Observations on the respiratory quotients and weight gain of man after eating large quantities of carbohydrate

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Every woman knows that carbohydrate is fattening: this is a piece of common knowledge, which few nutritionists would dispute. It is orthodox physiological teaching that the store of carbohydrate, as glycogen, in the human body is small and limited. Soskin & Levine (1952) give normal figures for an adult man as follows:

	Glycogen content	
	%	Total (g)
Liver	6·0	110
Muscle	0·7	250
Total	—	360

The glycogen in the liver cannot rise above 15% and it is stated in textbooks that the capacity of muscle to store glycogen is limited. It would be considered unlikely that this total store could be more than doubled. Hence, if an individual consumed 400 g of carbohydrate in excess of his energy requirements, then it would be expected that there would be a net conversion of carbohydrate into fat. As carbohydrate molecules contain more oxygen relative to carbon and hydrogen than do molecules of fatty acid, this conversion has a high respiratory quotient (RQ). RQs well above 1·0 have been recorded in animals which are laying down fat. The classical example is the marmot. Pembrey (1902) records RQs of 1·4 in these animals when preparing for hibernation. The conversion of carbohydrate into fat after a dietary carbohydrate excess should be easy to demonstrate in man by measuring the RQ and finding values of 1·0 or above. This paper records measurements under such conditions and also observations on the changes in weight of some of the subjects.

It will be shown that, in fact, it is difficult to raise the RQ of man to 1·0, even when the subject undergoes real discomfort from his enforced gluttony. Possible explanations of the apparently low RQ after excess carbohydrate are discussed. A preliminary account of some of these experiments has already been given (Passmore & Swindells, 1962).

EXPERIMENTAL

Three series of experiments were carried out by similar laboratory methods.

Subjects. These were all healthy students, technicians or research workers. None of them was obese or exceptionally thin. Between meals the subjects sat and read in

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easy chairs, except for brief periods when the respiratory exchanges were being measured whilst they walked on a treadmill. In the experiments lasting through the night, the subjects slept on camp beds in the laboratory.

Diet. The meals consisted of white bread, jam and a little tinned fruit. Tea was provided to drink, with sugar but no milk. The subjects were encouraged to eat as much as possible at each meal. The protein, fat and carbohydrate contents of these foods were determined by chemical analysis. The protein content was calculated by multiplying by 5·7 the value for the nitrogen content, obtained by Kjeldahl analysis. The fat content was measured by Soxhlet extraction, and the carbohydrate by the method of Trevelyan & Harrison (1952). All values for carbohydrate are expressed as polysaccharides.

Respiratory exchanges. Expired air was collected over 10 min periods in Douglas bags. For measurements when walking, the Max Planck respirometer was used.

Samples of expired air were analysed by the Haldane method, duplicates agreeing within $\pm 0{\cdot}02\%$.

Table 1. *First series of experiments. Oxygen utilization and carbon dioxide output of subject Nas. over 24 h*

Activity	Time (min)	O_2 used		CO_2 output	
		ml/min	Total (l.)	ml/min	Total (l.)
Lying	406	211	85·7	192	77·8
Sitting	922	247	227·7	225	207·4
Walking	52	1044	54·3	950	49·4
Up and about	60	500	30·0	455	27·3
Total	1440	—	397·7	—	361·9

Urinary N: 10·6 g/24 h.

Metabolic mixture. This was derived from the values for the total O_2 consumption and CO_2 output and the urinary N throughout the periods of observation. Total O_2 consumption and CO_2 output were calculated by multiplying the figures obtained during the sampling period by the overall times, as previously described (Passmore, Strong & Ritchie, 1958). An example is given in Table 1. With these figures the amounts of protein, carbohydrate and fat metabolized were calculated, on the assumption (Zuntz, 1897) that for oxidation

1 g protein utilizes 966 ml of O_2 and produces 782 ml of CO_2,

1 g carbohydrate utilizes 829 ml of O_2 and produces 829 ml of CO_2,

1 g fat utilizes 2019 ml of O_2 and produces 1427 ml of CO_2,

and that 1 g of urinary N is equivalent to 6·25 g of protein metabolized.

Weight changes. The subjects in the second series of experiments were weighed naked at the beginning and end of the 24 h period on a balance accurate to 1 g. For these subjects, a complete fluid balance was drawn up. Fluid intake was unrestricted but accurately measured. The water content of the foods consumed was determined by analysis and the metabolic water was calculated with the factors 0·41, 0·60 and 1·07 g of water produced for each g of protein, carbohydrate and fat metabolized.

The evaporative water loss was estimated from the invisible weight loss with the values for the weights of $CO_2 - O_2$ measured in the respiratory exchanges.

