DIGESTIVE FUNCTION OF THE INTESTINAL SURFACE IN RABBITS DURING THE FIRST WEEKS OF LIFE

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Numerous facts indicate that in the higher animals and man digestion takes place not only under the influence of enzymes entering the chyme as a constituent of the digestive juices, but also intracellularly (particularly as a result of pinocytosis), and on the external surface of the intestinal epithelium (parietal digestion), [6, 9]. In this connection it becomes necessary to determine the role of each of the different kinds of digestion described during the early post-embryonic stages. There are indications that intracellular digestion by means of pinocytosis is particularly well marked in mammals during the first few weeks after birth [7].

The histochemical studies of Clark [8] and Brodskii [1] who have investigated alkaline phosphatase indicated that the enzyme layer on the surface of the intestine is formed during the first days after birth. However the problem of to what extent the small intestine presents a functional digestive surface during the early postnatal period has not been studied in direct experiments.

In the present work we report the first results on this subject. We have studied digestion of partly broken down (dissolved) starch which could not penetrate within the cells of the small intestine of rabbits; the work was carried out between the 4th and 45th days after birth.

EXPERIMENTAL METHOD

Acute experiments were carried out on 10 rabbits aged 4-6 days, on 8 aged 14-16 days, on 8 aged 24-26 days, and on 2 aged $1\frac{1}{2}$ months. The animals were placed on a thermostaticatlly controlled table and an isolated segment od duodenum and small intestine 15-25 cm in length was perfused; pancreatic juice entering the perfused seg-

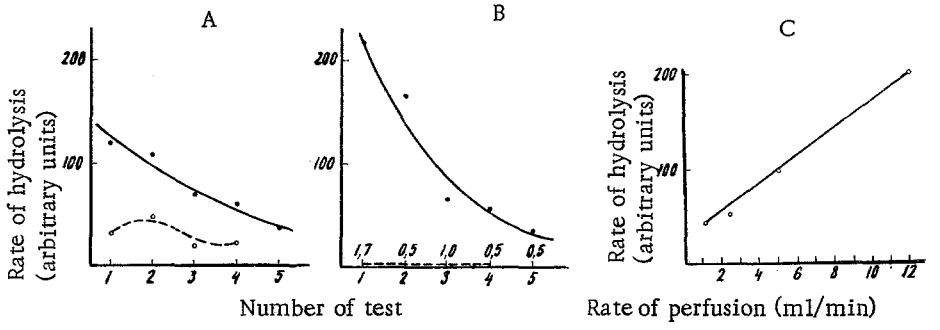

Fig. 1. Hydrolysis of soluble strach in rabbits 45(A) and 4(B) days old. C Change in the rate of hydrolysis plotted against perfusion rate. Dashes—hydrolysis in vivo, dots—in vitro. Tests made every three min.

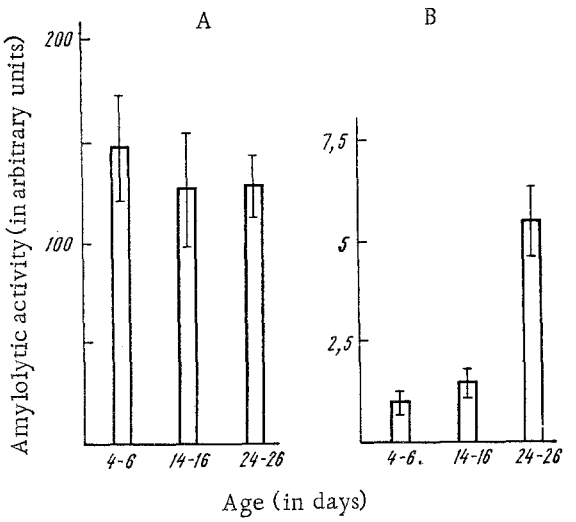

Fig. 2. Ratio of luminal to parietal digestion at early stages. A) Hydrolysis in vivo; B) in vitro.

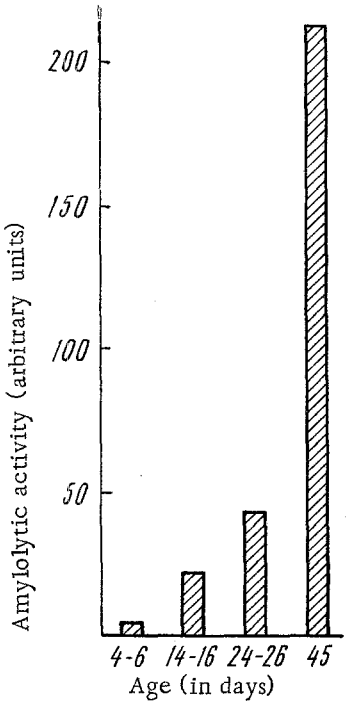

Fig. 3. Secretion of amylase per min at various periods. Amylolytic activity (arbitrary units).

ment was preserved. The hydrolysis of starch was determined by a reduction of the starch-iodine color, as measured photometrically by our modification of the Smith-Roy method [6]. In all age groups the rate of perfusion was approximately 2-5 ml/min. The results were treated statistically.

