XXX. THE RELATIVE VALUE OF FAT AND CARBOHYDRATE AS SOURCES OF MUSCULAR ENERGY.

WITH APPENDICES ON THE CORRELATION BETWEEN STANDARD METABOLISM AND THE RESPIRATORY QUOTIENT DURING REST AND WORK.

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INTRODUCTION.

A NUMBER of researches on isolated muscles, made most of them during the last decade by the Cambridge School of physiologists, have revived the old problem about the immediate source of muscular energy, in so far as their main results cannot be reconciled to the commonly accepted view, that the muscle is able to make use indiscriminately and with the same coefficient of utilisation of different sources of energy. According to this view, which is based mainly on the researches of Zuntz and his school, the muscular machine can transform a definite fraction of the energy liberated by the combustion of any available substance into mechanical work—provided the substance can be oxidised in the organism. According to the Cambridge school the muscular contraction itself does not depend at all upon an oxidative reaction but upon the splitting up of a definite unknown molecule, resulting in the formation of lactic acid, while other definite processes, involving the recombination of lactic acid into the molecule directly concerned in the contraction, are necessary to restore the contractility.

The researches on which the supposed isodynamic value for muscular work of very different oxidisable substances are based have, without exception, been made on the organism as a whole, and the general principle has been to feed a subject during a certain period upon a diet consisting chiefly of a single foodstuff (fat, protein or carbohydrate), to let the subject perform a definite amount of work and to study the relation between the work performed and the corresponding metabolism. When a number of such periods, which differed only in the character of the chief substance catabolised, were compared the conclusion was arrived at by Zuntz [1911] and his collaborators that the coefficient of utilisation is practically independent of the substance catabolised[1].

From the researches of Fletcher, Hopkins, A. V. Hill and their collaborators [see Fletcher and Hopkins, 1917] it must be inferred on the other hand that, when the muscular machine requires certain reactions to take place between definite substances which must be closely allied to carbohydrates, it is almost inconceivable that substances such as fats can be utilised without a transformation involving loss of energy, and one is led to expect therefore that the coefficient of utilisation should be lower for other substances than for carbohydrates.

We do not propose to enter upon a discussion of the Cambridge results, but the discrepancy between them and those of Zuntz has caused a growing feeling of uneasiness in our minds which has at last compelled us to take up the problem and to see whether Zuntz's conclusion will stand the test of a renewed experimental investigation.

The general plan of our proposed research was briefly as follows. A human subject should live for a certain number of days on a definite diet, containing a minimum of protein and a very decided preponderance of either fat or carbohydrate. During this period, or part of it, he should come to the laboratory in the morning before taking any food and with as little muscular effort as

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[1] It should be remembered, however, that the researches made in Zuntz's laboratory were not primarily intended to demonstrate the equal value of the different foodstuffs, but to examine whether the 30 % difference in value between fat and carbohydrate postulated by the hypothesis of Chauveau could be found or not.

possible. After a suitable period of complete rest, during which the standard metabolism could be measured, he should work on a bicycle ergometer for a certain length of time, which we fixed provisionally at two hours, and the rate at which work was performed should be kept constant throughout for the same subject. During the work a number of determinations of the respiratory exchange should be made. After a suitable number of days the diet should be altered and the determinations repeated.

The experimental difficulties involved in such an investigation are very considerable, and it was evident from the first that a definite solution of our problem could only be hoped for when the accuracy of all the determinations could be raised to a high standard. The reliability must depend (1) on the technical accuracy of the determinations themselves, (2) on the constancy of the external conditions to which the subject was exposed and (3) on the constancy of reaction on the part of the subject. The greatest difficulty is presented by the subject. During a total experimental period of three weeks or a month effects of training and probably other changes are likely to occur, and it was impossible to tell beforehand how these could best be avoided or their influence minimised. We arranged therefore to make several series of experiments and to use the results of the first to guide us in the planning of the following. It is evident that a condition for doing this is that we should be able to recognise which variations in the results must be due to the variations in the reaction of the subject and which to errors in the determinations, and it was imperative therefore that the technical accuracy of the determinations should be as great as possible.

We had to choose between determining the pulmonary gas exchange by measurements and analyses of the expired air and determining the total gas exchange in a chamber. Although the methods for measuring the pulmonary gas exchange can give very accurate results and have been used in almost all former researches bearing upon our problem we thought it better to discard them because they would involve that the subject should wear a respiration mask (or a mouthpiece) during a period of two hours, which would become rather disagreeable and might influence the metabolism in unaccountable ways[1].

When the determinations should be made by means of a respiration chamber we had to choose between the closed circuit (Regnault) and the air current (Jaquet) type of apparatus. The dangers and drawbacks of large Regnault apparatus have been pointed out by Krogh [1915, 2] and from the interesting control experiments reported by Carpenter [1915] it is clear,

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[1] In the excellent series of experiments on muscular work on an ergometer made by Benedict and Cathcart [1913] the subject was connected with the mouthpiece for a number of short periods only which were distributed over the time of riding the ergometer. This device appears to us to involve serious dangers. For a certain time after the putting on of a mouthpiece and noseclip the respiration is apt to be distinctly abnormal and though the absorption of oxygen is as a rule scarcely affected by such changes the CO_2 output may become abnormal by washing out, when the ventilation is increased, and storing up when it is diminished.

moreover, that the accurate determination of respiratory quotients in a closed circuit apparatus is—to say the least—very difficult to attain.

Carpenter has carried out extensive comparisons between respiration apparatus of various types. The comparisons were made between instruments of two types at a time by employing them for alternate determinations of the respiratory exchange of the same subject. Usually about six alternate determinations were made on each experimental day, and care was taken to change the order in which the instruments were used from day to day. This method of experimenting is extremely suitable to bring out both the uniformity of results (accidental variations) obtained with each type and its absolute reliability (systematic error). The accidental variations have been given by Carpenter in "probability curves" but the systematic differences between the types have not been discussed. It is obvious, however, that when the averages of long series of such determinations differ by more than double the mean error of each average the difference cannot be purely accidental, but must be due to some inherent peculiarity in one or both of the apparatus.

From the probability curves given by Carpenter it can be deduced that the mean error on the average of each separate series of determinations of the respiratory quotient is of the order ±0·005 and nearly the same for the different types of apparatus except the "Spirometer Unit" and the "Bed Calorimeter" which have slightly larger errors.

Table I.

Apparatus 1	Number of exp. 2	CO_2 cc./min. 3	O_2 cc./min. 4	R.Q. 5	R.Q. reduced 6
T.E. Unit	142	185	227	0·815	
Bed Cal.	95	190	223	0·85	0·865
T.E. Unit	31	197	231	0·855	
Sp. Unit	25	198	233	0·85±·005	0·83
T.E. Unit	36	190	224	0·85	
Zuntz-Gep.	35	186	227	0·82	0·80
Sp. Unit	74	182	219	0·83	
Zuntz-Gep.	58	176	220	0·80±·005	0·80
T.E. Unit	44	165	193	0·855	
Tissot	37	167	194	0·86	0·835
Sp. Unit	65	190	233	0·815	
Tissot	52	192	242	0·795	0·81
Sp. Unit	48	189	231	0·82	
Douglas	45	178	224	0·795	0·805

In Table I we have put together the average results of the various comparisons, compiled from Carpenter's book. The figures in column 5 show that while the "Tension Equaliser Unit" and the "Spirometer Unit" give the same average quotients, the differences found in the other comparisons are too large to be accidental.

In column 6 we have arranged a direct comparison between all the types of apparatus investigated by reducing the respiratory quotients found in the various series by means of the same apparatus (the "Spirometer Unit") to a uniform value put arbitrarily at 0·83 and it is seen that the "Bed Calorimeter," which is a large closed circuit apparatus, gives a much higher average quotient, while the Zuntz-Geppert and Douglas apparatus, in which the quotient depends exclusively on the results of a gas analysis, give only 0·80. (In the comparisons with the Tissot apparatus very special errors come into play which it is not deemed necessary to discuss.)

The respiratory quotient determined by gas analysis of the expired (and inspired) air correctly performed cannot have any *systematic* error, and it follows that the respiratory quotients determined by means of the closed circuit "Unit" apparatus are on an average 0·03 too high, while those found by means of the respiration calorimeter are 0·065 too high.

In a Jaquet apparatus on the other hand the accuracy of the respiratory quotient depends exclusively on the gas analysis. There is therefore no danger of systematic errors in the quotient while the limits of the accidental errors can always be controlled. A special gas analysis apparatus capable of analysing the respiratory gases to 0·001 % has been constructed for this and similar researches and described by Krogh [1920, 1].

DESCRIPTION OF APPARATUS AND METHOD.

Our Jaquet apparatus which has been constructed on the lines laid down by Grafe [1910] is shown in Fig. 1. The chamber consists of a framework of angle iron to which sheets of galvanised iron have been riveted and made airtight by soldering. The form and dimensions have been chosen with a view to accommodating the bicycle ergometer and the subject riding the machine. The floor is made from a single sheet of galvanised iron with the edges bent downwards into a U shaped rectangular groove (1, Fig. 1) which is filled with water. The chamber itself dips into the same water seal when closed during an experiment. As shown in the figure (at 2) one end can be lifted to let in the subject and put in apparatus. At the other end just above the groove where the movements are very slight a number of small tubes (3) are arranged to introduce wires etc. for the working of the ergometer, mixing fans, signals etc.

Near the top of the chamber are two wider tubes (4 and 5). Through a mouthpiece or mask, respiration valves and flexible tubing the subject can be connected with one of these (4) and through it with a dry meter placed outside the chamber. The air for inspiration has in such experiments been taken from the chamber and again returned to the chamber from the meter through the tube (5). This arrangement has been used during some introductory experiments to compare the pulmonary gas exchange with the total.

The chamber is ventilated with outside air from the street through a 60 mm. tube (6) which is connected up at the beginning of an experiment. At the other end of the chamber, a similar tube (7), which is likewise put in place when the chamber has been let down, connects it with the gas meter. The inlet tube simply opens into the chamber, but the outlet tube draws air simultaneously from three points distant about 50 cm. from each other (8).

During experiments the air in the chamber is mixed continuously by two revolving fans (9 and 10) each of which will move about 30 cb. meters per minute. The blast produced by these fans is rather disagreeable at first but during the work, when the temperature and moisture in the chamber rise, it is felt by the subject as very refreshing. Arrangements for controlling the temperature and moisture have not been put in though they would undoubtedly constitute a considerable improvement. As it is, work experiments can only be made during the cooler season of the year.

The chamber has been tested for tightness by closing it up and connecting it with a spirometer loaded so as to produce a negative pressure of about

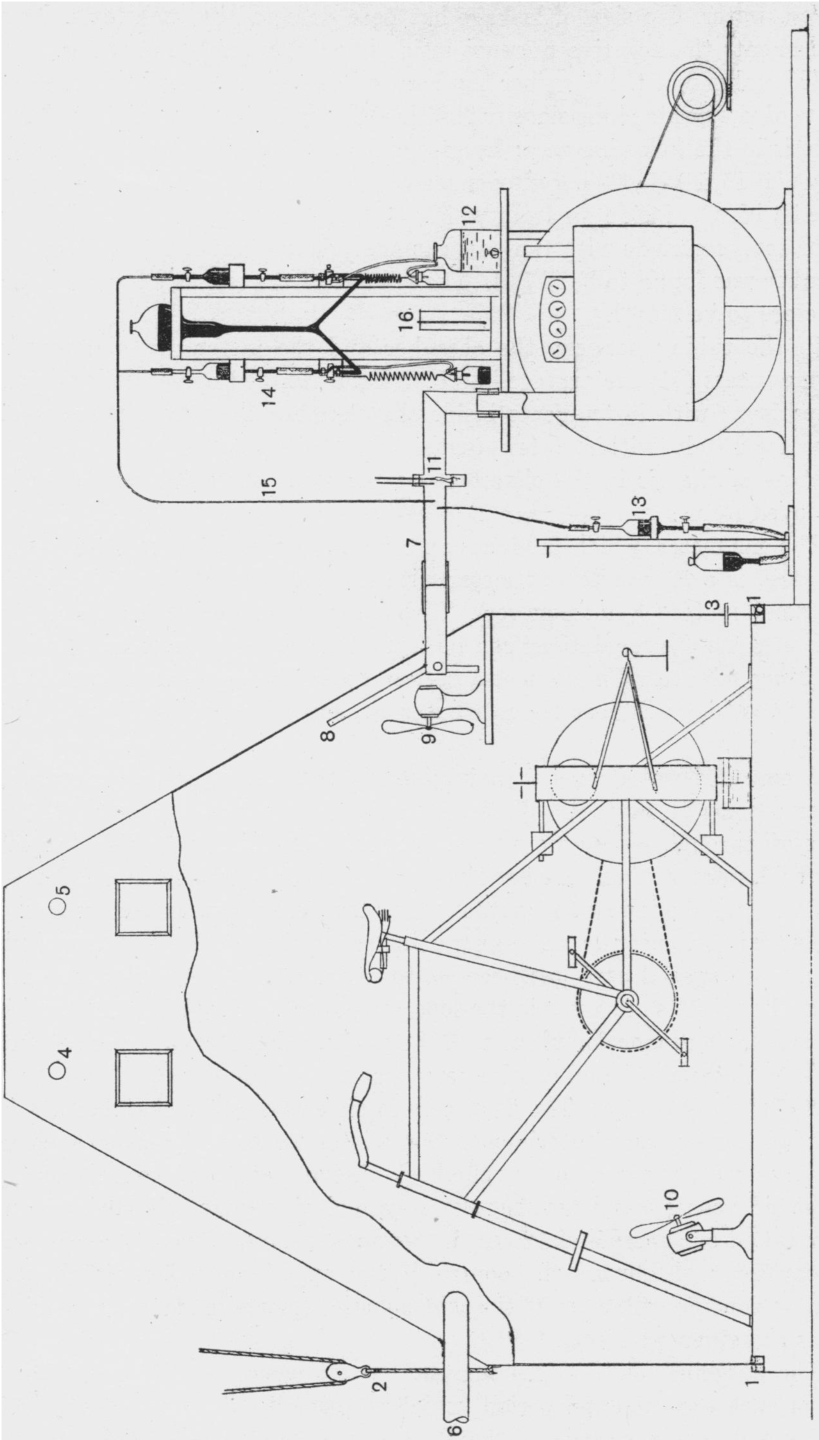

Fig 1.

20 mm. water. No sign of leakage has been detected by such tests. During experiments the negative pressure inside is only about ½ mm. water.

The volume of the chamber has been calculated from numerous measurements of the inside dimensions to 2267 l. This determination was tested by gas analysis in the following way: by means of a 1 litre glass bulb (described by Krogh [1915, 1]) 15·000 l. hydrogen were put into the chamber and thoroughly mixed with the inside air from which 15 l. had been previously withdrawn. From analyses made with the new gas analysis apparatus the volume of the chamber was found to be 2276 l. The volume of the empty chamber is taken therefore to be 2270 l.

In the tubing between the chamber and the meter dry and wet bulb thermometers (11) are arranged and we have satisfied ourselves by repeated comparisons with instruments inside the chamber that these thermometers show accurately within a few tenths of 1° the average temperature and moisture of the air in the chamber—at the rates of ventilation and mixing employed by us.

The gas meter, which produces and measures the air current through the chamber, is a 50 candle wet meter with a drum of 4 cb. feet. It is driven by a small motor ($\frac{1}{10}$ horse power). Through electrical resistances and suitable transmissions the revolutions can be regulated between about 1 in 3 minutes and 3 per minute. When set at a certain speed the motor is controlled by a regulator which will keep the rate constant, generally within ½ % and always within 1 %.

A constant water level is maintained in the meter by a slow current of water passing through it. Water is admitted from the 3 l. bottle (12) and flows off through an overflow tube. The rate at which water is admitted is about ¾ l. per hour and care has always been taken not to begin any measurements before the inflow and outflow of water were approximately equal.

As we had to use the meter at the rather rapid rate of nearly 2 revolutions per minute special care has been bestowed upon its calibration at various rates. The results are given in the separate paper by Krogh [1920, 2] and here it is sufficient to mention that at all the rates used the volume per revolution has been determined and can be kept constant within 0·1 %.

Sampling of the air. The atmospheric air entering the chamber has been sampled during each experiment. Sometimes we have taken two separate samples during short periods at the beginning and end of the experiment, but as the differences found between these were always extremely slight we have later taken one sample of 120 cc. in portions of about 20 cc. at more or less regular intervals during the course of the experiment. Details about the composition and constancy of the atmospheric air as taken from a Copenhagen street are given by Krogh [1919].

The outgoing air has been sampled in two ways. At the beginning and end of each experimental period, which is normally of 20 minutes duration, we have drawn a sample by hand in a sampling vessel of about 100 cc.

capacity (13). The taking of such an "intermediate sample" occupies about 1 minute. During the course of each experimental period an "average sample" has been drawn automatically by means of the apparatus shown at (14) which was employed in Greenland by A. and M. Krogh [1913] for a similar purpose. The mercury from the sampling vessel flows off into a bottle suspended by a spring which is so adjusted as to maintain constant within 1 cm. the vertical distance between the surface of the mercury in the sampling vessel and the point of the tube through which it flows out. The volume of air taken into the sampling vessel per minute is therefore practically constant, and as the volume transported by the meter is constant also the sample will represent accurately the average composition of the air even though this should vary considerably. During experiments with constant work the variations are extremely slight. The tubing connecting the sampling vessels with the pipe (7) is of 1 mm. bore. The volume of the tube (15) is about 1·2 cc. and as about 6 cc. are drawn per minute the sample is therefore 12 seconds behind the meter.

Analysis and calculation of experiments. The air samples have been analysed for CO_2 and O_2 in the special gas analysis apparatus constructed for the purpose and described in a separate paper [Krogh, 1920, 1] where the methods of calculating the increase in CO_2 percentage and the O_2 deficit in the outgoing air as well as the correction on the oxygen deficit, which is necessary when the ingoing and outgoing volumes of air are not identical, have also been given in detail and illustrated by an example. The atmospheric air has in all experiments been analysed in duplicate, and in all the experiments made in 1917 the average samples were likewise analysed in duplicate. As the double analyses practically never differed more than 0·001 % we have in the later series usually analysed only a single one of the average samples in duplicate.

Calculation of the gas exchange. We have in all cases taken experimental periods of the length of a whole number of revolutions of the meter (usually 38). By multiplication of the volume per revolution with the number and reduction to 0°, 760 mm. and dryness from the temperature of the meter (shown by the thermometer (16) placed in the outgoing current of air) and the barometric pressure, we obtain the reduced ventilation during the period, which is multiplied by the CO_2 increase and the corrected O_2 deficit found in the corresponding average sample.

