2. [ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [0-7167-1615-1](http://en.wikipedia.org/wiki/Special:BookSources/0-7167-1615-1).
  40. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-40) Jencks, William P. (1987). *Catalysis in chemistry and enzymology*. Mineola, N.Y: Dover.[ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [0-486-65460-5](http://en.wikipedia.org/wiki/Special:BookSources/0-486-65460-5).
  41. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-41) Villa J, Strajbl M, Glennon TM, Sham YY, Chu ZT, Warshel A (2000). ["How important are entropic contributions to enzyme catalysis?"](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC17266). *Proc. Natl. Acad. Sci. U.S.A.* **97**(22): 11899–904. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1073/pnas.97.22.11899](http://dx.doi.org/10.1073%2Fpnas.97.22.11899). [PMC](http://en.wikipedia.org/wiki/PubMed_Central) [17266](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC17266). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [11050223](http://www.ncbi.nlm.nih.gov/pubmed/11050223).
  42. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-42) Warshel A, Sharma PK, Kato M, Xiang Y, Liu H, Olsson MH (2006). "Electrostatic basis for enzyme catalysis". *Chem. Rev.* **106** (8): 3210–35. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1021/cr0503106](http://dx.doi.org/10.1021%2Fcr0503106). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [16895325](http://www.ncbi.nlm.nih.gov/pubmed/16895325).
  43. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-43) Eisenmesser EZ, Bosco DA, Akke M, Kern D (2002). "Enzyme dynamics during catalysis".*Science* **295** (5559): 1520–3. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1126/science.1066176](http://dx.doi.org/10.1126%2Fscience.1066176). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [11859194](http://www.ncbi.nlm.nih.gov/pubmed/11859194).
  44. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-44) Agarwal PK (2005). "Role of protein dynamics in reaction rate enhancement by enzymes". *J. Am. Chem. Soc.* **127** (43): 15248–56. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1021/ja055251s](http://dx.doi.org/10.1021%2Fja055251s). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [16248667](http://www.ncbi.nlm.nih.gov/pubmed/16248667).
  45. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-45) Eisenmesser EZ, Millet O, Labeikovsky W (2005). "Intrinsic dynamics of an enzyme underlies catalysis". *Nature* **438** (7064): 117–21. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1038/nature04105](http://dx.doi.org/10.1038%2Fnature04105). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [16267559](http://www.ncbi.nlm.nih.gov/pubmed/16267559).
  46. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-46) Yang LW, Bahar I (5 June 2005). ["Coupling between catalytic site and collective dynamics: A requirement for mechanochemical activity of enzymes"](http://www.cell.com/structure/abstract/S0969-2126%2805%2900167-X). *Structure* **13** (6): 893–904. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/j.str.2005.03.015](http://dx.doi.org/10.1016%2Fj.str.2005.03.015).[PMC](http://en.wikipedia.org/wiki/PubMed_Central) [1489920](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1489920). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [15939021](http://www.ncbi.nlm.nih.gov/pubmed/15939021).
  47. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-47) Agarwal PK, Billeter SR, Rajagopalan PT, Benkovic SJ, Hammes-Schiffer S. (5 March 2002). ["Network of coupled promoting motions in enzyme catalysis"](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC122427). *Proc Natl Acad Sci USA.* **99** (5): 2794–9. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1073/pnas.052005999](http://dx.doi.org/10.1073%2Fpnas.052005999).[PMC](http://en.wikipedia.org/wiki/PubMed_Central) [122427](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC122427). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [11867722](http://www.ncbi.nlm.nih.gov/pubmed/11867722).
  48. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-48) Agarwal PK, Geist A, Gorin A (2004). "Protein dynamics and enzymatic catalysis: investigating the peptidyl-prolyl cis-trans isomerization activity of cyclophilin A". *Biochemistry***43** (33): 10605–18. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1021/bi0495228](http://dx.doi.org/10.1021%2Fbi0495228).[PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [15311922](http://www.ncbi.nlm.nih.gov/pubmed/15311922).
