Enzyme

- Introduction
  - History
  - Nomenclature
  - Categories
- Character of Enzyme Catalyzed Reactions
  - Affect reaction rate, not the equilibria
  - Thermodynamic definition
  - Catalytic power and specificity
  - Weak interaction optimized at transition state
  - Specificity & catalysis as of binding
  - Catalysis strategy: acid-base, metal, covalent
- Enzyme kinetics
  - Nomenclature
  - Michaelis-Menton equation
  - Compare enzyme activity via kinetic parameter
  - Complex system
  - Inhibition
  - pH & temperature behavior
- Regulatory enzyme
  - Allosteric enzyme
  - Conformational change
  - Regulatory steps in pathway catalyzed by allosteric enzyme
  - Kinetics
  - Miscellaneous

Most Enzymes are Proteins

Cofactor
Coenzyme
Prosthetic group
Holoenzyme
Apoenzyme
Apoprotein

TABLE 6–1 Some Inorganic Ions That Serve as Cofactors for Enzymes

Ions	Enzymes
Cu^{2+}	Cytochrome oxidase
Fe^{2+} or Fe^{3+}	Cytochrome oxidase, catalase, peroxidase
K^{+}	Pyruvate kinase
Mg^{2+}	Hexokinase, glucose 6-phosphatase, pyruvate kinase
Mn^{2+}	Arginase, ribonucleotide reductase
Mo	Dinitrogenase
Ni^{2+}	Urease
Se	Glutathione peroxidase
Zn^{2+}	Carbonic anhydrase, alcohol dehydrogenase, carboxypeptidases A and B

Table 6-1
Lehninger Principles of Biochemistry, Fifth Edition

TABLE 6–2 Some Coenzymes That Serve as Transient Carriers of Specific Atoms or Functional Groups

Coenzyme	Examples of chemical groups transferred	Dietary precursor in mammals
Biocytin	CO_2	Biotin
Coenzyme A	Acyl groups	Pantothenic acid and other compounds
5′-Deoxyadenosylcobalamin (coenzyme B_{12})	H atoms and alkyl groups	Vitamin B_{12}
Flavin adenine dinucleotide	Electrons	Riboflavin (vitamin B_2)
Lipoate	Electrons and acyl groups	Not required in diet
Nicotinamide adenine dinucleotide	Hydride ion ($:H^-$)	Nicotinic acid (niacin)
Pyridoxal phosphate	Amino groups	Pyridoxine (vitamin B_6)
Tetrahydrofolate	One-carbon groups	Folate
Thiamine pyrophosphate	Aldehydes	Thiamine (vitamin B_1)

Note: The structures and modes of action of these coenzymes are described in Part II.

Table 6-2
Lehninger Principles of Biochemistry, Fifth Edition

Nomenclature

Remember the five basic reactions in biochemistry

TABLE 6–3 International Classification of Enzymes

Class no.	Class name	Type of reaction catalyzed
1	Oxidoreductases	Transfer of electrons (hydride ions or H atoms)
2	Transferases	Group transfer reactions
3	Hydrolases	Hydrolysis reactions (transfer of functional groups to water)
4	Lyases	Addition of groups to double bonds, or formation of double bonds by removal of groups
5	Isomerases	Transfer of groups within molecules to yield isomeric forms
6	Ligases	Formation of C—C, C—S, C—O, and C—N bonds by condensation reactions coupled to cleavage of ATP or similar cofactor

Table 6-3
Lehninger Principles of Biochemistry, Fifth Edition

Subclass	Name
EC 1	Oxidoreductases
EC 1.1	Acting on the CH-OH group of donors
EC 1.2	Acting on the aldehyde or oxo group of donors
EC 1.3	Acting on the CH-CH group of donors
EC 1.4	Acting on the CH-NH2 group of donors
EC 1.5	Acting on the CH-NH group of donors
EC 1.6	Acting on NADH or NADPH
EC 1.7	Acting on other nitrogenous compounds as donors
EC 1.8	Acting on a sulfur group of donors
EC 1.9	Acting on a heme group of donors
EC 1.10	Acting on diphenols and related substances as donors
EC 1.11	Acting on a peroxide as acceptor
EC 1.12	Acting on hydrogen as donor
EC 1.13	Acting on single donors with incorporation of molecular oxygen (oxygenases)
EC 1.14	Acting on paired donors, with incorporation or reduction of molecular oxygen
EC 1.15	Acting on superoxide radicals as acceptor
EC 1.16	Oxidising metal ions
EC 1.17	Acting on CH or CH_2 groups
EC 1.18	Acting on iron-sulfur proteins as donors
EC 1.19	Acting on reduced flavodoxin as donor
EC 1.20	Acting on phosphorus or arsenic in donors
EC 1.21	Acting on X-H and Y-H to form an X-Y bond
EC 1.97	Other oxidoreductases

EC 2	Transferases
EC 2.1	Transferring one-carbon groups
EC 2.2	Transferring aldehyde or ketonic groups
EC 2.3	Acyltransferases
EC 2.4	Glycosyltransferases
EC 2.5	Transferring alkyl or aryl groups, other than methyl groups
EC 2.6	Transferring nitrogenous groups
EC 2.7	Transferring phosphorus-containing groups
EC 2.8	Transferring sulfur-containing groups
EC 2.9	Transferring selenium-containing groups

EC 3	**Hydrolases**
EC 3.1	Acting on ester bonds
EC 3.2	Glycosylases
EC 3.3	Acting on ether bonds
EC 3.4	Acting on peptide bonds (peptidases)
EC 3.5	Acting on carbon-nitrogen bonds, other than peptide bonds
EC 3.6	Acting on acid anhydrides
EC 3.7	Acting on carbon-carbon bonds
EC 3.8	Acting on halide bonds
EC 3.9	Acting on phosphorus-nitrogen bonds
EC 3.10	Acting on sulfur-nitrogen bonds
EC 3.11	Acting on carbon-phosphorus bonds
EC 3.12	Acting on sulfur-sulfur bonds
EC 3.13	Acting on carbon-sulfur bonds

EC 4	**Lyases**
EC 4.1	Carbon-carbon lyases
EC 4.2	Carbon-oxygen lyases
EC 4.3	Carbon-nitrogen lyases
EC 4.4	Carbon-sulfur lyases
EC 4.5	Carbon-halide lyases
EC 4.6	Phosphorus-oxygen lyases
EC 4.99	Other lyases
EC 5	**Isomerases**
EC 5.1	Racemases and epimerases
EC 5.2	cis-trans-Isomerases
EC 5.3	Intramolecular isomerases
EC 5.4	Intramolecular transferases (mutases)
EC 5.5	Intramolecular lyases
EC 5.99	Other isomerases
EC 6	**Ligases**
EC 6.1	Forming carbon—oxygen bonds
EC 6.2	Forming carbon—sulfur bonds
EC 6.3	Forming carbon—nitrogen bonds
EC 6.4	Forming carbon—carbon bonds
EC 6.5	Forming phosphoric ester bonds
EC 6.6	Forming nitrogen—metal bonds

EC 1 Oxidoreductases

EC 1.1 Acting on the CH-OH group of donors

EC 1.1.1 With NAD+ or NADP+ as acceptor

EC 1.1.1.1 alcohol dehydrogenase
EC 1.1.1.2 alcohol dehydrogenase (NADP+)
EC 1.1.1.3 homoserine dehydrogenase
EC 1.1.1.4 (R,R)-butanediol dehydrogenase
EC 1.1.1.5 acetoin dehydrogenase
EC 1.1.1.6 glycerol dehydrogenase
EC 1.1.1.7 propanediol-phosphate dehydrogenase
EC 1.1.1.8 glycerol-3-phosphate dehydrogenase (NAD·
EC 1.1.1.9 D-xylulose reductase
EC 1.1.1.10 L-xylulose reductase
EC 1.1.1.11 D-arabinitol 4-dehydrogenase
EC 1.1.1.12 L-arabinitol 4-dehydrogenase
EC 1.1.1.13 L-arabinitol 2-dehydrogenase
EC 1.1.1.14 L-iditol 2-dehydrogenase
EC 1.1.1.15 D-iditol 2-dehydrogenase
EC 1.1.1.16 galactitol 2-dehydrogenase
EC 1.1.1.17 mannitol-1-phosphate 5-dehydrogenase
EC 1.1.1.18 inositol 2-dehydrogenase
EC 1.1.1.19 L-glucuronate reductase
EC 1.1.1.20 glucuronolactone reductase
EC 1.1.1.21 aldehyde reductase
EC 1.1.1.22 UDP-glucose 6-dehydrogenase

EC 1.1.1.23 histidinol dehydrogenase
EC 1.1.1.24 quinate dehydrogenase
EC 1.1.1.25 shikimate dehydrogenase
EC 1.1.1.26 glyoxylate reductase
EC 1.1.1.27 L-lactate dehydrogenase
EC 1.1.1.28 D-lactate dehydrogenase
EC 1.1.1.29 glycerate dehydrogenase
EC 1.1.1.30 3-hydroxybutyrate dehydrogenase
EC 1.1.1.31 3-hydroxyisobutyrate dehydrogenase
EC 1.1.1.32 mevaldate reductase
EC 1.1.1.33 mevaldate reductase (NADPH)
EC 1.1.1.34 hydroxymethylglutaryl-CoA reductase (NA
EC 1.1.1.35 3-hydroxyacyl-CoA dehydrogenase
EC 1.1.1.36 acetoacetyl-CoA reductase
EC 1.1.1.37 malate dehydrogenase
EC 1.1.1.38 malate dehydrogenase (oxaloacetate-deca
EC 1.1.1.39 malate dehydrogenase (decarboxylating)
EC 1.1.1.40 malate dehydrogenase (oxaloacetate-deca
EC 1.1.1.41 isocitrate dehydrogenase (NAD+)
EC 1.1.1.42 isocitrate dehydrogenase (NADP+)
EC 1.1.1.43 phosphogluconate 2-dehydrogenase
EC 1.1.1.44 phosphogluconate dehydrogenase (decarl
EC 1.1.1.45 L-gulonate 3-dehydrogenase
EC 1.1.1.46 L-arabinose 1-dehydrogenase
EC 1.1.1.47 glucose 1-dehydrogenase
EC 1.1.1.48 galactose 1-dehydrogenase
EC 1.1.1.49 glucose-6-phosphate dehydrogenase
EC 1.1.1.50 3a-hydroxysteroid dehydrogenase (B-spec
EC 1.1.1.51 3(or 17)b-hydroxysteroid dehydrogenase
EC 1.1.1.52 3a-hydroxycholanate dehydrogenase
EC 1.1.1.53 3a(or 20b)-hydroxysteroid dehydrogenase
EC 1.1.1.54 allyl-alcohol dehydrogenase
EC 1.1.1.55 lactaldehyde reductase (NADPH)
EC 1.1.1.56 ribitol 2-dehydrogenase
EC 1.1.1.57 fructuronate reductase
EC 1.1.1.58 tagaturonate reductase
EC 1.1.1.59 3-hydroxypropionate dehydrogenase
EC 1.1.1.60 2-hydroxy-3-oxopropionate reductase
EC 1.1.1.61 4-hydroxybutyrate dehydrogenase
EC 1.1.1.62 estradiol 17b-dehydrogenase
EC 1.1.1.63 testosterone 17b-dehydrogenase
EC 1.1.1.64 testosterone 17b-dehydrogenase (NADP+)
EC 1.1.1.65 pyridoxine 4-dehydrogenase
EC 1.1.1.66 w-hydroxydecanoate dehydrogenase
EC 1.1.1.67 mannitol 2-dehydrogenase
EC 1.1.1.68 now EC 1.7.99.5
EC 1.1.1.69 gluconate 5-dehydrogenase
EC 1.1.1.70 deleted, included in EC 1.2.1.3
EC 1.1.1.71 alcohol dehydrogenase [NAD(P)+]
EC 1.1.1.72 glycerol dehydrogenase (NADP+)
EC 1.1.1.73 octanol dehydrogenase
EC 1.1.1.74 deleted
EC 1.1.1.75 (R)-aminopropanal dehydrogenase
EC 1.1.1.76 (S,S)-butanediol dehydrogenase
EC 1.1.1.77 lactaldehyde reductase
EC 1.1.1.78 methylglyoxal reductase (NADH-dependen
EC 1.1.1.79 glyoxylate reductase (NADP+)
EC 1.1.1.80 isopropanol dehydrogenase (NADP+)
EC 1.1.1.81 hydroxypyruvate reductase
EC 1.1.1.82 malate dehydrogenase (NADP+)
EC 1.1.1.83 D-malate dehydrogenase (decarboxylating
EC 1.1.1.84 dimethylmalate dehydrogenase