As the volume of air which has passed through the chamber during a period is only about double the volume of the chamber itself we cannot take the composition of air in the chamber as unaltered but have to subtract the CO_2 increase and O_2 deficit in the chamber at the beginning of the period and add the corresponding figures for the end of the period. The volume of the chamber (– the ergometer, subject etc.) is therefore calculated for the beginning and end of each period and reduced to 0°, 760 mm. and dryness from the readings of the dry and wet bulb thermometers (11) and the barometric pressure. The water vapour tension corresponding to the dry and wet bulb readings is taken by interpolation from a psychometric table in Landolt-Börnstein's tables.

From the corrected gas exchange for the experimental period the gas exchange per minute is calculated by division with the length of the period and the respiratory quotient is made out. Finally the total heat production per minute is calculated from the oxygen intake and the respiratory quotient by means of Zuntz's table [1901] disregarding the protein metabolism.

A detailed example of the calculation is given below. The working out of the formulas on which the calculation of respiration experiments with intermediate samples is based is given in detail in the paper by A. and M. Krogh [1913] quoted above.

Rest experiments. In order to calculate the coefficients of efficiency in the muscular work experiments the standard metabolism of the subject must be determined and subtracted from the metabolism during the work periods. It would have been desirable to make these determinations also in a chamber, but for technical reasons this was impossible and we have therefore made them by means of the technique usually employed by us involving the use of a mouthpiece and respiration valves.

The subject who had taken no breakfast sat down in an easy chair on arriving in the laboratory and remained absolutely at rest for 20 minutes. Thereupon the mouthpiece and noseclip were put on, and the subject breathed for about 10 minutes through the valves and expired through a mixing vessel of about 3 l. capacity and a wet meter of 14·50 l. per revolution. During this period the duration of 1 revolution of the meter was observed repeatedly and when it had become approximately constant the determinations were begun. Each experimental period lasted for approximately 2 revolutions of the meter and was begun and finished at the end of an expiration. Two consecutive determinations were made each day. During each a sample of the expired air from the mixing vessel was taken into a 40 cc. sampling vessel of the type usually employed by us [Krogh, 1915, 1]. The sample was drawn by hand, about 2 cc. at a time. One sample of the air inspired from the room was taken in small portions during the two experimental periods. The analyses were reliable to about 0·01 %.

The general routine of making and calculating the experiments is best shown by an example taken from the protocol.

April 19, 1918. The subject O. H. arrived and sat down at 9 o'clock. Mouthpiece etc. at 9.22. Barometer 751·5 mm.

As soon as possible after the determinations of the standard metabolism the subject entered the respiration chamber and began riding the ergometer at 9.45. During the first nine minutes the chamber is not ventilated, to allow the inside air to attain the composition which will remain nearly constant during the whole of the experiment. The subject rides for about half-an-hour before the determinations begin, and during this time the general accommoda-

Rest experiment begun	Duration	Vol. expired l.	Temp. of meter	Samples	Atm. sample
9.31	4′ 27·3″	28·95	17·0°	1	3
	4′ 42·0″	29·20	17·0°	2	

Analyses:

	cc.		%				Expired %	Inspired	Corr.	Diff.
3.	9·988 9·980 7·893	0·008 2·087	0·08 CO_2 20·90 O_2	1.	9·996 9·601 7·931	0·395 1·670	3·95 16·71	0·08 20·90	 +0·08	*3·87* *4·27*
			20·98				20·66 20·98			
							0·265 × 0·32 = 0·08			
				2.	9·990 9·599 7·933	0·391 1·666	3·91 16·68	0·08 20·90	 +0·10	*3·82* *4·32*
							20·59 20·98			
							0·265 × 0·39 = 0·10			

Calculation:

	Duration m.	Ventilation per m. L. reduced	CO_2 increase %	O_2 deficit %	R.Q.	Per minute cc. CO_2	Per minute cc. O_2	Calories
1	4·455	5·81	3·87	4·27	0·905	225	248	1·23
2	4·70	5·67	3·82	4·32	0·885	216	245	1·215

tion of the subject to the work, of the temperature in the chamber, of the water level of the meter etc. will take place.

Exp. begun	Duration	Reading of meter	Ventilation revolutions	Temperature of chamber dry	Temperature of chamber moist	Temp. of meter	Samples Intermediate	Samples Average
10.16		9003		18·0°	14·4°	13·2°	1	
	20′ 44·5″		38					A
10.37		9041		19·5°	17·0°	13·2°	2	
	20′ 43·0″		38					B
10.58		9079		20·0°	18·4°	13·3°	3	
	20′ 45·3″		38					C
11.18		9117		20·2°	19·0°	13·4°	4	

Barometer 752 mm. Volume of meter per revolution 113·9 l.
Volume of chamber corrected 2170 l.

The analyses are left out as sufficient examples are given in the preceding paper. The CO_2 increases and O_2 deficits found are given in the calculation.

Calculation:

Sample	Barometer − vapour tension mm.	Temp.	Volume reduced l.	CO_2 increase hundredths of 1 %	O_2 deficit hundredths of 1 %	CO_2 increase litre	O_2 deficit litre
1	742	18·0°	1987	56·15	63·75	11·16	12·67
A	740·5	13·2°	4019	56·95	64·7	22·90	26·00
2	739	19·5°	1968	56·75	64·65	11·17	12·73
B	740·5	13·25°	4019	56·9	64·5	22·87	25·92
3	737·5	20·0°	1961	56·95	64·55	11·17	12·66
C	740·5	13·35°	4019	56·8	64·85	22·83	26·07
4	736·5	20·2°	1956	56·9	65·45	11·14	12·81

Period	Duration m.	CO_2 eliminated l.	O_2 absorbed l.	R.Q.	Per minute CO_2 cc.	Per minute O_2 cc.	Cal.
A	20·74	22·91	26·06	0·880	1105	1256	6·22
B	20·72	22·87	25·85	0·884	1104	1248	6·18
C	20·755	22·80	26·22	0·870	1099	1264	6·24

SOURCES OF ERROR AND ACCURACY.

The possible sources of error in the respiration experiments are few in number and not *a priori* likely to be serious. The ventilation recorded by the meter can be taken as correct to about 0·1 %, but the reduced volume of the chamber may possibly be erroneous to the extent of 0·2 %, if the recorded temperature and moisture differ from the true averages by ½° and ½ mm. vapour pressure. Such an error will influence the final result to the extent of 0·1 %.

Errors in the analyses may amount to 0·001 % and since the CO_2 percentage is generally about 0·5 % this will correspond to an error on the gas exchange of 0·2 %. If the CO_2 increase should be found, say, 0·001 % too low and the O_2 deficit 0·001 % too high the resulting error on the respiratory quotient would be 0·004.

A priori the possibility cannot be excluded that the samples analysed do not represent accurately the average composition of the air. This may be the case especially with the intermediate samples if the air in the chamber is not absolutely mixed.

To test this point we have made a small number of control experiments. In these we have added CO_2 from a cylinder to the chamber through a 1 litre meter. The CO_2 was washed with permanganate and the water in the meter

Control experiment 1.

Time	Duration seconds	CO_2 %
10.45	52	·5085
	57	·5085
	70	·508
	59	·5015
	70	·511
	9	·509
	31	·5085
	67	·5095
	7	·508
10.55	65	·509
		Average 0·5082
		Dispersion $\sigma = \pm 0{\cdot}0025$

Control experiment 2.

Time	Duration seconds	CO_2 %
10.38	33	·509
	60	·5105
	10	·510
	90	·513
	7	·5105
	70	·510
	15	·5075
	92	·5095
	16	·5035
	70	·5095
10.51	60	·510
	61	·514
	60	·5115
	13	·510
	55	·5125
11.00	55	·5035
		Average 0·5097
		Dispersion $\sigma = \pm 0{\cdot}0028$

was thoroughly saturated with the gas before any experiments were made. During the experiments CO_2 was added at an approximately constant rate of 1 l. per minute while the chamber was being ventilated at the rate used in actual work experiments. It is obvious that the CO_2 from a constant slow current of the pure gas is not so likely to become uniformly mixed with the air of the chamber as the expired air from a human subject, which contains only about 5 % CO_2.

The first control experiments consisted simply in taking intermediate samples as rapidly as possible and comparing their CO_2 percentage, which should remain constant.

The dispersions of the single samples do not differ significantly in both series, viz. about 0·5 % of the quantity of CO_2. If the CO_2 percentage in one of the intermediate samples is, say, 1 % too high the CO_2 production in the preceding 20 minutes period will be found 0·5 % too high, since the volume of the chamber is about half the ventilation during 20 minutes, while in the following period it will be 0·5 % too low.

We have made two complete control experiments consisting of five 15 minute periods during which CO_2 was added at an approximately constant rate. The results were as follows:

Control experiment 3.

No.	Duration m.	CO_2 found l.	CO_2 added l.	CO_2 per minute found cc.	CO_2 per minute added cc.	Difference %
1	15·395	14·21	14·33	922	930	−0·9
2	15·42	14·20	14·29	920	926	−0·7
3	15·37	14·28	14·32	928	931	−0·3
4	15·39	14·32	14·31	930	929	+0·1
5	15·355	14·54	14·26	946	928	+1·9
		71·55	71·51			

Control experiment 4.

No.	Duration m.	CO_2 found l.	CO_2 added l.	CO_2 per minute found cc.	CO_2 per minute added cc.	Difference %
1	16·54	15·29	15·43	924	932	−0·9
2	15·44	14·41	14·37	933	930	+0·3
3	15·41	14·24	14·37	924	932	−0·9
4	15·44	14·27	14·34	924	928	−0·7
5	15·44	14·26	14·39	924	931	−0·8
		72·17	72·90			

According to these control experiments we have every reason to expect that the error in the respiration experiments on a working subject in which the conditions for complete mixing of the air are distinctly more favourable than in the controls will practically never exceed 1 %.

In order finally to test the accuracy with which the respiratory quotient can be determined we have made a control experiment on a human subject, doing the normal amount of work on the ergometer, while the chamber was ventilated as usual, by taking a continuous series of "intermediate samples." We cannot of course expect that the gas exchange of the subject will remain constant during the whole period covered by the samples, but as the air in the chamber is only very gradually renewed the possible changes in the composition of the air and the respiratory quotient must obviously be very gradual. Since the air expired from the subject must show the same respiratory quotient whether it be mixed with a small or a large quantity of pure air, the oscillations observed in the respiratory quotient must be due chiefly to errors in the gas analysis, while oscillations in the CO_2 increase coincident with similar oscillations in the O_2 deficit must be due to incomplete mixing. The results were as follows:

Control experiment 5.

Time	Duration seconds	CO_2 increase °/ₒₒₒ	O_2 deficit °/ₒₒₒ	R.Q.
10.16	61	65·75	70·8	0·929
	69	65·1	70·4	0·925
	68	66·0	71·1	0·928
	91	65·95	71·3	0·925
	62	65·65	70·85	0·928
	47	66·0	70·85	0·932
	75	66·2	71·3	0·929
	83	66·4	71·65	0·927
10.28	70	66·7	71·8	0·930
			Average	0·928
			Dispersion $\sigma =$	$\pm 0{\cdot}002$

The variations in the respiratory quotient correspond closely to the unavoidable errors in the gas analysis, but the percentages of CO_2 and O_2 show somewhat larger variations especially in the second and fifth sample indicating deficiencies in the mixing amounting sometimes to ½ or even 1 % of the CO_2 increase or O_2 deficit.

In the calculation of the energy metabolism from the results of the respiration experiments we have like Benedict and Cathcart [1913] used the method introduced by Zuntz and Schumburg [1901]. We have not used the original table but the latest given by Zuntz and Loewy [1913]. This table which shows the caloric value of oxygen at quotients between 0·71 and 1·00 is partly reproduced on p. 310. It differs slightly from the earlier tables. The use of this table presupposes that anabolic processes do not take place, and it refers only to the catabolism of fats and carbohydrates, assuming that the oxygen and carbon dioxide corresponding to the protein metabolism are subtracted beforehand. Like Benedict and Cathcart, Loewy [1911] and others we have made our calculations on the basis that fats and carbohydrates are exclusively catabolised. It will be necessary to estimate the error resulting from this simplification. Almost all the experiments have been made on low protein diets, but it has not been practicable to collect the urine and determine the protein metabolism.

We can assume a protein metabolism of 75 g. per day as the maximum during our experiments. This corresponds to 12 g. nitrogen or 0·5 g. per hour.

0·5 g. nitrogen per hour requires per minute 49·4 cc. oxygen and produces 0·222 Calorie, while the same quantity of oxygen would when used to burn a mixture of fat and carbohydrate produce 0·242 Calorie. The maximum error committed by disregarding the protein metabolism is therefore 0·02 Calorie or 0·3–0·4 % of the metabolism during work.

The accuracy of the technique adopted for the respiration experiments during rest has been studied and discussed by Liljestrand [1916]. The error on a 5 minute experiment may amount to about 5 % or 10 cc. CO_2 or O_2 per minute. We have made a technical error in taking the samples of expired air from the mixing vessel synchronously with the periods of ventilation. As the volume of the lungs + tubing + mixing vessel is about 6 l. a change in ventilation will not correspond to a simultaneous change in the composition of the air from which the sample is drawn, but this change will on an average take place 6 respired liters or 1 minute later. The taking of samples should therefore have been begun 1 minute after the beginning of each period and continued for 1 minute after the end of it. With an absolutely uniform respiration no error can arise from this source, but the respiration during rest is seldom absolutely uniform. The large number of double determinations made by us furnish material for a statistical study of the accuracy which w be referred to below (Appendix I, p. 346).

The muscular work was in all our experiments performed on the bicycle ergometer constructed by Krogh [1913]. The instrument was provided with automatic control of the current [Krogh, 1915, 3]. A load of 10 g. is sufficient to bring about a contact actuating the adjusting motor, and the maximum error on the determination of the load is therefore 10 g. or 1 % of the load usually employed. When work is being performed it can be observed that the adjusting motor is generally actuated for a moment about every minute, now increasing now diminishing the load. This is due to the unavoidable small irregularities in the pedalling, but these oscillations must in our opinion counterbalance each other so that the final error on the effective load will be much below 1 %.

The rate of pedalling was controlled by a metronome which could be observed by the subject through one of the windows in the chamber. We soon found that it was difficult to control the rate by sight and installed an electric bell actuated by the metronome inside the chamber. After a minute or two a certain phase in the movements of the legs is synchronous with the signal, and the rate is maintained with a minimum of mental effort.

We found that the metronome employed by us would not work with absolute constancy and in most experiments the subject has therefore employed 10 minutes during each of the experimental periods in controlling the metronome by counting and comparing with a watch. This has the further advantage of relieving somewhat the monotony of the work. The maximum variation observed in the rate of the metronome is 0·4 %.

In preliminary tests with each subject the load and rate of pedalling were adjusted to the muscular strength and the convenience of the subject. Some preferred a rate of 60 revolutions per minute, but most of the experiments were done at the rate of about 50.

The subject always began to work just after entering the chamber and worked for half-an-hour before the experiments began. We have repeatedly made determinations of 10–20 minutes duration during this introductory period, but we have found that the results were distinctly less regular than they became later and these determinations have been left out of account in the working out of the results.

We have made several separate series of experiments and after each series we have reviewed the results secured and the technique employed to find out whether by suitable changes in the arrangement we might hope to avoid some of the irregularities encountered. As this is, in our opinion, one of the most important points in the research we propose to report the experiments in the order in which they were made, to set forth the reasons for the changes in routine adopted and discuss their results.

PRELIMINARY SERIES OF EXPERIMENTS.

Our first plan was worked out in collaboration with Dr G. Liljestrand of Stockholm who took part also in this series of experiments. We would make determinations on four subjects and would act alternately as subjects ourselves. On each subject we would make a preliminary experiment which should not be included in the series. After a suitable interval the subject should take a diet consisting either chiefly of carbohydrates or chiefly of fats. In the first experiments (on J. L. and G. L.) no precautions were taken regarding protein, but later it was provided that the experimental diets should contain a minimum of protein. The diet should be taken for two consecutive days and on the morning of the third day an experiment should be made before the subject took any food. During the third day the diet should be continued and a second experiment should be made on the morning of the fourth day. Each experiment should consist of 2 hours' work with 3 half-hour periods in which the metabolism should be determined. Thereupon the subject should have a rest of several days before taking the alternative diet. We hoped by taking two days' diet before the experiments to obtain very high or respectively very low quotients. It was arranged further that in the fat periods the subjects should take a certain amount of exercise to get rid of as much glycogen as possible.

Two of the subjects should begin with the carbohydrate diet and two with the fat diet, and we hoped in this way to neutralise the possible influence of training.

The technique was during these preliminary experiments not so elaborate and precise as it became later. The automatic device on the ergometer was not regularly controlled and the metronome was assumed to work at a constant rate when once set and was controlled only at long intervals. As the rate was found to have changed distinctly we had to obtain the rates in the experiments done during the interval by interpolation. The motor driving the gas meter was not provided with a regulator and its rate varied about 3 %. The revolutions of the meter were counted by an electrical device which proved not to be absolutely reliable. The length of the experimental periods was regulated by the rate of outflow of the mercury from the sampling vessels which differed somewhat in size; they varied therefore between 22 and 32 minutes. In a few cases, which will be duly noted, these imperfections may have caused errors in the determinations but usually their influence is imperceptible.

Determinations of the metabolism during rest were not made regularly on the first two subjects (J. L. and G. L.) but the standard metabolism must be deduced from 2–3 experiments.

Experiments were made on the following subjects:

J. L. Age 46 years. Weight 67 kg. Height 171 cm. Practised in bicycling but not specially trained.

G. L. Age 31 years. Weight 51 kg. Height 166 cm. Had very little practice in bicycling.

A. K. Age 42 years. Weight 67 kg. Height 176 cm. Practised in bicycling but not trained.

R. E. Age 25 years. Weight 64 kg. Height 170 cm. In moderate training as a bicyclist.

From the notes made by the subjects the following points are selected:

J. L. Fat diet, Jan. 13th to 15th (inclusive). Work on the ergometer on the 15th and 16th. The diet consisted chiefly of pork, eggs and meat with cabbage and butter. Some claret was taken at meals. The subject took plenty of food and had no digestive trouble.