  49. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-49) Tousignant A, Pelletier JN. (2004). "Protein motions promote catalysis". *Chem Biol.* **11** (8): 1037–42. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/j.chembiol.2004.06.007](http://dx.doi.org/10.1016%2Fj.chembiol.2004.06.007). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [15324804](http://www.ncbi.nlm.nih.gov/pubmed/15324804).
  50. ^ [Jump up to:***a***](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-OF_2005_50-0) [***b***](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-OF_2005_50-1) Flomenbom O, Velonia K, Loos D et al. (2005). ["Stretched exponential decay and correlations in the catalytic activity of fluctuating single lipase molecules"](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC548972). *Proc. Natl. Acad. Sci. U.S.A.* **102**(7): 2368–2372. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1073/pnas.0409039102](http://dx.doi.org/10.1073%2Fpnas.0409039102). [PMC](http://en.wikipedia.org/wiki/PubMed_Central) [548972](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC548972). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [15695587](http://www.ncbi.nlm.nih.gov/pubmed/15695587).
  51. ^ [Jump up to:***a***](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-English_2006_51-0) [***b***](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-English_2006_51-1) English BP, Min W, van Oijen AM et al. (2006). "Ever-fluctuating single enzyme molecules: Michaelis-Menten equation revisited". *Nature Chemical Biology* **2** (2): 87–94.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1038/nchembio759](http://dx.doi.org/10.1038%2Fnchembio759). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [16415859](http://www.ncbi.nlm.nih.gov/pubmed/16415859).
  52. ^ [Jump up to:***a***](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-Lu_1998_52-0) [***b***](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-Lu_1998_52-1) Lu H, Xun L, Xie X S (1998). "Single-molecule enzymatic dynamics". *Science* **282**(5395): 1877–1882. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1126/science.282.5395.1877](http://dx.doi.org/10.1126%2Fscience.282.5395.1877). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [9836635](http://www.ncbi.nlm.nih.gov/pubmed/9836635).
  53. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-53) Olsson, MH; Parson, WW; Warshel, A (2006). "Dynamical Contributions to Enzyme Catalysis: Critical Tests of A Popular Hypothesis". *Chem. Rev.* **106** (5): 1737–56.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1021/cr040427e](http://dx.doi.org/10.1021%2Fcr040427e). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [16683752](http://www.ncbi.nlm.nih.gov/pubmed/16683752).
  54. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-54) Neet KE (1995). "Cooperativity in enzyme function: equilibrium and kinetic aspects". *Meth. Enzymol*. Methods in Enzymology **249**: 519–67. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/0076-6879(95)49048-5](http://dx.doi.org/10.1016%2F0076-6879%2895%2949048-5). [ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [978-0-12-182150-0](http://en.wikipedia.org/wiki/Special:BookSources/978-0-12-182150-0).[PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [7791626](http://www.ncbi.nlm.nih.gov/pubmed/7791626).
  55. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-55) Changeux JP, Edelstein SJ (2005). "Allosteric mechanisms of signal transduction". *Science***308** (5727): 1424–8. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1126/science.1108595](http://dx.doi.org/10.1126%2Fscience.1108595). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [15933191](http://www.ncbi.nlm.nih.gov/pubmed/15933191).
  56. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-56) de Bolster, M.W.G. (1997). ["Glossary of Terms Used in Bioinorganic Chemistry: Cofactor"](http://www.chem.qmul.ac.uk/iupac/bioinorg/CD.html#34). International Union of Pure and Applied Chemistry. Retrieved 30 October 2007.
  57. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-57) de Bolster, M.W.G. (1997). ["Glossary of Terms Used in Bioinorganic Chemistry: Coenzyme"](http://www.chem.qmul.ac.uk/iupac/bioinorg/CD.html#33). International Union of Pure and Applied Chemistry. Retrieved 30 October 2007.
