THE RATE OF ABSORPTION OF GLUCOSE FROM THE GASTROINTESTINAL TRACT OF THE DOG

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(Received for publication, December 20, 1932)

20 years ago Fisher and Wishart (1) introduced known quantities of d-glucose into the stomachs of dogs and after experimental periods of varying lengths killed the animals and determined the quantity of sugar still remaining in the gastrointestinal tract. Using these data as a basis, Sansum and Woodyatt (2) several years later calculated the rate of absorption of this carbohydrate in relation to the weight of the animals and to the length of the experimental period. They concluded that the intact dog could absorb 1.6 to 1.7 gm. of d-glucose per hour for every kilo of its body weight. The value thus obtained has been quoted repeatedly and has been used frequently by subsequent investigators as a basis for calculations and comparisons.

As the preliminary step in undertaking a research of a different nature, we had occasion a few years ago to repeat the procedure of Fisher and Wishart several times. The absorption rates encountered were so much lower than those calculated by Sansum and Woodyatt that it was deemed necessary to explore the entire field once more. As a result we have reached the conclusion that, with its stomach and intestine functioning as a physiological unit, the dog can absorb glucose at a rate approximating only 1 gm. per hour per kilo of body weight, a value considerably lower than the one currently accepted.

Before presenting our own data we shall summarize briefly the procedure and the results of Fisher and Wishart. These authors used dogs weighing 8 to 9 kilos, which, after having been on a
uniform diet for several days, were fasted for 24 hours and then
given by mouth 50 gm. of glucose contained in 150 cc. of water.
At the end of the experimental period (1 to 4 hours) the animals
were killed by a blow upon the head, the contents of the stomach
and the intestine were collected separately, covered with 95 per
cent alcohol, and the sugar still present was determined by the
method of Allihn (3). In the five experiments recorded, the
quantities of ingested sugar not recovered from the gastrointestinal
tract were respectively: 41.5 gm. after 1 hour, 38.2 and 32.4 gm.
in the duplicate 2 hour experiments, 42.6 gm. after 3 hours, and
none at all after 4 hours. On the basis of these experiences, Fisher
and Wishart concluded that "the absorption of 50 grams of dex-
trose in dogs weighing between 8 and 9 kgs. is rapid and is com-
pleted during the fourth hour after the administration of the
sugar."

Reference should be made also to the recent work of Cori (4)
upon animals of a different species. This investigator has meas-
ured the rate of absorption of d-glucose (and a number of other
sugars) from the gastrointestinal tracts of rats. His researches
have standardized the procedure for studying absorption from the
intact alimentary canal and have placed the method upon a satis-
factory experimental basis. Especially noteworthy have been
his findings that for rats the rate of absorption of a sugar is a
linear function with respect to time and is independent of both
the concentration and the absolute quantity ingested.

EXPERIMENTAL

In its broad outlines our method of experimentation has been
similar to that of Fisher and Wishart. In the elaboration of a
number of details we have had the advantage of Cori's compre-
hensive description (4) of the technique which he employed in
studying absorption by rats. Since the use of larger animals as
subjects introduces some additional complications and since our
results are at variance with conclusions long accepted, we shall
describe our method of experimentation in detail.