EXPERIMENTAL RESULTS

The results shown in Fig. 1 of typical experiments on rabbits at the 45th (A) and 4th (B) day of life enables us to compare the hydrolysis of starch in animals at the early postnatal periods. In the 45-day-old rabbit hydrolysis of starch in the intestine takes place as described for various adult animals [2, 6, 7, 9]. Hydrolysis in vivo is 2-5 times more rapid than it is in vitro, which is an indication that only a certain portion of the substrate is broken down by enzymes acting within the cavity, and that a considerably greater amount of hydrolysis is brought about by enzymes fixed onto the intestinal surface.

The rate of hydrolysis in vivo in 4-day-old rabbits was no lower than it was in animals which were changing over to independent feeding. We must also note that the perfusate escaping did not contain amylase, whereas in the 45-day-old animals it was present in large quantities.

In 4-day-old rabbits we also noted a slowing down of starch hydrolysis during perfusion caused by amylase leaving the intestinal surface. Some of the differences of this process between newborn animals and adults, as revealed in our experiments cannot yet be considered to be completely established. However the very fact that starch hydrolysis was reduced during the course of the perfusion is a result typical of those kinds of intestinal digestion which occur through the action of enzymes which are loosely held by the intestinal surface.

Many authors have drawn attention to the fact that for catalytic actions of air at surfaces there is a characteristic relationship between the velocity of the fluid relative to the surface and the velocity of the reaction itself [7]. Figure 1B, shows that with increase in perfusion rate the rate of hydrolysis in vivo increases linearly within certain limits (see Fig. 1C). As can be seen from Fig. 2, in the youngest age group hydrolysis in vivo is approximately 150 times as rapid as in vitro.

We could find no statistically significant differences in the rate of hydrolysis of starch in the intestine of animals 4-6, 14-16, or 24-26 days old (postnatal), although from the youngest group luminal digestion was almost entirely absent, whereas in the older animals it was well shown.

The rate of spontaneous secretion of amylase, which in rabbits is continuous, was enhanced particularly strongly during the transition from milk to vegetable feeding (Fig. 3), an effect which is usually regarded as adaptive

We must note that our results concerning the entry of pancreatic amylase into the intestine, which determines the level of luminal digestion, agree with those of other authors. Indeed the fact that the secretion of enzymes

breaking down polysaccharides occurs quite late in life has been established by other authors who have studied this problem [3-5, 10].

If we consider only luminal digestion, then the conclusion follows that hydrolysis of polysaccharides in the lumen of the gut of new born animals is practically impossible. However the fact is, as has been shown above, that hydrolysis in vivo is well marked even during the first days of life, and its rate scarcely changes during the whole of the first month after birth.

Hence, it follows that the breakdown of starch during the first days of life is brought about by enzymes which act on the external surface of the cell membranes. This hypothesis has been confirmed by special experiments on the removal of amylase from the intestinal surface, and is in line with the fact that during the period of milk feeding the chief digestive glands are comparatively inactive, and that highly dispersed products, for example milk, do not require much previous treatment of the kind to which they are subjected in the lumen of the gastrointestinal tract. If this hypothesis is confirmed, the period of milk feeding could rightly be called a period of parietal digestion.

To conclude, we must emphasize that experiments with starch are a kind of model. Although the substrate used is not typical of the period of milk feeding it was chosen for the reason that it cannot penetrate the cell membrane, and therefore allows a clear distinction to be drawn between luminal and parietal digestion, and for intracellular digestion to be excluded.

Also the results obtained may have some practical significance, because they indicate the highly developed ability of the intestinal surface to break down the soluble starch, even in the period when enzymatic function of the pancreas is very little developed.

Finally, experiments on the hydrolysis of starch indicate that the intestinal surface on which parietal digestion occurs becomes functional earlier than does the secretory mechanism which enables various forms of luminal digestion to occur. Here, however,further investigations are required to determine the digestion of various food substances because there is evidence that the development of processes related to the breakdown of protein-lipids and polysaccharides are markedly different [4, 10].

SUMMARY

Acute experiments were carried out on rabbits 4-6, 14-16, 24-26, and 45 days old; it was shown that the pancreas secreted very little amylase during the first two weeks. Its secretion increased markedly by the end of the first postnatal month, and still more by the middle of the second month. Hydrolysis of soluble starch by enzymes sorbed onto the surface of the small intestine was well under way during the first days of life. It is suggested that parietal digestion is the dominant mechanism at the stage of milk feeding.

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