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THE ISODYNAMIC REPLACEMENT OF NUTRIENTS.

THIS term was introduced into physiology by Rubner about 1885 as a concise expression of the results of his experiments upon the relative values in nutrition of the three great classes of nutrients, the proteids, carbohydrates and fats.

It was already well established by the labors of previous investigators, notably of Pettenkofer and Voit in Munich, that, aside from a certain rather small amount of proteids which is indispensable, the animal body possesses a remarkable degree of flexibility as regards the nature of the material which it can use to support its vital processes. Aside from the necessary minimum of proteids, the metabolic activities of the body may be supported, now at the expense of the stored body fat, now by the body proteids, and again by the proteids, the fats or the carbohydrates of the food. Whatever may be true economically, physiologically the welfare of the mature animal is not conditioned upon any fixed relation between the classes of nutrients in its food supply, apart from the minimum requirement for proteids. The problem which Rubner proposed to himself was to determine the relative quantities of the several nutrients which were equivalent to each other in the vital processes of the animal—in other words, to substitute quantitative for qualitative knowledge.

It is well known that a fasting animal consumes the tissues of its own body to sustain its vital activities. Thus in one of Rubner's experiments a fasting dog oxidized per day the equivalent of 20.51 grams of dry muscular tissue (lean meat) and in addition 75.92 grams of his fat. He was then given 740 grams per day of fresh lean meat. On this ration he was found to oxidize the equivalent of 133.89 grams of dry muscular tissue, but only 30.72 grams of the fat of his body. In other words, the oxidation of 113.38 grams more of muscular tissue derived from the lean meat eaten diminished the draft upon the body-fat of the dog by 45.20 grams. Plainly, these two quantities were equivalent, or, after making some slight corrections, 243 parts of dry lean meat were equivalent to 100 parts of fat. A number of similar experiments were made with extracted meat and with various carbohydrates, while in a few cases fat and carbohydrates were interchanged in the food, and a series of ratios like the above were obtained, varying with the material experimented on.

All these results, however, are purely empirical. They explain nothing. The fact, however, that the nutrients can mutually replace each other through so wide a range, and the other fact that the animal body is essentially a transformer of the potential energy of the food into the kinetic energy of heat and motion, suggest that the nutrients replace each other because they all serve as sources of energy to the organism. Acting on this hint, Rubner proceeded to determine the amounts of energy which the several nutrients could liberate in the body. This, by a well-known principle of thermochemistry, is measured by the difference between the potential energy of the substance and that of the products of its decomposition. The potential energy of the nutrients is measured, for this purpose, by their heats of combustion. In the case of the carbohydrates and fats, the products of their decomposition in the body are (in the carnivora) substantially carbon dioxide and water, which contain no measurable amount of potential energy. With the proteids the case is different. Here we have various partially oxidized compounds contained in feces and urine, the potential energy of which Rubner summarily determined by determining the heats of combustion of the dried excreta. In this way he was able to determine how much energy a given amount of lean meat or fat or starch was capable of liberating in the animal organism, and this amount he called its physiological heat value.

When, now, he came to compare the amounts of the several nutrients from which equal quantities of energy could be liberated in the body with the amounts which were found to replace each other in actual feeding experiments, he obtained a most remarkable correspondence. The first column of the table shows the amounts of the several substances required to liberate the same amount of energy as 100 grams of fat, while the second column shows the amounts which were found to replace 100 grams of fat in the nutrition of the animal.

	Yielding Energy Equal to 100 Grams Fat.	Replacing 100 Grams Fat in the Body.
Lean meat......	235 grams.	243 grams.
Extracted meat..	213 "	225 "
Cane sugar......	235 "	234 "
Starch..........	229 "	232 "
Grape sugar.....	255 "	256 "

The teaching of these figures seems perfectly clear. The nutrients are the fuel of the body—its supply of energy—and they replace each other just in proportion to the energy they are capable of liberating.

This law Rubner called the law of isodynamic replacement.*

This law was based upon the conception that the same laws of energetics which control the chemical changes of so-called dead matter also rule the far more complex ones which occur in the living organism, and that the energy which the animal imparts to its surroundings is simply the transformed energy of its food, or, in other words, that the law of the conservation of energy applies to the animal body. Later experiments by Rubner, directed more specifically to this broader aspect of the question, went far to demonstrate the truth of this conclusion, while the later investigations of Laulanié and especially the very extensive ones of Atwater and his associates, Rosa and Benedict, seem to have placed it beyond question.