EC 1.1.1.85 3-isopropylmalate dehydrogenase
EC 1.1.1.86 ketol-acid reductoisomerase
EC 1.1.1.87 homoisocitrate dehydrogenase
EC 1.1.1.88 hydroxymethylglutaryl-CoA reductase
EC 1.1.1.89 deleted, included in EC 1.1.1.86
EC 1.1.1.90 aryl-alcohol dehydrogenase
EC 1.1.1.91 aryl-alcohol dehydrogenase (NADP+)
EC 1.1.1.92 oxaloglycolate reductase (decarboxylating
EC 1.1.1.93 tartrate dehydrogenase
EC 1.1.1.94 glycerol-3-phosphate dehydrogenase [NAI
EC 1.1.1.95 phosphoglycerate dehydrogenase
EC 1.1.1.96 diiodophenylpyruvate reductase
EC 1.1.1.97 3-hydroxybenzyl-alcohol dehydrogenase
EC 1.1.1.98 (R)-2-hydroxy-fatty-acid dehydrogenase
EC 1.1.1.99 (S)-2-hydroxy-fatty-acid dehydrogenase
EC 1.1.1.100 3-oxoacyl-[acyl-carrier-protein] reductase
EC 1.1.1.101 acylglycerone-phosphate reductase
EC 1.1.1.102 3-dehydrosphinganine reductase
EC 1.1.1.103 L-threonine 3-dehydrogenase
EC 1.1.1.104 4-oxoproline reductase
EC 1.1.1.105 retinol dehydrogenase
EC 1.1.1.106 pantoate 4-dehydrogenase
EC 1.1.1.107 pyridoxal 4-dehydrogenase
EC 1.1.1.108 carnitine 3-dehydrogenase
EC 1.1.1.109 now EC 1.3.1.28
EC 1.1.1.110 indolelactate dehydrogenase
EC 1.1.1.111 3-(imidazol-5-yl)lactate dehydrogenase
EC 1.1.1.112 indanol dehydrogenase
EC 1.1.1.113 L-xylose 1-dehydrogenase
EC 1.1.1.114 apiose 1-reductase
EC 1.1.1.115 ribose 1-dehydrogenase (NADP+)
EC 1.1.1.116 D-arabinose 1-dehydrogenase
EC 1.1.1.117 D-arabinose 1-dehydrogenase [NAD(P)+]
EC 1.1.1.118 glucose 1-dehydrogenase (NAD+)
EC 1.1.1.119 glucose 1-dehydrogenase (NADP+)
EC 1.1.1.120 galactose 1-dehydrogenase (NADP+)
EC 1.1.1.121 aldose 1-dehydrogenase
EC 1.1.1.122 D-threo-aldose 1-dehydrogenase
EC 1.1.1.123 sorbose 5-dehydrogenase (NADP+)
EC 1.1.1.124 fructose 5-dehydrogenase (NADP+)
EC 1.1.1.125 2-deoxy-D-gluconate 3-dehydrogenase
EC 1.1.1.126 2-dehydro-3-deoxy-D-gluconate 6-dehydr
EC 1.1.1.127 2-dehydro-3-deoxy-D-gluconate 5-dehydr
EC 1.1.1.128 L-idonate 2-dehydrogenase
EC 1.1.1.129 L-threonate 3-dehydrogenase
EC 1.1.1.130 3-dehydro-L-gulonate 2-dehydrogenase
EC 1.1.1.131 mannuronate reductase
EC 1.1.1.132 GDP-mannose 6-dehydrogenase
EC 1.1.1.133 dTDP-4-dehydrorhamnose reductase
EC 1.1.1.134 dTDP-6-deoxy-L-talose 4-dehydrogenase
EC 1.1.1.135 GDP-6-deoxy-D-talose 4-dehydrogenase
EC 1.1.1.136 UDP-N-acetylglucosamine 6-dehydrogena
EC 1.1.1.137 ribitol-5-phosphate 2-dehydrogenase
EC 1.1.1.138 mannitol 2-dehydrogenase (NADP+)
EC 1.1.1.139 deleted, included in EC 1.1.1.21
EC 1.1.1.140 sorbitol-6-phosphate 2-dehydrogenase
EC 1.1.1.141 15-hydroxyprostaglandin dehydrogenase
EC 1.1.1.142 D-pinitol dehydrogenase
EC 1.1.1.143 sequoyitol dehydrogenase
EC 1.1.1.144 perillyl-alcohol dehydrogenase
EC 1.1.1.145 3b-hydroxy-D5-steroid dehydrogenase

EC 1.1.1.146 11b-hydroxysteroid dehydrogenase
EC 1.1.1.147 16a-hydroxysteroid dehydrogenase
EC 1.1.1.148 estradiol 17a-dehydrogenase
EC 1.1.1.149 20a-hydroxysteroid dehydrogenase
EC 1.1.1.150 21-hydroxysteroid dehydrogenase (NAD+
EC 1.1.1.151 21-hydroxysteroid dehydrogenase (NADP
EC 1.1.1.152 3a-hydroxy-5b-androstane-17-one 3a-deh
EC 1.1.1.153 sepiapterin reductase
EC 1.1.1.154 ureidoglycolate dehydrogenase
EC 1.1.1.155 identical to EC 1.1.1.87
EC 1.1.1.156 glycerol 2-dehydrogenase (NADP+)
EC 1.1.1.157 3-hydroxybutyryl-CoA dehydrogenase
EC 1.1.1.158 UDP-N-acetylmuramate dehydrogenase
EC 1.1.1.159 7a-hydroxysteroid dehydrogenase
EC 1.1.1.160 dihydrobunolol dehydrogenase
EC 1.1.1.161 cholestanetetraol 26-dehydrogenase
EC 1.1.1.162 erythrulose reductase
EC 1.1.1.163 cyclopentanol dehydrogenase
EC 1.1.1.164 hexadecanol dehydrogenase
EC 1.1.1.165 2-alkyn-1-ol dehydrogenase
EC 1.1.1.166 hydroxycyclohexanecarboxylate dehydro
EC 1.1.1.167 hydroxymalonate dehydrogenase
EC 1.1.1.168 2-dehydropantolactone reductase (A-spe
EC 1.1.1.169 2-dehydropantoate 2-reductase
EC 1.1.1.170 3b-hydroxy-4a-methylcholestenecarboxyl
EC 1.1.1.171 now EC 1.5.1.20
EC 1.1.1.172 2-oxoadipate reductase
EC 1.1.1.173 L-rhamnose 1-dehydrogenase
EC 1.1.1.174 cyclohexane-1,2-diol dehydrogenase
EC 1.1.1.175 D-xylose 1-dehydrogenase
EC 1.1.1.176 12a-hydroxysteroid dehydrogenase
EC 1.1.1.177 glycerol-3-phosphate 1-dehydrogenase (N
EC 1.1.1.178 3-hydroxy-2-methylbutyryl-CoA dehydrog
EC 1.1.1.179 D-xylose 1-dehydrogenase (NADP+)
EC 1.1.1.180 deleted, included in EC 1.1.1.131
EC 1.1.1.181 cholest-5-ene-3b,7a-diol 3b-dehydrogena
EC 1.1.1.182 deleted, included in EC 1.1.1.198, EC 1.1.
EC 1.1.1.183 geraniol dehydrogenase
EC 1.1.1.184 carbonyl reductase (NADPH)
EC 1.1.1.185 L-glycol dehydrogenase
EC 1.1.1.186 dTDP-galactose 6-dehydrogenase
EC 1.1.1.187 GDP-4-dehydro-D-rhamnose reductase
EC 1.1.1.188 prostaglandin-F synthase
EC 1.1.1.189 prostaglandin-E2 9-reductase
EC 1.1.1.190 indole-3-acetaldehyde reductase (NADH)
EC 1.1.1.191 indole-3-acetaldehyde reductase (NADPH
EC 1.1.1.192 long-chain-alcohol dehydrogenase
EC 1.1.1.193 5-amino-6-(5-phosphoribosylamino)uracil
EC 1.1.1.194 coniferyl-alcohol dehydrogenase
EC 1.1.1.195 cinnamyl-alcohol dehydrogenase
EC 1.1.1.196 15-hydroxyprostaglandin-D dehydrogena
EC 1.1.1.197 15-hydroxyprostaglandin dehydrogenase
EC 1.1.1.198 (+)-borneol dehydrogenase
EC 1.1.1.199 (S)-usnate reductase
EC 1.1.1.200 aldose-6-phosphate reductase (NADPH)
EC 1.1.1.201 7b-hydroxysteroid dehydrogenase (NADP
EC 1.1.1.202 1,3-propanediol dehydrogenase
EC 1.1.1.203 uronate dehydrogenase
EC 1.1.1.204 now EC 1.17.1.4
EC 1.1.1.205 IMP dehydrogenase