Male animals were employed regularly as the subjects in a
majority of our absorption experiments. The few exceptions to
this rule are designated specifically in presenting the data. The
individuals chosen weighed between 10 and 20 kilos and were
selected so that only animals in good nutritional condition, neither fat nor thin, were used. For several days preceding the experiments these were under our direct observation and control. They were subjected to sham experiments and had opportunity to become accustomed to the surroundings to be encountered on the day of the experiment. They were given their final feeding of approximately 300 gm. of ground meat and 300 cc. of milk 18 to 24 hours before the experiment. Upon the day of the experiment the animal was permitted a short run in the yard, was weighed upon a scale accurate to 0.1 kilo, and a preliminary specimen of blood was taken. The dog then received by stomach tube an exactly measured quantity (100 to 300 cc.) of a solution of d-glucose (temperature 37°) of known concentration. A small measured quantity of water was employed to rinse the sugar container and the funnel of the stomach tube. A porcelain dish was held in position to receive the stomach tube as it was withdrawn. Later the interior and exterior of this tube were rinsed to recover the glucose which might have adhered to it. Routinely this was determined and allowance was made for it in calculating the quantity of glucose actually administered to the dog. (Regurgitation of fluid at the moment when the stomach tube is withdrawn, or shortly thereafter, constitutes the most serious hazard to the success of such an experiment. Training the animals by several sham experiments enabled us to minimize this difficulty.) After the sugar feeding, the animal was placed on the floor in a corner of the laboratory or returned to its cage in a quiet room. When it was desired to retain the animal at hand for the taking of blood samples, it was found that the presence beside it of a pet dog trained to lie quietly upon the floor had a decidedly soothing effect and usually led the subject of experimentation into a similar behavior. At the conclusion of the absorption period the animal was placed upon a table, and given a rapid intravenous injection (saphenous vein) of amytal (100 mg. per kilo), which caused death to ensue immediately and without a struggle. Throughout this last procedure it is important that the animal's head should be raised to a slightly elevated position and maintained thus until an incision can be made into the neck and the upper end of the esophagus ligated. Failure to observe this precaution may permit fluid to flow out of the esophagus into the pharynx and trachea.
thus escaping observation and collection. If the abdominal cavity be opened first and the stomach manipulated even slightly in ligating the lower end of the esophagus, the probability is very great that error from this source will occur when dogs are being used. It is obvious that loss of sugar in this way would lead to apparent absorption rates higher than actually exist. How extensively this error may have entered into previous work it is not possible to judge.

Immediately after the ligation of the upper end of the esophagus it was our custom to open the abdomen with a mid-line incision and to place stout ligatures at the pylorus, the ileocecal valve, and around the rectum at the lowest level possible. The stomach with the esophagus attached, the small intestine, and the large intestine were all dissected from their attachments and lifted out individually. The contents of the stomach and of the intestine were collected separately and the volume of each measured. Each organ was washed out repeatedly with 5 to 7 portions (50 to 100 cc,) of distilled water until the final washing was clear and gave a negative test for the presence of reducing substances.

In only a few instances did the large intestine contain fluid at the termination of the experiment. As a matter of routine this was always tested for reducing substances but in only one case was the quantity found a significant fraction of the total recovered from the gastrointestinal tract. The urine in the bladder was always collected and subjected to Benedict's (5) qualitative test for sugar. The result was uniformly negative.

Analytical Procedures—The method of titration described by Folin and McEllroy (6) and Folin and Peck (7) was used to determine the concentrations of glucose existing in the solutions prepared for ingestion and those recovered from the alimentary tract. Before making measurements upon the latter solutions it was our custom to remove protein by the addition of approximately 0.1 volume each of 10 per cent sodium tungstate and \( \frac{3}{8} \) N sulfuric acid as in the Folin-Wu (8) procedure for blood. The intestinal contents were clarified further by shaking with Lloyd's reagent (9). In control experiments it was found that the recovery of sugar from stomach extracts was substantially the same whether the titration was made directly upon untreated stomach contents, upon a filtrate to which tungstic acid had been added, or upon the latter after it had been shaken with Lloyd's reagent.
When the sugar content of the intestinal extracts was too low to be titrated, it was measured by diluting the Lloyd's reagent filtrate to volumes such that the revised Folin-Wu (10) colorimetric procedure could be employed. In control experiments it was determined that the quantity of the non-fermentable reducing substances which remained after treatment of these filtrates with washed yeast by Benedict's procedure (11) was very slight and of the same order of magnitude as that found in extracts from intestines of fasting dogs (see later sections). For determinations of blood sugar either the copper reduction method of Folin and Wu (10) or the microferrocyanide procedure of Folin (12) was employed. Glucose from the Bureau of Standards served for standardization of reagents.

Control Experiments

Reducing Substances Normally Present in Stomach and Intestine of Fasting Dog—In five instances the stomachs of fasting dogs were washed out and after treatment with tungstic acid and Lloyd's reagent the reducing material was measured by the revised Folin-Wu blood sugar method (10). The quantities found calculated as glucose were 13, 3, 51, 1.4, and 4 mg. In a similar manner 36, 22, and 34 mg. of reducing substances were found in the small intestine of three fasting dogs. Because of the small magnitude of these quantities no correction for them was made in our calculations.

