PARIETAL (CONTACT) DIGESTION

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For more than 100 years it has been generally supposed that digestion in the higher animals takes place as follows:

The food passes into the cavity of the digestive tract, becomes finely divided and mixed with the secretions of various glands so as to form a chyme. In the chyme, under the influence of various enzymes the food becomes broken down into nonspecific constituent elements capable of being absorbed.

This view, although generally accepted, involves certain serious contradictions. In particular, in spite of great advances in our knowledge of the physiology of digestion and the chemistry of enzymes, until now it has not been possible to reproduce in vitro those rapid breakdown processes which occur in vivo.

In attempting to understand the conditions which govern digestive hydrolysis in the living animal, we have studied the hydrolysis of starch by amylase in the presence of small pieces of intestine. During the course of the work we obtained results which indicated that cavity digestion (throughout the whole mass of chyme) is not the only or even the main mechanism which brings about the breakdown and absorption of food, and that in addition there are other very important and hitherto unknown processes which we have referred to collectively as parietal or contact digestion.

METHOD

We have studied the effect of small portions of living rat small intestine having a surface of serosa of 1-1.5 cm^2 on the hydrolysis of starch by amylase in vitro.

The rate of hydrolysis was determined photometrically in terms of the amount of starch destroyed, using the Smith-Row method and incubating for 30 minutes at 38° in a phosphate buffer at pH 7.5 containing 0.85% NaCl, or in Ringer's solution; the results obtained by both methods were almost identical.

In the first set of experiments we compared the activity of 1 ml of diluted pancreatic amylase, the activity of a piece of small intestine in 1 ml of phosphate buffer, and the activity of 1 ml of amylase to which a piece of small intestine was added during the period of incubation with starch.

In subsequent experiments we used the "trichloracetic" models of the esophagus, stomach, and small and large intestines.

These were prepared as follows: The animal was decapitated and portions of intestine, stomach, etc., rapidly removed and washed several times in physiological saline cooled to 3-5°. The portions were then transferred for 1½-2 hours to a 10% solution of trichloracetic acid (TCA). After being treated for two days with TCA, the intestine was washed in several changes of Ringer at a temperature of approximately 0°.

RESULTS

It can be seen from Fig. 1 that in the presence of a portion of living intestine, the rate of enzymatic hydrolysis of starch increases, so that it becomes considerably greater than the summed effects of the amylase solution and the intestine when incubated separately with the standard amount of starch. This effect cannot be ascribed exclusively to the activity of the living structures of the intestine or to the presence in the gut of particular enzymes, because the pieces of intestine previously killed by treatment with 10% TCA increase the activity of the amylase, although they themselves have no enzymatic activity.

As can be seen from Table 1, the presence of pieces of dead intestine caused a marked increase in enzymatic activity.

The following explanation of the phenomenon may be advanced: The intestine contains substances which pass into solution and increase the action of amylase, or alternatively the increase in amylolytic activity results from the fact that the intestine exerts an influence on the kinetics of the enzymatic reaction by presenting an active porous surface.

We have shown that the addition of aqueous or saline extracts of small intestine to the amylase cause no appreciable effect on the hydrolysis of starch as is shown by comparing it with a control mixture containing the same amount of enzyme but no intestinal extract.

It can be deduced from these experiments that the increase in amylolytic breakdown of starch caused by adding intestine is not due to the presence in it of substances activating amylase.

If we suppose that under the conditions of our experiments there is an increase in the activity of the amylase in solution, then it would be expected that first incubating the amylase with pieces of intestine would cause an increased hydrolysis of starch when the latter was added after the intestine had been removed (by analogy with the activation of trypsinogen by enterokinase). However, it can be seen from Table 2, that after incubating with pieces of intestine there is never any increase in amylase activity, but in most cases there is some reduction. These results do not accord with the hypothesis that substances activating amylase pass from the intestine into the solution, or that the enzymatic activity of amylase in the solution is increased.

From this table it can be seen that after incubating with amylase, the intestine acquires a considerable enzymatic activity several times greater than the loss of the enzyme in the original amylase solution. The experiments demonstrate that a certain amount of amylase must be adsorbed onto the surface of the intestine in such a way as to increase the activity of the adsorbed enzyme considerably.