It is practically to Rubner, then, whatever suggestions may have been made previously, that we owe the effective introduction into physiology of the conception that the relative values of the several nutrients, except as to the special functions of the proteids, are measured by their physiological heat values, or 'fuel values' as they are called by Atwater. This conception has proved to be a fruitful one and has profoundly influenced the study of animal nutrition.

As is so often the case, however, further study has revealed the necessity for modifications and has shown that in its first form the law of isodynamic replacement was, after all, but a partial statement of the truth.

Rubner's experiments were made with animals in a state of rest and with amounts of food insufficient to cause any storing up of flesh or fat in the body. Under these conditions all the energy set free by the burning of food or tissue to support the vital activities, whatever forms it may temporarily take, finally appears as heat which is imparted to the surroundings of the animal. The law of isodynamic replacement, now, implies that the heat production of such an animal is unaffected, at least below the maintenance requirement, by changes in the amount and kind of food consumed. Thus, if the animal oxidizes while fasting 100 grams of body fat, and if it be then given an amount of starch equivalent in energy to 100 grams of fat, viz., 229 grams, this starch should be burned in place of the fat. That is, there will be simply a substitution of one kind of fuel for another, but no increase in the total heat production.

It is, however, an observation as old as the time of Lavoisier that the consumption of food tends to *increase* the heat production, and the fact has been fully established by a host of subsequent investigators. The taking of food calls into activity a whole set of organs that were previously in a state of relative inactivity. The mastication and swallowing of the food and its passage through the alimentary canal involve a not inconsiderable amount of muscular work. In addition to this the various secreting glands are called into action to supply the digestive fluids, while the resulting chemical and fermentative changes in the food itself add their quota to the heat arising from the muscular and glandular activity. This heat, of course, may aid in keeping the animal warm, but otherwise, so far as we know, it is of no direct use to the organism, while often the body has already a superabundant supply and is really engaged in getting rid of heat.

It appears, then, that the mere supplying of more energy to the body in the shape of food sets up a demand for more energy to

* Conclusions very similar, although not based upon their own investigations, had been previously announced by v. Hoesslin and by Danilewsky.

digest and assimilate this food. The case is analogous to that of a steam-boiler which is fired by means of a mechanical stoker driven by steam from the same boiler. Each pound of coal fed into the fire-box is capable of evolving a certain amount of heat, and that heat is capable of producing a certain quantity of steam. A definite fraction of the latter, however, is required to introduce the next pound of coal into the furnace and, therefore, is not available for driving the main engine.

It is plain, however, that this view of the matter is inconsistent with the law of isodynamic replacement as above stated. If the consumption of food causes an increased expenditure of energy by the body, then we do not have simply a replacement of one kind of fuel by another, such as the law of isodynamic replacement predicates, but in addition an actual stimulation of the combustion. To recur to the previous illustration, to prevent the oxidation of 100 grams of fat in the fasting animal would require not only the 229 grams of starch equivalent in energy to the 100 grams of fat, but also enough more to supply the energy required to digest and assimilate the starch. As a matter of fact, Rubner actually did find that slightly more than the theoretical amount of starch was required, viz., 232 grams instead of 229 grams, and the same was true with the other materials experimented on with the exception of cane sugar.

Such substances as meat, starch and sugar, however, are comparatively easy of digestion, and the latter two, at least, do not call for any large expenditure of energy, so that it is difficult to decide whether the small differences in Rubner's figures are significant or not. A material requiring more digestive work would obviously furnish a more decisive test. Such materials are offered in the food of herbivora, particularly in the so-called 'coarse fodders' (hay, straw, etc.), and the recent completion at the Pennsylvania Experiment Station of a respiration-calorimeter * for experiments with cattle afforded an opportunity to test the question with these animals.

The feed used was a rather coarse timothy hay. The steer was fed a very light ration of the hay, together with a little linseed meal, the whole 'basal ration' being much less than was required to support the animal. On this basal ration the steer produced 9,229 calories of heat in 24 hours. During the same time it was shown that he oxidized 49.2 grams of the proteids and 259 grams of the fat of his body, equivalent to 2,578 calories of energy.