Exercise: a 2–3 hours' walk on the 13th and 14th. Very tired afterwards. Indisposition with fever and headache began on the 14th and continued throughout the period. Body temperatures: 15th morning, 37·5°, night, 38·2°; 16th, 36·7°, 37·4°; 17th, night, 39·2°; 18th, 38·0°, 37·0°; 19th, 36·0°, 37·0°. Pulse rate: 15th, 77; 17th, 90 and 19th, 58 which latter figure is normal for the subject.

Work on the ergometer on the 15th. Moderate perspiration, tired afterwards. On the 16th, profuse perspiration, work performed with great difficulty. Extremely tired during the afternoon.

Carbohydrate diet, Jan. 30th to Feb. 1st. The diet consisted chiefly of porridge, bread, cakes, sugar, honey, marmalade, green vegetables.

No particular exercise was taken.

Work on the ergometer on Feb. 1st and 2nd, performed with ease.

G. L. Carbohydrate diet, Jan. 16th to 18th, same as for J. L. A meal of cakes was taken late in the evening on the 17th and 18th. No exercise.

Work on the ergometer 18th and 19th performed without difficulty.

Fat diet, Jan. 23rd to 25th, same as for J. L.

Exercise: about two hours' walk on the 23rd and 24th.

Table II.

SERIES I. GENERAL TABLE OF EXPERIMENTS.

	Rest				Work					
Date and subject	Vent. l. per min. 0°, 760 mm.	O_2 per min. cc.	R.Q.	Cal. per min.	Length of per.[1]	O_2 per min. cc.	R.Q.	Cal. per min.	Revolut. per min.	Techn. work Cal. per min.
J. L.				*c*				*b*	*a*	
15. i.					32	1220	0·772	5·92		
					30	1256	0·756	6·07	60·2[2]	0·918
					29	1316	0·760	6·46		
16. i.					27	1256	0·767	6·08		
					24	1247[3]	0·771	6·05	60·3[2]	0·920
					22	1265	0·791	6·16		
1. ii.	4·03	218	0·77	1·055	26	1156	0·846	5·68		
	4·11	216	0·81	1·055	25	1151	0·873	5·68	61·3[2]	0·935
					26	1163	0·868	5·74		
2. ii.	3·99	203	0·81	0·995	28	1187	0·846	5·84		
	3·92	205	0·80	1·00	26	1194	0·843	5·87	61·5[2]	0·937
					28	1186	0·836	5·82		
G. L.										
18. i.					25	860	0·906	4·28		
					29	898	0·885	4·45	60·5[2]	0·645
					28	902	0·867	4·45		
19. i.					32	944	0·927	4·72		
					28	936	0·913	4·66	60·7[2]	0·647
					29	903	0·900	4·48		
25. i.	5·17	228	0·765	1·10	31	957	0·766	4·63		
	5·29	229	0·765	1·11	24	970	0·777	4·71	61·0[2]	0·650
					26	1014	0·751	4·90		
26. i.	4·80	216	0·765	1·045	28	989[4]	0·762	4·79		
	4·89	210	0·80	1·025	29	995	0·757	4·81	61·1[2]	0·651
					28	1009	0·762	4·88		
26. ii.	5·32	212	0·80	1·035	28	931	0·863	4·59		
	4·43	196	0·79	0·955	30	971	0·857	4·78	62·3	0·663
					23	954	0·833	4·68		
A. K.										
12. ii.	6·50	209	0·875	1·035	27	1053	0·896	5·22		
	6·60	213	0·87	1·05	26	1070	0·867	5·28	61·7[2]	0·940
					28	1087[5]	0·861[5]	5·36[5]		
13. ii.	6·51	215	0·88	1·065	27	1081	0·909	5·38		
	6·68	206	0·94	1·03	27	1090	0·893	5·41	61·8	0·941
					29[6]	1132	0·883	5·60		

[1] The length of the period has been given in whole minutes.

[2] Revolutions obtained by interpolation from countings of metronome on the 13th Jan. and 13th Feb. and following days.

[3] Recorded revolutions of meter 46, corrected according to the rate in the first and third period to 47. (See also notes 4 and 6.)

[4] Counter on meter failed. Number of revolutions calculated from ventilation in second and third period.

[5] The last "intermediate" sample of air was lost. As the composition of the air in the preceding samples was approximately constant the composition was assumed in accordance with these.

[6] Counter on meter was seen to fail just before the reading.

Table II *continued.*

	Rest				Work					
Date and subject	Vent. l. per min. 0°, 760 mm.	O_2 per min. cc.	R.Q.	Cal. per min.	Length of per.[1]	O_2 per min. cc.	R.Q.	Cal. per min.	Revolut. per min.	Techn. work Cal. per min.
A. K.				*c*				*b*	*a*	
19. ii.	6·96	254	0·725	1·22	28	1094[2]	0·781	5·31[2]		
	6·14	215	0·75	1·04	28	1134	0·774	5·50	61·9	0·941
					28	1135	0·755	5·49		
20. ii.	6·88	241	0·70	1·15	26	1221	0·757	5·90		
	6·91	246	0·73	1·185	26	1238	0·762	5·99	62·0	0·945
					26	1255	0·757	6·07		
1. iii.	6·18	225	0·83	1·10	22	1068	0·891	5·30		
	6·20	222	0·885	1·10	30	1122	0·870	5·54	62·4	0·950
					22	1145	0·846	5·63		
R. E.										
20. iii.	5·59	234	0·85	1·15	31	1092	0·854	5·38		
	5·44	233	0·83	1·14	30	1096	0·836	5·38	49·8	0·986
					32	1112	0·817	5·44		
25. iii.					29	1210	0·747	5·84	49·8	0·986
	6·09	290	0·73	1·395	30	1308	0·742	6·30	?	?
	5·61	276	0·71	1·32	29	1406	0·751	6·79	(57·2)[3]	(1·13)
26. iii.	5·48	258	0·745	1·245	28	1194	0·742	5·76		
	5·48	264	0·76	1·275	27	1221	0·730	5·87	49·8	0·986
					29	1250	0·738	6·02		
6. iv.	6·40	269	0·93	1·34	29	1054	0·891	5·23		
	6·05	263	0·90	1·305	26	1052	0·895	5·22	49·9	0·988
					30	1056	0·879	5·23		
7. iv.	5·71	250	0·93	1·25	30	1064	0·932	5·32		
	5·91	253	0·95	1·27	25	1086	0·918	5·41	49·9	0·988
					31	1140[4]	0·897	5·66[4]		

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[1] See note 1 on preceding page.

[2] See note 4 on preceding page.

[3] Several countings showed that the subject was not keeping time with the metronome.

[4] Duration of last period slightly uncertain. The figure for the metabolism possibly 1 % too high.

Felt very tired on the 24th.

Work on the ergometer 25th and 26th performed with considerable difficulty. After the work the subject was very tired.

A. K. Carbohydrate diet, Feb. 10th to 12th. Food: potatoes, flour, bread, cakes, marmalade, sugar. A meal of cakes and marmalade with a little alcohol taken late (about 11 p.m.) on the 11th and 12th. No special exercise.

Work on the ergometer 12th and 13th performed with ease. No perspiration.

Fat diet, Feb. 17th to 19th. Very fat bacon, cream, butter, eggs, and cabbage. Plenty of food taken on the 17th and 18th. Less on the 19th. Some diarrhoea on the 18th.

Exercise: 3½ hours' walk (about 18 km.) on the 18th. Felt tired afterwards.

Work on the ergometer 19th performed with some difficulty. Rather tired afterwards. On the 20th work carried through with extreme difficulty. Very tired for several hours afterwards.

R. E. Fat diet, March 22nd to 25th. Food: fat bacon, butter, cream, cabbage. Three meals a day. Felt hungry between meals

Exercise: 1 hour's walk and a little gymnastics each day.

Work on the ergometer 25th and 26th performed without difficulty.

Carbohydrate diet, April 4th to 6th. Food: bread, cakes, apples, potatoes and green peas. No special exercise.

Had very little sleep between the 5th and the 6th.

Work on the ergometer on the 6th. Felt tired and sleepy. Work appeared difficult. 7th, work easier but apparently not easier than on the fat diet.

An inspection of the columns R.Q. and Cal. in the general table shows an unmistakeable tendency for the amount of energy, expended to perform a practically constant amount of muscular work, to vary inversely as the quotient, which means that the energy value of fat and carbohydrate for work is not the same. The value of fat is smaller than that of carbohydrate.

The difference in value for muscular work of fat and carbohydrate can be expressed quantitatively either as a difference in percentage muscular efficiency or as a difference in the number of Calories expended to perform 1 Calorie of external work. Representing by a the output of external work in Calories per minute, by b the total amount of energy expended per minute, while doing the work, and by c the energy output per minute during rest we have the percentage "gross efficiency" $\frac{100a}{b}$ and the corresponding "net efficiency" $\frac{100a}{b-c}$, while the corresponding expenditure of Calories per unit work are gross $\frac{b}{a}$ and net $\frac{b-c}{a}$. There is a general agreement that valid comparisons can only be obtained by using "net" values, but certain differences of opinion exist about the most correct definitions for a and c.

Lindhard [1915] has shown in detail that the amount of work recorded by a bicycle ergometer is considerably lower than the total amount actually performed in riding. The real efficiency is therefore greater than the apparent or "technical" efficiency obtained from the amount of work directly recorded. Since, however, we have to deal with differences only it does not much matter for our purposes whether the efficiencies calculated by us are true or only technical efficiencies, provided we are justified in assuming that there is a constant or approximately constant relation between the technical and the true efficiency. It has been shown by Lindhard [1915] that the relation between the true and the technical efficiency varies with the rate of pedalling and also to a certain extent with the load, but we have every reason to believe that when both the load and the rate are kept constant throughout each series of determinations the use of technical efficiencies for comparison purposes will give correct results.

A further point of difficulty and controversy in calculating efficiencies or expenditure of Calories per unit work is the choice of a proper value for c, the "base line" of the work. Benedict and Cathcart [1913] have made calculations of efficiencies from several different base lines, viz. complete rest, rest in a sitting posture on the ergometer, riding on an ergometer without load and riding on an ergometer which was revolved by a motor while the legs of the subject followed the motion passively. Lindhard [1915] has criticised these base lines and shown that complete rest and rest in the position in which the work is performed furnish the most reliable base lines. In our case we must expect that any difference between the value of carbohydrates and fats will exercise its influence equally upon all kinds of muscular work and also on the work of maintaining a certain posture on the ergometer, and it follows therefore that we must take complete rest as our logical base line.

The question remains as to whether the rest experiments of each day should be used for combination with the work experiment of the same day or whether a large number of rest experiments should be averaged and the average standard metabolism used as base line for all the work experiments. Lindhard [1915] has pointed out that if the variation in the rest experiments is purely accidental there is no reason to suppose that the same accidental factors (*e.g.* slight movements of the subject, small technical errors in the determination) will influence the work experiments of the same day in the same direction, and it will therefore be safer and give more correct results to average all the available determinations made during rest. In our experiments it is possible, though *a priori* not very probable, that the variations in diet may have an influence upon the resting metabolism. If that should be the case rest experiments on a certain diet should be used as base line for work experiments on the same diet.

In the above tables the rest experiments are too few in number to decide whether the diet has any influence or not upon the standard metabolism, though there is in the experiments on A. K. and R. E. some indications of a slightly increased metabolism when the quotient is very low. We have therefore averaged the rest experiments done on each subject and used the averages as base lines c in the calculations mentioned above.

When we began working out the results of this research we calculated "net efficiencies" $\frac{100a}{b-c}$ in accordance with the principles indicated above, but we found later that the reciprocal values $\frac{b-c}{a}$ (expenditure of energy per unit work) were better suited for the comparisons between the value of fat and carbohydrate. What we want to find is the difference in value between fat and carbohydrate or the waste of energy resulting from the combustion of fats. Putting $b - c = d$ we have, when fats alone are the source of energy during muscular work, the expenditure of energy per unit work $e_F = \frac{d_F}{a}$ and for carbohydrates $e_C = \frac{d_C}{a}$. The difference between these figures $e_F - e_C = w$ represents the waste of energy from fat and $\frac{100w}{e_F}$ the percentage waste of energy.

As we are unable to obtain experimentally a catabolism exclusively of fat (R.Q. = 0·71) or exclusively of carbohydrate (R.Q. = 1·00) and may obtain all possible quotients between these limits it becomes necessary to make out the quantitative relation between the respiratory quotient and the relative amounts of fat and carbohydrate catabolised. Table III, which is calculated from the corresponding table of Zuntz, shows for quotients varying from 0·71 to 1·00 the relative amounts of energy derived from carbohydrate and fat respectively.

Table III.

R.Q.	Energy value of 1 l. O_2 Cal.	Cal. from carbohydrate	Cal. from fat	Per cent. energy from fat	$\frac{100\,(1-\text{R.Q.})}{1{\cdot}00-0{\cdot}71}$
0·71	4·795	0	4·795	100	100
0·75	4·829	0·647	4·182	86·6	86·3
0·80	4·875	1·530	3·345	68·6	69·0
0·85	4·921	2·411	2·510	51·0	51·8
0·90	4·967	3·295	1·672	33·65	34·5
0·95	5·012	4·175	0·837	16·7	17·2
1·00	5·058	5·058	0	0	0

The calculation shows that the percentage amount of energy derived from fat is approximately a straight line function of the respiratory quotient and can be expressed by the formula $\frac{100\,(1-\text{R.Q.})}{1{\cdot}00-0{\cdot}71}$.

If, therefore, we take as our theoretical basis the hypothesis that the energy output per unit work can be expressed as the sum of a certain amount of energy derived from carbohydrate, which can be utilised "directly," and another amount derived from fat, which can only be utilised after a "conversion" involving the loss of a definite fraction of the energy, we can deduce as consequences of this hypothesis (1) that the curve expressing the relation between the energy output per unit work $\frac{d}{a} = e$ as ordinate and the respiratory quotient as abscissa should be a straight line and (2) that the percentage waste of energy from fat should be the same for different subjects.

The percentage waste of energy from fat $\frac{100\,(e_F - e_C)}{e_F}$ can be found from any two points of the curve by computation and graphically by extrapolation of the curve to the quotients 0·71 and 1·00. When we have the energy per unit work at the quotient q_1 to be e_1 and at the quotient q_2 to be e_2 we get

$$e_F - e_C = \frac{e_1 - e_2}{q_2 - q_1}\,0{\cdot}29 \text{ and } e_F = e_1 + \frac{e_1 - e_2}{q_2 - q_1}\,(q_1 - 0{\cdot}71).$$

In Table IV the determinations on each subject are arranged in series according to the quotients. By means of the dates and numbers given each period can be referred back to the general table. In the figures 2–5 the results have been plotted with the quotients as abscissae and the expenditure of energy per unit work e as ordinates. The first periods of each experiment have been denoted by ×, the second by • and the third by o. It is seen that the third periods deviate in certain cases and notably at low quotients from

Table IV.

Date and number	R.Q. work	Work Cal.	Rest Cal.	Difference	Cal. per unit of work	Technical work Cal.	Deviation from curve
J. L.		*b*	*c*	*d*	*e*	*a*	δ
15. i. 2	·756	6·07	1·03	5·04	5·49	0·918	
15. i. 3	·760	6·46		5·43	5·91	0·918	
16. i. 1	·767	6·08		5·05	5·49	0·920	
16. i. 2	·771	6·05[1]		5·02	5·46	0·920	
15. i 1	·772	5·92		4·89	5·33	0·918	
16. i. 3	·791	6·16		5·13	5·58	0·920	
2. ii. 3	·836	5·82		4·79	5·12	0·937	
2. ii. 2	·843	5·87		4·84	5·17	0·937	
1. ii. 1	·846	5·68		4·65	4·97	0·935	
2. ii. 1	·846	5·84		4·81	5·14	0·937	
1. ii. 3	·868	5·74		4·71	5·04	0·935	
1. ii. 2	·873	5·68		4·65	4·97	0·935	
G. L.							
25. i. 3	·751	4·90	1·04	3·86	5·94	0·650	+0·2
26. i. 2	·757	4·81		3·77	5·79	0·651	+0·07
26. i. 1	·762	4·79		3·75	5·76	0·651	+0·05
26. i. 3	·762	4·88		3·84	5·90	0·651	+0·19
25. i. 1	·766	4·63		3·59	5·52	0·650	−0·18
25. i. 2	·777	4·71		3·67	5·64	0·650	−0·03
26. ii. 3	·833	4·68		3·64	5·49	0·663	−0·03
26. ii. 2	·857	4·78		3·74	5·64	0·663	+0·18
26. ii. 1	·863	4·59		3·55	5·36	0·663	−0·08
18. i. 3	·867	4·45		3·41	5·29	0·645	−0·15
18. i. 2	·885	4·45		3·41	5·29	0·645	−0·10
19. i. 3	·900	4·48		3·44	5·32	0·647	−0·03
18. i. 1	·906	4·28		3·24	5·02	0·645	−0·32
19. i. 2	·913	4·66		3·62	5·60	0·647	+0·28
19. i. 1	·927	4·72		3·68	5·69	0·647	+0·41
						Sum	+0·47
A. K.							
19. ii. 3	·755	5·49	1·10	4·39	4·67	0·941	−0·25
20. ii. 1	·757	5·90		4·80	5·08	0·945	+0·16
20. ii. 3	·757	6·07		4·97	5·26	0·945	+0·34
20. ii. 2	·762	5·99		4·89	5·18	0·945	+0·28
19. ii. 2	·774	5·50		4·40	4·68	0·941	−0·19
19. ii. 1	·781	5·31[1]		4·21	4·48	0·941	−0·37
1. iii. 3	·846	5·63		4·53	4·77	0·950	+0·09
12. ii. 3	·861	5·36		4·26	4·53	0·940	−0·11
12. ii. 2	·867	5·28		4·18	4·45	0·940	−0·18
1. iii. 2	·870	5·54		4·44	4·68	0·950	+0·06
13. ii. 3	·883	5·60		4·50	4·78	0·941	+0·19
1. iii. 1	·891	5·30		4·20	4·42	0·950	−0·14
13. ii. 2	·893	5·41		4·31	4·58	0·941	+0·02
12. ii. 1	·896	5·22		4·12	4·38	0·940	−0·17
13. ii. 1	·909	5·38		4·28	4·55	0·941	+0·03
						Sum	−0·24
R. E.							
26. iii. 2	·730	5·87	1·27	4·60	4·67	0·986	+0·02
26. iii. 3	·738	6·02		4·75	4·82	0·986	+0·20
26. iii. 1	·742	5·76		4·49	4·55	0 986	−0·06
25. iii. 1	·747	5·84		4·57	4·63	0·986	+0·04
20. iii. 3	·817	5·44		4·17	4·23	0·986	−0·12
20. iii. 2	·836	5·38		4·11	4·17	0·986	−0·11
20. iii. 1	·854	5·38		4·11	4·17	0·986	−0·05
6. iv. 3	·879	5·23		3·96	4·01	0·988	−0·13
6. iv. 1	·891	5·23		3·96	4·01	0·988	−0·09
6. iv. 2	·895	5·22		3·95	4·00	0·988	−0·08
7. iv. 3	·897	5·66		4·39	4·44	0·988	+0·36
7. iv. 2	·918	5·41		4·14	4·19	0·988	+0·19
7. iv. 1	·932	5·32		4·05	4·10	0·988	+0·15
						Sum	+0·32

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[1] Slightly uncertain.

the rest and give higher values for *e*. This must be ascribed to the fatigue which was repeatedly very pronounced.

