ENZYMES OF DIGESTION

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Summary

The enzymes of digestion are produced and secreted from almost all parts of the digestive system: salivary glands, lingual glands, stomach, pancreas, liver and intestinal mucosa. Often the final steps of digestion take place in the villi of enterocytes. These enzymes are almost all hydrolases. The digestion of carbohydrates begins in mouth by the salivary amylase and continues in the small intestine by pancreatic amylase and the intestinal and mucosal oligo- and disaccharidases. The enzymes involved in fat

digestion are the lingual, gastric, pancreatic and intestinal lipases. However, the main digestion of fats occurs in the small intestine by pancreatic lipase with the contribution of bile acids. The digestion of proteins begins in the stomach by pepsins, the active form of pepsinogens which is secreted from the chief cells of the gastric glands. The proteolytic enzymes of the pancreas, i.e. trypsin, chymotrypsin and carboxypolipeptidase, which are also secreted in inactive forms, continue protein digestion. The end products of protein digestion are amino acids, produced by the action of intestinal and mucosal dipeptidases.

1. Introduction

Preparation of foods contributes to their digestibility. Foods contain several autolytic enzymes. Many foods are fermented i.e. bacterial enzymes contribute to the digestibility of their components. Cooking denatures proteins, breaks cell walls, etc. and again the digestibility is promoted.

Almost all the enzymes of digestion are hydrolases. They are secreted by the salivary glands and gastric glands, pancreas and liver and the intestinal enterocytes. The actions of the digestive enzymes are similar to those of the lysosomal enzymes of the cells, except that they have different pH optima. Lysosomal enzymes are mostly active at acidic pH, whereas the digestive enzymes except pepsins have their activity optima at a pH of 6.5 to 7.5.

Many of the digestive enzymes have trivial names, such as pepsin and trypsin, since they were the first enzymes to be discovered before the systematic nomenclature was developed.

Although the basic principles of digestion are the same in most species we humans are intrerested, theree are still significant differences between e.g. herbivoric and omnivoric species compared with predators, which have much shorter guts (see also *Alimentary Systems in Some Homeothermic Vertebrates*).

2. Hydrolysis

If an organic molecule is split by addition of water, the reaction is called hydrolysis. Three major types of food, carbohydrates, lipids and proteins, are all digested by hydrolysis, but the enzymes catalyzing the reactions are different in each case.

Almost all the carbohydrates of the human diet are large polysaccharides or disaccharides, and they are combinations of monosaccharides bound to one another by condensation. The first stage of this reaction is the removal of a hydrogen ion from a monosaccharide and then a hydroxyl ion from another one. The two monosaccharides are then combined with each other at the sites of removal, and the hydrogen and hydroxyl ions combine to form water. When the carbohydrates are digested back into monosaccharides, specific enzymes return the hydrogen and hydroxyl ions to the polysaccharides and thereby separate the monosaccharides from each other.

The majority of fats in the diet consist of triglycerides (neutral fats), which are combinations of three fatty acid molecules condensed with a single glycerol molecule. Phospholipids consist of a phosphate and two fatty acid molecules. Cholesterol esters consist of a cholesterol and one fatty acid molecule. In the digestion of triglycerides, the fat-digesting enzymes return water to the triglyceride molecule, thereby splitting the fatty acid molecules away from the glycerol.

Finally, proteins are composed of amino acids bound together by peptide linkages. In this linkage, a hydroxyl ion is removed from one amino acid and a hydrogen ion is removed from the next one in condensation. In their digestion, the proteolytic enzymes return water to the peptide bonds to release the constituent amino acids.

3. Enzymes of Digestion According to their Sites of Secretion

Table 1 listed the sources, activators, substrates, actions and end products of the enzymes of digestion.

Source	Enzyme	Activator	Substrat	Action	Products
Salivary glands	Salivary α-amylase (ptyalin)	Cl^-	Starch	Hydrolyzes 1:4α linkages	α-Limit dextrins, maltoriose, and maltose
Lingual glands	Lingual lipase		Triglycerides		Fatty acids and 1,2-diacylgliserols
Stomach	Pepsins (pepsinogens)	HCl	Proteins and polypeptides	Cleave peptide bonds adjacent to aromatic amino acids	Proteoses, peptons and polypeptides
	Gasrtic lipase		Triglyserides	Lipolysis	Fatty acids and glycerol
Pancreas	Endopptidases Trypsin (Trypsinogen)	Enterokinase and trypsin	Proteins and polypeptides	Cleaves peptide bonds adjacent to arginine or lysine	Polypeptides and amino acids
	Chymotrypsins (chymotrypsinogens)	Trypsin	Proteins and polypeptides	Cleaves peptide bonds adjacent to arginine or lysine	Polypeptides and amino acids
	Elastase (proelastase)	Trypsin	Elastin, some other proteins	Cleaves peptide bonds adjacent to aliphatic amino acis	Polypeptides and amino acids
	Carboxypeptidase A (procarboxypeptidase A)	Trypsin	Proteins and polypeptides	Cleaves carboxy-terminal amino acids that have aromatic or bramched	Polypeptides and amino acids