  58. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-58) Fisher Z, Hernandez Prada JA, Tu C, Duda D, Yoshioka C, An H, Govindasamy L, Silverman DN and McKenna R. (2005). "Structural and kinetic characterization of active-site histidine as a proton shuttle in catalysis by human carbonic anhydrase II". *Biochemistry.* **44** (4): 1097–115. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1021/bi0480279](http://dx.doi.org/10.1021%2Fbi0480279).[PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [15667203](http://www.ncbi.nlm.nih.gov/pubmed/15667203).
  59. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-59) Wagner, Arthur L. (1975). *Vitamins and Coenzymes*. Krieger Pub Co. [ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [0-88275-258-8](http://en.wikipedia.org/wiki/Special:BookSources/0-88275-258-8).
  60. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-60) [BRENDA The Comprehensive Enzyme Information System](http://www.brenda.uni-koeln.de/). Retrieved 4 April 2007.
  61. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-61) Törnroth-Horsefield S, Neutze R (2008). ["Opening and closing the metabolite gate"](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2604989). *Proc. Natl. Acad. Sci. U.S.A.* **105**(50): 19565–6. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1073/pnas.0810654106](http://dx.doi.org/10.1073%2Fpnas.0810654106). [PMC](http://en.wikipedia.org/wiki/PubMed_Central) [2604989](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2604989). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [19073922](http://www.ncbi.nlm.nih.gov/pubmed/19073922).
  62. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-Nicholls_62-0) Ferguson, S. J.; Nicholls, David; Ferguson, Stuart (2002). *Bioenergetics 3* (3rd ed.). San Diego: Academic. [ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [0-12-518121-3](http://en.wikipedia.org/wiki/Special:BookSources/0-12-518121-3).
  63. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-63) Henri, V. (1902). "Theorie generale de l'action de quelques diastases". *Compt. Rend. Hebd. Acad. Sci. Paris* **135**: 916–9.
  64. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-64) Sørensen,P.L. (1909). "Enzymstudien {II}. Über die Messung und Bedeutung der Wasserstoffionenkonzentration bei enzymatischen Prozessen". *Biochem. Z.* **21**: 131–304.
  65. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-65) Michaelis L., Menten M. (1913). "Die Kinetik der Invertinwirkung". *Biochem. Z.* **49**: 333–369. [English translation](http://web.lemoyne.edu/~giunta/menten.html). Retrieved 6 April 2007.
  66. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-66) Briggs G. E., Haldane J. B. S. (1925). ["A note on the kinetics of enzyme action"](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1259181). *Biochem. J.* **19** (2): 339–339.[PMC](http://en.wikipedia.org/wiki/PubMed_Central) [1259181](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1259181). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [16743508](http://www.ncbi.nlm.nih.gov/pubmed/16743508).
  67. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-XX_2006_67-0) Xue X, Liu F, Ou-Yang ZC (2006). "Single molecule Michaelis-Menten equation beyond quasistatic disorder". *Phys. Rev. E* **74** (3): 030902. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1103/PhysRevE.74.030902](http://dx.doi.org/10.1103%2FPhysRevE.74.030902). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [17025584](http://www.ncbi.nlm.nih.gov/pubmed/17025584).
  68. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-68) Radzicka A, Wolfenden R. (1995). "A proficient enzyme". *Science* **267** (5194): 90–931.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1126/science.7809611](http://dx.doi.org/10.1126%2Fscience.7809611).[PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [7809611](http://www.ncbi.nlm.nih.gov/pubmed/7809611).
  69. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-69) Ellis RJ (2001). "Macromolecular crowding: obvious but underappreciated". *Trends Biochem. Sci.* **26** (10): 597–604. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/S0968-0004(01)01938-7](http://dx.doi.org/10.1016%2FS0968-0004%2801%2901938-7). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [11590012](http://www.ncbi.nlm.nih.gov/pubmed/11590012).
  70. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-70) Kopelman R (1988). "Fractal Reaction Kinetics". *Science* **241** (4873): 1620–26.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1126/science.241.4873.1620](http://dx.doi.org/10.1126%2Fscience.241.4873.1620).[PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [17820893](http://www.ncbi.nlm.nih.gov/pubmed/17820893).