It is obvious that the experiments are too few and too discordant to allow of a quantitative estimate of the energy waste from fat. It is possible to draw rather different curves which will suit the determinations at least as well as the straight lines which we have drawn. In the case of J. L. we have not drawn any curve. On account of his illness during the fat period we think it better to disregard the experiments made on this subject.

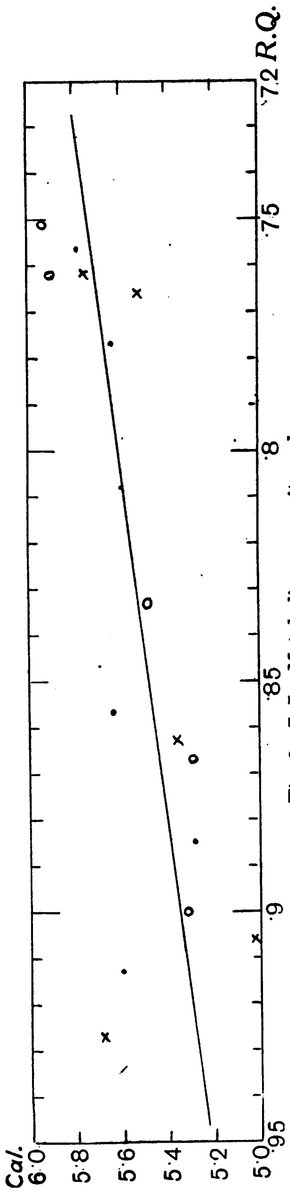

Fig. 2. J. L. Metabolism per unit work.

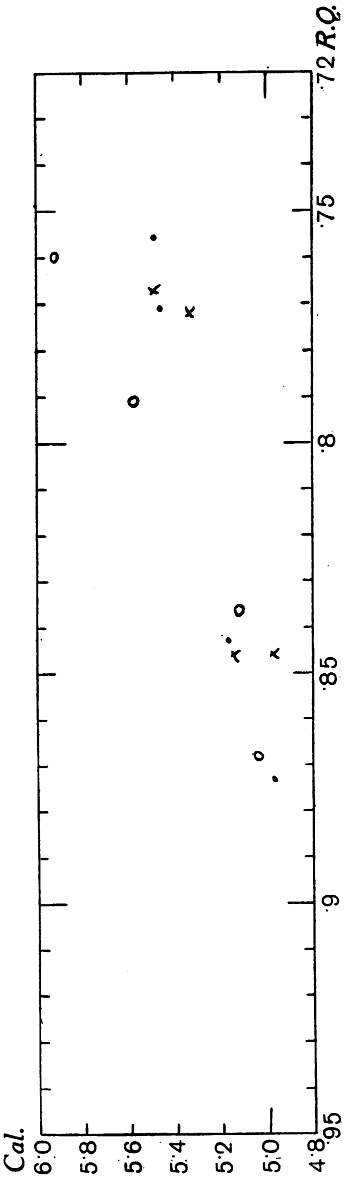

Fig. 3. G. L. Metabolism per unit work.
× First experimental period, • second, o third period.

We have measured the vertical distance (in Cal. per unit work) of each point in Figs. 2–5 from the curve to which it belongs and these distances have been given in the last column of Table IV as the deviation from the curve (δ). If the curves were correctly drawn and all the determinations were of equal weight the algebraic sum of these deviations should be 0. From the deviations given the dispersion (σ) or "standard deviation" has been calculated for each curve according to the formula $\sigma = \sqrt{\frac{\Sigma\delta^2}{n-1}}$ and we have further

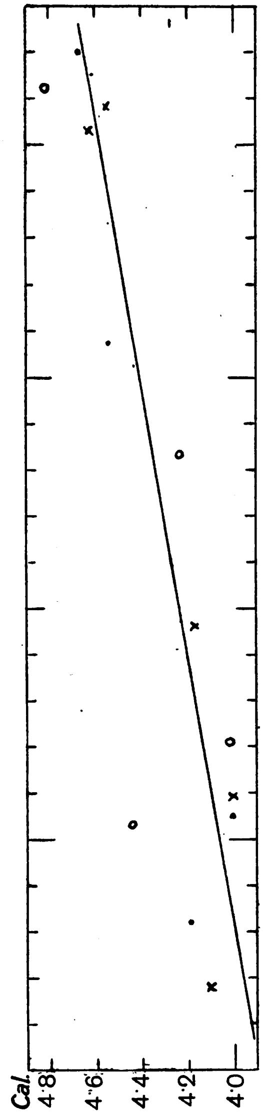

Fig. 4. A. K. Metabolism per unit work.

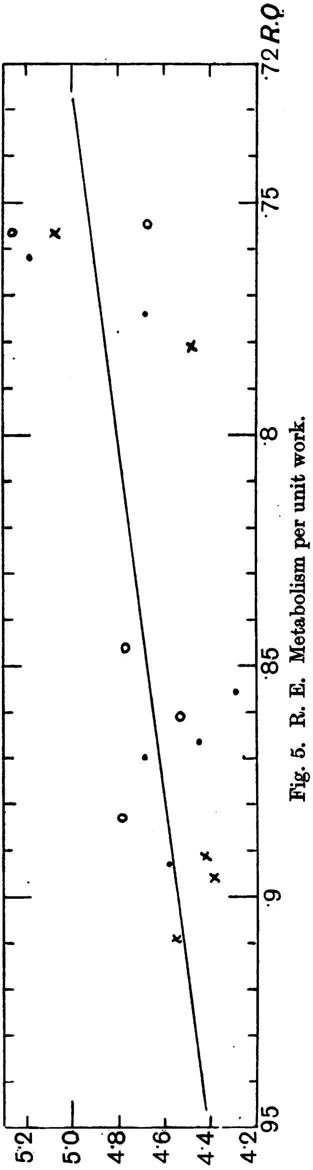

Fig. 5. R. E. Metabolism per unit work.
x First experimental period, • second, o third period.

calculated the dispersion in per cent. of the average metabolism per unit work $e_{0·85}$. We find

Table V.

	G. L.	A. K.	R. E.
n	15	15	13
$e_{0·85}$ Cal.	5·48	4·17	4·24
σ Cal.	0·20	0·21	0·155
σ %	3·6	4·4	3·7

When the waste of energy is calculated from the straight lines drawn we obtain the following results:

Table VI.

	G. L.	A. K.	R. E.
e_F Cal.	5·84	5·04	4·72
e_C Cal.	5·09	4·28	3·72
Waste from fat Cal.	0·75	0·76	1·00
Waste %	12·9	15·1	21·2
Efficiency on carbohydrate $\frac{100}{e_C}$	19·6	23·4	26·8

The low efficiency of the subject G. L. is probably to be explained by his want of training as a bicycle rider.

The results are obviously of very limited value quantitatively and it should be specially pointed out that the exercise taken during the fat periods and not during the carbohydrate periods may constitute a systematic error.

SECOND SERIES OF EXPERIMENTS.

As a result of the preliminary series of experiments several improvements were introduced into the technique and routine. The purely technical improvements have been alluded to above. As we ourselves were evidently not suitable as subjects, partly because our other duties made it impossible for us to lead an absolutely uniform life during the experimental period, we resolved to secure the assistance of an intelligent student who should be, as far as possible, a trained athlete both generally and as a bicyclist, hoping thereby to minimise the influence of training. We would further shorten the dietary periods and make a larger number of determinations also at intermediate quotients to obtain data for determining the form of the efficiency curve. The length of the experimental periods should be somewhat reduced to minimise the influence of fatigue.

We were very fortunate in securing the services as subject of Mr Olaf Hansen a student of languages and gymnastics who possessed all the qualifications desired.

His age was 23 years, weight 80 kg. and height 179 cm. He is a trained athlete and was in good form at the time but lately he had practised bicycling to a very limited extent only. He was carefully instructed with regard to the experimental routine, and the most suitable load on the machine and rate of pedalling were found by trials. No hint whatever was given of the subjective results expected from the different diets, but the subject was asked to make notes both of the food eaten and of the influence of the work upon his well-being and physical fitness. From these notes, which gave very full information, we have made the following extract.

From May 6th (1917) to 11th mixed diet, poor in protein. Went for a walk of 7 km. on the 6th. Otherwise no exercise. Work on the ergometer 7th, 8th, 10th and 11th. Not the least tired after each day's work. Weight on the 9th, 80 kg.

Carbohydrate diet 12th to 18th. Three meals a day on the experiment days, otherwise four. Last meal in the evening between 7 and 10 o'clock. Food chiefly porridge, bread, potatoes and other vegetables, sugar, honey, marmalade and fruit. Exercise: walk of 7 km. on the 13th, cycling about 17 km. on the 17th. This tour was taken in the afternoon after work on the ergometer in the morning. No fatigue whatever was felt. Work on the ergometer 14th, 15th, 16th and 17th performed with very slight perspiration and not in the least fatiguing. The work was felt to be easier than in the preceding week and on the 14th the subject asked if the load had not been diminished. Weight on the 16th, 79·5 kg.

Fat diet 19th to 24th. On the experiment days a cup of tea without sugar or milk was taken in the morning and large meals at 12 noon and 7 night. Cocoa and cream in the afternoon at 3. Food: ham, eggs, bacon, butter, cream and green vegetables. Exercise: cycling about 38 km. on the 20th in slow time, 25 km. on the 23rd in the evening; felt tired in the legs especially during first half of the tour. No experiments on these days. Cycling about 9 km. on the 24th, in the evening after an experiment. Felt very tired during the whole week and could not do the usual amount of mental work. Work on the ergometer 21st and 22nd. Perspiration profuse, extremely tired during the latter part of the day's work and afterwards and had to rest during most of the afternoons. Took some bread in the evening of the 22nd and the morning of the 23rd. Work again on the 24th and 25th. Profuse perspiration but not quite so tired as on the preceding days. Weight on the 25th, 76·5 kg. The technical work on the ergometer was 1·12 Cal. per minute throughout.

A simple inspection of the general table shows:

1. Somewhat irregular variations of the standard metabolism with a distinct tendency to become higher during the last days of the period when the quotient was very low.
2. The correlation between the quotient and the total metabolism during work is marked when the changes from day to day are considered, but it is unmistakable at the same time that the metabolism at a constant quotient becomes gradually lower during the period. We take this lowering to be due to training.

In order to find the most reliable numerical expression for the function studied we have examined and combined the experimental results in several ways.

Table VII.

General Table of Experiments.

	Rest				Work					
Date	Ventilation l. per min.	O_2 per min. cc.	R.Q.	Cal. per min.	Length of period	O_2 per min. cc.	R.Q.	Cal. per min.	Revolut. per min.	Tech. work Cal. per min.
O.H. I				c				b		a
1917	5·93	261	0·82	1·275	30	1399	0·836	6·86	49·4	1·123
8. v.	5·93	258	0·82	1·265	26	1393	0·829	6·83		
					29	1405	0·818	6·87		
10. v.	6·05	290	0·82	1·42	31	1395	0·814	6·82	49·4	1·123
	6·44	292	0·81	1·425	29	1395	0·803	6·81		
					32	1395	0·810	6·82		
11. v.	5·97	303	0·79	1·475	24	1365	0·830	6·69	49·4	1·123
	6·35	296	0·84	1·455	25	1347	0·835	6·61		
					23	1375	0·814	6·72		
14. v.	6·34	276	0·92	1·375	24	1353	0·864	6·68	49·4	1·123
	6·21	258	0·96	1·295	24	1336	0·870	6·60		
					23	1320	0·876	6·53		
15. v.	6·24	291	0·945	1·455	24	1303	0·929	6·50	49·4	1·123
	6·28	279	0·945	1·395	24	1312	0·922	6·54		
					23	1306	0·919	6·51		
17. v.	6·16	280	0·92	1·395	24	1276	0·904	6·34	49·4	1·123
	6·43	272	0·99	1·375	25	1301	0·896	6·45		
					23	1314	0·881	6·50		
18. v.	5·95	276	0·93	1·38	23	1337	0·839	6·56	49·4	1·123
	6·06	286	0·89	1·42	24	1366	0·817	6·68		
					24	1375	0·799	6·70		
21. v.	5·77	300	0·71	1·435	23	1419	0·731	6·82	49·3	1·120
	5·70	307	0·705	1·47	24	1427	0·715	6·85		
					22	1434	0·714	6·88		
22. v.	5·94	291	0·71	1·395	23	1398	0·717	6·71	49·3	1·120
	6·25	291	0·75	1·405	25	1396	0·709	6·70		
					23	1413	0·719	6·78		
24. v.	6·22	324	0·71	1·55	22	1363	0·735	6·56	49·4	1·123
	6·35	317	0·73	1·53	25	1387	0·734	6·63		
					23	1325[1]	0·765[1]	6·42		
25. v.	5·61	292	0·69	1·395	22	1384	0·744	6·68	49·4	1·123
	5·78	304	0·72	1·46	26	1387	0·731	6·68		
					22	1385	0·746	6·68		

[1] The exceptionally large increase in quotient and decrease in metabolism must arouse suspicion but no reason can be found for doubting the technical accuracy of the results.

The determinations of the resting metabolism have been plotted in Fig. 6 as ordinates with the dates as abscissae. The curve drawn shows that the average standard metabolism remained practically constant except during the last few days when the quotients were very low. We observed in the earlier experiments on A. K. and R. E. that with a low quotient the standard metabolism shows a tendency to rise and we may add that this is borne out also by the later series of determinations given below. We have therefore no hesitation in concluding that the standard metabolism remained constant during the whole period except for the variations correlated with the variations in quotient. The determinations have accordingly been plotted a second time (Fig. 7) with the quotient as abscissa and a curve drawn to represent them.

We have now the material to combine the standard metabolism *c* with the metabolism during work *b* in three different ways. We can either:

1. Use the determination of *c* for each particular day in combination with the determinations of *b* for the same day.

2. Use the average value for *c* from all the determinations in combination with each *b*.

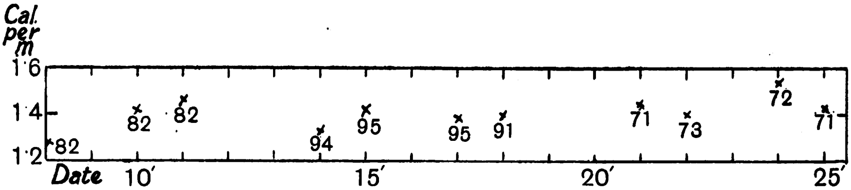

Fig. 6. O. H. Standard metabolism. Variations from day to day. Figures: respiratory quotients.

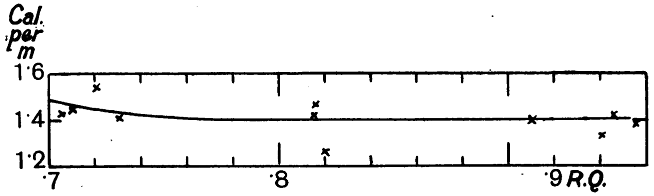

Fig. 7. O. H. Standard metabolism. Variation with respiratory quotient.

3. Use for combination with each *b* a value for *c* selected from the curve Fig. 7, on the principle that the respiratory quotient during rest is the same as that during work. Though this latter assumption might seem to be somewhat arbitrary an inspection of Table VII shows unmistakably that there is a very close connection between the quotient during rest and the quotient during work just afterwards, the difference being seldom more than a few per cent.[1]

The alternatives 1 and 2 have been tested in a preliminary calculation of the efficiency at varying quotients the results of which are given in the curves, Fig. 8[2]. When the standard metabolism *c* found on a particular day depended mainly on some cause which would act also during the work on the same day the combination of the values obtained each day ought to give the most concordant results, but if the variations in the *c* values are purely accidental and have nothing to do with the results obtained in the corresponding work

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[1] This point will be discussed in detail below. Appendix III, p. 354.

[2] In these curves corrections have been introduced for the effect of training according to the principles given below, p. 320.

experiments (which have likewise their own accidental variations) the elimination of the accidental variations of the *c* values ought to diminish the variability of the final results.

It is seen at a glance that the individual determinations of efficiency show considerably larger deviations from the curve when the *c* values for each day are utilised than when they are replaced by the average value. A numerical expression for the difference is obtained when the dispersions of the two sets of values are calculated. For Curve I we find a dispersion $\sigma = 0{\cdot}38$ and for Curve II $\sigma = 0{\cdot}31$.

As it might be thought that the correction for the effect of training applied to the curves, Fig. 8, might influence the result of the comparison we have made a similar comparison between the uncorrected values for the expenditure of energy per unit work, using in one case the *c* values for each day and in the other the *c* values taken from the curve, Fig. 7, according to the third alternative. The results of this comparison are shown in Fig. 9. It is obvious that the *c* values taken from the curve make the final results much more uniform than those obtained day by day, and in our opinion this furnishes conclusive evidence in favour of discarding the single determinations and using either the simple average of a number of determinations or a graph in which the accidental variations have been smoothed out[1]. In the final calculations we have also rejected the second alternative (an average *c*), because it would increase the apparent metabolism per unit work at low quotients, and the later experiments show that there is no reason to doubt the reality of the observed increase in resting metabolism at low quotients.

