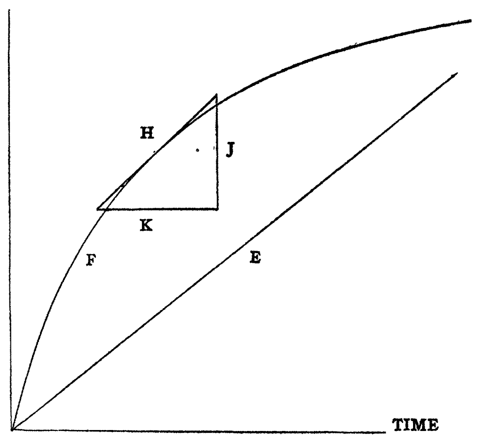

Fig. 2. Curves of a normal biological process E proceeding at a constant rate, and the same process under abnormal conditions with a variable rate, F.

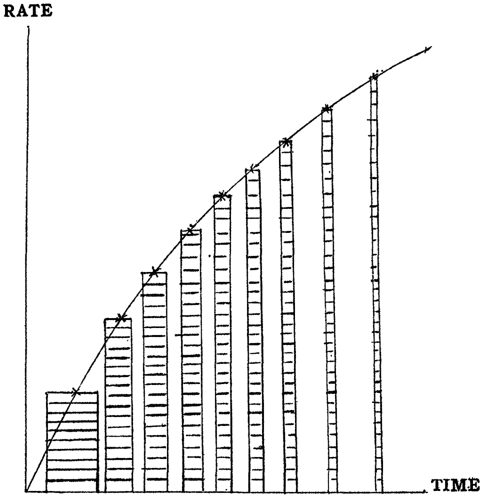

Fig. 3. Curve of a biological process which is studied by measurements of its rate made at frequent intervals. The shaded portions represent periods during which measurements are made. The unshaded portions represent intervals during which there are no measurements.

mine the rate at various periods as shown in Fig. 3, in which the periods during which the rate is measured are shaded while the intervals during which no measurements are made are unshaded.

We can determine the time necessary to perform a given amount of work and take its reciprocal as the rate: this rate is of course an average for the whole period. If the rate is changing during the period the average rate probably occurs near the middle of the period; hence we may place the ordinate representing the rate in the middle of the period as shown in the figure. The resulting curve can be transformed into a curve of the type shown in Fig. 2 by finding the total amount of work performed at any given time: this is accomplished by finding the area enclosed by the curve and the ordinate of the time chosen (since this area is the product of rate by time, it gives the amount of work performed).

Summary.—Measurements of the relative rates of biological processes are frequently made in a faulty manner which may easily be avoided by a slight change of method.

Usually it is preferable to compare the times required to perform a given amount of work (or to bring the reaction to the same stage) rather than to compare the amounts of work performed in a given time.

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HOW FOOD AND EXERCISE INCREASE OXIDATION IN THE BODY

Lavoisier,[1] shortly after his discovery that oxygen supported combustion, showed that physical work increased oxidation in the body, thus giving rise to the energy for the work. He also found that the ingestion of food increased oxidation. Rubner[2] showed that of the food-stuffs, meat increased oxidation most, fat next, and sugar least. The present investigation was begun in an attempt to find out how physical work and the ingestion of food increase oxidation in the body.[3] We had already found that whatever increased oxidation in the body also stimulated the liver to an increased output of catalase, an enzyme

[1] Lavoisier, *Mem. de l'Acad. des Sc.*, 1780.

[2] Rubner, "Energiegesetze," 322.

[3] Burge, Neill and Ashman, *American Journal of Physiology*, Vol. XLV., No. 4, pp. 388–395, 500–506.

in the tissues possessing the property of liberating oxygen from hydrogen peroxide. Hence the conclusion was drawn that catalase is the enzyme in the body principally responsible for oxidation. Stated more specifically, the present investigation was carried out to determine if the end products of digestion of food, when absorbed from the alimentary tract and carried to the liver, stimulate this organ to an increased output of catalase, which being taken to the muscles and tissues increase oxidation, and if during exercise the liver was also stimulated to an increased output of catalase, thereby increasing oxidation in the muscles and thus furnish the energy for exercise.

The animals used were cats, rabbits and dogs. The catalase in 0.5 c.c. of the blood of the animals was determined by adding this amount of blood to hydrogen peroxide in a bottle at 22° C. and as the oxygen gas was liberated, it was conducted through a rubber tube to an inverted burette previously filled with water. After the volume of gas thus collected in ten minutes had been reduced to standard atmospheric pressure, the resulting volume was taken as a measure of the amount of catalase in the 0.5 c.c. of blood. The material was shaken at a fixed rate of one hundred and eighty double shakes per minute during the determinations. The animals were exercised in a tread-wheel seven feet in diameter and two feet wide. The food materials were carbohydrates (maltose, levulose, dextrose, lactose, honey, cane sugar, cornstarch, dextrin, wheat flour, corn meal, rice flour and fruits (oranges, lemons, apples, bananas, grape-bean flour); fats (olive oil, bacon, cream, cod-liver oil, glycerine, palmitic acid and lard); fruit and rhubarb); proteins (egg, beef, beef extract, beef juice, aminoids and peptone); beverages (coffee, milk, chocolate, tea and cocoa).