  71. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-71) Savageau MA (1995). "Michaelis-Menten mechanism reconsidered: implications of fractal kinetics". *J. Theor. Biol.* **176** (1): 115–24. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1006/jtbi.1995.0181](http://dx.doi.org/10.1006%2Fjtbi.1995.0181). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [7475096](http://www.ncbi.nlm.nih.gov/pubmed/7475096).
  72. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-72) Schnell S, Turner TE (2004). "Reaction kinetics in intracellular environments with macromolecular crowding: simulations and rate laws". *Prog. Biophys. Mol. Biol.* **85** (2–3): 235–60. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/j.pbiomolbio.2004.01.012](http://dx.doi.org/10.1016%2Fj.pbiomolbio.2004.01.012). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [15142746](http://www.ncbi.nlm.nih.gov/pubmed/15142746).
  73. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-73) Xu F, Ding H (2007). "A new kinetic model for heterogeneous (or spatially confined) enzymatic catalysis: Contributions from the fractal and jamming (overcrowding) effects". *Appl. Catal. A: Gen.* **317** (1): 70–81. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/j.apcata.2006.10.014](http://dx.doi.org/10.1016%2Fj.apcata.2006.10.014).
  74. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-74) Garcia-Viloca M., Gao J., Karplus M., Truhlar D. G. (2004). "How enzymes work: analysis by modern rate theory and computer simulations". *Science* **303** (5655): 186–95.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1126/science.1088172](http://dx.doi.org/10.1126%2Fscience.1088172).[PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [14716003](http://www.ncbi.nlm.nih.gov/pubmed/14716003).
  75. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-75) Olsson M. H., Siegbahn P. E., Warshel A. (2004). "Simulations of the large kinetic isotope effect and the temperature dependence of the hydrogen atom transfer in lipoxygenase". *J. Am. Chem. Soc.* **126** (9): 2820–8. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1021/ja037233l](http://dx.doi.org/10.1021%2Fja037233l). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [14995199](http://www.ncbi.nlm.nih.gov/pubmed/14995199).
  76. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-76) Masgrau L., Roujeinikova A., Johannissen L. O., Hothi P., Basran J., Ranaghan K. E., Mulholland A. J., Sutcliffe M. J., Scrutton N. S., Leys D. (2006). "Atomic Description of an Enzyme Reaction Dominated by Proton Tunneling". *Science* **312** (5771): 237–41.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1126/science.1126002](http://dx.doi.org/10.1126%2Fscience.1126002).[PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [16614214](http://www.ncbi.nlm.nih.gov/pubmed/16614214).
  77. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-77) Cleland, W.W. (1963). "The Kinetics of Enzyme-catalyzed Reactions with two or more Substrates or Products 2. {I}nhibition: Nomenclature and Theory". *Biochim. Biophys. Acta* **67**: 173–87.
  78. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-78) Price, NC. (1979). "What is meant by 'competitive inhibition'?". *Trends in Biochemical Sciences* **4** (11): pN272. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/0968-0004(79)90205-6](http://dx.doi.org/10.1016%2F0968-0004%2879%2990205-6).
  79. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-79) Dick, Ronald M. (2011). "Chapter 2. Pharmacodynamics: The Study of Drug Action". In Ouellette, Richard G.; Joyce, Joseph A. *Pharmacology for Nurse Anesthesiology*. Jones & Bartlett Learning. [ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [978-0-7637-8607-6](http://en.wikipedia.org/wiki/Special:BookSources/978-0-7637-8607-6).
  80. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-Poulin_80-0) R Poulin; Lu, L; Ackermann, B; Bey, P; Pegg, AE (5 January 1992). "Mechanism of the irreversible inactivation of mouse ornithine decarboxylase by alpha-difluoromethylornithine. Characterization of sequences at the inhibitor and coenzyme binding sites". *Journal of Biological Chemistry* **267** (1): 150–8. [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [1730582](http://www.ncbi.nlm.nih.gov/pubmed/1730582).