Error Due to Destructive Action of Bacteria in Alimentary Tract—In his experiments with rats, Cori (4) found that the destructive action of bacteria normally present in the stomach and intestine was sufficient to account for only an insignificant fraction of the total sugar which disappeared from this region during an absorption period. That this agency contributed very little to the disappearance of glucose from the gastrointestinal tract of our dogs was demonstrated by observations made during our research. In the paragraphs which follow some of our data upon this point are presented.

Under amytal anesthesia the abdomen of a dog was opened and ligatures were placed around the lower end of the esophagus and the pylorus and 48.86 gm. of glucose in 32 per cent solution were allowed to flow into the stomach through a hollow needle. After 1.5 hours the animal was killed and the contents of its stomach
were washed out into a volumetric flask. The sugar recovered was 99.2 per cent of that originally ingested.

In another experiment under amytal anesthesia the small intestine was ligated at both ends, dissected free of its mesentery, and lifted into an evaporating dish. A solution (approximately 150 cc.) previously warmed to 37° and containing 6.13 gm. of glucose was introduced into the intestine through a hollow needle. After the solution had been uniformly distributed throughout the intestine, the latter was placed in the hot room and maintained at 37° for 2 hours. At the close of that period the intestine was washed out and the sugar remaining was determined. The quantity recovered was 6.18 gm.

Results

In Table I we present a record of the quantities of d-glucose which were administered to the experimental animals and of the amounts which were recovered from the stomach and from the small intestine after intervals of 1, 2, and 3 hours respectively. It may be noted that the average rate of absorption found for the fifteen male dogs was 0.99 ± 0.17 gm. per kilo per hour, and that substantially the same value was obtained for each series. The individual results for the 1 hour experiments vary more from each other and from the average of the entire group than do those which extended over longer periods. It is believed that the wider fluctuations encountered in the short experiments may be ascribed to (a) unavoidable irregularities in the technique of handling the experimental animals, and (b) the occasional activity of the pylorus\(^1\) in delaying the passage of the sugar solution to the region where the most rapid absorption occurs. Both of these factors would have greater opportunity to produce conspicuous variations in the rates when the time for absorption is brief. Therefore, lengthening the absorption period should minimize the effects of extraneous influences of the character just mentioned upon the rates actually observed. That this expectation has been realized is shown by the greater uniformity of the rates found for the 2 and the 3 hour series. With the data for these two periods only, the

\(^1\) A series of observations bearing particularly upon the effect of the activity of the pylorus upon absorption rates has been made and will be presented elsewhere.
magnitude of the mean deviation is considerably reduced and the average rate becomes $0.99 \pm 0.05$ gm. per kilo per hour. Since

\[
\text{TABLE I}
\]

\textit{Rate of Absorption of d-Glucose from Gastrointestinal Tract of Male Dogs}

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Weight of dog kg.</th>
<th>Absorption period hrs.</th>
<th>Glucose Given gm. per cent</th>
<th>Recovered gm.</th>
<th>Total gm.</th>
<th>Rate per kilo per hr. mg. per cent</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>12.4</td>
<td>3</td>
<td>44.40 13.9</td>
<td>4.11 2.38</td>
<td>6.49 38.11</td>
<td>1.02 104</td>
</tr>
<tr>
<td>13</td>
<td>16.9</td>
<td>3</td>
<td>65.55 20.2</td>
<td>9.71 3.75</td>
<td>13.46 52.09</td>
<td>1.02 133</td>
</tr>
<tr>
<td>15</td>
<td>14.1</td>
<td>2</td>
<td>25.70 8.9</td>
<td>6.39 0.43</td>
<td>6.82 10.82</td>
<td>0.74 153</td>
</tr>
<tr>
<td>17</td>
<td>15.5</td>
<td>1</td>
<td>23.18 9.5</td>
<td>9.90 2.46</td>
<td>12.36 10.82</td>
<td>0.74 153</td>
</tr>
<tr>
<td>16</td>
<td>11.2</td>
<td>2</td>
<td>27.76 11.1</td>
<td>5.71 1.75</td>
<td>7.46 20.30</td>
<td>0.91 130</td>
</tr>
<tr>
<td>15</td>
<td>14.2</td>
<td>2</td>
<td>36.99 11.5</td>
<td>6.97 1.05</td>
<td>8.02 28.97</td>
<td>1.02 154</td>
</tr>
<tr>
<td>11</td>
<td>18.6</td>
<td>2</td>
<td>53.67 15.1</td>
<td>15.51 1.08</td>
<td>16.59 36.43</td>
<td>0.98 93</td>
</tr>
<tr>
<td>12</td>
<td>15.0</td>
<td>2</td>
<td>46.21 16.1</td>
<td>14.47 2.97</td>
<td>17.44 30.77</td>
<td>1.02 173</td>
</tr>
<tr>
<td>10</td>
<td>16.5</td>
<td>2</td>
<td>60.60 20.2</td>
<td>26.72 0.95</td>
<td>27.67 32.83</td>
<td>1.00 126</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.00 126</td>
<td></td>
</tr>
</tbody>
</table>