				aliphatic side chains	
	Carboxypeptidase B (procarboxypeptidase B)	Trypsin	Proteins and polypeptides	Cleaves carboxy-terminal amino acids that have basic side chains	Polypeptides and amino acids
	Colipase (procolipase)	Trypsin	Fat droplets	Facilitates exposure of active site of pancreatic lipase	
	Pancreatic lipase	...	Triglycerides	Lipolysis	Monoglycerides and fatty acids
	Cholesteryl ester hydrolase	...	Cholesteryl esters		Cholesterol and fatty acids
	Pancreatic α-amylase	Cl^- ...	Starch	Hydrolyzes 1:4α linkages	α-Limit dextrins, maltoriose, and maltose
	Ribonuclease	...	RNA		Nucleotides
	Deoxyribonuclease	...	DNA		Nucleotides
	Phospholipase A_2 (prophospholipase A_2)	Trypsin	Phospholipids		Fatty acids, lysopholipids
Intestinal mucosa	Dipeptidase	...	Dipeptides		Amino acids
	Maltase	...	Maltose, maltotriose		Glucose
	Lactase	...	Lactose		Galactose and glucose
	Sucrase	...	Sucrose		Fructose and glucose
	α-Limited dextrinase	...	A-Limit dextrins		Glucose
	Nuclease and related enzymes	...	Nucleic acids		Pentoses and purine and pyrimidine bases
Cytoplasm of mucosal cels	Various peptidases	...	Di, tri, and tetrapeptides		Amino acids

Table 1. The sources, activators, substrates, actions and end products of the enzymes of digestion.

3.1. Ptyalin (α- amylase)

The only enzyme having physiological significance in saliva is ptyalin (α- amylase). It is secreted mainly by the parotid glands. Ptyalin starts the digestion of carbohydrates such as plant starch and muscle glycogen. Starch is our main source of energy. Salivary amylase can hydrolyze starch into the disaccharide maltose and other small polymers of glucose such as maltotriose and α limit dextrins that originate from the branch points of the starch molecule. However, because ptyalin can only act on the food for a short period, oral digestion has limited significance. Carbohydrate digestion continues in stomach for a while. Explanation for the continuation of ptyalin action is slow penetration of hydrochloric acid into the swallowed bolus The optimal pH of salivary

amylase is 6.7. When a food bolus enters the stomach, its action is inhibited by the acidic gastric juice, which has a pH of 4.0 or less. The salivary α- amylase hydrolyzes 1:4α linkages but not 1:6α linkages—terminal 1:4α linkages, and the 1:4α linkages next to branching points.

Probably, not more than 5% of all the starches that are ingested become hydrolyzed within the mouth before the food is swallowed. Starch digestion by ptyalin continues in the corpus and fundus of the stomach for as long as an hour, and, therefore, as much as 30 to 40% of the starch may be hydrolyzed mainly to maltose before the food becomes mixed with the acidic gastric juice.

3.2. Lingual Lipase

The serous lingual glands (Ebner's glands), on the dorsal surface of the tongue, secrete lingual lipase. As much as 30% of dietary triglyceride is digested in the stomach by the actions of lingual and gastric lipases together, producing fatty acids and 1,2-diacylglycerols. Lingual lipase appears to have little practical importance in lipid digestion. On the other hand, in premature infants in whom pancreatic lipase is insufficiently secreted or in children with congenital deficiency of pancreatic lipase, about half of dietary triacylglycerols can be digested and, therefore, absorbed, presumably due to the action of these lipases.

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Biographical Sketches

Prof. Dr. Senol DANE was born in 1963, in Konya, Turkey. He graduated from Ege University, Medical Faculty, Izmir, Turkey, in 1986. He completed his specialization in Physiology in 1990 in Ataturk University, Medical Faculty. Currently, he is serving as a Professor of Physiology and head of the Physiology Department in the Medical Faculty of Atatürk University, Erzurum, Turkey. He is a member of the Turkish Physiological Society, Neuroscience Society of Turkey, International Brain Research Organisation and New York Academy of Sciences. He is married and the father of four children.

Dr Osmo Otto Päiviö Hänninen, DMS, Ph..D., Professor of Physiology, Chairman of the Department, University of Kuopio, Finland. Born 1939, Lahti, Finland. He studied at the University of Helsinki and the University of Turku, Finland, where he received his Master of Sciences (Biochemistry) in 1962, Licentiate of Medicine (MD) in 1964, Doctor of Medical Sciences (DMS) in 1966, and passed his dissertation in biochemistry for his Ph.D. in 1968. He has also studied genetics. He has been a specialist in sports medicine since 1986. He served as the Research Assistant of Professor K. Hartiala, 1962–4; Assistant of Physiology, 1964–5; Laborator of Physiology, 1966–7; Docent of Physiology, from 1967, and Associate Professor of Biochemistry, 1969–71, at the University of Turku; Acting Professor in the Planning Office, 1971–2; and from 1972, Professor of Physiology and Chairman of the Department of Physiology, University of Kuopio; Vice-President of the University of Kuopio, 1972–9; and President, University of Kuopio, 1981–4. Furthermore, he served as Visiting Professor of Physiology at Shanghai Medical University, China, 1991–2, and at Sun Yat Sen Medical University, Guangzhou, China, 1998–9; as Foreign Member of the Russian Academy of Natural Sciences, from 1994; and as Secretary General, International Council for Laboratory Animal Science, 1988–95. He was the President of Societas Physiologica Finlandiae, 1990–9, and has been President of the International Society for Pathophysiology and a Member of the Executive Committee since 1994, and the Treasurer of the International Union of Biological Sciences since 1997.

His special interests in research are:

1. - Biotransformation and adaptation to chemical loading, biomonitoring of toxicants, and comparative biochemical toxicology.

2. - Muscle metabolism and function.

3. - Ergonomics.

He has contributed 266 papers in refereed journals and seventy-two in proceedings, and written fifty-five reviews, and thirty books or book chapters. He serves on the editorial board of four international journals and is at present the European Journal Editor of *Pathophysiology*.

Of his post-graduate students (thirty-two in biotransformation, twenty-seven in muscle metabolism and physiology, and five others), twelve serve as professors in China, Finland, Greece, Sweden, and the United States.