  81. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-81) Yoshikawa S and Caughey WS. (15 May 1990). "Infrared evidence of cyanide binding to iron and copper sites in bovine heart cytochrome c oxidase. Implications regarding oxygen reduction". *J Biol Chem.* **265** (14): 7945–58. [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [2159465](http://www.ncbi.nlm.nih.gov/pubmed/2159465).
  82. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-82) Hunter T. (1995). "Protein kinases and phosphatases: the yin and yang of protein phosphorylation and signaling". *Cell.* **80** (2): 225–36. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/0092-8674(95)90405-0](http://dx.doi.org/10.1016%2F0092-8674%2895%2990405-0). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [7834742](http://www.ncbi.nlm.nih.gov/pubmed/7834742).
  83. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-83) Berg JS, Powell BC, Cheney RE (1 April 2001). ["A millennial myosin census"](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC32266). *Mol. Biol. Cell* **12** (4): 780–94.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1091/mbc.12.4.780](http://dx.doi.org/10.1091%2Fmbc.12.4.780). [PMC](http://en.wikipedia.org/wiki/PubMed_Central) [32266](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC32266). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [11294886](http://www.ncbi.nlm.nih.gov/pubmed/11294886).
  84. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-84) Meighen EA (1 March 1991). ["Molecular biology of bacterial bioluminescence"](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC372803). *Microbiol. Rev.* **55** (1): 123–42.[PMC](http://en.wikipedia.org/wiki/PubMed_Central) [372803](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC372803). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [2030669](http://www.ncbi.nlm.nih.gov/pubmed/2030669).
  85. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-85) Mackie RI, White BA (1 October 1990). "Recent advances in rumen microbial ecology and metabolism: potential impact on nutrient output". *J. Dairy Sci.* **73** (10): 2971–95.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.3168/jds.S0022-0302(90)78986-2](http://dx.doi.org/10.3168%2Fjds.S0022-0302%2890%2978986-2). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [2178174](http://www.ncbi.nlm.nih.gov/pubmed/2178174).
  86. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-86) Faergeman NJ, Knudsen J (1997). ["Role of long-chain fatty acyl-CoA esters in the regulation of metabolism and in cell signalling"](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1218279).*Biochem. J.* **323** (Pt 1): 1–12. [PMC](http://en.wikipedia.org/wiki/PubMed_Central) [1218279](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1218279). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [9173866](http://www.ncbi.nlm.nih.gov/pubmed/9173866).
  87. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-87) Doble B. W., Woodgett J. R. (2003). ["GSK-3: tricks of the trade for a multi-tasking kinase"](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3006448). *J. Cell. Sci.* **116** (Pt 7): 1175–86.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1242/jcs.00384](http://dx.doi.org/10.1242%2Fjcs.00384). [PMC](http://en.wikipedia.org/wiki/PubMed_Central) [3006448](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3006448). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [12615961](http://www.ncbi.nlm.nih.gov/pubmed/12615961).
  88. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-88) Carr C. M., Kim P. S. (2003). "A spring-loaded mechanism for the conformational change of influenza hemagglutinin". *Cell* **73** (4): 823–32. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/0092-8674(93)90260-W](http://dx.doi.org/10.1016%2F0092-8674%2893%2990260-W). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [8500173](http://www.ncbi.nlm.nih.gov/pubmed/8500173).
  89. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-89) [Phenylketonuria: NCBI Genes and Disease](http://www.ncbi.nlm.nih.gov/books/bv.fcgi?call=bv.View..ShowSection&rid=gnd.section.234). Retrieved 4 April 2007.
  90. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-90) ["Pseudocholinesterase deficiency"](http://ghr.nlm.nih.gov/condition/pseudocholinesterase-deficiency). U.S. National Library of Medicine. Retrieved 5 September 2013.