Urine and faeces. These were collected for the appropriate period of experiment in each series. Faeces were passed by only four subjects in series 2: they were weighed, but not analysed; all the stools were well formed and the water content was taken as 75%. Urinary N was determined by the Kjeldahl method. The sodium and potassium contents of the urine were estimated by flame photometry.

RESULTS

First series of experiments. The subjects, three men and five women, received four meals rich in carbohydrate at 3 h intervals and their respiratory exchanges were followed over periods of about 14 h. Table 2 shows the ranges and means of the RQs after each meal. Table 3 shows mean values for the total intake each day and the calculated metabolic mixture. Of the sixty-three measurements of RQ, when the subjects were at rest, only seventeen were 0·95 or above and only three reached 1·00.

Table 2. *First series of experiments. Respiratory quotients of eight subjects at rest and when walking after four successive meals rich in carbohydrate and low in fat*

	At rest		Walking	
	Range	Mean	Range	Mean
Basal	0·77–0·85	0·82	—	—
Before meal 1	—	—	0·83–0·87	0·85
After meal 1:				
1 h	0·86–0·96	0·90	—	—
2 h	0·81–0·92	0·88	0·91–0·96	0·93
After meal 2:				
1 h	0·88–1·00	0·92	—	—
2 h	0·85–1·01	0·93	0·90–0·97	0·95
After meal 3:				
1 h	0·85–0·96	0·92	—	—
2 h	0·90–0·97	0·93	0·92–0·96	0·95
After meal 4:				
1 h	0·84–1·02	0·94	—	—
2 h	0·89–0·97	0·94	0·92–0·99	0·96

Table 3. *First series of experiments. Mean values for eight subjects for diet, metabolic mixture and proportions of the calories of the mixture derived from protein, carbohydrate and fat during 14 h with meals rich in carbohydrate and low in fat*

	Protein	Carbohydrate	Fat	Calories
Diet	45 g	421 g	2 g	1870 kcal
Metabolic mixture	36 g	242 g	31 g	1430 kcal
Calorie contribution to metabolic mixture	10%	70%	20%	—

It will be seen that the mean values for the RQs did not rise above 0·94 at the end of the day and that, despite the very low dietary intake of fat and the excess dietary calories, fat still appeared to be mobilized and used. Accordingly a second series of

experiments was planned, in which the dietary intake was increased and the period of observations extended to 24 h.

Second series of experiments. The subjects, nine men, two of whom had been in the first series, were given five meals at each of which they were encouraged to eat to their maximum capacity, which varied greatly from 2610 to 5120 kcal/day. All of the subjects suffered some abdominal discomfort, but there was no vomiting or diarrhoea. Indeed, only four of the subjects passed a stool during the period of observation. The respiratory exchanges were measured at intervals over 24 h periods. Table 4 shows the ranges and means of the RQ after each meal and throughout the night and early morning. Table 5 shows the mean values for the dietary intake and metabolic mixture and also the values for one subject. He ate the greatest amount (1·17 kg of carbohydrate), and only his values indicated a net conversion of carbohydrate into fat. Of the sixty-six measurements of RQ, when the subjects were at rest, twenty-five were 0·95 or above; fifteen reached 1·00, but only three exceeded 1·05.

Table 4. *Second series of experiments. Respiratory quotients of nine subjects at rest and when walking during a 24 h period when receiving excess of a diet rich in carbohydrate*

Day	Approx. time	At rest		Walking	
		Range	Mean	Range	Mean
1	9.00 Meal	0·73–0·86	0·80	—	—
	11.00 Meal	0·78–0·94	0·88	0·89–1·01	0·95
	14.00 Meal	0·75–1·01	0·90	0·90–0·99	0·95
	17.00 Meal	0·84–1·05	0·92	0·90–1·00	0·95
	20.00 Meal	0·88–1·06	0·96	0·92–1·01	0·96
	23.00	0·85–1·03	0·96	—	—
2	2.00	0·87–1·09	0·99	—	—
	5.00	0·87–0·98	0·95	—	—
	8.00	0·77–0·98	0·88	—	—

Table 5. *Second series of experiments. (A) Mean values for nine subjects and (B) values for one subject, Wil., for diet, metabolic mixture and proportions of the calories of the mixture derived from protein, carbohydrate and fat during 24 h when receiving excess of a diet rich in carbohydrate*

	Protein	Carbohydrate	Fat	Calories
		A		
Diet	86 g	884 g	3 g	3910 kcal
Metabolic mixture	76 g	452 g	30 g	2440 kcal
Calories contributed to the metabolic mixture	13 %	76 %	11 %	
		B		
Diet	101 g	1172 g	3 g	5120 kcal
Metabolic mixture	58 g	650 g	−18 g	2740 kcal
Calories contributed to the metabolic mixture	9 %	97 %	−6 %	

(The negative sign indicates formation of fat from carbohydrate)

Table 6 shows the gain in weight of each subject over the 24 h expressed in g/65 kg. The subjects have been arranged in descending order of their calorie excess, calculated from the net calorie value of the diet consumed minus the estimated energy expenditure. The figure for water in the table is for the complete water balance, determined as described above. The figures for protein, carbohydrate and fat are the differences between the net dietary intake and the calculated metabolic mixture.