EC 1.1.1.206 tropine dehydrogenase
EC 1.1.1.207 (-)-menthol dehydrogenase
EC 1.1.1.208 (+)-neomenthol dehydrogenase
EC 1.1.1.209 3(or 17)a-hydroxysteroid dehydrogenase
EC 1.1.1.210 3b(or 20a)-hydroxysteroid dehydrogenas
EC 1.1.1.211 long-chain-3-hydroxyacyl-CoA dehydroge
EC 1.1.1.212 3-oxoacyl-[acyl-carrier-protein] reductase
EC 1.1.1.213 3a-hydroxysteroid dehydrogenase (A-spe
EC 1.1.1.214 2-dehydropantolactone reductase (B-spe
EC 1.1.1.215 gluconate 2-dehydrogenase
EC 1.1.1.216 farnesol dehydrogenase
EC 1.1.1.217 benzyl-2-methyl-hydroxybutyrate dehydr
EC 1.1.1.218 morphine 6-dehydrogenase
EC 1.1.1.219 dihydrokaempferol 4-reductase
EC 1.1.1.220 6-pyruvoyltetrahydropterin 2'-reductase
EC 1.1.1.221 vomifoliol 4'-dehydrogenase
EC 1.1.1.222 (R)-4-hydroxyphenyllactate dehydrogena
EC 1.1.1.223 isopiperitenol dehydrogenase
EC 1.1.1.224 mannose-6-phosphate 6-reductase
EC 1.1.1.225 chlordecone reductase
EC 1.1.1.226 4-hydroxycyclohexanecarboxylate dehyd
EC 1.1.1.227 (-)-borneol dehydrogenase
EC 1.1.1.228 (+)-sabinol dehydrogenase
EC 1.1.1.229 diethyl 2-methyl-3-oxosuccinate reductas
EC 1.1.1.230 3a-hydroxyglycyrrhetinate dehydrogenas
EC 1.1.1.231 15-hydroxyprostaglandin-I dehydrogenas
EC 1.1.1.232 15-hydroxyicosatetraenoate dehydrogena
EC 1.1.1.233 N-acylmannosamine 1-dehydrogenase
EC 1.1.1.234 flavanone 4-reductase
EC 1.1.1.235 8-oxocoformycin reductase
EC 1.1.1.236 tropinone reductase
EC 1.1.1.237 hydroxyphenylpyruvate reductase
EC 1.1.1.238 12b-hydroxysteroid dehydrogenase
EC 1.1.1.239 3a(17b)-hydroxysteroid dehydrogenase (I
EC 1.1.1.240 N-acetylhexosamine 1-dehydrogenase
EC 1.1.1.241 6-endo-hydroxycineole dehydrogenase
EC 1.1.1.242 now EC 1.3.1.69 zeatin reductase
EC 1.1.1.243 carveol dehydrogenase
EC 1.1.1.244 methanol dehydrogenase
EC 1.1.1.245 cyclohexanol dehydrogenase
EC 1.1.1.246 pterocarpin synthase
EC 1.1.1.247 codeinone reductase (NADPH)
EC 1.1.1.248 salutaridine reductase (NADPH)
EC 1.1.1.249 reinstated as EC 2.5.1.46
EC 1.1.1.250 D-arabinitol 2-dehydrogenase
EC 1.1.1.251 galactitol-1-phosphate 5-dehydrogenase
EC 1.1.1.252 tetrahydroxynaphthalene reductase
EC 1.1.1.253 now EC 1.5.1.33
EC 1.1.1.254 (S)-carnitine 3-dehydrogenase
EC 1.1.1.255 mannitol dehydrogenase
EC 1.1.1.256 fluoren-9-ol dehydrogenase
EC 1.1.1.257 4-(hydroxymethyl)benzenesulfonate dehy
EC 1.1.1.258 6-hydroxyhexanoate dehydrogenase
EC 1.1.1.259 3-hydroxypimeloyl-CoA dehydrogenase
EC 1.1.1.260 sulcatone reductase
EC 1.1.1.261 glycerol-1-phosphate dehydrogenase [NA
EC 1.1.1.262 4-hydroxythreonine-4-phosphate dehydr
EC 1.1.1.263 1,5-anhydro-D-fructose reductase
EC 1.1.1.264 L-idonate 5-dehydrogenase
EC 1.1.1.265 3-methylbutanal reductase

EC 1.1.1.266 dTDP-4-dehydro-6-deoxyglucose reductase
EC 1.1.1.267 1-deoxy-D-xylulose-5-phosphate reductoisomerase
EC 1.1.1.268 2-(R)-hydroxypropyl-CoM dehydrogenase
EC 1.1.1.269 2-(S)-hydroxypropyl-CoM dehydrogenase
EC 1.1.1.270 3-keto-steroid reductase
EC 1.1.1.271 GDP-L-fucose synthase
EC 1.1.1.272 (R)-2-hydroxyacid dehydrogenase
EC 1.1.1.273 vellosimine dehydrogenase
EC 1.1.1.274 2,5-didehydrogluconate reductase
EC 1.1.1.275 (+)-trans-carveol dehydrogenase
EC 1.1.1.276 serine 3-dehydrogenase
EC 1.1.1.277 3b-hydroxy-5b-steroid dehydrogenase
EC 1.1.1.278 3b-hydroxy-5a-steroid dehydrogenase
EC 1.1.1.279 (R)-3-hydroxyacid ester dehydrogenase
EC 1.1.1.280 (S)-3-hydroxyacid ester dehydrogenase
EC 1.1.1.281 GDP-4-dehydro-6-deoxy-D-mannose reductase
EC 1.1.1.282 quinate/shikimate dehydrogenase
EC 1.1.1.283 methylglyoxal reductase (NADPH-dependent)
EC 1.1.1.284 S-(hydroxymethyl)glutathione dehydrogenase
EC 1.1.1.285 3"-deamino-3"-oxonicotianamine reductase
EC 1.1.1.286 isocitrate—homoisocitrate dehydrogenase
EC 1.1.1.287 D-arabinitol dehydrogenase (NADP+)

EC 1.1.1.1

Common name: alcohol dehydrogenase
Reaction: an alcohol + NAD^+ = an aldehyde or ketone + NADH + H^+
Other name(s): aldehyde reductase; ADH; alcohol dehydrogenase (NAD); aliphatic alcohol dehydrogenase; ethanol dehydrogenase; NAD-dependent alcohol dehydrogenase; NAD-specific aromatic alcohol dehydrogenase; NADH-alcohol dehydrogenase; NADH-aldehyde dehydrogenase; primary alcohol dehydrogenase; yeast alcohol dehydrogenase
Systematic name: alcohol:NAD^+ oxidoreductase
Comments: A zinc protein. Acts on primary or secondary alcohols or hemi-acetals; the animal, but not the yeast, enzyme acts also on cyclic secondary alcohols.
CAS registry number: 9031-72-5

References:

1. Brändén, G.-I., Jörnvall, H., Eklund, H. and Furugren, B. Alcohol dehydrogenase. In: Boyer, P.D. (Ed.), *The Enzymes*, 3rd ed., vol. 11, Academic Press, New York, 1975, p. 103-190.
2. Jörnvall, H. Differences between alcohol dehydrogenases. Structural properties and evolutionary aspects. *Eur. J. Biochem.* 72 (1977) 443-452. [Medline UI: 77115786]
3. Negelein, E. and Wulff, H.-J. Diphosphopyridinproteid ackohol, acetaldehyd. *Biochem. Z.* 293 (1937) 351-389.
4. Sund, H. and Theorell, H. Alcohol dehydrogenase. In: Boyer, P.D., Lardy, H. and Myrbäck, K. (Eds.), *The Enzymes*, 2nd ed., vol. 7, Academic Press, New York, 1963, p. 25-83.
5. Theorell, H. Kinetics and equilibria in the liver alcohol dehydrogenase system. *Adv. Enzymol. Relat. Subj. Biochem.* 20 (1958) 31-49.

[EC 1.1.1.1 created 1961]

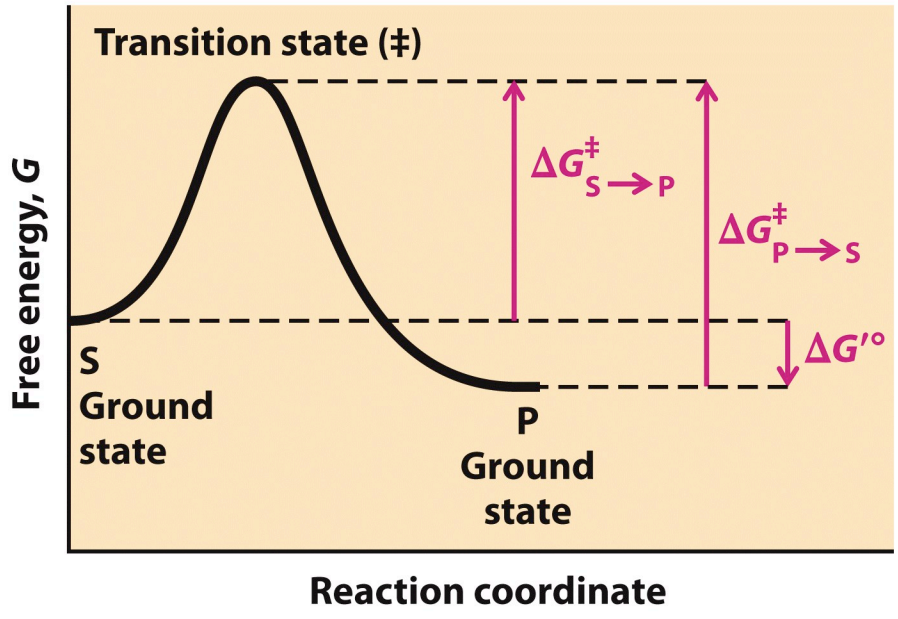


Figure 6-2
Lehninger Principles of Biochemistry, Fifth Edition

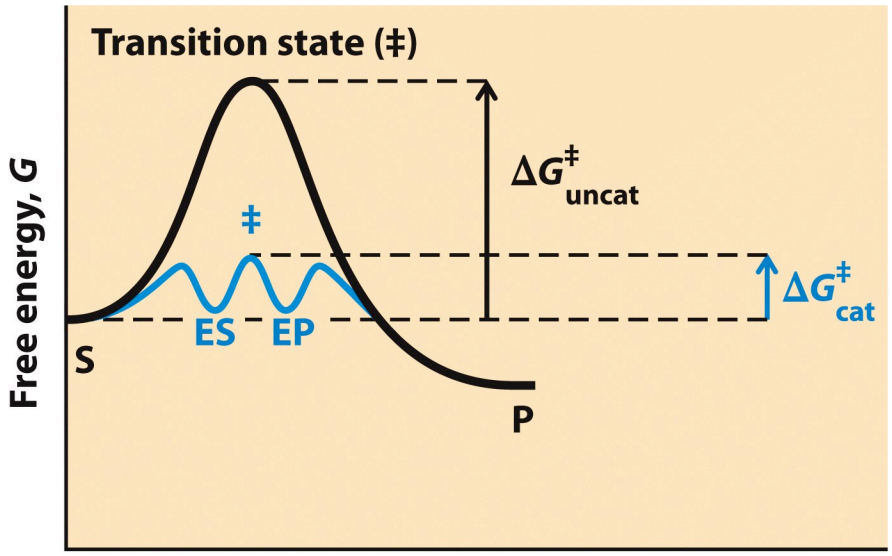


Figure 6-3
Lehninger Principles of Biochemistry, Fifth Edition

- Ground state
- Standard free-energy change
- Biochemical standard free-energy change
- Transition state
- Activation energy
- Reaction intermediate
- Rate-limiting step
- Rate-determining step
- Equilibrium constant
- Rate constant
- Rate equation
- Binding energy

TABLE 6–4 Relationship between K'_{eq} and $\Delta G'^{\circ}$

K'_{eq}	$\Delta G'^{\circ}$ (kJ/mol)
10^{-6}	34.2
10^{-5}	28.5
10^{-4}	22.8
10^{-3}	17.1
10^{-2}	11.4
10^{-1}	5.7
1	0.0
10^{1}	−5.7
10^{2}	−11.4
10^{3}	−17.1

Note: The relationship is calculated from $\Delta G'^{\circ} = -RT \ln K'_{eq}$ (Eqn 6–3).