  91. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-91) Fuhrmann G, Leroux JC (2011). ["In vivo fluorescence imaging of exogenous enzyme activity in the gastrointestinal tract"](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3107327).*Proceedings of the National Academy of Sciences* **108** (22): 9032–9037.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1073/pnas.1100285108](http://dx.doi.org/10.1073%2Fpnas.1100285108).[PMC](http://en.wikipedia.org/wiki/PubMed_Central) [3107327](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3107327). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [21576491](http://www.ncbi.nlm.nih.gov/pubmed/21576491).
  92. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-92) The complete nomenclature can be browsed at [Enzyme Nomenclature](http://www.chem.qmul.ac.uk/iubmb/enzyme/). Recommendations of the Nomenclature Committee of the International Union of Biochemistry and Molecular Biology on the Nomenclature and Classification of Enzymes by the Reactions they Catalyse. Nomenclature Committee of the International Union of Biochemistry and Molecular Biology (NC-IUBMB)
  93. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-93) Shen, HB; Chou, KC (2007). "EzyPred: A top-down approach for predicting enzyme functional classes and subclasses". *Biochemical and Biophysical Research Communications***364** (1): 53–9. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/j.bbrc.2007.09.098](http://dx.doi.org/10.1016%2Fj.bbrc.2007.09.098). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [17931599](http://www.ncbi.nlm.nih.gov/pubmed/17931599).
  94. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-94) Qiu, JD; Huang, JH; Shi, SP; Liang, RP (2010). "Using the concept of Chou's pseudo amino acid composition to predict enzyme family classes: An approach with support vector machine based on discrete wavelet transform". *Protein and peptide letters* **17** (6): 715–22.[doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.2174/092986610791190372](http://dx.doi.org/10.2174%2F092986610791190372).[PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [19961429](http://www.ncbi.nlm.nih.gov/pubmed/19961429).
  95. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-95) Zhou, X. B., Chen, C., Li, Z. C. & Zou, X. Y. (2007). "Using Chou's amphiphilic pseudo-amino acid composition and support vector machine for prediction of enzyme subfamily classes".*Journal of Theoretical Biology* **248** (3): 546–551. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/j.jtbi.2007.06.001](http://dx.doi.org/10.1016%2Fj.jtbi.2007.06.001). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [17628605](http://www.ncbi.nlm.nih.gov/pubmed/17628605).
  96. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-96) Chou, K. C. (2005). "Using amphiphilic pseudo amino acid composition to predict enzyme subfamily classes". *Bioinformatics* **21** (1): 10–19. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1093/bioinformatics/bth466](http://dx.doi.org/10.1093%2Fbioinformatics%2Fbth466). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [15308540](http://www.ncbi.nlm.nih.gov/pubmed/15308540).
  97. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-97) Renugopalakrishnan V, Garduno-Juarez R, Narasimhan G, Verma CS, Wei X, Li P. (2005). "Rational design of thermally stable proteins: relevance to bionanotechnology". *J Nanosci Nanotechnol.* **5** (11): 1759–1767. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1166/jnn.2005.441](http://dx.doi.org/10.1166%2Fjnn.2005.441). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [16433409](http://www.ncbi.nlm.nih.gov/pubmed/16433409).
  98. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-98) Hult K, Berglund P. (2003). "Engineered enzymes for improved organic synthesis". *Current Opinion in Biotechnology* **14** (4): 395–400. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1016/S0958-1669(03)00095-8](http://dx.doi.org/10.1016%2FS0958-1669%2803%2900095-8). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [12943848](http://www.ncbi.nlm.nih.gov/pubmed/12943848).
  99. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-99) Jiang L, Althoff EA, Clemente FR (2008). ["De novo computational design of retro-aldol enzymes"](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3431203). *Science* **319** (5868): 1387–91. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1126/science.1152692](http://dx.doi.org/10.1126%2Fscience.1152692).[PMC](http://en.wikipedia.org/wiki/PubMed_Central) [3431203](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3431203). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [18323453](http://www.ncbi.nlm.nih.gov/pubmed/18323453).