The curves, Fig. 9, show an increase in *e* (energy per unit work) when the quotient falls from 0·93 to 0·8, but a slight decrease on the further fall from 0·8 to 0·71. This, as well as certain other irregularities, is due in the main to the fact that the metabolism, when determined at an approximately constant quotient, is evidently decreasing during the 18 days occupied by the series of experiments. In order to examine this decrease we have arranged Table VIII giving for each experimental day the respiratory quotient for the three determinations during work, taken together, the corresponding Calories per minute (*b*), the metabolism during rest *c* as found from the curve, Fig. 7, by means of the quotient in column 1, the difference $b-c$, the amount of technical work *a* and the metabolism per unit work *e*. The figures in this latter column have been plotted in Fig. 10 as ordinates with the dates as abscissae. All the results corresponding to quotients between 0·78 and 0·88 have been marked by a × and the others by a small •, and it has been attempted to draw a curve representing the variation of the metabolism with time at a quotient of about 0·83. This curve is called the "training curve" and is taken to represent the change in metabolism per unit work depending, as we

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[1] We have also in the later series of experiments made similar comparisons between average and individual *c* values with the same result as that illustrated above, but we do not think it necessary to reproduce them.

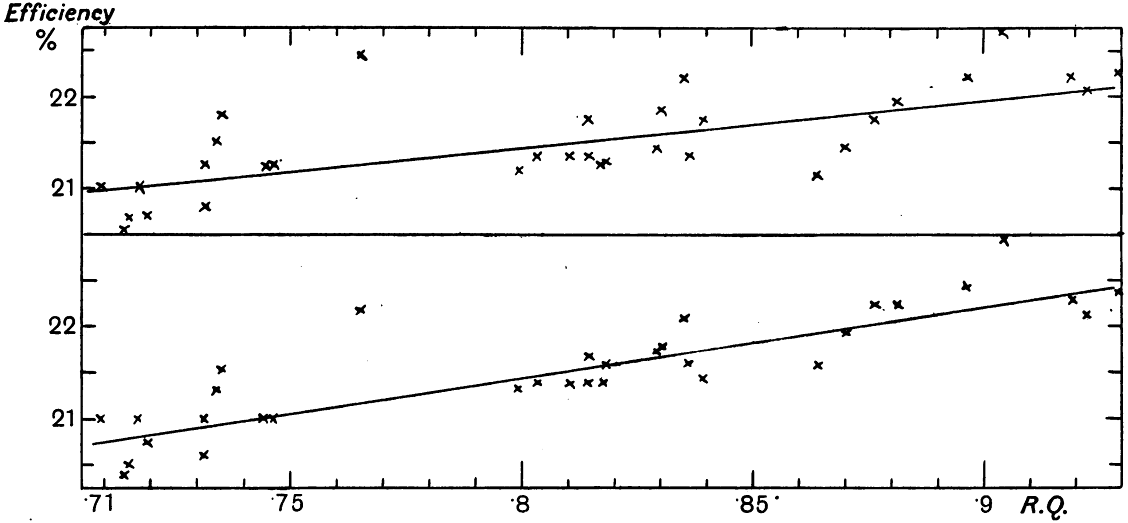

Fig. 8. O. H. Efficiency of muscular work.
Lower curve: average value for standard metabolism. Upper curve: day to day values for standard metabolism.

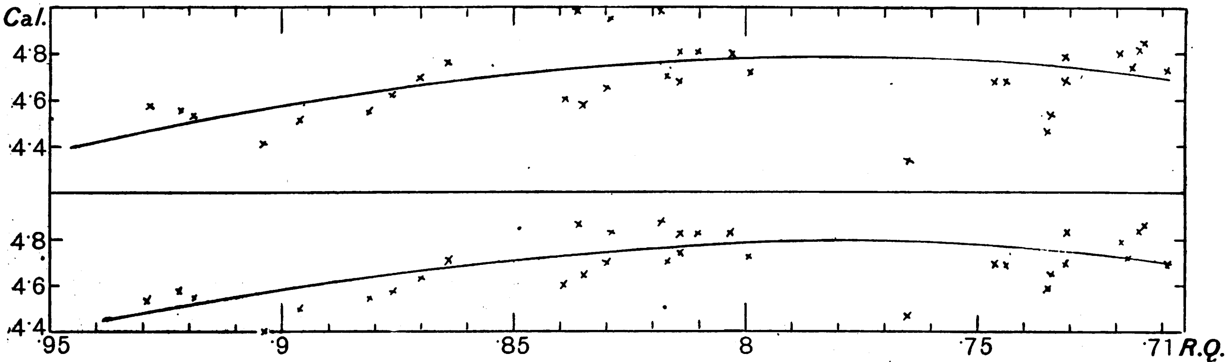

Fig. 9. O. H. Metabolism per unit work.
Lower curve: values for standard metabolism from curve, Fig. 7. Upper curve: day to day values for standard metabolism.

think, upon the increasing training of the subject. Unfortunately we have no determinations at suitable quotients after the 18th and for the last week we have had therefore to extrapolate the training curve as best we might. We have thought it safest to assume a very slight influence of the training after that date.

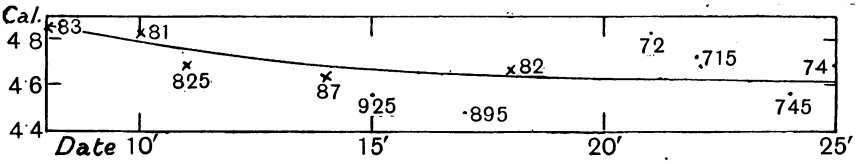

Fig. 10. O. H. Metabolism per unit work. Influence of training.

At the end of the experimental period we assume that the metabolism per unit work at a quotient of 0·83 would have decreased to 4·62 Cal. as shown by the curve, and by finding from the curve the corresponding figure for each experimental day and dividing 4·62 by the same we have obtained a series of figures, increasing from 0·950 on the 8th to 1·000 on the 22nd to 25th, given in the last column of Table VIII as the "correction for training." In the final Table IX the effect of the training has been eliminated by multiplying each *e* value by the correction coefficient for the day.

Table VIII.

Date 1917	R.Q.	Average Cal. during work *b*	Cal. at rest from curve *c*	Difference *d*	Technical work *a*	Cal. per unit of work *e*	Training correction (from Fig. 10)
8. v.	·83	6·85	1·40	5·45	1·123	4·85	·950
10. v.	·81	6·82	1·40	5·42	1·123	4·83	·967
11. v.	·825	6·67	1·40	5·27	1·123	4·69	·973
14. v.	·87	6·60	1·40	5·20	1·123	4·63	·985
15. v.	·925	6·52	1·40	5·12	1·123	4·56	·989
17. v.	·895	6·43	1·40	5·03	1·123	4·48	·993
18. v.	·82	6·65	1·40	5·25	1·123	4·67	·996
21. v.	·72	6·85	1·44	5·41	1·120	4·83	·998
22. v.	·715	6·73	1·45	5·28	1·120	4·72	1·000
24. v.	·745	6·54	1·41	5·13	1·123	4·57	1·000
25. v.	·74	6·68	1·41	5·27	1·123	4·69	1·000

We are fully aware that objections can be raised against this method of attempting an elimination of the training effect. We must admit of course that the training curve as drawn is more or less arbitrary, but we have convinced ourselves that even if the training curve is drawn differently from the one we have adopted in any way compatible with the actual experiments on which it must be based, the resulting effect on the final curve will be very slight.

It must be conceded further that the effect of training is not necessarily the same at all quotients. This point will be touched upon below, p. 334.

Table IX.

Date and number	R.Q.	Cal. work	Cal. obs.	Rest from curve	Difference		Calories per unit work			Deviation from curve δ
		b	c_I	c_{II}	d_I	d_{II}	e_I	e_{II}	e_{II} corrected	
May 1917										
22 2	·709	6·70	1·40	1·45	5·30	5·25	4·73	4·69	4·69	−·10
21 3	·714	6·88	1·45	1·43	5·43	5·45	4·85	4·865	4·855	+·075
21 2	·715	6·85	1·45	1·43	5·40	5·42	4·82	4·84	4·83	+·05
22 1	·717	6·71	1·40	1·42	5·31	5·29	4·74	4·72	4·72	−·055
22 3	·719	6·78	1·40	1·42	5·38	5·36	4·80	4·79	4·79	+·02
21 1	·731	6·82	1·45	1·40	5·37	5·42	4·79	4·84	4·83	+·08
25 2	·731	6·68	1·43	1·40	5·25	5·28	4·68	4·70	4·70	−·05
24 2	·734	6·63	1·54	1·40	5·09	5·23	4·54	4·66	4·66	−·085
24 1	·735	6·56	1·54	1·40	5·02	5·16	4·47	4·60	4·60	−·14
25 1	·744	6·68	1·43	1·40	5·25	5·28	4·68	4·70	4·70	−·03
25 3	·746	6·68	1·43	1·40	5·25	5·28	4·68	4·70	4·70	−·025
24 3	·765	6·42	1·54	1·40	4·88	5·02	4·34	4·47	4·47	−·225
18 3	·799	6·70	1·40	1·40	5·30	5·30	4·72	4·72	4·70	+·06
10 2	·803	6·81	1·42	1·40	5·39	5·41	4·80	4·82	4·66	+·02
10 3	·810	6·82	1·42	1·40	5·40	5·42	4·81	4·825	4·665	+·04
10 1	·814	6·82	1·42	1·40	5·40	5·42	4·81	4·825	4·665	+·05
11 3	·814	6·72	1·47	1·40	5·25	5·32	4·68	4·74	4·61	±·00
18 2	·817	6·68	1·40	1·40	5·28	5·28	4·70	4·70	4·68	+·07
8 3	·818	6·87	1·27	1·40	5·60	5·47	4·99	4·87	4·625	+·015
8 2	·829	6·83	1·27	1·40	5·56	5·43	4·95	4·84	4·60	+·01
11 1	·830	6·69	1·47	1·40	5·22	5·29	4·65	4·71	4·58	−·01
11 2	·835	6·61	1·47	1·40	5·14	5·21	4·58	4·64	4·515	−·065
8 1	·836	6·86	1·27	1·40	5·59	5·46	4·98	4·86	4·615	+·035
18 1	·839	6·56	1·40	1·40	5·16	5·16	4·60	4·60	4·58	±·00
14 1	·864	6·68	1·34	1·40	5·34	5·28	4·76	4·705	4·63	+·095
14 2	·870	6·60	1·34	1·40	5·26	5·20	4·69	4·63	4·56	+·04
14 3	·876	6·53	1·34	1·40	5·19	5·13	4·62	4·57	4·50	−·015
17 3	·881	6·50	1·39	1·40	5·11	5·10	4·55	4·54	4·51	+·005
17 2	·896	6·45	1·39	1·40	5·06	5·05	4·51	4·50	4·47	−·01
17 1	·904	6·34	1·39	1·40	4·95	4·94	4·41	4·40	4·37	−·10
15 3	·919	6·51	1·43	1·40	5·08	5·11	4·53	4·55	4·50	+·055
15 2	·922	6·54	1·43	1·40	5·11	5·14	4·55	4·58	4·53	+·09
15 1	·929	6·50	1·43	1·40	5·13	5·10	4·57	4·54	4·49	+·06
									Sum	−·035

In Table IX all the determinations have been arranged in the order of increasing quotients and in the last column but one the *e* values are corrected for training by means of the figures given in Table VIII. These corrected *e* values have been plotted in Fig. 11, which shows very distinctly the regular variation of the expenditure of energy per unit work with the respiratory quotient. It should be noted that the determinations number 3 which are marked o are on the whole slightly above the curve probably on account of fatigue. The determination R.Q. = 0·765 (No. 3, May 24th) forms a very striking exception to this rule and deviates from all the rest in that the third period shows a marked rise in quotient and a great fall in metabolism. As pointed out above (Table VII, note 1) there is no reason to doubt the technical accuracy of this determination.

In the last column of Table IX are given the deviations of the determinations from the curve. Their number is 33 and the dispersion works out as $\sigma = 0{\cdot}072$ Cal. or 1·55 % of the average metabolism $e_{0\cdot 85} = 4{\cdot}56$ Cal., a very striking improvement on the results of the preliminary series.

The straight line drawn corresponds to an $e_F = 4{\cdot}79$ Cal. and $e_C = 4{\cdot}32$ Cal. The waste of energy from fat is therefore $w = 0{\cdot}47$ Cal. or 9·8 %.

THIRD SERIES OF EXPERIMENTS.

The second series of determinations would have been quite satisfactory if the curve of training and the corrections based upon this curve had not been a little uncertain, and we resolved therefore to change the routine so as to insure the best possible data from which to construct a curve of training and at the same time to make the influence of the training as uniform as possible throughout the series. This end we hoped to attain by making determinations each day on the same subject during a period of three weeks and letting the subject undergo repeated changes of diet from carbohydrate to fat and *vice versa* beginning and ending the series on a mixed diet and effecting the changes through the interpolation of one day's mixed diet.

The experiments of this series were carried out in January and February 1918 on Mr A. Möller Nielsen (age 24 years, height 174·5 cm.) a student of languages and gymnastics who kindly undertook to act as a subject and carried out his part of the work very carefully. From his notes which were not so elaborate as those of O. H. we give the following essential points.

Jan. 28th to 30th, ordinary mixed diet, poor in protein. Work on the ergometer from the 29th. Weight on the 29th, 63 kg. No exercise. Carbohydrate diet 31st to Feb. 4th. Mixed diet on the 5th. Went for a short walk (2 km.) in the evening. Fat diet 6th to 9th. A short walk every evening. Felt tired in the evening on the 6th. Mixed diet on the 10th and 11th. Carbohydrate diet 12th and 13th. Fat diet 14th to 16th. Diarrhoea in the afternoon on the 14th. Very tired in the evening. Severe headache on the 15th. Slightly unwell on the 16th. Mixed diet 17th to 19th. Weight on the 19th, 69·8 kg.

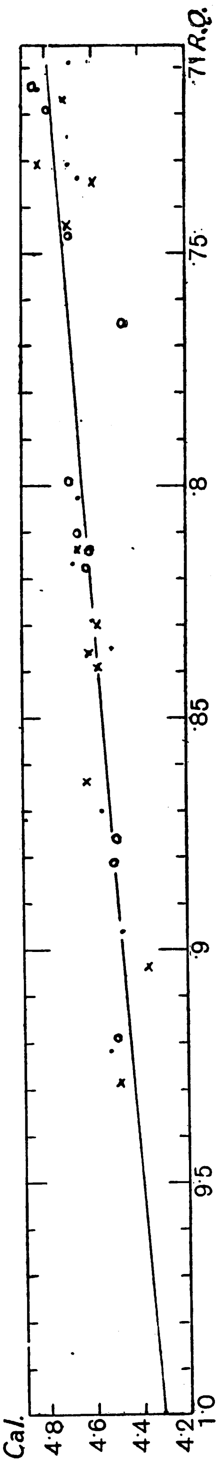

Fig. 11. O.H. Metabolism per unit work. Corrected for training.

Table X.

GENERAL TABLE OF EXPERIMENTS.

	Rest				Work					
Date	Ventilation l. per min.	O$_2$ per min. cc.	R.Q.	Cal.	Length	O$_2$ per min. cc.	R.Q.	Cal.	Revolutions per min.	Techn. work Cal.
A. M. N.				*c*				*b*		*a*
1918	6·79	236	·845	1·16	Normal period of work. Training experiment					
29. i.	7·30	226	·855	1·11						
					25	1234	·848	6·07		
30. i.	6·15	231	·82	1·13	21	1080	·873	5·335		
	6·38	212	·84	1·04	22	1075	·862	5·30	49·3	·910
					22	1102	·855	5·43		
31. i.	6·20	221	·87	1·09	20	1050	·890	5·205		
	5·97	213	·87	1·05	20	1057	·888	5·24	49·3	·910
					20	1074	·883	5·32		
1. ii.	6·41	242	·85	1·19	21	1075	·850	5·29		
	6·20	244	·86	1·20	21	1090	·846	5·36	49·3	·910
					21	1113	·846	5·475		
2. ii.	6·00	245	·90	1·215	21	1049	·886	5·20		
	5·60	235	·88	1·165	21	1067	·870	5·27	49·2	·9085
					21	1080	·872	5·335		
3. ii.	6·17	238	·895	1·18	21	1141	·910	5·68		
	6·11	242	·89	1·195	21	1135	·896	5·635	49·2	(1·05[1])
					21	1145	·892	5·68		
4. ii.	6·20	235	·98	1·185	Work as usual but no determinations on account of trouble with ergometer regulator and gas analysis apparatus					
	6·55	242	·99	1·22						
5. ii.	5·61	234	·93	1·175	21	1049	·882	5·19		
	6·01	227	1·01	1·15	21	1039	·907	5·165	49·2	·908
					21	1065	·876	5·265		
6. ii.	5·80	231	·88	1·14	21	1034	·876	5·11		
	5·83	231	·88	1·14	21	1029	·876	5·09	49·2	·908
					21	1054	·868	5·205		
7. ii.	5·00	231	·83	1·13	21	1057	·787	5·14		
	5·07	223	·83	1·095	21	1080	·782	5·25	49·2	·9075
					21	1063	·805	5·19		
8. ii.	5·29	231	·79	1·125	21	1106	·770	5·36		
	5·33	239	·77	1·16	21	1112	·761	5·38	49·2	·9075
					21	(1112)[2]	·764[2]	5·38		
9. ii.	5·17	230	·775	1·115	21	(1060)[3]	(·768)[3]	(5·125)[3]		
	4·81	224	·78	1·085	21	1110	·764	5·375	49·5	·9135
					21	1109	·760	5·365		
10. ii.	5·28	233	·75	1·125	21	1087	·770	5·27		
	5·28	223	·78	1·08	21	1093	·763	5·295	49·5	·9135
					20	1113	·761	5·385		

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[1] Regulator on ergometer did not work. The load was determined after the experiment.

[2] Oxygen determination in last average sample lost. Percentage determined by interpolation between remaining samples which were practically constant.

[3] Oxygen determination in first intermediate sample not quite reliable.