Table 6-4
Lehninger Principles of Biochemistry, Fifth Edition

TABLE 6–5 Some Rate Enhancements Produced by Enzymes

Cyclophilin	10^{5}
Carbonic anhydrase	10^{7}
Triose phosphate isomerase	10^{9}
Carboxypeptidase A	10^{11}
Phosphoglucomutase	10^{12}
Succinyl-CoA transferase	10^{13}
Urease	10^{14}
Orotidine monophosphate decarboxylase	10^{17}

Table 6-5
Lehninger Principles of Biochemistry, Fifth Edition

Weak interactions optimized in the

transition state

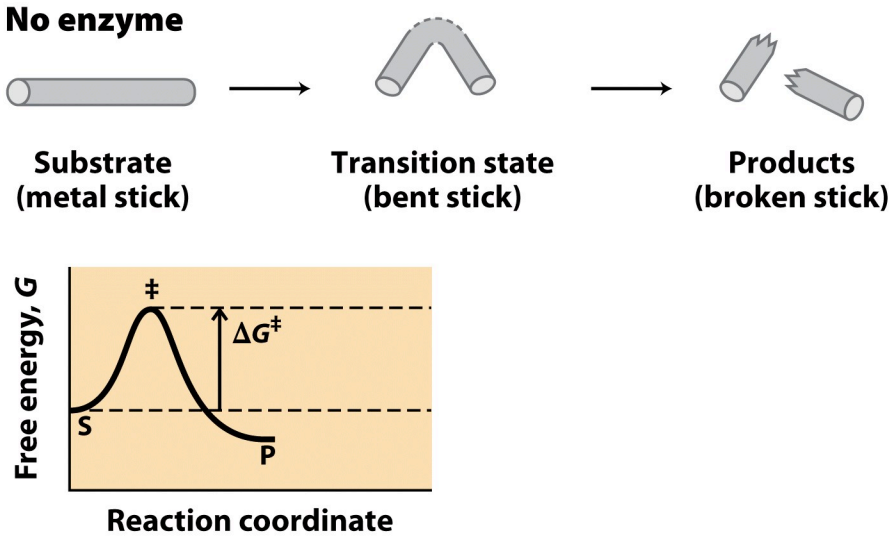


Figure 6-5a
Lehninger Principles of Biochemistry, Fifth Edition

Enzyme complementary to substrate

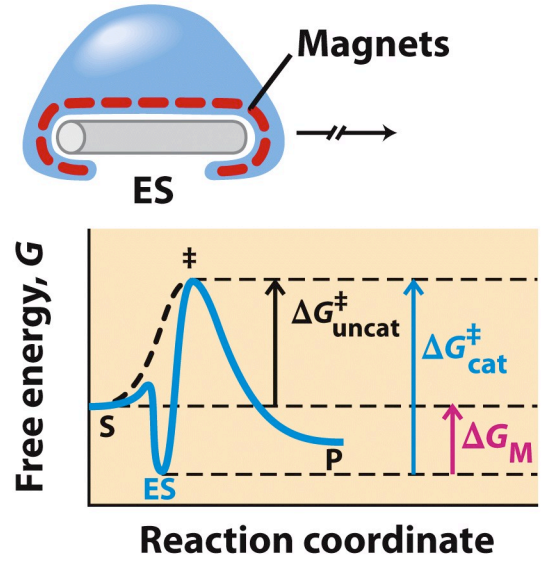


Figure 6-5b
Lehninger Principles of Biochemistry, Fifth Edition

Enzyme complementary to transition state

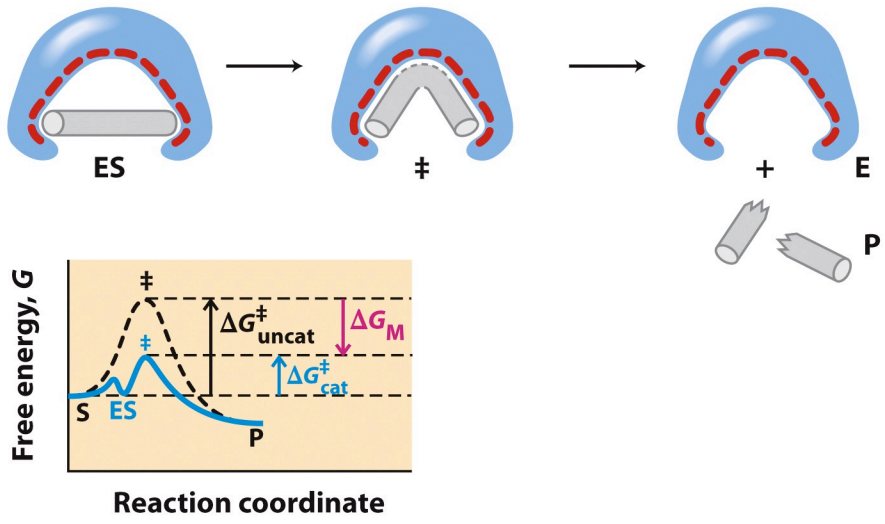


Figure 6-5c
Lehninger Principles of Biochemistry, Fifth Edition

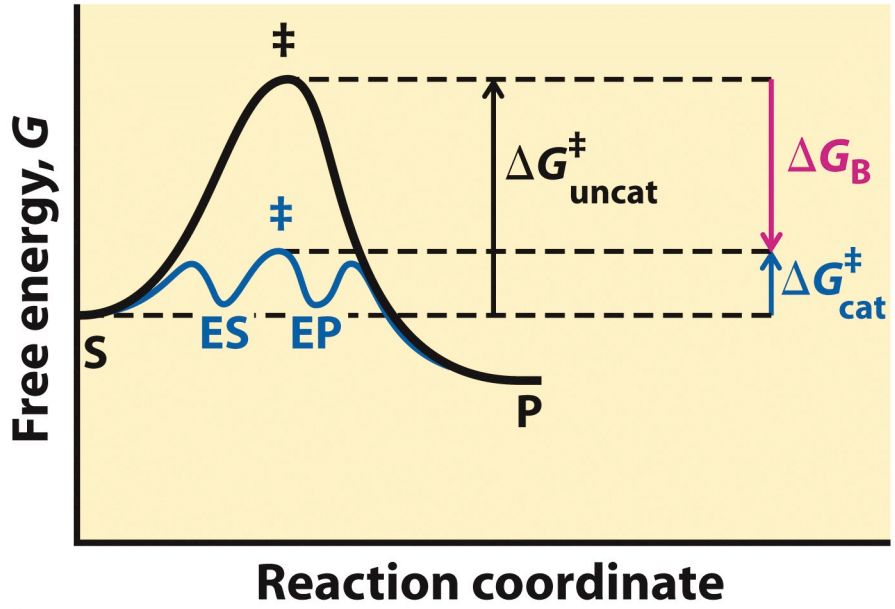


Figure 6-6
Lehninger Principles of Biochemistry, Fifth Edition

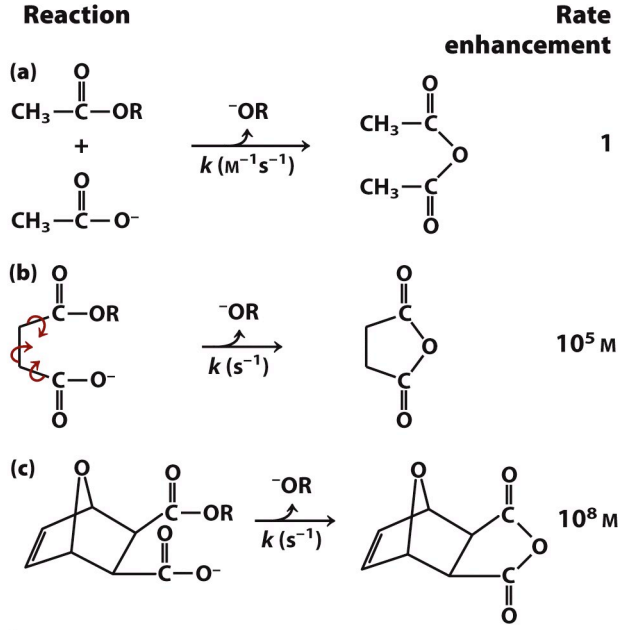


Figure 6-7
Lehninger Principles of Biochemistry, Fifth Edition

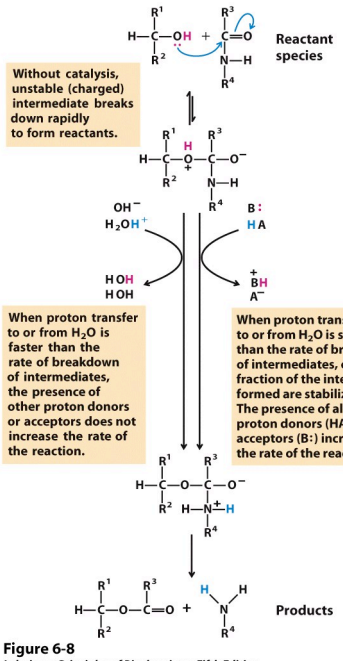


Figure 6-8
Lehninger Principles of Biochemistry, Fifth Edition

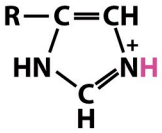
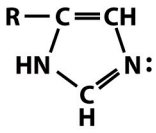
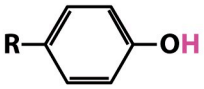
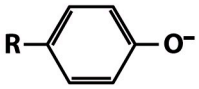
Amino acid residues	General acid form (proton donor)	General base form (proton acceptor)
Glu, Asp	R—COOH	R—COO⁻
Lys, Arg	R—$\overset{+}{N}$H$_3$	R—NH$_2$
Cys	R—SH	R—S⁻
His		
Ser	R—OH	R—O⁻
Tyr		