Table 6. *Second series of experiments. Changes in weight and in body composition (per 65 kg body-weight) of nine men who ate five meals containing large quantities of carbohydrate in excess of their calorie needs*

Subject	Calorie excess (kcal)	Weight (g)	Water (g)	Protein (g)	Carbohydrate (g)	Fat (g)
Har.	2270	538	−40	−3	600	−21
Nim.	2110	1636	1130	25	480	3
Wil.	2080	1225	740	36	440	15
Pas.	1680	1518	1060	−9	510	−38
Ste.	1420	415	70	4	340	0
Nas.	1340	1439	1060	16	400	−41
Pic.	1070	446	160	−6	310	−18
New.	670	11	−240	11	310	−69
Bow.	320	−350	−560	−10	330	−105

Third series of experiments. In these, we ourselves acted as subjects. We studied the response to a large midday meal of carbohydrate for a period of 6 h over 8 days. On the first 2 days we ate our normal diets. On the next 4 days, we deliberately restricted the fat in our diet, but ate according to normal appetite. On the last 2 days we stuffed ourselves with carbohydrate and as far as possible excluded all fat from the diet. In this process, Y.E.S. gained 2·8 kg in weight, but R.P. only 0·3 kg.

Table 7. *Third series of experiments. Respiratory quotients after a heavy meal rich in carbohydrate and low in fat. Mean values for eight observations each day taken over a 6 h period*

Day	Previous diet	Subject	
		Y.E.S.	R.P.
1	Normal	0·89	—
2	Normal	0·90	—
5	Reduced fat	0·92	0·94
6	Reduced fat	0·92	0·94
7	Excess carbohydrate	0·94	0·95
8	Excess carbohydrate	1·00	0·96

Table 8. *Third series of experiments. Metabolic mixture over a 6 h period after a meal rich in carbohydrate. For the previous 2 days the subjects had eaten carbohydrates in excess of calorie needs*

	Protein	Carbohydrate	Fat
Meal (g)	24	204	1
Metabolic mixture (g/6 h):			
Subject Y.E.S.	16	111	−5
Subject R.P.	15	102	5

Table 7 shows the mean of the RQs after the test meal. It will be seen that even on day 8 it did not rise above 1·0. The calculated metabolic mixtures (Table 8) indicate that even after this longer period of restriction of fat and forcing of carbohydrate, conversion of carbohydrate into fat occurred in trivial amounts in one subject only.

DISCUSSION

In each of the three series of experiments described above, it was found to be difficult to raise the RQs of the subjects significantly above 1·00. Thus, despite the large intakes of carbohydrate, there was no evidence of the net conversion of carbohydrate into fat in substantial amounts within 24 h. There are three possible explanations.

First, in measuring the respiratory exchanges, the CO_2 output might have been consistently underestimated. The interpretation of measurements of the RQ may not be simple. A single RQ reading may represent the sum of three processes: (1) the relative combustion rates of fat, carbohydrate and protein, (2) the sum of the transformation carbohydrate $\rightleftarrows$ fat, and (3) the result of any change in the bicarbonate content of the tissue fluids, secondary to variations in acidity. When moderate exercise is associated with the development and recovery from a metabolic acidosis, the uncorrected RQ cannot be used as a measure of metabolic changes. This situation has long been known and has led to a discounting of the value of RQ measurements in

Table 9. *Comparison of the theoretical respiratory quotient of the food intake with the mean value of all the measurements of the* RQ *made on subjects carrying out various activities at irregular intervals throughout the day*

Subjects	No. of subjects	No. of measurements of RQ	Observed RQ (mean)	Calculated RQ of diet	Reference
Colliery clerks	10	210	0·84	0·86	Garry, Passmore, Warnock & Durnin (1955)
Thin male students	2	46	0·82	0·85	Passmore, Meiklejohn, Dewar & Thow (1955)
Fat young women	2	72	0·86	0·86	Passmore, Strong, Swindells & el Din (1963)

All subjects were on diets that approximately met their calorie needs: there was no evidence of gains or losses of weight.

metabolic research. Cathcart & Markowitz (1927) have discussed the limitation of interpretation of the RQ in a well-known paper. In mice the measured RQ has been shown to correspond accurately to the theoretical RQ of the diet and to rise and fall linearly in relation to an increase or decrease in the amount of food eaten (Dewar & Newton, 1948). Such observations are entirely consistent with the concepts of the classical physiology of metabolism. That in human beings, under conditions which are not precisely controlled, measurements of the RQ do reflect the metabolic changes is

indicated by Table 9. The mean of a large number of RQ measurements obtained whilst the subjects were occupied in various activities, not involving heavy exercise, and at all times of the day, unrelated to meals, is compared with the theoretical RQ of their diets. The dietary intake at the time of the measurements was determined by dietary survey, or prescribed if the subjects were living in the metabolic ward of a hospital. There was no evidence that any of these subjects was not in calorie balance at the time. The general agreement between the observed and calculated RQ values suggests that mean values for the quotients, obtained as described in this paper, do reflect with some accuracy the sum of the metabolic changes in the body.