It is usually supposed that the epithelium of the small intestine performs the functions both of absorption and secretion. No experimental study has been made of the problem of how the large surface area affects the course of the enzymatic reactions in the

TABLE 1 Effect of TCA Model of the Small Intestine on Amylase Activity

Number of experiment	Amylolytic activity of hydrolyzed starch, %		
	amylase	intestine	amylase and intestine
1	28	0	46
2	31	0	52
3	19	0	34
4	12	0	20
5	47	0	57

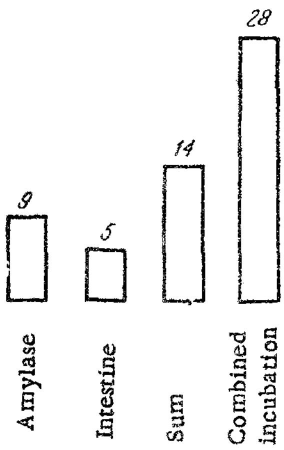

Fig. 1. Effect of a piece of living intestine on the breakdown of starch by amylase. The activity is shown as a percentage of the substrate hydrolyzed. From left to right: activity of a preparation of pancreatic amylase, innate amylolytic activity of the strip of intestine, some of the two activities, activity shown during combined incubation with amylase and intestine.

lumen. Nevertheless it is well known that the rate of enzymatic processes on a surface is very different from that occurring in a fluid medium.

Our results indicate that the large surface of the small intestine performs a further important function – that of reconstituting a living porous adsorbant. Under normal conditions, part of the digestive enzymes remain in solution, and bring about digestion in the lumen, and until now this has been considered the only mechanism responsible for the breakdown of food, while the remaining part of the enzymes are adsorbed on to the surface of the mucosa where they bring about contact or parietal digestion.

Evidently, parietal digestion will be best developed in the small intestine. We have compared the increase in the amylolytic breakdown of starch under the influences of pieces of mucosa from the esophogus, stomach, and small and large intestines (experiments on models previously treated with TCA). It can be seen from Fig. 2, that the enhancing effect is comparatively small for pieces of stomach and large intestine, negligible for fragments of esophogus, but well shown for fragments of small intestine.

This differentiation of the digestive tract does not arise by chance. We have compared the rates of breakdown of soluble (partially hydrolyzed) amylose and insoluble amylose by the enzyme in solution and the enzyme adsorbed onto intestine. It was found that the larger amylose molecules are more intensely attacked by the dissolved enzyme, while the smaller molecules (previously partially hydrolyzed) on the contrary were more rapidly broken down in the parietal layer by the adsorbed enzymes.

Evidently, the very first stages in digestion take place chiefly in the lumen of the digestive tract, and subsequently on the surface of the intestine. This view agreed well with the results given previously which showed that parietal digestion occurs chiefly in the small intestine, i.e., where the greatest amount of hydrolyzed substrate is to be found. The arrangement

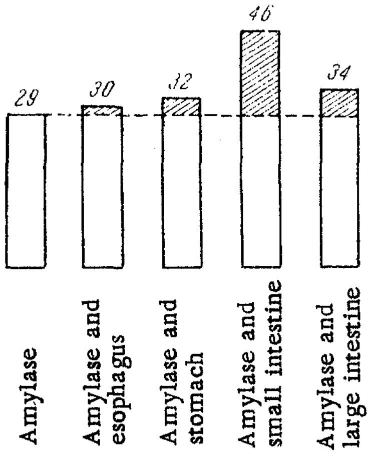

Fig. 2. Effect of equal areas of esophagus, stomach, small and large intestine (treated with TCA) on the activity of pancreatic amylase.

whereby parietal hydrolysis represents the chief supply of absorbable products and takes place directly on the surface of the villi constitutes extremely favorable conditions for absorption. A rough estimate based on our figures shows that the concentration of the starch breakdown products in the immediate neighborhood of the intestinal wall ought to be several times greater than in the chyme. Possibly absorption is not determined by the concentration gradient between chyme and blood, but by that between the parietal layer and the blood.

Because the enzymatic layer on the intestinal surface is related not only to the hydrolysis of food but also to its absorption it ought perhaps to be referred to as the "digestive-transport" layer.

We have found that the adsorbed enzymes are quite firmly fixed to the intestinal surface, and only pass back into solution with difficulty. This indicates that the classical view of the enzymes moving with the chyme along the intestine where they quite soon enter the large intestine to be further broken down or voided to the outside, needs to be refined considerably.

It is usual to suppose that the action of enzymes is limited to the particular portion of chyme into which they have passed when secreted, and that the digestive enzymes pass quite rapidly out of the small intestine together with the chyme, so that at each new act of digestion there ought to be a complete renewal of the enzymes which bring about the breakdown of food. We consider that as a result of adsorption quite a stable enzymatic layer is formed. The result is that the enzymes act on the whole of the food passing past a given section of intestine, and not only on one particular portion of chyme. It is still more important, however, that thanks to the parietal digestion the useful life (if we may call it that) of the digestive enzymes is increased several times. By being adsorbed it is likely that they do not take part merely in one but in several digestive acts.