Figure 6-9
Lehninger Principles of Biochemistry, Fifth Edition

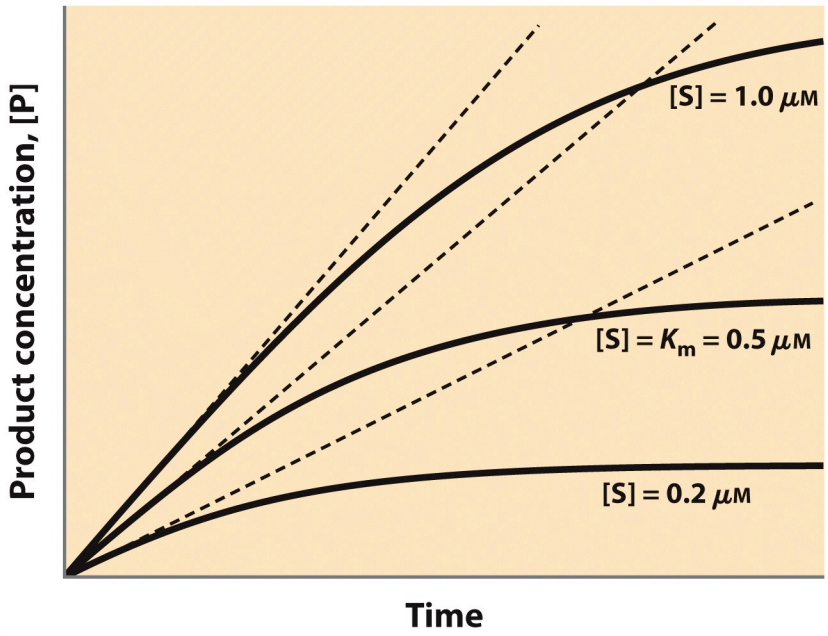
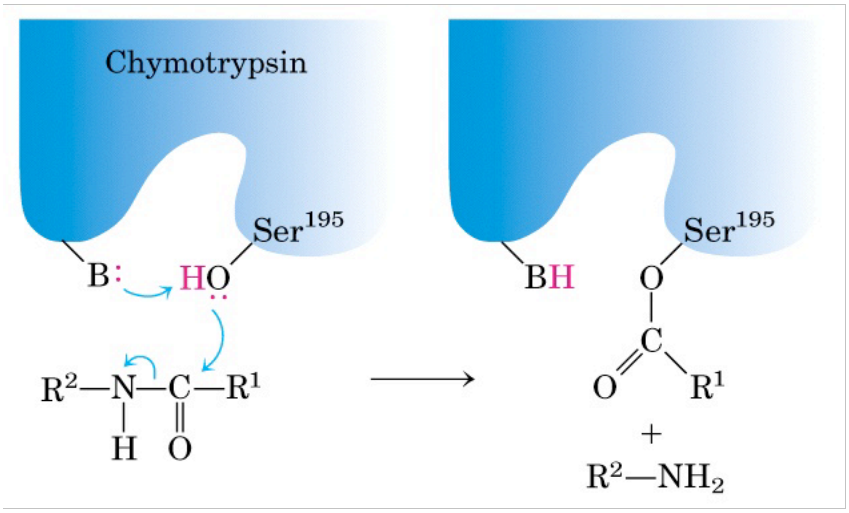


Figure 6-10
Lehninger Principles of Biochemistry, Fifth Edition



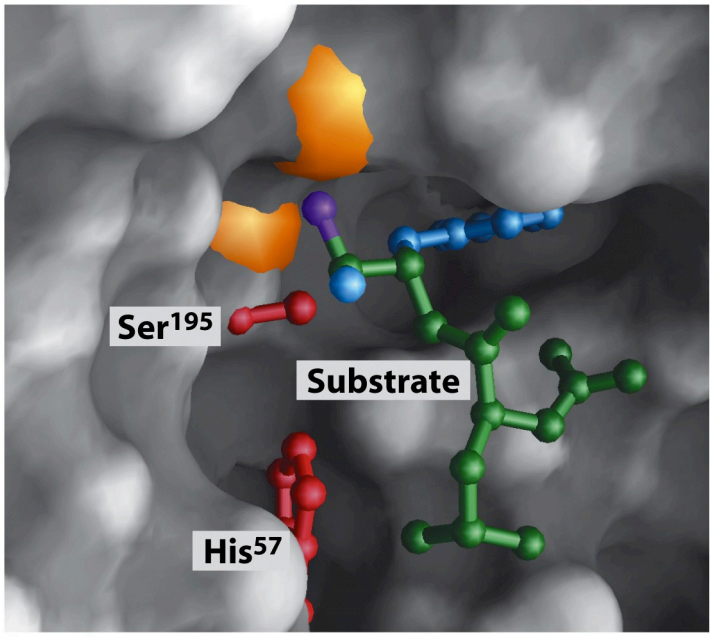


Figure 6-18d
Lehninger Principles of Biochemistry, Fifth Edition

Enzyme Kinetics

Enzyme kinetics

Initial rate (or initial velocity)

Maximum velocity

Pre-steady state

Steady state

Steady-state kinetics

Steady-state assumption

Michaelis constant

Michaelis-Menten equation

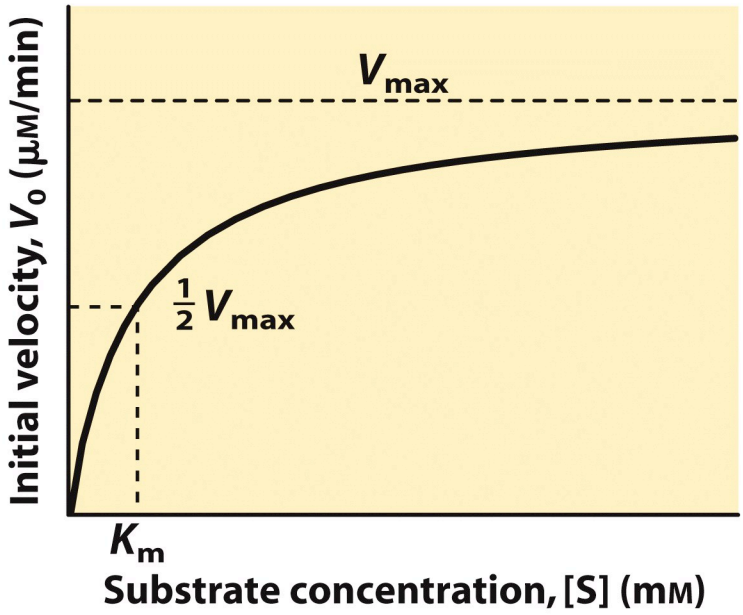


Figure 6-11
Lehninger Principles of Biochemistry, Fifth Edition

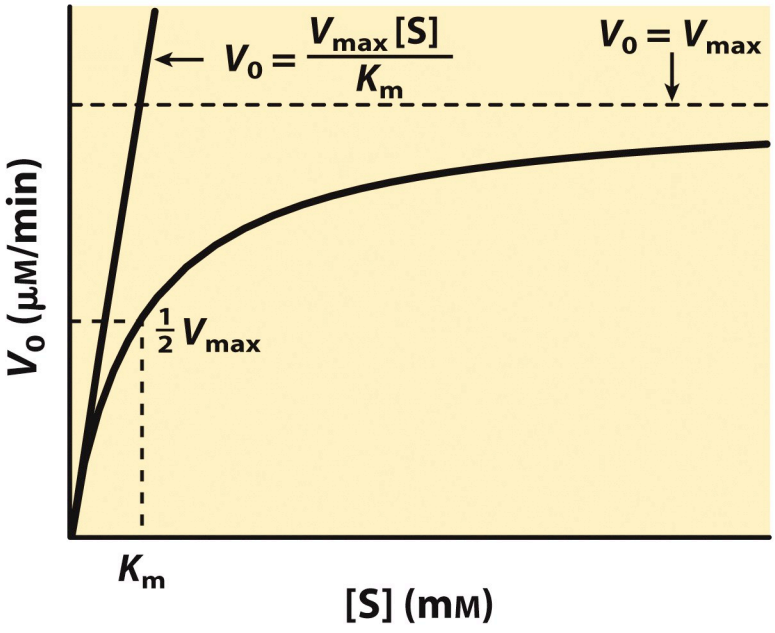


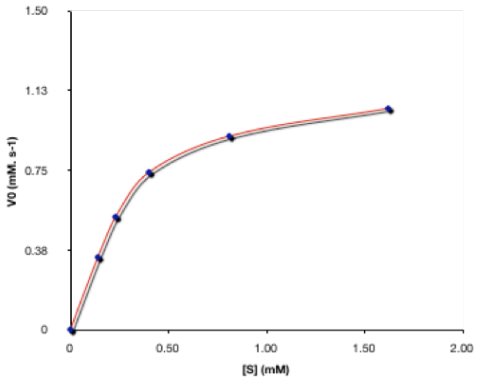
Figure 6-12
Lehninger Principles of Biochemistry, Fifth Edition

Double-reciprocal plot

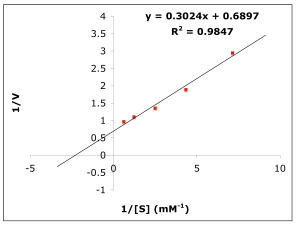
Dissociation constant

Turnover number

[S] (μM)	v_0 (mM. s^{-1})
0.14	0.34
0.23	0.53
0.4	0.74
0.81	0.91
1.62	1.04



Lineweaver-Burk Plot

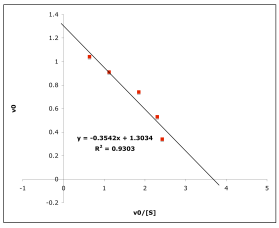


V_{max} = 1/0.6897 = 1.45

K_m = -1/(-2.28) = 0.44 μM)

Eadie-Hofstee Plot

$$v_0 = V_{\max} - K_m \frac{v_0}{[S]}$$

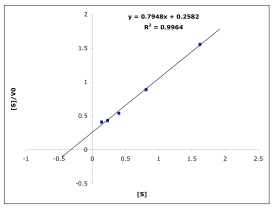


V_{max} = 1.30

K_m = 0.354

Haynes-Woolf Plot

$$\frac{[S]}{V_0} = [S](\frac{1}{V_{\max}}) + \frac{K_M}{V_{\max}}$$



$K_m = 0.32$

$V_{max} = 0.80$

Eisenthal-Cornish-Bowden Direct Plot
Direct Linear Plot

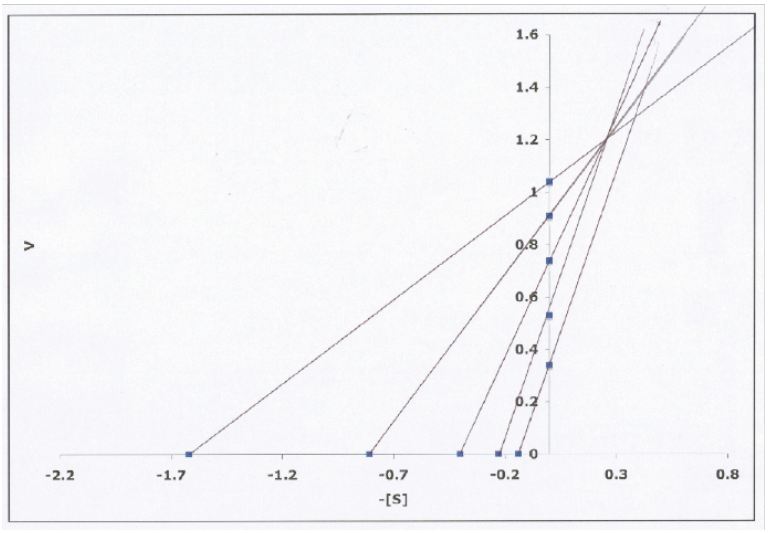


TABLE 6–6 K_m for Some Enzymes and Substrates

Enzyme	Substrate	K_m (mM)
Hexokinase (brain)	ATP	0.4
	D-Glucose	0.05
	D-Fructose	1.5
Carbonic anhydrase	HCO_3^-	26
Chymotrypsin	Glycyltyrosinylglycine	108
	N-Benzoyltyrosinamide	2.5
β-Galactosidase	D-Lactose	4.0
Threonine dehydratase	L-Threonine	5.0