Secondly, some of the O_2 consumed might be used to oxidize hydrogen in fats with consequent desaturation of the fat without the production of CO_2 in the following manner:

$$—CH_2—CH_2— + O = —CH=CH— + H_2O.$$

That this process occurs was suggested by Furnass (1960) who also failed to observe high RQs when feeding patients on diets rich in carbohydrate. We know of no evidence in man either to support or refute this suggestion. However, when pigs were fed on a diet rich in carbohydrate, the fat became 'harder' (Ellis, 1933). Ellis noted the following changes in the body fat of young pigs when their carbohydrate intake was increased by feeding them on maize, in place of a diet based on groundnuts: the iodine value was reduced from 93 to 63, the percentage of saturated fatty acids increased from 19 to 33 and the percentage of linoleic acid was reduced from 23 to 9. Likewise, Longenecker (1939) observed a decrease from 84 to 78 in the percentage of unsaturated fatty acids in the depot fats of rats when fed on a diet rich in carbohydrate.

Thirdly, the capacity of the carbohydrate store in the human body may be greater than has been generally considered. Perhaps the conversion into fat may take place slowly and only after an interval which may be many hours or even days. As none of our subjects excreted significant amounts of glucose in their urine, this store could not be in the form of glucose in the blood. More likely it would be as glycogen. Glycogen can be stored in liver, adipose tissue and muscle. In a normal man there will be about 1·5 kg of liver, 9 kg of adipose tissue and 30 kg of muscle. Although the liver is known to be able to store glycogen up to 10% concentration, the total glycogen store in the liver can only amount to 150 g. On the other hand, although the concentration of glycogen in muscle is usually much less than in the liver, the total amount present in muscle will be more than that in the liver. To store an extra 500 g the muscle glycogen would have to rise by 1·7 g/100 g. This is not impossible. Information about the glycogen content of human muscle is scanty. Analyses of post-mortem material and of samples obtained at operation will not throw light on normal values, much less values after excessive feeding. The sampling of muscle by biopsy is now an established clinical technique. Hildes, Sherlock & Walshe (1949) have measured the glycogen content of human muscle samples so obtained. Figures from 0·72 to 3·89 g/100 g were found, and varied for different muscles in the same subject. After reading their paper, we concluded that to get an indication of a change in total muscle glycogen we should have had to ask our subjects to submit to a veritable pin-cushion

of punctures. High concentrations of glycogen in muscle are certainly possible and indeed in glycogen-storage disease amounts up to 12 g/100 g have been found (Illingworth, 1961).

Although we have no positive evidence to support this conclusion, we think it most likely that an excess of carbohydrate taken in the diet is first stored as glycogen, predominantly in the muscles, and only slowly converted into fat.

In the second series of experiments, the individual differences in weight gain (Table 6) were not surprising. Large day-to-day variations in body-weight are commonly observed (Durnin, 1961; Adam, Best & Edholm, 1961). Our results confirm previous findings that short-term changes in body-weight are usually closely related to changes in body water. Only four of the subjects (Nim., Wil., Pas. and Nas.) retained substantial amounts of water (mean 996 g) and these four were also in positive sodium balance (mean value +159 m-equiv.). This suggests retention of extracellular fluid, since the mean potassium balance for these four subjects was −6 m-equiv. In the other subjects the changes in sodium and potassium were very small, but Bow., who lost 560 g water, also lost 34 m-equiv. sodium. The immediate retention of sodium after glucose administration to obese subjects who had previously fasted for several days was recently reported by Bloom (1962). Table 6 also shows that in some of the subjects the consumption of large quantities of carbohydrate did not appear to suppress the mobilization of fat.

SUMMARY

1. In three series of experiments healthy human subjects were fed on diets rich in carbohydrates and containing calories in excess of their requirements. The respiratory exchanges were measured at intervals for periods of up to 24 h.

2. The values for the RQ rose after each meal, but not as much as would be expected if the excess carbohydrate was being converted into fat. The RQ was seldom significantly above 1·0.

3. It is suggested that the immediate disposal of an excess of dietary carbohydrate is storage as glycogen, mostly in muscle. There is probably a delay before conversion into fat.

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