Then 1.2 kilograms of the hay were added to the basal ration. It was shown that, after deducting the various unoxidized wastes, this hay represented a fuel value of 2,840 calories; that is, oxidized to the fullest extent to which the organism was capable of carrying it, could liberate that amount of energy. If, now, the law of isodynamic replacement is applicable to this case, that is, if it was simply a question of substituting one kind of fuel for another, the digestible matter of the hay, yielding 2,840 calories of energy, should have prevented the oxidation of an equivalent amount of body tissue. As a matter of fact it fell far short of doing this. On the increased ration, the daily loss by the body of the animal was 7.2 grams of proteids and 80.6 grams of fat, equivalent to 791 calories of energy, while the heat production in 24 hours was 10,249 calories as compared with 9,229 calories on the smaller

* The apparatus is modeled after that of Atwater and Rosa. It was constructed and is being operated in cooperation by the Bureau of Animal Industry of the U. S. Department of Agriculture and The Pennsylvania State College Agricultural Experiment Station.

ration. While the addition of the hay considerably diminished the loss of tissue by the animal, it at the same time caused an increase of over ten per cent. in the heat production; that is, a portion of its fuel value, instead of taking the place of energy previously derived from the oxidation of tissue, was required for the various processes incident to the digestion and assimilation of the hay and ultimately appeared as heat. The loss of tissue was diminished by 1,787 calories by the addition of hay having a fuel value of 2,840 calories. In round numbers, then, only 63 per cent. of the fuel value of the hay was used by the body in place of the energy previously derived from the oxidation of tissue, instead of 100 per cent. as required by the law of isodynamic replacement, while the remaining 37 per cent. became practically an excretum.

The results of a single experiment are, of course, to be accepted with reserve. At the same time, however, the discrepancy is far too great to be accounted for by any possible errors in the determinations of the amounts of energy involved, while there was not the slightest indication of anything abnormal in the state of the animal or in the conditions of the experiment. We are forced to the conclusion that in this case at least the digestible matter of the food was not isodynamic with body substance, or in other words, that its fuel value was not, as has been ordinarily assumed, a measure of its value for maintenance.

It may perhaps be objected that the mixture of ill-known materials digested from hay is a very different thing from the nearly pure nutrients employed in Rubner's experiments, and that it very naturally has a lower nutritive value. Such an objection, however, while perfectly true, would be irrelevant. It is precisely because these materials require the expenditure upon them of a considerable amount of energy, mechanical and chemical, to fit them for the metabolism of the body, that there is this large loss. The difference is one of degree rather than of kind. The cellulose of hay, for example, undergoes an extensive fermentation in the first stomach of ruminants, yielding methane, carbon dioxide and various organic acids. This fermentation is accompanied by an evolution of heat which becomes largely or wholly waste, since the animal body appears to be unable to convert heat into other forms of energy. Undoubtedly this escape of energy during fermentation constitutes a part, and not improbably a large part, of the 37 per cent. of loss observed with the steer. When starch is fed to a dog, it is converted into dextrins, maltose and isomaltose and finally into dextrose by the action of the various digestive ferments. In this process there is likewise a loss of energy, very much smaller it is true than in the case of the cellulose, but just as really a loss. Similarly, the mechanical work of digestion is far less with pure nutrients than with hay, but is by no means equal to zero.

It was noted above that Rubner's own equivalents show that slightly more than the theoretical amounts of nutrients were required to replace body tissue. The writer recently made a careful compilation of all accessible results bearing on this question. After rejecting two experiments by Rubner with cane sugar, in which values considerably over 100 per cent. were obtained, and which Rubner himself considers of doubtful value, all the other trials give values less than 100 per cent. except one experiment on fat and one early one by Pettenkofer and Voit which gives the impossible value of 115 per cent. The deficit is often small and in some cases may not exceed the probable experimental error, but the general tendency appears significant, especially when taken in connection with the very marked result of the experiment on hay.

Quite recently Rubner has published in book form * an elaborate discussion of this question, including the results of later experiments on dogs, in which amounts of fats, carbohydrates or proteids considerably in excess of those required for the simple maintenance of the body were fed. Under these conditions he finds that all these nutrients, but especially the proteids, may cause a marked increase in the heat production of the animal. In other words, he shows that what appears to be true of ruminants below the maintenance requirement is equally true of carnivora when the amount of food consumed is relatively large.

It would appear, then, that the law of isodynamic replacement as it has been commonly taught must be modified. That law, as stated above, is that the 'fuel values,' or 'physiological heat values,' of the several nutrients represent their relative worth to the animal body except for the peculiar constructive function of the proteids. In other words, the food is regarded as the fuel of the vital furnace. The fundamental error of this view lies in the fact that it more or less consciously assumes that the production of heat in the body is an end in itself. The truth appears to be that it is, in a physiological sense, an incident. The energy of the food is needed for the performance of the vital processes. During these processes it undergoes various transformations, but finally the larger part, or in the resting animal all, is degraded into heat, which incidentally serves to maintain the temperature of the body, and, as it would seem, is amply sufficient for this purpose under a wide range of conditions.