Table 6-6
Lehninger Principles of Biochemistry, Fifth Edition

TABLE 6–7 Turnover Numbers, k_{cat}, of Some Enzymes

Enzyme	Substrate	k_{cat} (s^{-1})
Catalase	H_2O_2	40,000,000
Carbonic anhydrase	HCO_3^-	400,000
Acetylcholinesterase	Acetylcholine	14,000
β-Lactamase	Benzylpenicillin	2,000
Fumarase	Fumarate	800
RecA protein (an ATPase)	ATP	0.5

Table 6-7
Lehninger Principles of Biochemistry, Fifth Edition

TABLE 6–8 Enzymes for Which k_{cat}/K_m Is Close to the Diffusion-Controlled Limit (10^8 to 10^9 $M^{-1}s^{-1}$)

Enzyme	Substrate	k_{cat} (s^{-1})	K_m (M)	k_{cat}/K_m ($M^{-1}s^{-1}$)
Acetylcholinesterase	Acetylcholine	1.4×10^4	9×10^{-5}	1.6×10^8
Carbonic anhydrase	CO_2	1×10^6	1.2×10^{-2}	8.3×10^7
	HCO_3^-	4×10^5	2.6×10^{-2}	1.5×10^7
Catalase	H_2O_2	4×10^7	1.1×10^0	4×10^7
Crotonase	Crotonyl-CoA	5.7×10^3	2×10^{-5}	2.8×10^8
Fumarase	Fumarate	8×10^2	5×10^{-6}	1.6×10^8
	Malate	9×10^2	2.5×10^{-5}	3.6×10^7
β-Lactamase	Benzylpenicillin	2.0×10^3	2×10^{-5}	1×10^8

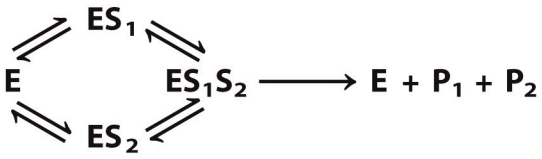
Source: Fersht, A. (1999) *Structure and Mechanism in Protein Science*, p. 166, W. H. Freeman and Company, New York.