  100. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-100) Guzmán-Maldonado H, Paredes-López O (1995). "Amylolytic enzymes and products derived from starch: a review". *Critical reviews in food science and nutrition* **35** (5): 373–403. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1080/10408399509527706](http://dx.doi.org/10.1080%2F10408399509527706). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [8573280](http://www.ncbi.nlm.nih.gov/pubmed/8573280).
  101. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Enzyme&printable=yes#cite_ref-101) Dulieu C, Moll M, Boudrant J, Poncelet D (2000). "Improved performances and control of beer fermentation using encapsulated alpha-acetolactate decarboxylase and modeling".*Biotechnology progress* **16** (6): 958–65. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1021/bp000128k](http://dx.doi.org/10.1021%2Fbp000128k). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [11101321](http://www.ncbi.nlm.nih.gov/pubmed/11101321).

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| **Etymology and history**   * Cornish-Bowden, Athel, ed. (1997). [*New Beer in an Old Bottle: Eduard Buchner and the Growth of Biochemical Knowledge*](http://bip.cnrs-mrs.fr/bip10/buchner.htm). Universitat de València. [ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [84-370-3328-4](http://en.wikipedia.org/wiki/Special:BookSources/84-370-3328-4)., A history of early enzymology. * Williams, Henry Smith (1904). [*A History of Science: in Five Volumes*. *Volume IV: Modern Development of the Chemical and Biological Sciences*](http://etext.lib.virginia.edu/toc/modeng/public/Wil4Sci.html). Harper and Brothers., A textbook from the early 20th century. * Kleyn J, Hough J (1971). "The microbiology of brewing". *Annu. Rev. Microbiol.***25**: 583–608. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1146/annurev.mi.25.100171.003055](http://dx.doi.org/10.1146%2Fannurev.mi.25.100171.003055). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [4949040](http://www.ncbi.nlm.nih.gov/pubmed/4949040).   **Enzyme structure and mechanism**   * Fersht, Alan (1999). *Structure and mechanism in protein science: a guide to enzyme catalysis and protein folding*. San Francisco: W.H. Freeman. [ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [0-7167-3268-8](http://en.wikipedia.org/wiki/Special:BookSources/0-7167-3268-8). * Walsh C (1979). *Enzymatic reaction mechanisms*. San Francisco: W. H. Freeman. [ISBN](http://en.wikipedia.org/wiki/International_Standard_Book_Number) [0-7167-0070-0](http://en.wikipedia.org/wiki/Special:BookSources/0-7167-0070-0). * Page, M. I., and Williams, A. (Eds.). *Enzyme Mechanisms*. Royal Society of Chemistry, 1987. [ISBN 0-85186-947-5](http://en.wikipedia.org/wiki/Special:BookSources/0851869475). * Bugg, T. *Introduction to Enzyme and Coenzyme Chemistry*. (2nd edition), Blackwell Publishing Limited, 2004. [ISBN 1-4051-1452-5](http://en.wikipedia.org/wiki/Special:BookSources/1405114525). * Warshel, A. *Computer Modeling of Chemical Reactions in enzymes and Solutions*. John Wiley & Sons Inc., 1991. [ISBN 0-471-18440-3](http://en.wikipedia.org/wiki/Special:BookSources/0471184403).   **Thermodynamics**   * ["Reactions and Enzymes"](http://www.emc.maricopa.edu/faculty/farabee/BIOBK/BioBookEnzym.html)Chapter 10 of on-line biology book at Estrella Mountain Community College. | **Kinetics and inhibition**   * Cornish-Bowden, Athel. *Fundamentals of Enzyme Kinetics*. (3rd edition), Portland Press, 2004. [ISBN 1-85578-158-1](http://en.wikipedia.org/wiki/Special:BookSources/1855781581). * Segel Irwin H. *Enzyme Kinetics: Behavior and Analysis of Rapid Equilibrium and Steady-State Enzyme Systems*. (New Ed edition), Wiley-Interscience, 1993.