Probably owing to the presence of two hydrolytic mechanisms (cavity and parietal) and through the interaction of these two mechanisms conditions are established for very effective action on the food. Here, probably the first stages of digestion are brought about chiefly in the lumen (the molecules of the enzymes being oriented with respect to the large portions of substrate), and subsequently hydrolysis takes place on the surface of the villi (the substrate molecules being orientated with respect to the fixed molecules of the enzyme).

Adsorption makes it possible for a particular enzymatic molecule to come into contact with many portions of chyme moving past a given section of intestine. The time of action of the enzymes in the digestive tract is thus increased, and the loss of enzyme is reduced. Finally, the features of parietal digestion as described establish extremely favorable conditions for absorption.

I. P. Pavlov compared the digestive system to a highly perfected chemical factory. The part played in modern chemical engineering by catalysts absorbed on to surfaces helps us to understand the significance of

TABLE 2 Effect on Activity of Incubating a TCA Model of Intestine in an Amylase Solution

Number of experment	Amylase activity of hydrolyzed starch, %			
	original amylase activity	original intestinal activity	amylase activity after incubating with intestine	intestinal activity after incubating with amylase
1	47	0	47	20
2	47	0	44.5	25.5
3	63	0	56	19
4	59	0	57	20
5	46	0	40	29

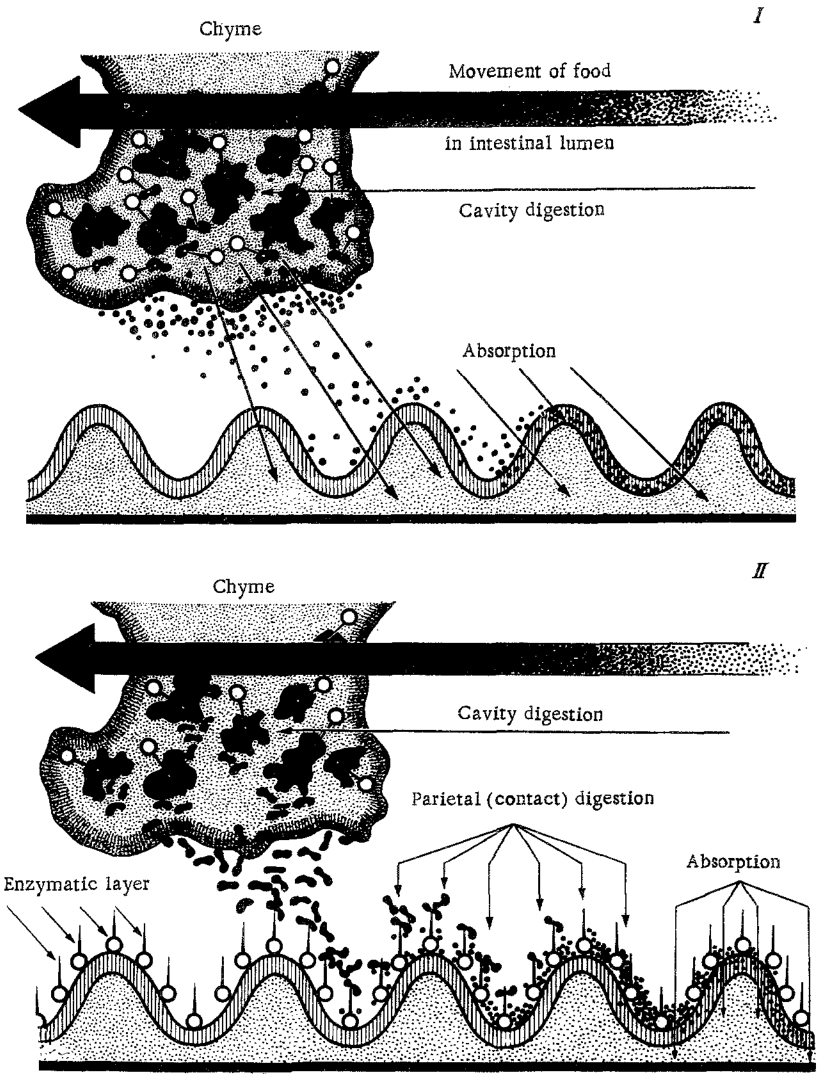

Fig. 3. General scheme of digestion. I) as usually accepted; II) taking into account parietal hydrolysis.

contact digestion in the activity of the living factory which brings about the breakdown and assimilation of food.

The last diagram (Fig. 3) shows the general course of digestion and indicates how cavity and parietal (contact) hydrolyses take place. Above, the usually accepted scheme for digestion is illustrated.

SUMMARY

The evidence presented shows that in higher animals cavity digestion is not the only or even the principal mechanism of breakdown and assimilation of food, but that along with it there is a system of hitherto unknown processes which we here refer to as parietal or contact digestion. The latter occurs under the influence of enzymes adsorbed onto the surface of the mucosa which is concerned in the hydrolysis and absorption of food; a number of specific features of this process are described.