Table X *continued.*

	Rest				Work					
Date	Ventilation l. per min.	O_2 per min. cc.	R.Q.	Cal.	Length	O_2 per min. cc.	R.Q.	Cal.	Revolutions per min.	Techn. work Cal.
A. M. N.				*c*				*b*		*a*
11. ii.	5·05	212	·85	1·045	21	1043	·829	5·11		
	5·10	206	·87	1·02	21	1045	·830	5·125	49·5	·9135
					20	1066	·825	5·22		
12. ii.	5·46	217	·94	1·085	20	1000	·889	4·96		
	5·13	214	·90	1·06	21	1000	·884	4·95	49·5	·9135
					21	1026	·876	5·07		
13. ii.	6·16	216	·97	1·085	21	988	·930	4·935		
	6·19	219	·99	1·105	21	995	·925	4·965	49·5	·9135
					20	1020	·928	5·09		
14. ii.	6·23	214	1·06	1·095	21	(1030)[1]	(·926)[1]	(5·14)[1]		
	6·00	212	1·03	1·075	20	1023	·924	5·10	49·5	·9135
					20	1030	·940	5·15		
15. ii.	5·30	216	·83	1·06	21	1016	·841	4·99		
	4·81	205	·84	1·005	21	1031	·838	5·06	49·5	·9135
					21	1040	·842	5·11		
16. ii.	5·16	221	·79	1·075	21	1063	·793	5·16		
	4·94	212	·81	1·035	21	1089	·779	5·275	49·4	·912
					21	1052	·802	5·13		
17. ii.	5·10	214	·81	1·045						
	5·38	213	·79	1·035	70	1120	·719	5·375	49·4	·912
18. ii.	5·56	208	·97	1·045	22	(998)[2]	(·843)[2]	(4·91)[2]		
	5·35	204	·92	1·02	21	1011	·829	4·96	49·4	·9115
					21	1033	·833	5·065		
19. ii.	4·98	206	·86	1·015	21	1007	·844	4·95		
	5·10	209	·85	1·03	21	1020	·846	5·015	49·4	·9115
					21	1022	·840	5·02		

[1] The oxygen determination in the first average sample is probably erroneous. The first intermediate sample gave an O_2 deficit of 0·493 % the second gave 0·4935, while the intervening average sample gave 0·5085 %. The probable values would be oxygen per min. 1004 cc., R.Q. 0·95, calories 5·025.

[2] First average sample lost. Values obtained by interpolation between intermediate samples.

During each day's work on the ergometer this subject noticed no distinct difference between the effects of the different diets and never became very tired. The technical work per minute was 0·91 Cal.

The determinations of the standard metabolism show a very marked decline during the whole of the experimental period, a decline which is brought out very clearly when the results are arranged graphically with the dates as abscissae (Fig. 12). The three first determinations give low values, but otherwise there is a steady and extremely regular decrease from first to last. The low values observed on the three first days are probably due to a fall in the body temperature. When the subject suppressed all movements, as he did very carefully throughout, he complained of feeling cold. In all the later determinations he was carefully wrapped up and felt warm. The decrease in standard metabolism, taking place at all events from Feb. 1st to 19th, is remarkable, and the more so as the subject gained in weight from 63 to 70 kg. As the diet during the experimental period was poor in protein it is conceivable that the decrease may be due to the elimination of a nitrogen reserve from the body as in the recent experiments of Benedict and his collaborators [1918], but we have no observations to support such a hypothesis.

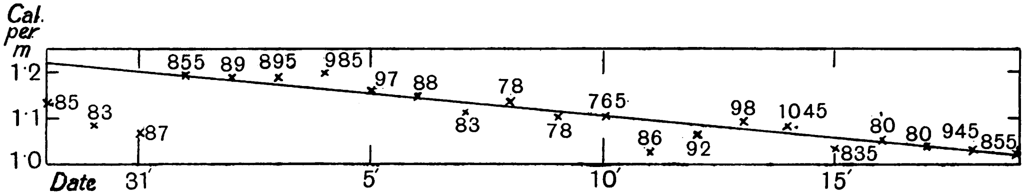

Fig. 12. A. M. N. Standard metabolism. Variation from day to day.

As the quotient during rest has in all experiments been above 0·77 there is very little influence of the quotient upon the resting metabolism to be detected, and we have therefore used the values for standard metabolism deduced from the straight line curve, Fig. 12, in the subsequent treatment of the material.

Table XI.

Date	R.Q. work	Average Cal. during work	Cal. at rest from curve	Difference	Technical work	Cal. per unit work	Training correction (from Fig. 13)
1918		*b*	*c*	*d*	*a*	*e*	
30. i.	·865	5·355	1·21	4·145	·910	4·555	·952
31. i.	·885	5·255	1·20	4·055	·910	4·46	·957
1. ii.	·85	5·375	1·19	4·185	·910	4·60	·962
2. ii.	·875	5·27	1·18	4·09	·9085	4·50	·969
3. ii.	·90	5·665	1·17	4·495	(1·05)[1]	(4·35)[1]	·973
5. ii.	·89	5·205	1·15	4·055	·908	4·47	·982
6. ii.	·875	5·135	1·14	3·995	·908	4·40	·985
7. ii.	·79	5·19	1·13	4·06	·9075	4·47	·989
8. ii.	·765	5·37	1·12	4·25	·9075	4·685	·991
9. ii.	·76	5·36	1·115	4·245	·9135	4·65	·993
10. ii.	·765	5·32	1·105	4·215	·9135	4·615	·995
11. ii.	·83	5·15	1·095	4·055	·9135	4·44	·997
12. ii.	·885	4·995	1·085	3·91	·9135	4·28	·999
13. ii.	·93	5·00	1·075	3·925	·9135	4·30	1·000
14. ii.	·93	5·13	1·07	4·06	·9135	4·445	1·000
15. ii.	·84	5·055	1·06	3·995	·9135	4·375	1·000
16. ii.	·79	5·19	1·05	4·14	·912	4·54	1·001
17. ii.	·72	5·375	1·04	4·335	·912	4·755	1·002
18. ii.	·83	5·00	1·03	3·97	·9115	4·355	1·002
19. ii.	·845	4·995	1·02	3·975	·9115	4·36	1·002

[1] Doubtful.

In Table XI the determinations during work done on each day have been averaged and the metabolism per unit work calculated for each separate day taken as a whole, and in Fig. 13 these results have been plotted with the dates as abscissae. By means of the values showing quotients between 0·82 and 0·89 a training curve has been constructed. The distribution of the determinations on which this curve is based shows that its possible errors must be comparatively slight. Owing to the distribution of the fat and carbohydrate periods the difference between the efficiency of these diets for work comes out about as distinctly and practically the same quantitatively with no correction whatever for training. See Figs. 14 and 15.

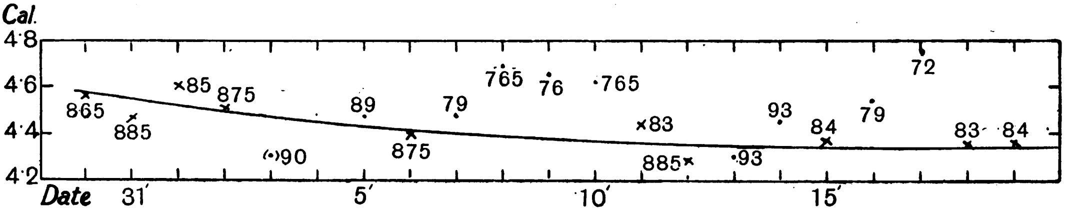

Fig. 13. A. M. N. Metabolism per unit work. Influence of training.

In the final Tables XII–XIII the determinations are arranged as usual according to their quotients, and as an inspection of the general Table X shows that the metabolism in the third experimental periods is generally a little higher than in periods 1 and 2, the third periods have been sorted out and arranged in the separate Table XIII. The results have been plotted and curves drawn to represent them in Figs. 14 and 15. In drawing the curves we have *not* attempted to represent all the determinations as nearly as possible. That would obviously mean curves which were not straight lines but slightly convex towards the abscissa, but such curves would be incompatible with our theoretical conception.

We can safely maintain, however, that the lines, drawn straight to be in accordance with theory, are perfectly compatible with the determinations, since the dispersion of these is only $\sigma = 0{\cdot}074$ Cal. or 1·7 % for the curve representing periods 1 and 2 and $\sigma = 0{\cdot}080$ Cal. or 1·8 % for the curve representing period 3.

It should be pointed out that the comparatively large deviation of a few determinations *upwards* from the curve as at R.Q. = 0·924 in Fig. 14 and at 0·940 in Fig. 15 is a thing which must be expected in experiments of this kind. A slight indisposition on the part of the subject will be enough to account for them.

The straight line, Fig. 14, representing periods 1 and 2 corresponds to an $e_F = 4{\cdot}70$ Cal. and $e_C = 4{\cdot}02$. The waste of energy from fat is therefore 0·68 Cal. or 14·5 %. The line in Fig. 15 representing the third experimental periods corresponds to $e_F = 4{\cdot}74$ Cal. and $e_C = 4{\cdot}11$ Cal. or a waste of energy from fat of 0·63 Cal. = 13·3 %.

FOURTH SERIES OF EXPERIMENTS.

Our fourth and final series of determinations was again made on the subject O. H. on whom we had obtained in 1917 the remarkably constant results given above pp. 314—322. Mr H. had been working hard for his degree during the preceding term and his general physical training was therefore below his usual standard. During a fortnight preceding the experiments he undertook to make a bicycle ride of about 30 km. every day. We hoped thereby to induce such an amount of bicycle training that the training effect of the experiments themselves, which had been so pronounced in the two preceding series, would be greatly diminished. As will be seen below this hope was in the main disappointed. In all other respects the routine was the same as that adopted in the third series.

Table XII.

Date and number Jan. and Feb. 1918		R.Q. work	Work Cal. *b*	Rest Cal. *c*	Difference *d*	Cal. per unit work *e*	*e* corrected	Deviation from curve *δ*
8	2	·761	5·38	1·12	4·26	4·69	4·645	+·065
10	2	·763	5·295	1·105	4·19	4·59	4·57	±·00
9	2	·764	5·375	1·115	4·26	4·665	4·635	+·065
9	1	(·768)	(5·125)	1·115	(4·01)	(4·39	4·36)[1]	
8	1	·770	5·36	1·12	4·24	4·67	4·625	+·065
10	1	·770	5·27	1·105	4·165	4·56	4·54	−·02
16	2	·779	5·275	1·05	4·225	4·63	4·635	+·095
7	2	·782	5·25	1·13	4·12	4·54	4·49	−·04
7	1	·787	5·14	1·13	4·01	4·42	4·37	−·15
16	1	·793	5·16	1·05	4·11	4·51	4·515	+·01
11	1	·829	5·11	1·095	4·015	4·395	4·38	−·04
18	2	·829	4·96	1·03	3·93	4·31	4·32	−·10
11	2	·830	5·125	1·095	4·03	4·41	4·40	−·02
15	2	·838	5·06	1·06	4·00	4·38	4·38	−·02
15	1	·841	4·99	1·06	3·93	4·305	4·305	−·085
18	1	·843	(4·91)	1·03	(3·88)	(4·26	4·27)[2]	
19	1	·844	4·95	1·02	3·93	4·31	4·32	−·06
1	2	·846	5·36	1·19	4·17	4·585	4·41	+·03
19	2	·846	5·015	1·02	3·995	4·385	4·395	+·15
1	1	·850	5·29	1·19	4·10	4·51	4·34	−·03
30	2	·862	5·30	1·21	4·09	4·495	4·28	−·06
2	2	·870	5·27	1·18	4·09	4·50	4·36	+·04
30	1	·873	5·335	1·21	4·125	4·535	4·32	±·00
6	1	·876	5·11	1·14	3·97	4·375	4·31	±·00
6	2	·876	5·09	1·14	3·95	4·35	4·285	−·025
5	1	·882	5·19	1·15	4·04	4·45	4·37	+·075
12	2	·884	4·95	1·085	3·865	4·23	4·225	−·065
2	1	·886	5·20	1·18	4·02	4·425	4·29	+·005
31	2	·888	5·24	1·20	4·04	4·44	4·25	−·03
12	1	·889	4·96	1·085	3·875	4·24	4·235	−·045
31	1	·890	5·205	1·20	4·005	4·40	4·21	−·07
3	2	·896	5·635	1·17	4·46	(4·3	4·2)[3]	
5	2	·907	5·165	1·15	4·015	4·42	4·34	+·10
3	1	·910	5·68	1·17	4·51	(4·3	4·2)[3]	
14	2	·924	5·10	1·07	4·03	4·41	4·41	+·21
13	2	·925	4·965	1·075	3·89	4·26	4·26	+·065
14	1	(·926)	5·14	1·07	4·07	(4·455	4·455)[4]	
13	1	·930	4·935	1·075	3·86	4·225	4·225	+·04
							Sum	+·185

[1] Slightly uncertain. [2] Slightly uncertain. [3] Doubtful. [4] Doubtful.

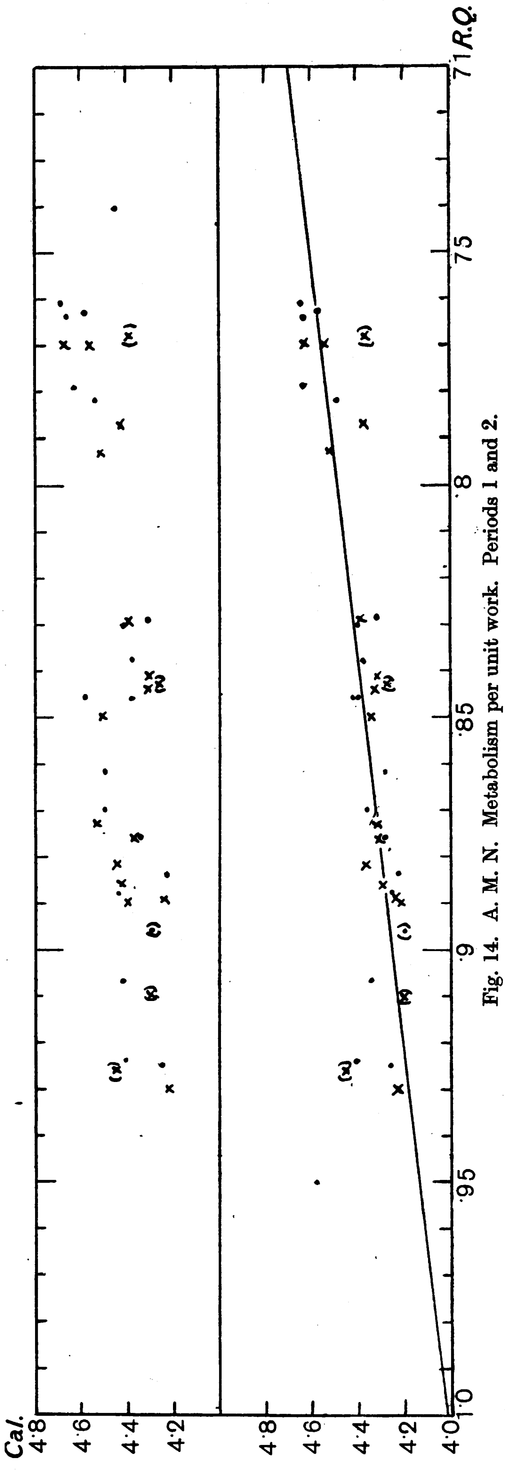

Fig. 14. A. M. N. Metabolism per unit work. Periods 1 and 2.
Lower section: values corrected for training. Upper section: values not corrected for training.

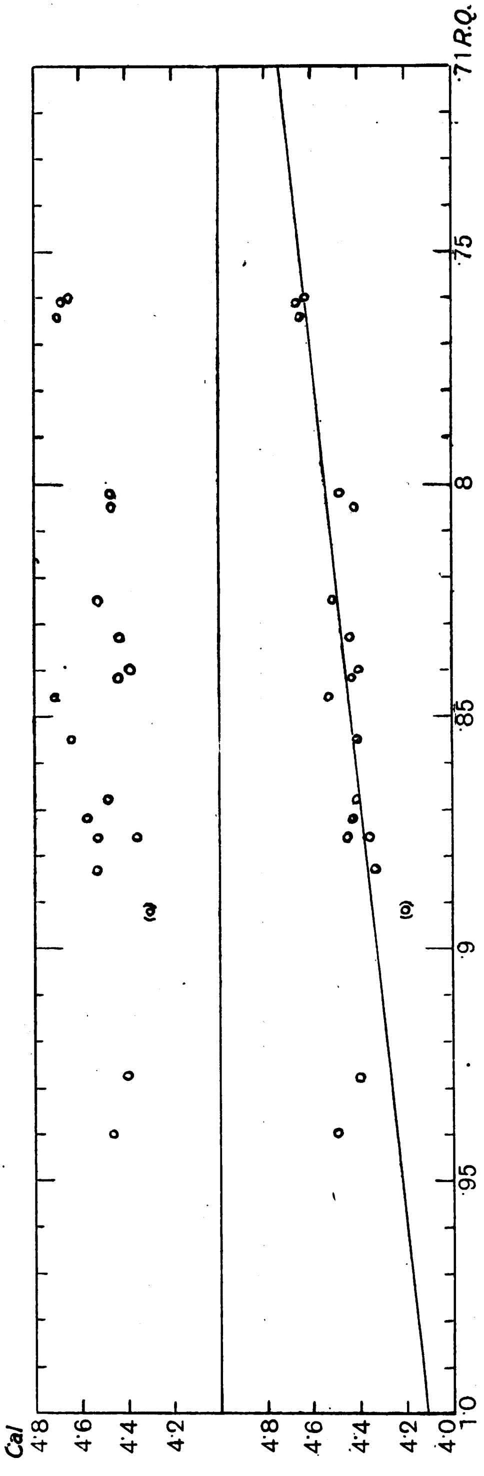

Fig. 15. A. M. N. Metabolism per unit work. Third periods.
Lower section: values corrected for training. Upper section: values not corrected for training.

Table XIII.

9	3	·760	5·365	1·115	4·25	4·655	4·625	−·01
10	3	·761	5·385	1·105	4·28	4·685	4·665	+·03
8	3	·764	5·38	1·12	4·26	4·695	4·65	+·03
16	3	·802	5·13	1·05	4·08	4·475	4·48	−·06
7	3	·805	5·19	1·13	4·06	4·47	4·42	−·11
11	3	·825	5·22	1·095	4·125	4·52	4·51	+·02
18	3	·833	5·065	1·03	4·035	4·43	4·44	−·03
19	3	·840	5·02	1·02	4·00	4·39	4·40	−·055
15	3	·842	5·11	1·06	4·05	4·435	4·435	−·015
1	3	·846	5·475	1·19	4·285	4·71	4·53	+·085
30	3	·855	5·43	1·21	4·22	4·64	4·41	−·01
6	3	·868	5·205	1·14	4·065	4·48	4·41	+·015
2	3	·872	5·335	1·18	4·155	4·575	4·43	+·04
5	3	·876	5·265	1·15	4·115	4·53	4·45	+·07
12	3	·876	5·07	1·085	3·985	4·365	4·36	−·015
31	3	·883	5·32	1·20	4·12	4·53	4·335	−·025
3	3	·892	5·68	1·17	4·51	(4·3	4·2)[1]	
13	3	·928	5·09	1·075	4·015	4·40	4·40	+·135
14	3	·940	5·15	1·07	4·08	4·47	4·47	+·23
							Sum	+·145

[1] Doubtful.