[ISBN 0-471-30309-7](http://en.wikipedia.org/wiki/Special:BookSources/0471303097). * Baynes, John W. *Medical Biochemistry*. (2nd edition), Elsevier-Mosby, 2005.[ISBN 0-7234-3341-0](http://en.wikipedia.org/wiki/Special:BookSources/0723433410), p. 57.   **Function and control of enzymes in the cell**   * Price, N. and Stevens, L. *Fundamentals of Enzymology: Cell and Molecular Biology of Catalytic Proteins*. Oxford University Press, 1999. [ISBN 0-19-850229-X](http://en.wikipedia.org/wiki/Special:BookSources/019850229X). * ["Nutritional and Metabolic Diseases"](http://www.ncbi.nlm.nih.gov/books/bv.fcgi?rid=gnd.chapter.86). Chapter of the on-line textbook *Introduction to Genes and Disease* from the NCBI.   **Enzyme-naming conventions**   * [Enzyme Nomenclature](http://www.chem.qmul.ac.uk/iubmb/enzyme/), Recommendations for enzyme names from the Nomenclature Committee of the International Union of Biochemistry and Molecular Biology. * Koshland, D. *The Enzymes*, v. I, ch. 7. Acad. Press, New York, 1959.   **Industrial applications**   * ["History of industrial enzymes"](http://www.mapsenzymes.com/History_of_Enzymes.asp), Article about the history of industrial enzymes from the late 1900s to the present times. |

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| * [Structure/Function of Enzymes](http://mcdb-webarchive.mcdb.ucsb.edu/sears/biochemistry/), Web tutorial on enzyme structure and function. * [Enzymes in diagnosis](http://www.science2day.info/2008/02/enzyme-test-or-cpk-test-what-is-it.html) Role of enzymes in diagnosis of diseases. * [Enzyme spotlight](http://www.ebi.ac.uk/intenz/spotlight.jsp) Monthly feature at the European Bioinformatics Institute on a selected enzyme. * [AMFEP](http://www.amfep.org/), Association of Manufacturers and Formulators of Enzyme Products * [BRENDA](http://www.brenda-enzymes.org/) database, a comprehensive compilation of information and literature references about all known enzymes; requires payment by commercial users. * [Enzyme Structures](http://pdbe.org/ec) Explore 3-D structure data of enzymes in the [Protein Data Bank](http://en.wikipedia.org/wiki/Protein_Data_Bank). * [Enzyme Structures Database](http://www.ebi.ac.uk/thornton-srv/databases/enzymes/) links to the known 3-D structure data of enzymes in the[Protein Data Bank](http://en.wikipedia.org/wiki/Protein_Data_Bank). * [ExPASy enzyme](http://enzyme.expasy.org/) database, links to [Swiss-Prot](http://en.wikipedia.org/wiki/Swiss-Prot)sequence data, entries in other databases and to related literature searches. | * [KEGG: Kyoto Encyclopedia of Genes and Genomes](http://www.genome.jp/kegg/) Graphical and hypertext-based information on biochemical pathways and enzymes. * [[1]](http://www.enzyme-database.org/) enzyme database * [MACiE](http://www.ebi.ac.uk/thornton-srv/databases/MACiE/) database of enzyme reaction mechanisms. * [MetaCyc](http://en.wikipedia.org/wiki/MetaCyc) database of enzymes and metabolic pathways * [Face-to-Face Interview with Sir John Cornforth who was awarded a Nobel Prize for work on stereochemistry of enzyme-catalyzed reactions](http://www.vega.org.uk/video/programme/19) Freeview video by the Vega Science Trust * [Sigma Aldrich Enzyme Assays by Enzyme Name](http://www.sigmaaldrich.com/life-science/metabolomics/enzyme-explorer.html)—Hundreds of assays sorted by enzyme name. * Bugg TD (2001). "The development of mechanistic enzymology in the 20th century". *Nat Prod Rep* **18** (5): 465–93. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1039/b009205n](http://dx.doi.org/10.1039%2Fb009205n). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [11699881](http://www.ncbi.nlm.nih.gov/pubmed/11699881). |

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