The catalase of the blood of the animals was determined before as well as at fixed intervals after the introduction of the food materials. It was found that the ingestion of the simple sugars, dextrose, etc., increased the catalase of the blood very quickly and in some cases as much as 40 per cent. above the normal. The starchy foods, flour, etc., increased the catalase of the blood, but not so quickly as did the simple sugars. The quicker action of the simple sugars was attributed to the fact that these substances are absorbed immediately and taken to the liver, whereas the starchy foods had to be digested before absorption. Proof that the simple sugars increase the catalase of the blood by stimulating the digestive glands, particularly the liver, to an increased output of catalase, is offered in the following experiment. After etherizing a dog, the abdominal wall was opened and the liver exposed. A comparison was made of the amount of catalase in the blood taken directly from the liver with the amount of blood coming from the tissues, that in the blood of the jugular vein, for example. The blood in the liver or coming directly from the liver was always found to be richer in catalase by 15 to 20 per cent. than the blood taken from any other part of the body. This comparison was made in a great number of animals and is taken to mean that the liver is continually replenishing the catalase of the blood which is being continually used up in the oxidative processes of the tissues. After introducing a simple sugar, such as dextrose, into the etherized animal with its abdominal wall opened, the catalase of the blood taken from the liver was increased much more extensively and rapidly than the blood from a vein such as the jugular. This observation is interpreted to mean that after absorption the sugar was taken to the liver and stimulated this organ to an increased output of catalase. The end products of digestion of the other food-stuffs were tried in a similar manner and all these substances were found to stimulate the liver to an increased output of catalase, meat digest being most effective, fat next, and sugar least.

Of the fats both the olive oil and bacon produced a very quick and pronounced increase in the catalase of the blood, whereas the cream, lard and butter did not act so quickly, due presumably to their slower absorption from the alimentary tract. Coffee, milk, cocoa and tea did not produce an appreciable increase in catalase, while chocolate did. The stimulating effect of chocolate was attributed to the high fat content of this beverage. Very ripe fruit increased the catalase of the blood quickly and extensively, while less ripe fruit did not. This was attributed to the fact that the very ripe fruit contained much sugar, which was quickly absorbed, taken to the liver, and stimulated this organ to an increased output of catalase, whereas the less ripe fruit contained less sugar and hence did not stimulate the liver so strongly. The meat digest increased the catalase of the blood very quickly and extensively, whereas meat, eaten as such, did not act so quickly, due presumably to the time taken for digestion. The meat extract and beef juice produced a small increase in catalase.

Dogs were used in studying the effect of moderate exercise on catalase. The animal was placed in a treadwheel and by a little coaxing was induced to run and thus turn the the wheel at a rate of about five miles per hour. The catalase in 0.5 c.c. of blood taken from the external jugular was determined before the exercise as well as at 15-minute intervals during the exercise. It was found that the effect of moderate exercise was to increase the catalase of the blood from 15 to 20 per cent. in most of the dogs used.

Domestic rabbits were used in studying the effect of strenous exercise and fatigue on catalase. The rabbits were also placed in the wheel, which was turned slowly by hand so that the direction in which the wheel was rotated could be changed to suit the direction in which the rabbit took a notion to run. A few slow turns of the wheel was sufficient to tire and fatigue the rabbit. Every precaution was taken not to abuse or injure the animal in any way. It was found that the strenuous exercise and fatigue decreased the catalase of the blood in some cases by as much as 30 per cent. and that during rest for an hour, the catalase returned to the normal amount and in fact above normal in several instances.

We had already shown that the output of catalase from the liver was increased by stimulating electrically the nerves (splanchnics) distributed to the liver. The explanation that suggested itself for the increase in catalase during moderate exercise was the stimulation of the liver over the splanchnics to an increased output of this enzyme, while the decrease in catalase during violent exercise and fatigue was due to the using up of catalase in the oxidative processes of the muscles more rapidly than it was being replenished by the liver. The increase in catalase during the periods of rest after hard exercise was attributed to the fact that the liver was putting out catalase in the blood more rapidly that it was being used up in the muscles.

According to the chemical theory as set forth by Ranke,[4] fatigue is due to the accumulation of substances, acid in nature, such as lactic acid, which inhibits or depresses the power of the muscles to contract. It is recognized that the accumulation of these acid substances is due to incomplete or defective oxidation. The decrease in catalase observed in the experiments reported in this paper is offered as the cause for the defective oxidation during hard muscular work and fatigue while the helpful effect of moderate exercise is attributed, in part at least, to the increase in catalase produced in this type of exercise.

From the experiments reported in this paper, the conclusion is drawn that food and exercise produce an increase in catalase with resulting increase in oxidation by stimulating the liver to an increased output of this enzyme.

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[4] Ranke, "Tetanus," Leipzig, 1865.

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