H. W. DAVENPORT

PHYSIOLOGY OF THE DIGESTIVE TRACT

SECOND EDITION

HORACE W. DAVENPORT, Ph.D., D.Sc. (Oxon.)
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The University of Michigan

THE DIGESTIVE TRACT

An Introductory Text

SECOND EDITION

YEAR BOOK MEDICAL PUBLISHERS INCORPORATED
35 EAST WACKER DRIVE, CHICAGO

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Preface to Second Edition

THE PURPOSE of this book is to make the basic facts of gastroenterological physiology readily available to medical and graduate students who are beginning their study of the digestive tract. The standards I have used are expressed in the questions: What should a generally well-informed student of physiology know of alimentary functions? What is the body of knowledge a student must command when he prepares himself for advanced study of the physiology of digestion? The standard is subjective and its application equally so. This book is intended to contain material answering the first question and to serve as a point of departure for the student who needs to know more.

The book's center of reference is the function of the normal human digestive tract. Although in some respects more is known about man than about any other animal, much human function must be inferred from observations on a wide variety of other species. I have selected experimental observations on other forms for their probable relevance to man, and I have tried to make clear on what species each statement is based. Unless otherwise specified, a statement can be assumed to apply to man. Aside from reporting a few amusing oddities, I have left unexplored the wide and fascinating field of comparative physiology of digestion. Likewise, I have used sparingly information derived from study of disease, and then chiefly when it explains or illustrates healthy function. I am sure that I can trust both students and teachers to understand the importance of knowing the normal before they attempt to interpret disordered behavior.

The plan of this book is to conduct the reader on three journeys through the alimentary canal, the first two showing him the mechanisms available for propulsion and secretion. Finally, we repeat the trip, accompanying aliments in the process of being digested and absorbed, observing to the best of our ability how and to what extent the mechanisms of motility, secretion and their control are actually used. The usually relentlessly downward gradient of the digestive tract imposes tedious repetitiveness on this method of exposition, but I find the task of adding variety by beginning with an enema and ending with an eructation beyond my powers.

I have made no attempt to document the text, for I estimate that on the average each sentence contains my interpretation of two scientific papers. The student who wants to know what lies behind the façade of textbook dogmatism and who has access to a good library can readily discover where our knowledge came from and where our research is going by using the references at the end of each section. These have been chosen because they are likely to be helpful guides to further study; most have excellent bibliographies.

It is a pleasure to thank those who have been helpful. Authors, editors and publishers have generously permitted me to reproduce published material; acknowledgment is specified in each instance where copyrighted material is used. Many persons have done special favors in supplying me with originals for illustrations, in sending me unpublished data or in giving critical advice on specific points. I must especially thank Lloyd Barr, Paul Bass, Felix D. Bertalanffy, R. W. Brauer, Hazel Brumby, G. Burnstock, W. I. Card,

J. N. Correa, Peter Curran, Virginia D. Davenport, R. E. Davies, Maynard Dewey, I. S. Edelman, Jean Frank, Arthur French, Rhoda Grant, Eugene Grim, A. Douglas Hally, F. J. Hodges, Adrian Hogben, Franklin Hollander, Henry Janowitz, Leon Miller, Bengt Nordgren, George E. Palade, Patricia C. Phelps, Robert Rushmer, E. C. Texter, Jr., Arthur Storey, S. C. Truelove, B. E. Vaughan, S. A. Weinberg, Fred S. Wright, J. Walter Woodbury and E. R. Woodward.

Three pre-eminent gastroenterologists are responsible for improvements in the second edition. J. N. Hunt supplied corrections and suggestions as well as fresh data drawn literally from his own stomach. Morton Grossman gave me both encouragement and welcome advice, once in a letter 19 pages long and in numerous shorter communications. Charles Code, over many years, and especially during the ten happy months I spent in his laboratory at the Mayo Clinic while on sabbatical leave from The University of Michigan, helped me in many practical ways and set a standard of comprehensive and critical knowledge for me to emulate. To all I give my affectionate gratitude.

Once more, I will gladly receive corrections and suggestions which may improve future editions.

H.W.D.

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PART I
MOTILITY

1

Chewing and Swallowing

FOOD IS TAKEN into the mouth in bites ranging from a few cubic millimeters upward; there it is broken up, mixed with saliva and lubricated. The act of chewing is partly voluntary; but the act of swallowing, once initiated, is entirely reflex. From the mass in the mouth, a bolus of 5–15 cu cm is separated and projected back into the pharynx, where it is engulfed by the stereotyped swallowing reflex, which moves it through the hypopharynx into the esophagus. During swallowing, the passages from the pharynx to the nose and trachea are closed, and respiration is briefly inhibited. The bolus is moved down the esophagus either by gravity or in the grip of a peristaltic wave and enters the stomach by passing through the inferior esophageal sphincter, which opens before it and shuts after it.

Chewing

The extent to which a mouthful of food is chewed varies among species; in some, such as the dog and the cat, food is reduced in size only enough to permit swallowing. In man, particles are usually reduced to a few cubic millimeters, but the amount a mouthful is chewed depends on the nature of the food, habit, incidental conversation and early training. The extent of chewing has a negligible effect on the chemical processes of digestion, but the bolting of unchewed food, especially when nervous tension is high, often causes epigastric distress. In chewing, the force which can be exerted by the incisors of an adult man is between 11 and 25 kg and by the molars from 29 to 90 kg. The jaw is normally kept closed in opposition to gravity; but the tactile stimulus of food particles against the gums, the upper and lower teeth and the anterior part of the hard palate evokes reflex inhibition of the closing muscles. This in turn reduces the strength of the stimulus causing inhibition, and contraction of the closing muscles follows. Thus the rhythmic act of chewing continues at an involuntary level. An animal deprived of its higher nervous centers above the mesencephalon chews reflexly when food is placed in its mouth. If the jaw is divided, the reflex is found to be unilateral, for stimulus on one side causes relaxation, followed by contraction on that side and not on the other. As a result, the force of chewing is brought to bear asymmetrically on the side of the mouth which is full. However, voluntary chewing and chewing movements caused by stimulation of the cerebral cortex are bilaterally synchronized. Most persons chew a bolus on one side of the mouth at a time, but some divide the bolus to chew it on both sides simultaneously.