Such being the case, the value of a food is not measured by the amount of heat which it can liberate in the body, but by the extent to which its energy is available for the vital processes. When, as in the case of the hay, 37 per cent. of the fuel value is consumed in separating the valuable from the worthless portions and in transporting the former to the point of use, the final net advantage to the animal is represented by the remaining 63 per cent. If the gross receipts of a business are one hundred dollars per day and the running expenses thirty-seven dollars, it is plain that the net receipts are only sixty-three dollars, no matter how necessary the expenses may be.

Of course this has a limit. As the temperature to which an animal is exposed falls, and the consequent draft on the body for heat increases, a point will be reached at which the production of heat is just equal to the demand. Below this point, cold seems actually to stimulate in some way the heat production of the animal. Under these circumstances Rubner appears to have demonstrated that the heat produced by the processes of digestion and assimilation may be of use indirectly by obviating the necessity of burning more tissue to supply the necessary heat, and that consequently at relatively low temperatures the fuel value of the food may be the measure of its worth, that is, that isodynamic replacement may occur. Above a certain temperature and a certain amount of food, however, varying with the kind of animal and with the nature of the food, the law ceases to hold and the specific differences in the availability of nutrients or foods reveal themselves.

But while it thus appears that the law of isodynamic replacement is of but limited application, this should not blind us to the vast importance of Rubner's earlier work. It established a new point of view and

* 'Die Gesetze des Energieverbrauchs bei der Ernährung.'

gave a unity to our conceptions of the function of nutrition which they previously lacked. The law of isodynamic replacement is but a single phase of the question. The fundamental idea is that the vital activities are manifestations of the same energy which is seen in operation throughout the universe, are subject to the same laws and may be studied by similar methods. It is his firm grasp of this broad conception, and not the exact scope or accuracy of a single expression of it, which has given Rubner's investigations their preeminent value.

H. P. Armsby.

*METHODS OF METEOROLOGICAL INVESTIGATION.**

In opening the proceedings of the subsection devoted to cosmical physics, which we may take to be the application of the methods and results of mathematics and physics to problems suggested by observations of the earth, the air or the sky, I desire permission to call your attention to some points of general interest in connection with that department which deals with the air. My justification for doing so is that this is the first occasion upon which a position in any way similar to that which I am now called upon to fill has been occupied by one whose primary obligations are meteorological. That honor I may with confidence attribute to the desire of the council of the association to recognize the subject so admirably represented by the distinguished men of science who have come across the seas to deliberate upon those meteorological questions which are the common concern of all nations, and whom we are specially glad to welcome as members of this subsection. Their presence and their scientific work are proof, if proof is required, that meteorologists can not regard meteorological problems as dissociable from Section A; that the prosecution of meteorological research is by the study of the kinematics, the mechanics, the physics or the mathematics of the data compiled by laborious observation of the earth's atmosphere.

* Address before the Subsection of Astronomy and Meteorology, British Association for the Advancement of Science. Opening address by the chairman, Southport meeting, 1903.

But this is not the first occasion upon which the address from the chair of the subsection has been devoted to meteorology. Many of you will recollect the trenchant manner in which a university professor, himself a meteorologist, an astronomer, a physicist and a mathematician, dealt candidly with the present position of meteorology. After that address I am conscious that I have no claim to be called a meteorologist according to the scientific standard of Section A. Professor Schuster has explained—and I can not deny it—that the responsible duty of an office from which I can not dissociate myself is signing weather reports; and I could wish that the duty of making the next address had been intrusted to one of my colleagues from across the sea. But as Professor Schuster has set forth the aspect of official meteorology as seen from the academic standpoint with a frankness and candor which I think worthy of imitation, I shall endeavor to put before you the aspect which the relation between meteorology and academic science wears from the point of view of an official meteorologist whose experience is not long enough to have hardened into that most comfortable of all states of mind, a pessimistic contentment.

Meteorology occupies a peculiar position in this country. From the point of view of mathematics and physics, the problems which the subject presents are not devoid of interest, nor are they free from that difficulty which should stimulate scientific effort in academic minds. They afford a