From the notes of the subject we give the following extract:

When the experiments began on April 2nd the general athletic training was distinctly lower than in 1917 but the special training for bicycling was better. The fatigue *during* work on the ergometer did not become very pronounced, but in the afternoon the subject was almost constantly tired and had to take rest on a couch for 1½ to 2 hours. The difference between the fatigue on fat days and carbohydrate days was less pronounced than in 1917 but on several occasions very distinct, nevertheless. Work was performed on the ergometer each day throughout the period and no other exercise was taken except in a few instances specified below.

Mixed diet from 2nd to 5th. Somewhat tired in the afternoon and evening. Weight on the 4th, 84·3 kg.

Fat diet, 6th to 8th. Not distinctly fatigued during the riding, but repeatedly suspected the metronome to be too fast, though as a matter of fact it was rather slower than the normal rate of pedalling of the subject. Somewhat tired during each afternoon and evening.

Mixed diet on the 9th. Weight, 81·5 kg.

Carbohydrate diet, 10th to 13th. On the 11th less tired than usual, took no rest in the afternoon. 12th tired for a short period during the work, tired in the afternoon with feeling of "pressure" in the abdomen. No objective symptoms of digestive trouble. 13th, symptoms and fatigue less pronounced. Weight, 83·5 kg. 14th, felt well during the work. No abdominal "pressure." Very slight fatigue afterwards.

Mixed diet, 14th to 17th. 15th, 18th, again rather tired in the afternoon. Weight on the 15th, 83·1 kg., on the 18th 82·2 kg.

Table XIV.

GENERAL TABLE OF EXPERIMENTS.

	Rest				Work					
Date	Ventilation l. per min.	O_2 per min. cc.	R.Q.	Cal.	Length of per.	O_2 per min. cc.	R.Q.	Cal.	Revolutions per min.	Techn. work Cal.
O.H. II				c				b		a
1918	5·71	263	·79	1·28	21	1304	·855	6·42		
3. iv.	(6·50	260	·86)[1]	1·28	21	1317[2]	·843	6·475	49·3	1·122
					21	1316[2]	·845	6·47		
4. iv.	5·95	275	·815	1·345	21	1347	·840	6·62		
	5·32	242	·80	1·18	21	1334	·839	6·555	49·5	1·127
					21	1327	·831	6·508		
5. iv.	5·63	269	·84	1·32	20	1290	·858	6·36		
	5·39	266	·815	1·30	20	1284	·846	6·315	49·4	1·125
					20	1321	·826	6·47		
6. iv.	5·52	263	·785	1·28	20	1300	·819	6·36		
	5·505	256	·795	1·25	20	1275	·839	6·26	49·3	1·122
					20	1300	·830	6·375		
7. iv.	5·58	288	·75	1·39	20	1339	·768	6·49		
					20	1345	·766	6·52	49·4	1·125
					20	1355	·763	6·56		
8. iv.	5·13	282	·695	1·35	21	1381	·728	6·64		
	5·67	285	·725	1·38	21	1361	·740	6·56	49·5	1·128
					21	1386	·732	6·67		
9. iv.	5·38	314	·645	(1·42)[3]	21	1333	·751	6·44		
	5·20	292	·66		21	1366	·737	6·58	49·5	1·128
					21	1348	·748	6·51		
10. iv.	5·75	254	·83	1·245	21	1333	·797	6·50		
	5·64	252	·84	1·24	21	1320	·804	6·44	49·5	1·130
					21	1347	·804	6·57		
11. iv.	6·23	248	·985	1·25	21	1270	·904	6·315		
	6·38	252	·995	1·275	21	1271	·903	6·32	49·5	1·128
					21	1280	·902	6·36		
12. iv.	6·47	255	1·00	1·29	21	1244	·944	6·225		
	6·33	260	·97	1·31	21	1231	·945	6·16	49·4	1·126
					21	1261	·917	6·28		
13. iv.	6·49	248	·985	1·25	21	1227	·961	6·16		
	6·63	266	·94	1·33	21	1217	·967	6·12	49·4	1·127
					21	1250	·944	6·26		
14. iv.	6·55	244	1·01	1·25	21	1211	·974	6·10		
	7·05	274	1·00	1·385	21	1255	·938	6·275	49·5	1·128
					21	1236	·940	6·185		
15. iv.	6·36	260	·845	1·275	21	1221	·904	6·07		
	6·19	263	·855	1·295	26	1235	·895	6·13	49·4	1·126
					21	1250	·882	6·185		

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[1] The high quotient certainly due to over-ventilation.

[2] Oxygen determination in intermediate sample 3 obviously erroneous. Value obtained by interpolation.

[3] Caloric value of oxygen by extrapolation in Zuntz's table.

Table XIV *continued.*

	Rest				Work					
Date	Ventilation l. per min.	O_2 per min. cc.	R.Q.	Cal.	Length of per.	O_2 per min. cc.	R.Q.	Cal.	Revolutions per min.	Techn. work Cal.
O.H. II				*c*				*b*		*a*
1918	5·78	256	·83	1·255	21	1254	·862	6·18		
16. iv.	5·80	262	·805	1·275	21	1268	·851	6·24	49·5	1·129
					21	1269	·849	6·24		
17. iv.	5·90	260	·79	1·265	21	1282	·816	6·27		
	5·96	277	·80	1·35	21	1289	·811	6·30	49·4	1·126
					21	1338	·791	6·51		
18. iv.	5·52	261	·77	1·265	21	1285	·808	6·275[1]		
	5·81	261	·79	1·27	21	1287	·808	6·28	49·5	1·127
					21	1310	·800	6·39		
19. iv.	5·81	248	·905	1·23	21	1256	·880	6·22		
	5·67	245	·885	1·215	21	1248	·884	6·18	49·4	1·126
					21	1264	·870	6·24		
20. iv.	6·54	266	·94	1·33	21	(1183	·966	5·945)[2]		
	6·43	261	·95	1·31	21	1225	·935	6·12	49·4	1·127
					21	1236	·937	6·18		
21. iv.	6·43	248	·98	1·25	21	1209	·950	6·055		
	6·52	261	·98	1·315	21	1204	·939	6·02	49·4	1·124
					21	1192	·970	6·00		
22. iv.	6·15	201	1·13		21	1192	·951	5·98		
	6·81	262	·97	1·32	21	1192	·935	5·96	49·4	1·126
					21	1210	·949	6·06		
23. iv.	5·32	213	·84	1·045	21	1255	·796	6·11		
	5·64	223	·87	1·10	21	1276	·788	6·21	49·5	1·128
					21	1295	·778	6·29		
24. iv.	6·46	275	·73	1·32	21					
	5·91	264	·725	1·27	21	(1332	·752	6·44)[3]	49·3	1·124
					21	1334	·760	6·455		
25. iv.	6·59	258	·855	1·27	21	1252	·832	6·14		
	6·35	244	·88	1·205	21	1260[4]	·822	6·17	49·4	1·124
					21	1264[4]	·829	6·20		
26. iv.	6·03	254	·875	1·255	21	1249	·838	6·13		
	5·59	245	·825	1·20	20	1255	·846	6·17	49·4	1·124
					21	1247	·848	6·135		
27. iv.	5·84	240	·86	1·185	21	1227	·890	6·08		
	6·05	254	·87	1·255	18	1212	·907	6·03	49·3	1·124
					21	1233	·892	6·11	Average:	1·126

---

[1] All the average samples lost. Experiments calculated from intermediate samples which varied little and regularly.

[2] Oxygen determination in first average sample somewhat improbable; O_2 deficit in sample 1 0·645 %, sample A 0·6175 %, sample 2 0·625 %.

[3] Intermediate samples 1 and 2 lost. 2 obtained by interpolation.

[4] Intermediate sample 3 lost. Value obtained by interpolation.

Carbohydrate diet, 18th to 21st. Distinctly less tired than before but more so than on the corresponding diet in 1917. On the 21st went for a walk of 10 km. (Had not felt any inclination to take exercise during the preceding days of the experimental period.) Weight on the 22nd, 83·1 kg.

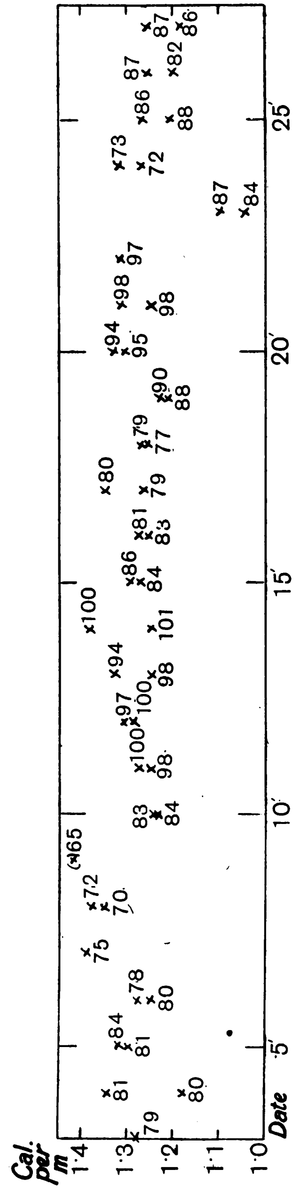

Fig. 16. O. H., 1918. Standard metabolism. Variations from day to day.

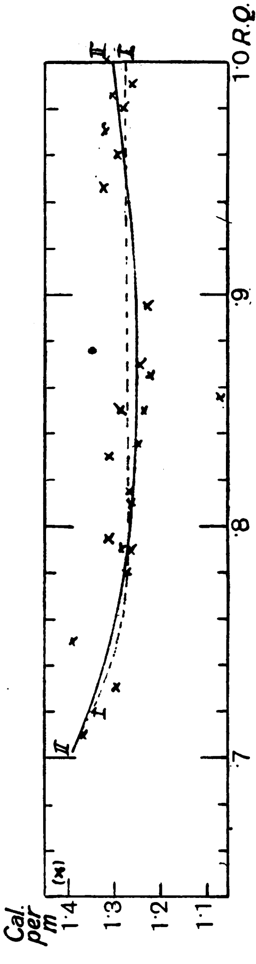

Fig. 17. O. H., 1918. Standard metabolism. Variations with respiratory quotient.

Fat diet, 22nd to 23rd. Very tired in the evening of the 22nd. Tired during the work on the 23rd. Very tired and hungry in the afternoon and evening. Work on the 24th very difficult to perform though somewhat easier during the last half hour. Weight on the 24th, 81·3 kg.

Mixed diet, 24th to 26th. Distinctly less tired after and especially during the work on the 25th to 27th. Weight on the 27th, 82·8 kg.

In Fig. 16 the single experiments made during rest have been plotted with the dates as abscissae and it is seen that while the standard metabolism does not vary with the time the determinations showing a low quotient are distinctly higher than the rest. In Fig. 17 the results (averages for each day) have therefore been plotted again with the respiratory quotient as abscissa. The standard metabolism appears to be distinctly lower at intermediate quotients than it is at low or very high ones. The full line curve drawn represents, we think, fairly accurately all the results except the single one at 0·855. As the increase in metabolism at high quotients might possibly be due to accidental errors we have drawn also the dotted line curve shown, and all the succeeding calculations of the metabolism per unit work have been carried out with both sets of values for the resting metabolism. A discussion of the influence of the quotient upon the standard metabolism will be given below in Appendix II dealing with all the determinations made on the various subjects.

Table XV.

Date	R.Q. work	Average Cal. during work b	Cal. at rest from Curve I c_{I}	Cal. at rest from Curve II c_{II}	Difference d_{I}	d_{II}	Cal. per unit work e_{I}	e_{II}	Training correction (from Fig. 18)
3. iv.	·85	6·455	1·27	1·25	5·185	5·205	4·605	4·62	·937
4. iv.	·835	6·56	1·27	1·25	5·29	5·31	4·70	4·715	·941
5. iv.	·845	6·38	1·27	1·25	5·11	5·13	5·54	4·56	·945
6 iv.	·83	6·33	1·27	1·25	5·06	5·08	4·495	4·515	·949
7. iv.	·765	6·52	1·27	1·29	5·25	5·23	4·66	4·645	·952
8. iv.	·735	6·62	1·31	1·33	5·31	5·29	4·72	4·70	·955
9. iv.	·745	6·51	1·295	1·31	5·215	5·20	4·63	4·62	·958
10. iv.	·80	6·50	1·27	1·26	5·23	5·24	4·645	4·655	·962
11. iv.	·905	6·33	1·27	1·26	5·06	5·07	4·495	4·505	·964
12. iv.	·935	6·22	1·27	1·27	4·95	4·95	4·395	4·395	·968
13. iv.	·955	6·18	1·27	1·275	4·91	4·905	4·36	4·36	·971
14. iv.	·95	6·19	1·27	1·27	4·92	4·92	4·37	4·37	·973
15. iv.	·895	6·13	1·27	1·255	4·86	4·875	4·32	4·33	·976
16. iv.	·855	6·22	1·27	1·25	4·95	4·97	4·395	4·415	·979
17. iv.	·805	6·36	1·27	1·26	5·09	5·10	4·52	4·53	·981
18. iv.	·805	6·315	1·27	1·26	5·045	5·055	4·48	4·49	·983
19. iv.	·88	6·21	1·27	1·25	4·94	4·96	4·39	4·405	·985
20. iv.	·935	6·15	1·27	1·265	4·88	4·885	4·335	4·34	·987
21. iv.	·95	6·025	1·27	1·27	4·755	4·755	4·225	4·225	·989
22. iv.	·945	6·00	1·27	1·27	4·73	4·73	4·20	4·20	·991
23. iv.	·79	6·20	1·27	1·27	4·93	4·93	4·38	4·38	·993
24. iv.	·76	6·455	1·28	1·295	5·175	5·16	4·595	4·585	·995
25. iv.	·83	6·17	1·27	1·25	4·90	4·92	4·35	4·37	·9965
26. iv.	·845	6·145	1·27	1·25	4·875	4·895	4·33	4·35	·998
27. iv.	·895	6·07	1·27	1·255	4·80	4·815	4·265	4·28	·999

In Table XV the determinations are averaged for each day and arranged for the construction of a training curve which is given in Fig. 18. As only the experiments showing quotients between 0·8 and 0·9 are utilised for the construction of the curve the difference between the two sets of values for e will be the same throughout and we have therefore utilised the second set only for drawing the curve. A training curve corresponding to e_{I} would be parallel to the one drawn but lie 0·02 Cal. lower. It is evident that training curves representing the determinations with quotients from 0·73 to 0·8 or with quotients between 0·9 and 0·96 would be very nearly parallel to the curve drawn in Fig. 18, and it follows therefore that the training effect is substantially the same at different quotients—as it ought to be theoretically.

It is worthy of note that the training effect of the experiments is considerable and persistent in spite of the measures taken to reduce it (the fortnight's preliminary training). There is no approach to a constant level, and the only advantage we have gained is that we have avoided the steep initial part of the training curves, Figs. 10 and 13, which makes the correction of the first experiments somewhat uncertain.

In the final Tables XVI and XVII we have again sorted out the third periods which show a slightly higher metabolism than the first and second. We have made the calculations with the two sets of values for the standard metabolism c_{I} and c_{II} obtained from curves I and II, Fig. 17 and corrected them for training by means of the figures given in Table XV. Both sets of corrected values and one set of the uncorrected have been plotted in Figs. 19 and 20 and curves drawn to represent them.

The lower curves in Fig. 19 and Fig. 20, corresponding to the standard metabolism curve II, Fig. 17, which gave the most accurate representation of the rest experiments and showed an increase in metabolism both at very high and at low quotients, are practically straight lines while the best curves (middle curves Fig. 19 and Fig. 20) corresponding to the values e_{I} are slightly convex towards the abscissa. We believe that the straight line curves are the most reliable.

The curves representing the results e_{II} as uncorrected for training are likewise straight and show about the same waste of energy from fat as do the corrected curves. This is due of course to the experiments with high and low quotients being suitably distributed. Had the experiments with low quotients been all made first the apparent waste would have become greater, and it could have been almost abolished by making the experiments at

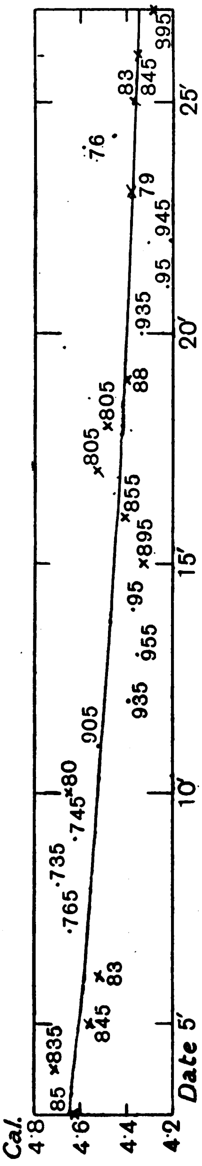

Fig. 18. O. H., 1918. Metabolism per unit work. Influence of training.

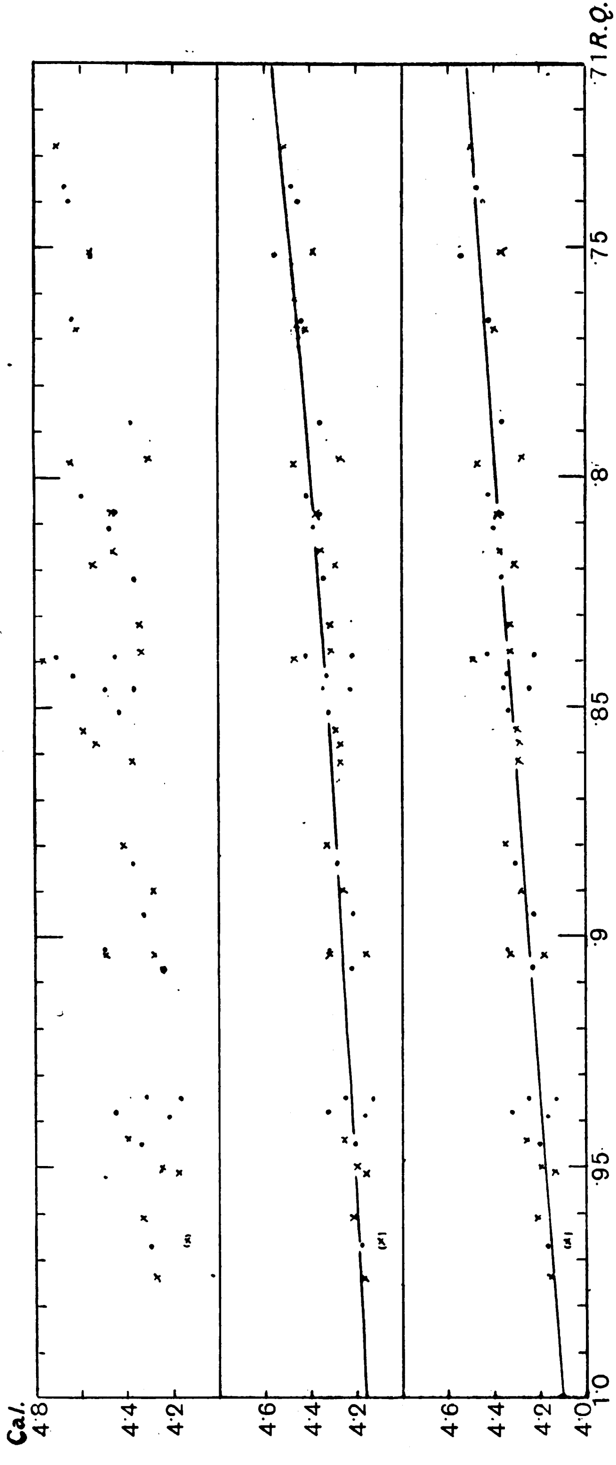

Fig. 19. O. H., 1918. Metabolism per unit work. Periods 1 and 2.