Mouth Movements in Swallowing

The digestive tract moves its contents by creating a pressure gradient. At the beginning of a swallow, the tip of the tongue separates a bolus from the rest of the material in the mouth and brings it into the midline between the anterior portion of the tongue and the hard palate. The jaw shuts, and the soft palate is elevated. The forepart of the tongue is pressed firmly against the roof of the mouth and, together with the closed lips, seals off the anterior portion of the mouth. The palate and the contracted palatopharyngeal muscles form a partition between the

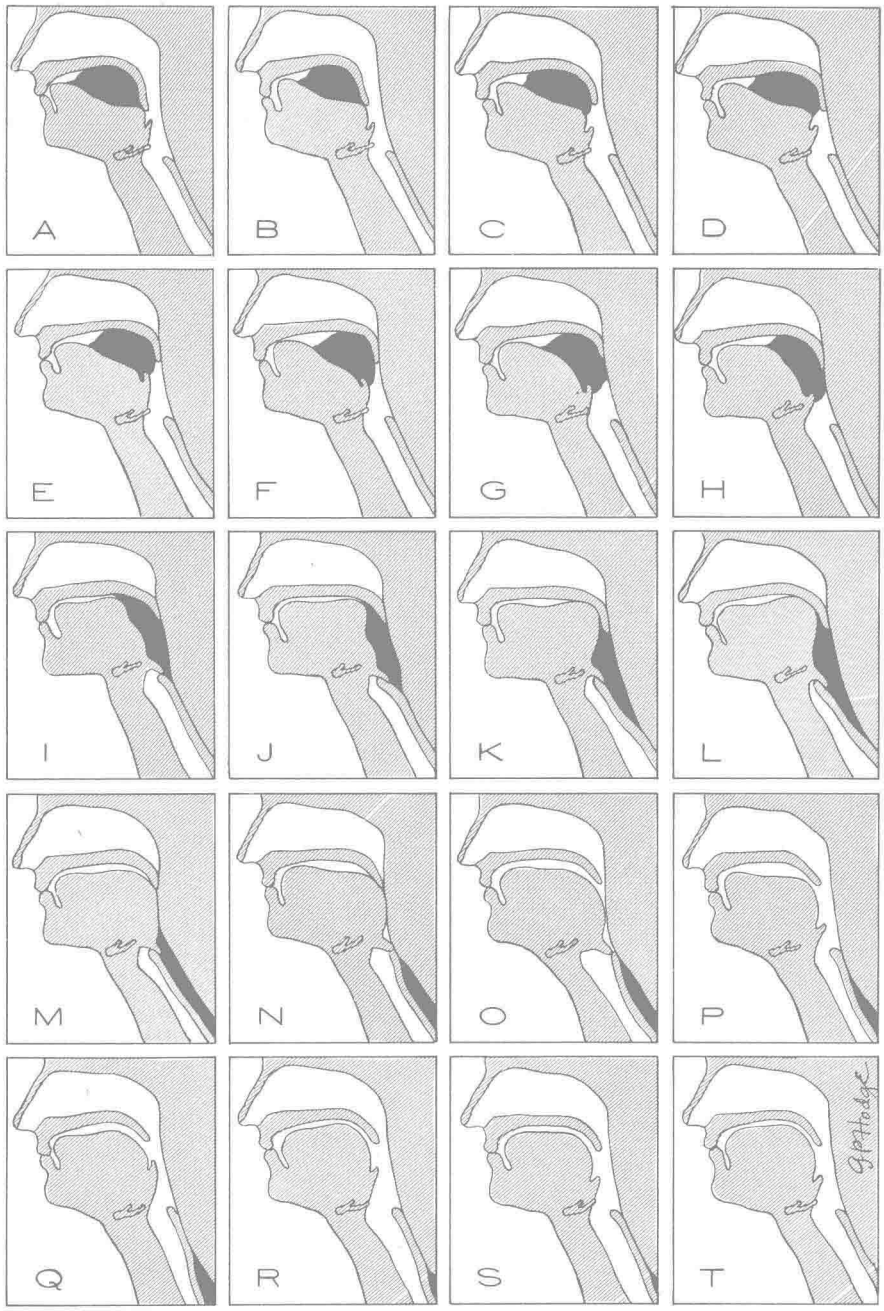

Fig. 1.—Sequence of events during swallowing. **A** and **B**, the soft palate forms a partition extending to the base of the tongue. **C**, **D**, **E** and **F**, the soft palate is elevated to obstruct the nasopharynx as the bolus moves backward over the tongue. **G**, **H** and **I**, the bolus tilts the epiglottis backward. From H through R the glottis, not shown, cuts off the laryngeal airway. **J** and **K**, the bolus passes smoothly over the convex epiglottis, and the tongue moves backward as a piston. **K**, the bolus is slightly delayed at the hypopharyngeal sphincter. **O** and **P**, the soft palate relaxes, and the epiglottis ascends. **Q**–**T**, the bolus moves down the esophagus. The entire sequence occupies one and a third seconds. (Adapted from Rushmer, R. F., and Hendron, J. A.: J. Appl. Physiol. 3:622–630, 1951.)