Table 6-8
Lehninger Principles of Biochemistry, Fifth Edition

More complex systems

(a) Enzyme reaction involving a ternary complex

Random order



Ordered

(b) Enzyme reaction in which no ternary complex is formed

Figure 6-13
Lehninger Principles of Biochemistry, Fifth Edition

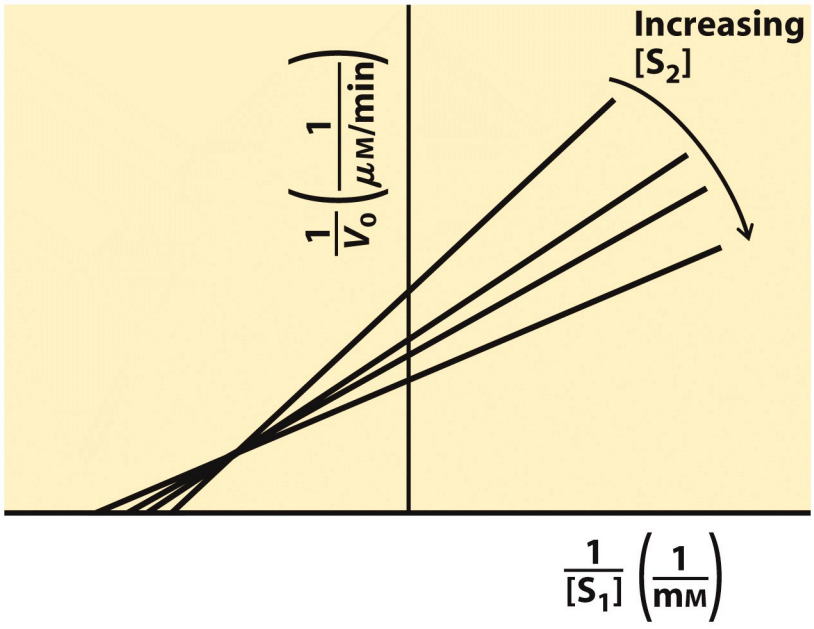


Figure 6-14a
Lehninger Principles of Biochemistry, Fifth Edition

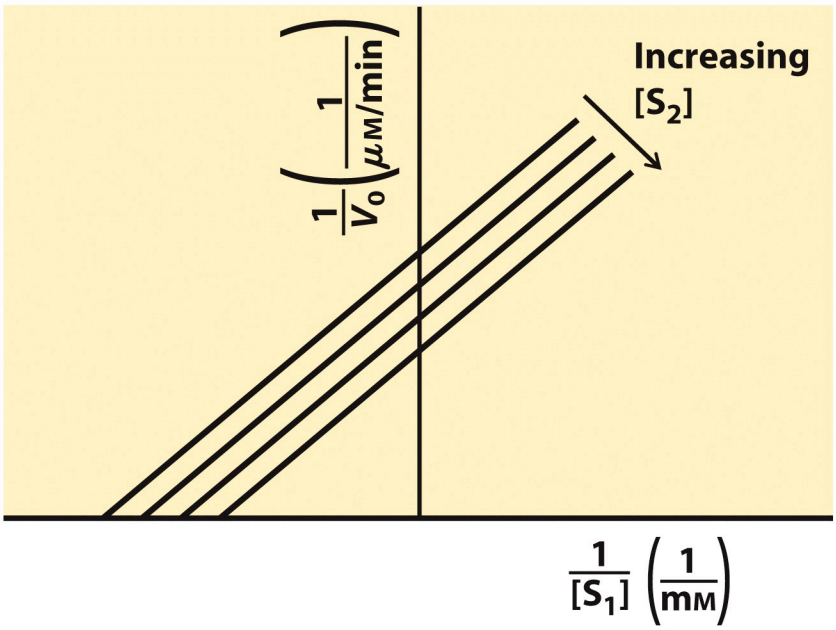


Figure 6-14b
Lehninger Principles of Biochemistry, Fifth Edition

Reversible Inhibition

Competitive inhibition

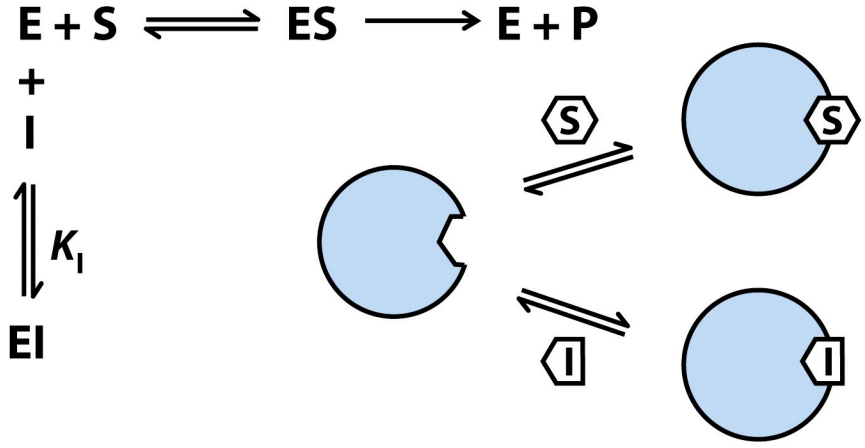


Figure 6-15a
Lehninger Principles of Biochemistry, Fifth Edition

Uncompetitive inhibition

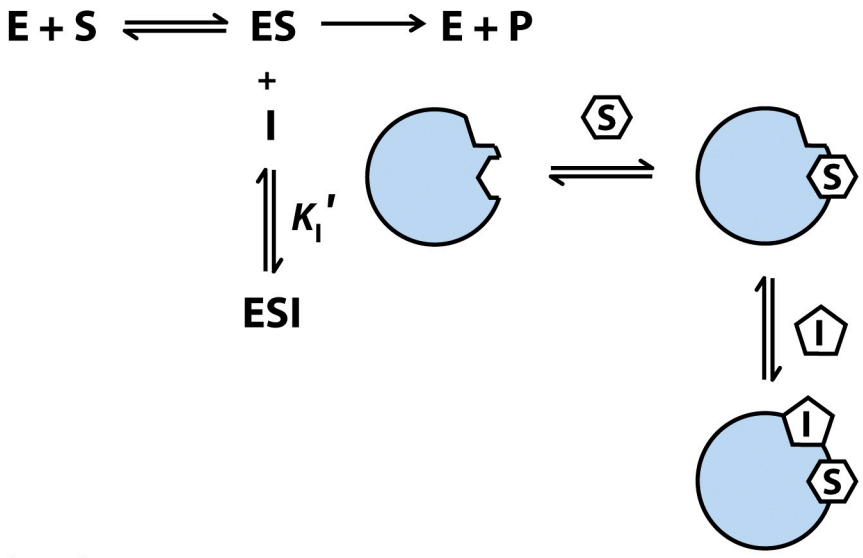


Figure 6-15b
Lehninger Principles of Biochemistry, Fifth Edition

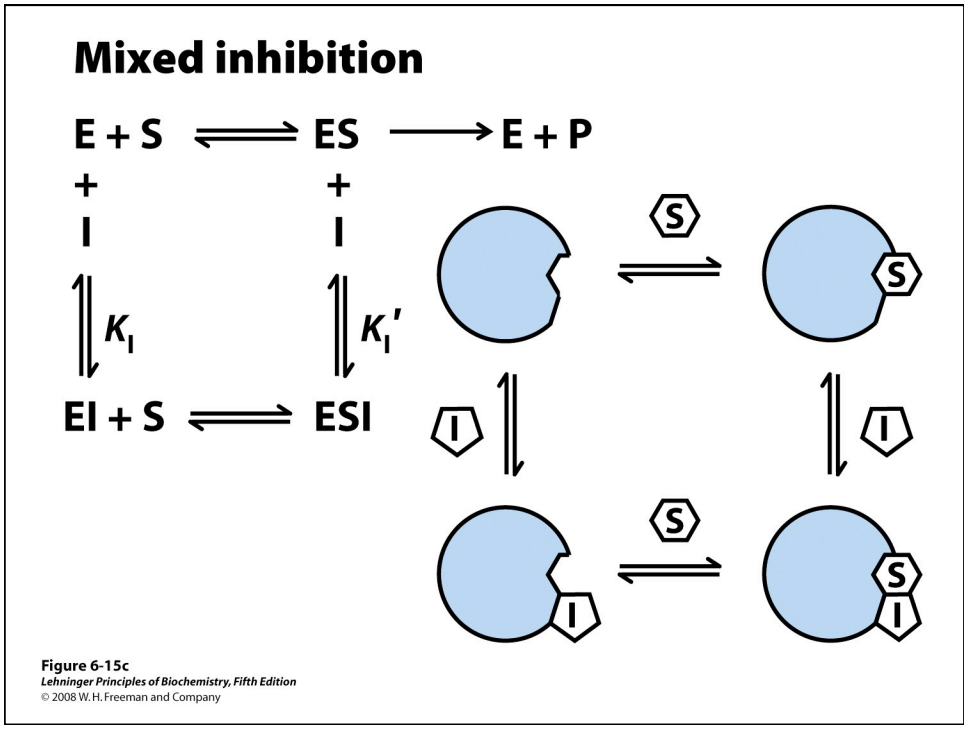
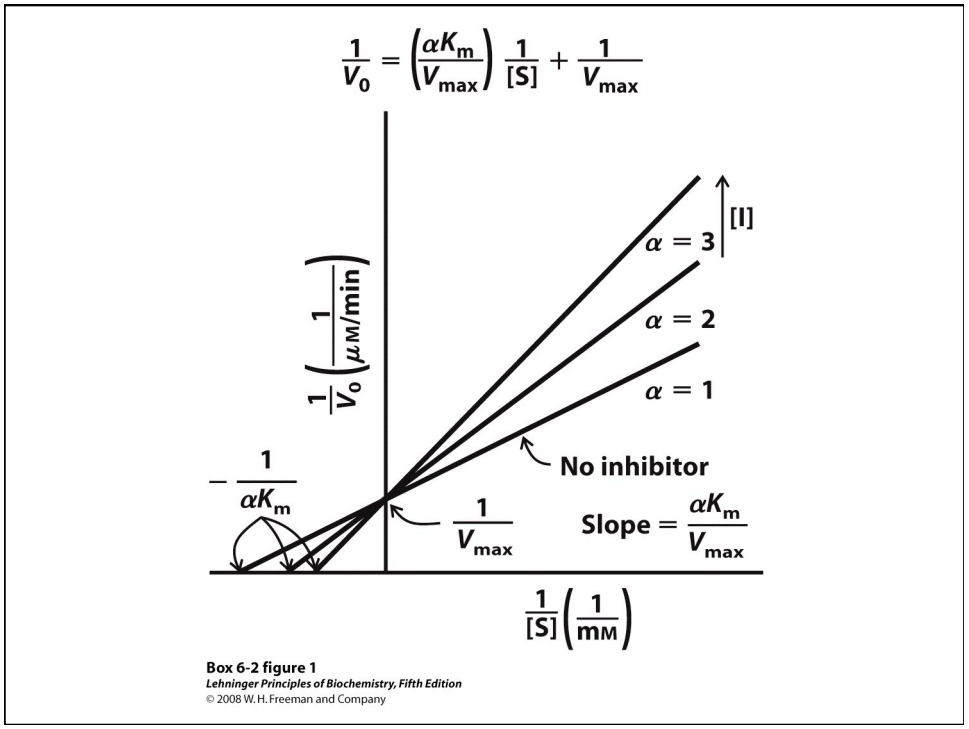
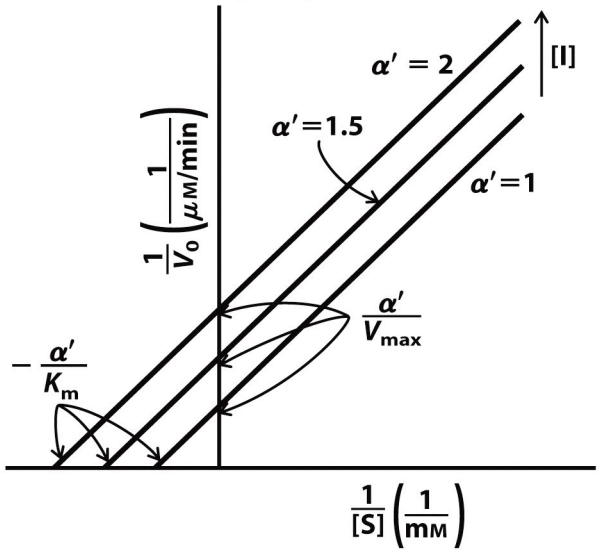


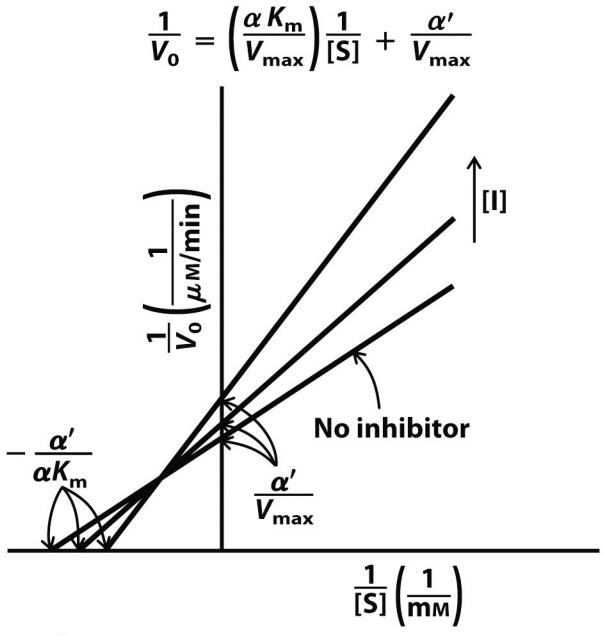
Figure 6-15c
Lehninger Principles of Biochemistry, Fifth Edition



Box 6-2 figure 1
Lehninger Principles of Biochemistry, Fifth Edition



Box 6-2 figure 2
Lehninger Principles of Biochemistry, Fifth Edition



Box 6-2 figure 3
Lehninger Principles of Biochemistry, Fifth Edition

TABLE 6–9 Effects of Reversible Inhibitors on Apparent V_{max} and Apparent K_m

Inhibitor type	Apparent V_{max}	Apparent K_m
None	V_{max}	K_m
Competitive	V_{max}	αK_m
Uncompetitive	V_{max}/α'	K_m/α'
Mixed	V_{max}/α'	$\alpha K_m/\alpha'$