Average................................................. 0.99 ± 0.07

Grand average, male dogs only = 0.99 ± 0.17; all experiments = 0.99 ± 0.15

* Including 8.10 gm. in large intestine.
† Female dogs, data not included in average.

the measurements of the rate were continued until the grand average for the entire series had become stabilized within a limited
range, we conclude that the normal male dog has the capacity to absorb during 1 hour approximately 1 gm. of glucose per kilo of body weight.

Cori (4) observed that rats continued to absorb sugar at a uniform rate until at least 90 per cent of the ingested sugar had disappeared. In no one of our experiments had this limit been reached and in only a few cases was it even approached. In fact, the quantity of sugar still present in the stomach and the intestine at the termination of a majority of the experiments was sufficient to have permitted absorption to have continued at the then existing rate for at least 1 hour longer. Therefore, the fact that the rates of absorption observed by us are lower than the value hitherto accepted cannot be explained on the basis of lack of a glucose supply sufficient to keep the dog's absorption process in action at its maximum physiological rate.

Holtz and Schreiber (13) in a brief section (p. 51) of a recent paper have mentioned that they have observed glucose absorption in dogs at rates ranging from 0.85 to 0.95 gm. per kilo per hour. Neither the experimental data supporting that statement nor a description of their methods was presented in that or in subsequent communications which we have found.

The individual experiments (Table I) are tabulated in an order such that in each of the three groups the concentration in solution of the sugar administered increases as one reads down the table. It will be evident that the individual rates of absorption are not related in any regular manner to this factor. If one cares to group the absorption rates recorded in relation either to the dosage per kilo, to the absolute weight of sugar ingested, or to the weight of the experimental animals, it will be disclosed that the results obtained fluctuate independently of each of these variables. In respect to these factors our experiences have proved quite similar to the observations upon rats reported by Cori (4).

Effect of Sex—The average absorption rate obtained is believed to reflect adequately the absorbing capacity of male dogs. In the few instances observed, female dogs also happened to show rates similar to those for males. These experiments, however, are not sufficiently extensive to warrant any general conclusion.

Effect of Experimental Manipulations—In most instances the animals were subjected to venepuncture at intervals throughout
the course of the experiment. In three cases (Experiments 12, 13, and 14) immediately after ingesting the sugar the dogs were returned to their cage in an animal room (otherwise empty) where they remained undisturbed for 2 or 3 hours. The average rate of absorption for these three experiments was 1.02 gm. per kilo per hour. Since this is so close to the average for the entire series, we conclude that excitement played no rôle as a factor in our experiments. (In this connection see a previous section where the routine procedure in handling the animals during experimentation is described.)

Effect of Absorption upon Blood Sugar—The blood of the animals used was sampled before the glucose was ingested and at definite periods thereafter. When the observations upon the concentrations of the sugar in the blood obtained in the different experiments were all plotted upon the same graph it was found that the various curves overlapped and interwove with each other very extensively. Since the shapes of the individual curves bear no regular relation either to the dosage of glucose per kilo of the animal’s weight, to the concentration of the sugar in the solution ingested, or to the rate of absorption, the data obtained are not recorded in detail. One feature which does stand out strikingly in several experiments warrants presentation. This concerns the concentration of sugar in the venous blood and the lack of significance of its return to the normal range as an index of the completion of the absorption process. Concrete instances showing how data of this nature might lead to an interpretation of events which would be totally erroneous is disclosed by the blood pictures for Dogs 11 and 7 recorded in Table II. The averages of the concentrations existing at the corresponding intervals in the entire series of experiments are presented in order that a comparison may be made.