Table 6-9
Lehninger Principles of Biochemistry, Fifth Edition

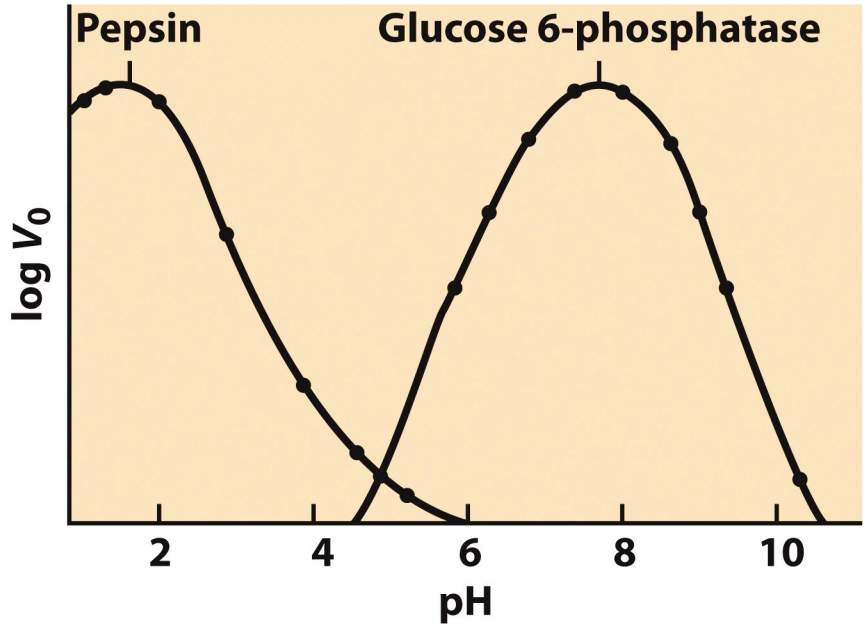


Figure 6-17
Lehninger Principles of Biochemistry, Fifth Edition

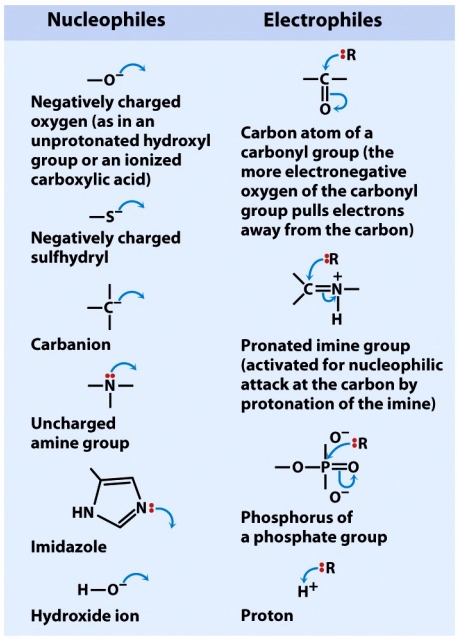


Figure 6-21 part 1
Lehninger Principles of Biochemistry, Fifth Edition

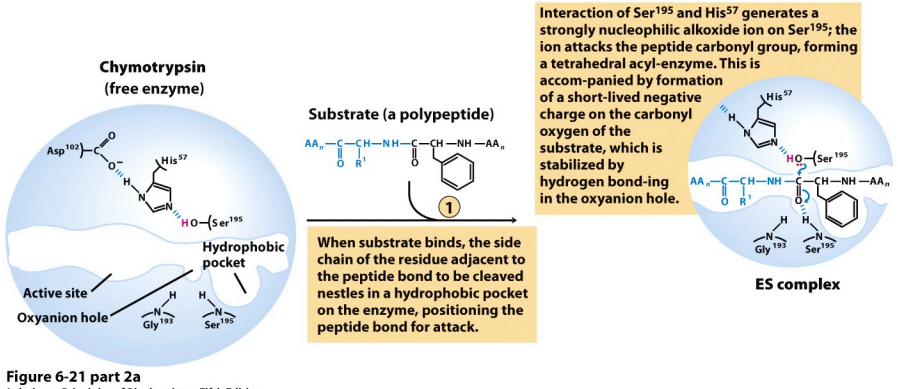


Figure 6-21 part 2a
Lehninger Principles of Biochemistry, Fifth Edition

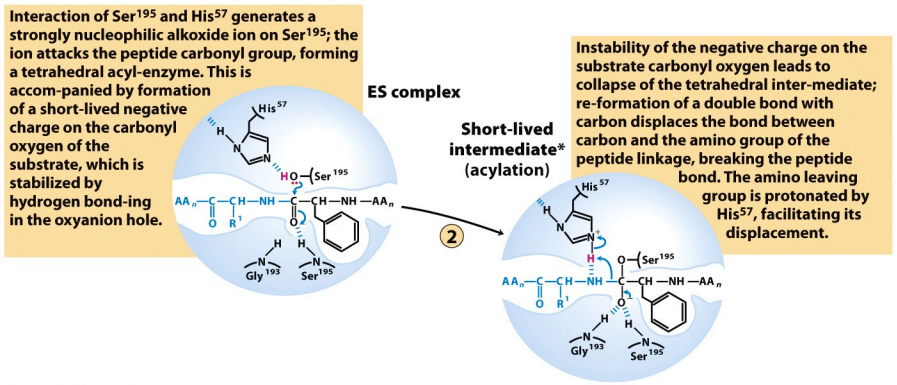


Figure 6-21 part 2b
Lehninger Principles of Biochemistry, Fifth Edition

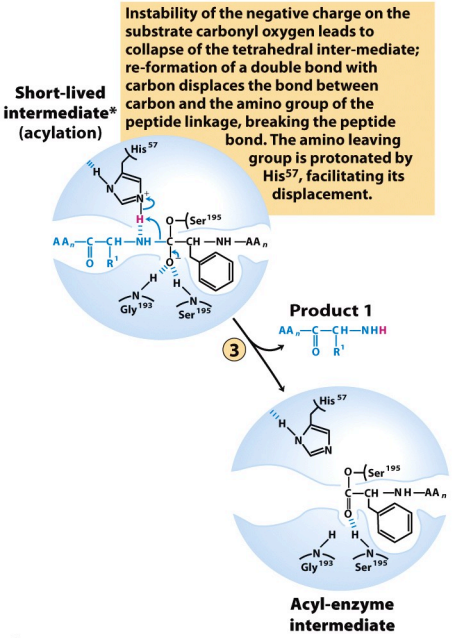


Figure 6-21 part 2c
Lehninger Principles of Biochemistry, Fifth Edition

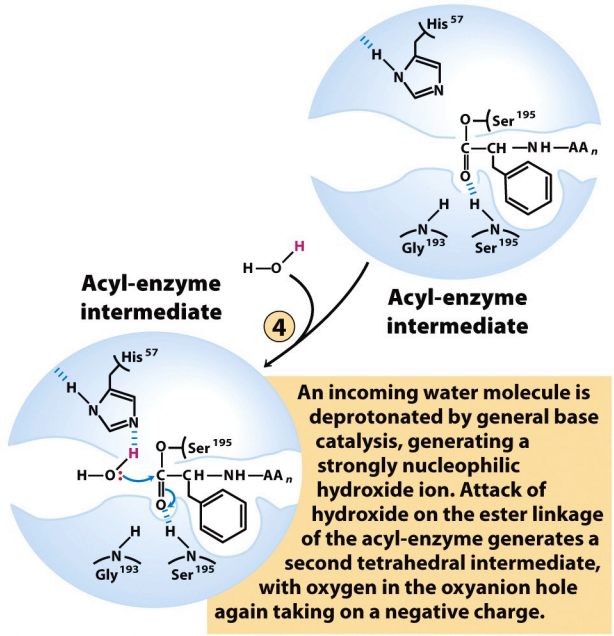


Figure 6-21 part 2d
Lehninger Principles of Biochemistry, Fifth Edition

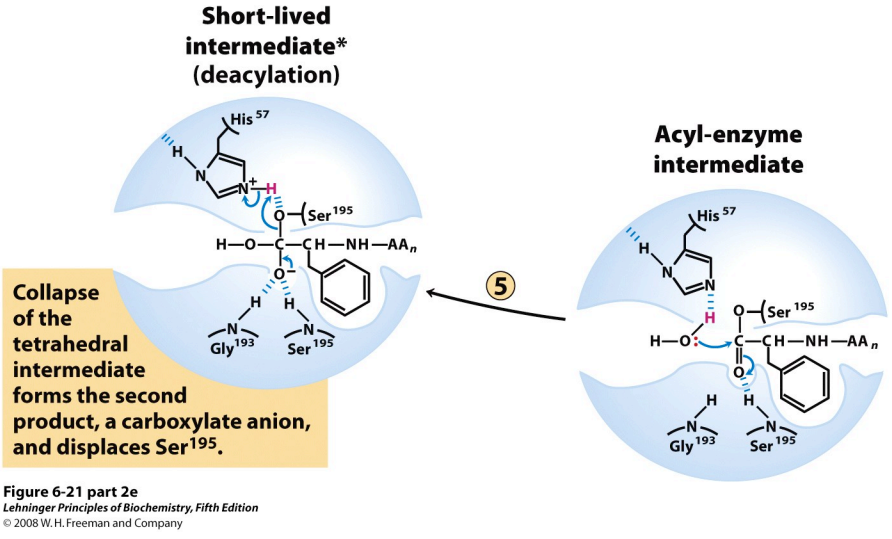


Figure 6-21 part 2e
Lehninger Principles of Biochemistry, Fifth Edition

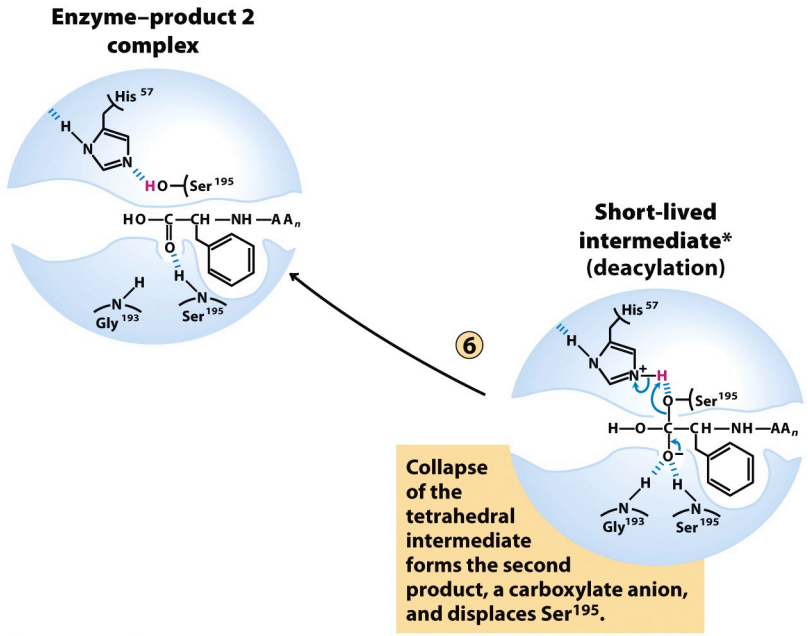


Figure 6-21 part 2f
Lehninger Principles of Biochemistry, Fifth Edition

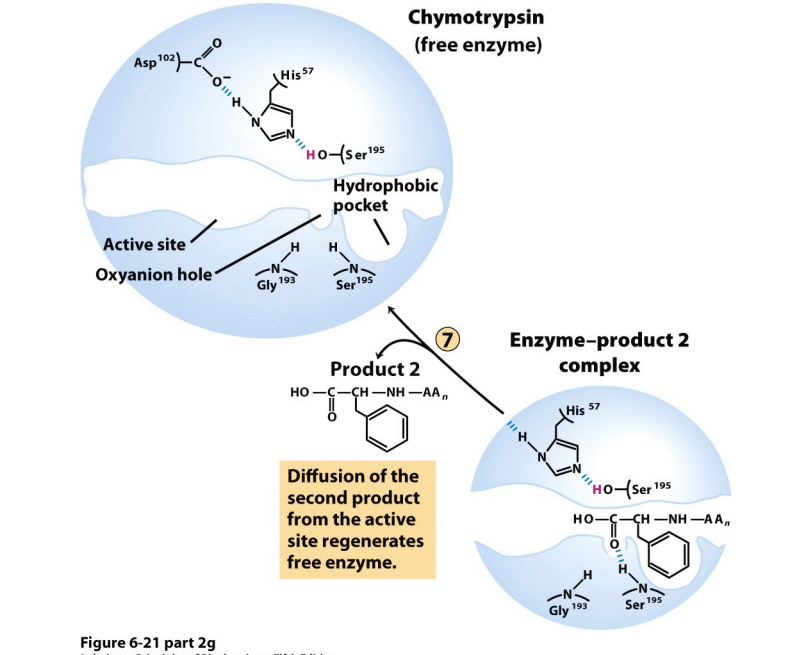
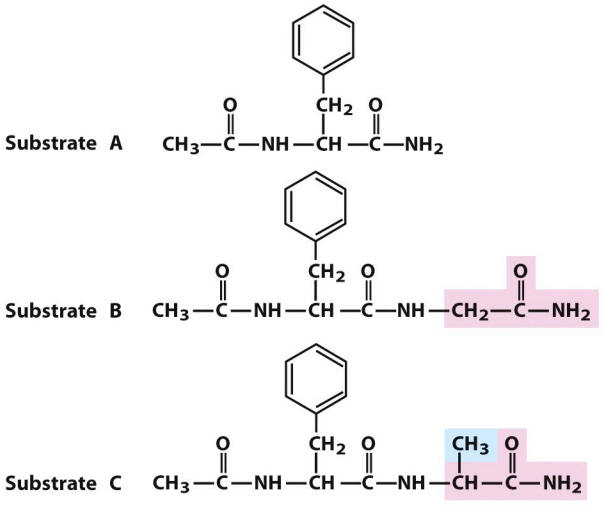


Figure 6-21 part 2g
Lehninger Principles of Biochemistry, Fifth Edition



k_{cat} (s^{-1})	K_m (mM)	k_{cat}/K_m ($M^{-1}\,s^{-1}$)
0.06	31	2
0.14	15	10
2.8	25	114

Box 6-3 figure 1
Lehninger Principles of Biochemistry, Fifth Edition

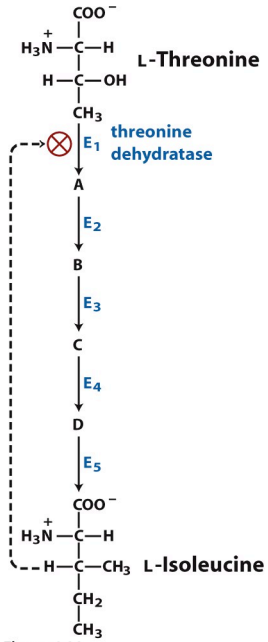


Figure 6-33
Lehninger Principles of Biochemistry, Fifth Edition