In the experiment with Dog 11 the blood sugar rose 15 mg. during the first quarter hour and then (with very moderate fluctuations) remained at a level which many would consider normal for a fasting animal. Actually 36.42 gm. of sugar were being absorbed at a rate of 0.98 gm. per kilo per hour, and yet the resulting activity produced only a slight increase in the venous blood during the period when all this transfer was in progress. Likewise, in the case of Dog 7, those who rely upon venous blood concentrations as an index of absorption activity would have concluded that
the process had been completed when actually 33 of the original 45 gm. remained unabsorbed. Search of our records has disclosed four other instances of venous blood sugar curves which remained nearly flat for several hours after the dogs had ingested glucose. At the time when these were obtained we wondered whether any absorption had taken place. Since recovery studies were not made upon the animals involved at the appropriate time, no conclusions regarding the actual course of events were possible either then or now. However, these experiences serve to strengthen our belief that curves of a type as flat as that of Dog 11 may be encountered much more frequently than is generally suspected. It would seem appropriate, therefore, that reliance upon normal venous blood sugar values as evidence that absorption has been completed should be abandoned entirely and that conclusions based upon older data of this sort should be carefully scrutinized once more. In particular it may be pointed out that in many experiments in which successive doses of glucose have been ingested by dogs the time allowed for absorption of the first quantity has not been sufficient for this process to have been completed. Therefore the failure of the second dose to affect the level of sugar in the venous blood is explained by the overlapping of the successive doses while in the intestinal tract so that the second became merely a continuation of the first.

**DISCUSSION**

*Comparison of Physiological Rate for Introducing d-Glucose into and Removing It from Circulating Blood of Dog*—Woodyatt, San-

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### TABLE II

**Sugar in Venous Blood after Glucose Ingestion**

Concentrations are expressed in mg. per cent.

<table>
<thead>
<tr>
<th>Before ingestion</th>
<th>Intervals after ingestion</th>
<th>Absorption rate (gm. per kg. per hr.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>15 min.</td>
<td>30 min.</td>
</tr>
<tr>
<td>Dog 11.............</td>
<td>85</td>
<td>100</td>
</tr>
<tr>
<td>&quot; 7.................</td>
<td>80</td>
<td>102</td>
</tr>
<tr>
<td>Average values in 13 experiments........</td>
<td>85</td>
<td>103</td>
</tr>
</tbody>
</table>
sanum, and Wilder (2, 14) demonstrated in 1915 that dogs can receive glucose intravenously at a rate of 0.85 gm. per kilo per hour for long periods without producing a glycosuria sufficient to yield a qualitative reduction test with Fehling’s or with Haines’ solutions. If the initial velocity of infusion was only slightly greater than that just mentioned, then a pronounced glycosuria resulted within a very brief interval—usually less than 30 minutes. In the later and more exact measurements recorded by Felsher and Woodyatt (15) the critical rates of injection which called forth a definite and pronounced glycosuria averaged 1.0 gm. per kilo per hour. These contributions of Woodyatt and coworkers served to introduce and to establish in the literature the concept that a rate of 0.85 to 1.0 gm. of glucose per kilo per hour represented the maximum speed at which the tissues of a dog which has just broken a short fast are prepared to remove d-glucose from the circulating blood and to dispose of it in a physiological manner.

It was in connection with these same investigations that San-
sum and Woodyatt made their recalculation of the absorption data of Fisher and Wishart to which we have referred in an earlier section. As a consequence of that computation the opinion also became current that the quantity 1.7 gm. per kilo per hour represents the normal physiological rate at which glucose (ingested alone) may be introduced into the blood of the dog through the gastrointestinal route.

Ever since these publications a rather anomalous situation has existed. It appeared to have been established that nature had provided for the entrance of d-glucose (under physiological circumstances) into the blood of a dog at a velocity approximately twice the maximum rate at which the animal’s tissues are prepared to remove it from the circulation and to dispose of it without waste. This anomaly was removed, in part, by the observation of Felsher and Woodyatt ((15) p. 738) that the mechanism for removing sugar from the blood and for disposing of it in a physiological manner can be stimulated to increased activity by a preliminary injection of glucose. Somewhat later Jordan (16) in confirming and amplifying this observation, injected animals intravenously for 2 hours at the subtolerant rate of 0.7 gm. per kilo per hour and followed this with an injection at a velocity of 1.5 gm. per kilo per hour without provoking a gross glycosuria. Thus
it was shown that the rate of removal of glucose from the blood may be elevated to a value nearly double that initially exhibited by a dog just after the termination of a short fast.

After the experiments of Jordan had been recorded, the situation with regard to the relation of the rate of absorption of glucose to the rate of its disposal in the dog had reached the following state. It appeared to have been established that the velocity initially available in the dog for withdrawing glucose from the blood and for disposing of it is less than that at which it may enter from the gastrointestinal tract. Also it had been shown that the withdrawal mechanism could be stimulated to activity at an increased velocity. However, the maximum velocity at which this mechanism had been observed to function and still prevent loss of sugar through the kidneys was not quite equal to the generally accepted value for the maximum possible rate of entrance of glucose into the blood from the gastrointestinal tract.

This discrepancy is now completely clarified by the data which we have presented above. These show that the physiological rate at which glucose may enter the blood from the digestive tract of a dog which has just terminated a short fast, does not exceed the maximum speed initially attainable (i.e., within the first half hour) for the removal of this substance from the circulatory system and for its disposition in a normal manner. Thus this long recognized anomaly seems to have been based upon inadequate data and to have been really non-existent.

Absorption Rates in Other Species—In connection with the discussion contained in the preceding section it is of interest to point out that a similar close relation appears to exist between the velocity with which glucose may normally enter the blood of the rat and the speed initially available for withdrawing it and disposing of it in a physiological manner. The evidence for this has been supplied in the publications of Cori and Cori from which the values that follow have been drawn or computed. These authors have reported that rats which have been fasted 48 hours can introduce glucose into their blood stream at average rates of 1.78 (4) and 1.87 (17) gm. per kilo per hour. When the rats were

References to the reports of others who have observed indications of greater activity of the withdrawal mechanism after a stimulation are included in the paper by Jordan.
fasted just 24 hours the rates of entrance found averaged 2.66 (18) and 2.05 (19) gm. per kilo per hour. The initial rate at which amyatalized rats (both fasting and non-fasting) were able to remove injected glucose from the blood in a physiological manner was found to range between 2.2 and 2.5 (20) gm. per kilo per hour—values which are intermediate between the various rates of entrance that have been recorded.

For the human species some data have been recorded concerning the rate at which glucose can be withdrawn from the blood without loss to the organism. Wilder and Sansum (21) have shown that men who have fasted over a night cannot tolerate an intravenous infusion of d-glucose at a rate greater than 0.85 gm. per kilo per hour without a gross glycosuria resulting. Regarding the rate at which glucose may enter the blood of man from the digestive tract, there is at present no information available that is at all comparable in accuracy with that which has been obtained from studies of the dog and the rat.

**SUMMARY**

In fifteen experiments covering periods of 1 to 3 hours upon male dogs ranging in weight from 11 to 20 kilos, the average rate of absorption of d-glucose from the gastrointestinal tract was 0.99 ± 0.17 gm. per kilo per hour. In the 2 and 3 hour experiments the rates observed were in closer agreement and averaged 0.99 ± 0.05 gm. per kilo per hour.

Variations in (a) the concentrations and (b) the absolute weight of glucose ingested, (c) the lengths of the absorption periods, (d) the weights of the animals used, and (e) the excitement occasioned by experimentation, have been considered in regard to their influence upon the rates of absorption observed. No definite relationship to any one of these factors has been detected.

That the concentrations of sugar existing in venous blood during absorption may fail to reflect either the course or the completion of the process is shown by some of the observations presented.

The absorption rate for glucose in dogs reported in this communication is less than two-thirds the value which has been currently accepted for a number of years. Therefore it is believed that many conceptions evolved by use of the older and higher value must again be scrutinized with regard to the necessity for their revision.
Rate of Absorption of Glucose

Acknowledgment is made of a grant from a Fund for Research upon Diabetes given by Mr. Francis P. Garvan to Dr. Elliott P. Joslin.

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