Upper curve: not corrected for training. Standard metabolism from curve II, Fig. 17.
Middle curve: corrected for training. Standard metabolism from curve I, Fig. 17.
Lower curve: corrected for training. Standard metabolism from curve II, Fig. 17.
The middle curve has been drawn about 0·02 Cal. too high.

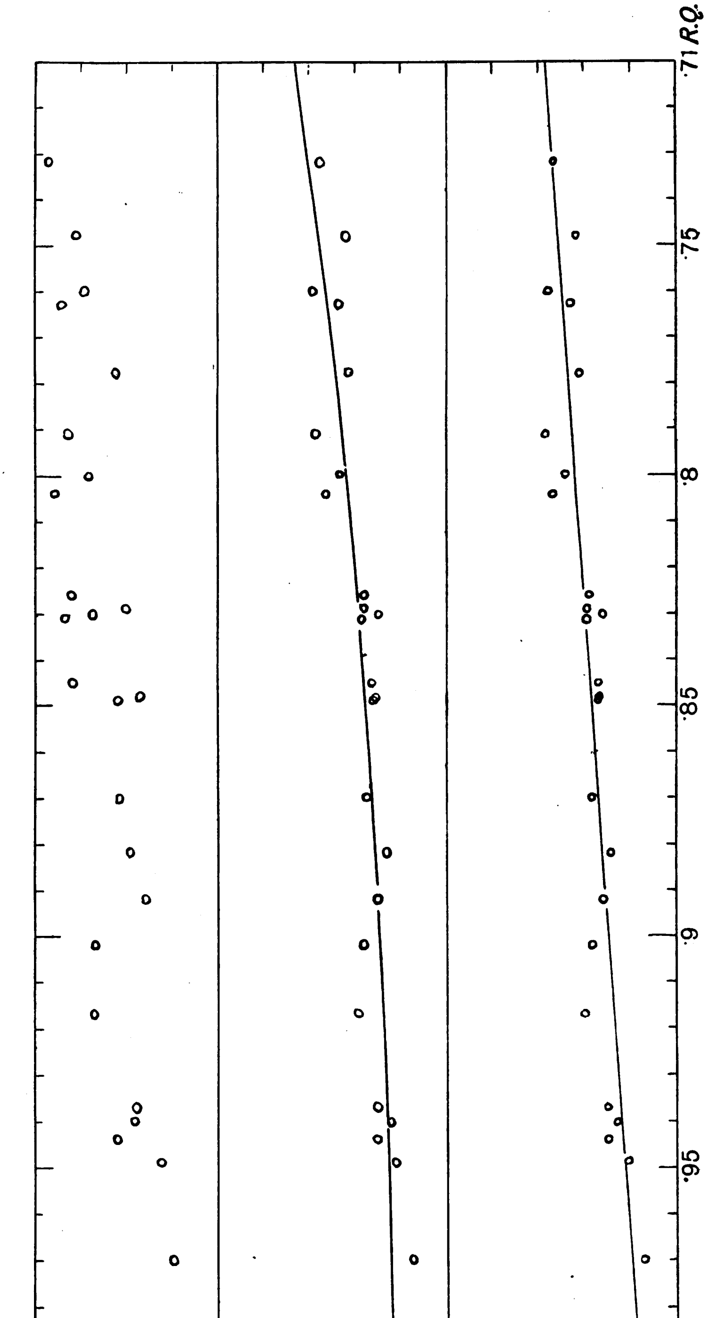

Fig. 20. O. H., 1918. Metabolism per unit work. Third periods.

Upper curve: not corrected for training. Standard metabolism from curve II, Fig. 17.
Middle curve: corrected for training. Standard metabolism from curve I, Fig. 17.
Lower curve: corrected for training. Standard metabolism from curve II, Fig. 17.

Table XVI.

Date and number April 1918	R.Q. work	Work Cal.	Rest	Cal.	Difference		Cal. per unit work				Deviation from curve (e_{II} corr.)
		b	c_I	c_{II}	d_I	d_{II}	e_I	e_{II}	e_I corr.	e_{II} corr.	δ
8. 1	·728	6·64	1·32	1·34	5·32	5·30	4·725	4·71	4·51	4·50	+·01
9. 2	·737	6·58	1·305	1·325	5·275	5·255	4·685	4·67	4·49	4·475	±·00
8. 2	·740	6·56	1·30	1·32	5·26	5·24	4·67	4·655	4·46	4·45	−·03
9. 1	·751	6·44	1·29	1·305	5·15	5·135	4·575	4·56	4·38	4·37	−·09
24. 2	·752	6·44	1·29	1·305	5·15	5·135	4·575	4·56	4·55	4·54[1]	+·08
7. 2	·766	6·52	1·27	1·29	5·25	5·23	4·66	4·645	4·44	4·42	−·02
7. 1	·768	6·49	1·27	1·29	5·22	5·20	4·64	4·62	4·42	4·40	−·04
23. 2	·788	6·21	1·27	1·27	4·94	4·94	4·39	4·39	4·36	4·36	−·045
23. 1	·796	6·11	1·27	1·265	4·84	4·845	4·30	4·305	4·27	4·275	−·125
10. 1	·797	6·50	1·27	1·265	5·23	5·235	4·645	4·65	4·47	4·47	+·075
10. 2	·804	6·44	1·27	1·26	5·17	5·18	4·59	4·60	4·42	4·43	+·04
18. 1	·808	6·275	1·27	1·255	5·005	5·02	4·445	4·46	4·37	4·38[2]	±·00
18. 2	·808	6·28	1·27	1·255	5·01	5·025	4·45	4·465	4·37	4·39[2]	+·01
17. 2	·811	6·30	1·27	1·255	5·03	5·045	4·47	4·48	4·39	4·40	+·02
17. 1	·816	6·27	1·27	1·25	5·00	5·02	4·44	4·46	4·36	4·38	+·01
6. 1	·819	6·36	1·27	1·25	5·09	5·11	4·52	4·54	4·29	4·31	−·055
25. 2	·822	6·17	1·27	1·25	4·90	4·92	4·355	4·37	4·34	4·36	±·00
25. 1	·832	6·14	1·27	1·25	4·87	4·89	4·325	4·345	4·31	4·33	−·01
26. 1	·838	6·13	1·27	1·25	4·86	4·88	4·32	4·335	4·31	4·33	−·005
4. 2	·839	6·555	1·27	1·25	5·285	5·305	4·695	4·71	4·42	4·43	+·09
6. 2	·839	6·26	1·27	1·25	4·99	5·01	4·435	4·45	4·21	4·22	−·12
4. 1	·840	6·62	1·27	1·25	5·35	5·37	4·75	4·77	4·47	4·49	+·155
3. 2	·843	6·475	1·27	1·25	5·205	5·225	4·625	4·64	4·33	4·345	+·015
5. 2	·846	6·315	1·27	1·25	5·045	5·065	4·48	4·50	4·23	4·25	−·075
26. 2	·846	6·17	1·27	1·25	4·90	4·92	4·355	4·37	4·35	4·36	+·035
16. 2	·851	6·24	1·27	1·25	4·97	4·99	4·415	4·435	4·32	4·34	+·02
3. 1	·855	6·42	1·27	1·25	5·15	5·17	4·575	4·59	4·29	4·30	−·01
5. 1	·858	6·36	1·27	1·25	5·09	5·11	4·52	4·54	4·27	4·29	−·02
16. 1	·862	6·18	1·27	1·25	4·91	4·93	4·36	4·38	4·27	4·29	−·01
19. 1	·880	6·22	1·27	1·25	4·95	4·97	4·40	4·415	4·33	4·35	+·07
19. 2	·884	6·18	1·27	1·25	4·91	4·93	4·36	4·38	4·29	4·31	+·04
27. 1	·890	6·08	1·27	1·255	4·81	4·825	4·27	4·285	4·265	4·28	+·015
15. 2	·895	6·13	1·27	1·255	4·86	4·875	4·315	4·33	4·21	4·23	−·03
11. 2	·903	6·32	1·27	1·255	5·05	5·065	4·485	4·50	4·32	4·34	+·095
11. 1	·904	6·315	1·27	1·255	5·045	5·06	4·48	4·495	4·32	4·33	+·09
15. 1	·904	6·07	1·27	1·255	4·80	4·815	4·265	4·28	4·16	4·18	−·06
27. 2	·907	6·03	1·27	1·26	4·76	4·77	4·23	4·24	4·225	4·235	±·00
20. 2	·935	6·12	1·27	1·265	4·85	4·855	4·31	4·315	4·255	4·26	+·06
22. 2	·935	5·96	1·27	1·265	4·69	4·695	4·17	4·17	4·13	4·13	−·07
14. 2	·938	6·275	1·27	1·27	5·005	5·005	4·45	4·45	4·33	4·33	+·135
21. 2	·939	6·02	1·27	1·27	4·75	4·75	4·22	4·22	4·17	4·17	−·02
12. 1	·944	6·225	1·27	1·27	4·955	4·955	4·40	4·40	4·26	4·26	+·075
12. 2	·945	6·16	1·27	1·27	4·89	4·89	4·345	4·345	4·205	4·205	+·025
21. 1	·950	6·055	1·27	1·275	4·785	4·78	4·25	4·245	4·20	4·20	+·025
22. 1	·951	5·98	1·27	1·275	4·71	4·705	4·185	4·18	4·15	4·14	−·035
13. 1	·961	6·16	1·27	1·28	4·89	4·88	4·345	4·335	4·22	4·21	+·05
20. 1	(·966	5·945)	1·27	1·28	(4·675	4·665	4·155	4·145	4·10	4·09)[3]	−·06
13. 2	·967	6·12	1·27	1·28	4·85	4·84	4·31	4·30	4·185	4·175	+·025
14. 1	·974	6·10	1·27	1·29	4·83	4·81	4·29	4·275	4·175	4·16	+·02
										Sum	+·355

[1] Slightly uncertain. [2] Slightly uncertain. [3] Determination rather doubtful.

high quotients first. The uncorrected curves are therefore of little value quantitatively.

Table XVII.

Date April 1918	R.Q. work	Work Cal. b	Rest c_I	Cal. c_{II}	Difference d_I	Difference d_{II}	Cal. per unit work e_I	e_{II}	e_I corr.	e_{II} corr.	Deviation from curve (e_{II} corr.) δ
8.	·732	6·67	1·315	1·33	5·355	5·34	4·76	4·745	4·55	4·53	–·01
9.	·748	6·51	1·29	1·31	5·22	5·20	4·635	4·62	4·44	4·43	–·08
24.	·760	6·455	1·28	1·295	5·175	5·16	4·60	4·585	4·58	4·56	+·06
7.	·763	6·56	1·275	1·29	5·285	5·27	4·695	4·68	4·47	4·46	–·035
23.	·778	6·29	1·27	1·28	5·02	5·01	4·46	4·45	4·43	4·42	–·05
17.	·791	6·51	1·27	1·265	5·24	5·245	4·655	4·66	4·57	4·57	+·115
18.	·800	6·39	1·27	1·26	(5·12	5·13)	4·55	4·56	4·47	4·48[1]	+·04
10.	·804	6·57	1·27	1·26	5·30	5·31	4·71	4·72	4·53	4·54	+·105
5.	·826	6·47	1·27	1·25	5·20	5·22	4·62	4·635	4·365	4·38	–·02
25.	·829	6·20	1·27	1·25	4·93	4·95	4·38	4·40	4·36	4·385	–·01
6.	·830	6·375	1·27	1·25	5·105	5·125	4·535	4·55	4·30	4·32	–·075
4.	·831	6·505	1·27	1·25	5·235	5·255	4·65	4·67	4·37	4·39	±·00
3.	·845	6·47	1·27	1·25	5·20	5·22	4·62	4·635	4·33	4·34	–·035
26.	·848	6·135	1·27	1·25	4·865	4·885	4·32	4·34	4·31	4·33	–·04
16.	·849	6·24	1·27	1·25	4·97	4·99	4·415	4·435	4·32	4·34	–·03
19.	·870	6·24	1·27	1·25	4·97	4·99	4·415	4·435	4·35	4·37	+·03
15.	·882	6·185	1·27	1·25	4·915	4·935	4·365	4·385	4·26	4·28	–·04
27.	·892	6·11	1·27	1·255	4·84	4·855	4·30	4·315	4·30	4·31	±·00
11.	·902	6·36	1·27	1·255	5·09	5·105	4·52	4·535	4·36	4·37	+·075
12.	·917	6·28	1·27	1·26	5·11	5·12	4·54	4·55	4·39	4·40	+·13
20.	·937	6·18	1·27	1·27	4·91	4·91	4·36	4·36	4·30	4·30	+·06
14.	·940	6·185	1·27	1·27	4·915	4·915	4·365	4·365	4·25	4·25	+·01
13.	·944	6·26	1·27	1·27	4·99	4·99	4·435	4·435	4·30	4·30	+·07
22.	·949	6·06	1·27	1·275	4·79	4·785	4·255	4·25	4·22	4·21	–·01
21.	·970	6·00	1·27	1·285	4·73	4·715	4·20	4·19	4·15	4·14	–·05
										Sum	+·21

[1] Slightly uncertain.

The dispersion about the curve of the corrected e_{II} values of the first and second periods is $\sigma = 0·06$ Cal. or 1·4 % of the average metabolism $e_{0·85} = 4·32$ Cal. For the third periods the corresponding dispersion is likewise $\sigma = 0·06$ Cal. or 1·35 % of $e_{0·85} = 4·37$ Cal. As the unavoidable technical errors of the determinations are on an average about 1 %, it is obvious that the variations due to the subject are very slight indeed.

The straight line representing periods 1 and 2 corresponds to an $e_F = 4·52$ Cal. and $e_C = 4·10$ Cal. The waste of energy from fat is therefore 0·42 Cal. or 9·3 %. The straight line, Fig. 20, representing the third experimental periods corresponds to $e_F = 4·57$ Cal. and $e_C = 4·15$ Cal. or a waste of energy from fat of 0·42 Cal. = 9·2 %.

THE GENERAL RESULTS OF THE FOUR SERIES OF EXPERIMENTS.

1. *The fatigue at different quotients.*

The subjects J. L., G. L., A. K. and O. H. observed distinct differences in the facility (or difficulty) with which the prescribed amount of work was performed, coincident with changes in diet and noted that on fat diets the fatigue became considerable and sometimes excessive. For several hours after the work on the ergometer these subjects were generally very tired when on a fat diet and much less tired or not tired at all when on carbohydrates. In the notes of O. H. indications are found of a perceptible difference also between work on a mixed diet and on a carbohydrate diet.

The subjects R. E. and A. M. N. failed to observe any appreciable difference between work on different diets. They never became very tired, either during or after the work. As the subjective estimate of the load upon an ergometer is liable to very considerable errors, especially when work done on different days has to be compared, the failure of the two subjects to notice the difference need not mean that such a difference was absent. On the other hand we think it rather probable that work at low quotients has not the same effect upon different individuals. The variations in fatigue may for instance be correlated with individual differences in the liability to acidosis. The clearing up of this point will require a special investigation in which the hydrogen ion concentration of the blood will have to be determined during and after the work.

2. *The waste of energy from fat.*

It is obvious that the objective difference in the economy of work at different quotients cannot be due to any incomplete oxidations at low quotients, since the difference is apparent at all quotients and is on the whole a straight line function of the quotient.

As mentioned above, p. 310, we took as our starting point the hypothesis that fats have to undergo a certain definite transformation involving loss of heat before they can be utilised for the production of muscular energy, and we deduced as necessary consequences of the hypothesis that the curves representing the relation between the expenditure of energy per unit work and the respiratory quotient should be straight lines and should show the same percentage waste of energy from fats in different individuals.

The first of these deductions has been verified by our experiments belonging to the second and fourth series. The best curve for the third series is very nearly a straight line, while in the preliminary series the experiments are too few and too discordant to decide anything quantitatively.

The three straight lines found for O. H. in the second and fourth series of determinations show practically the same waste of energy from fat, viz. 9·8, 9·3 and 9·2 % respectively, but the two straight lines representing the third series on A. M. N. give somewhat higher values, viz. 14·4 and 13·3 %.

We are unable to decide whether the difference between the result of the third series and the other two is real or due to the unavoidable errors with which our determinations of the waste of energy are infested. As the "best" curves for A. M. N. are not absolutely straight there is also the possibility that the metabolism at the lowest quotients has been slightly increased by some special influence. All the determinations (periods 1 and 2) made at quotients above 0·78 can be very accurately represented by a straight line giving $e_F = 4{\cdot}6$ Cal. and $e_C = 4{\cdot}1$ Cal. or $w = 0{\cdot}5$ Cal. $= 10{\cdot}9$ %.

Table XVIII.

Subject and series	Calories per unit work		Difference		Number of exp.	Dispersion Cal.	Weight		Average efficiency %
	from fat	from carbohydrate	Cal.	%					
	e_F	e_C	w	$\frac{100w}{e_F}$	n	σ	$\frac{n}{\sigma}$	$\frac{100wn}{e_F\sigma}$	$\frac{200}{e_F+e_C}$
J. L.	5·69	4·59	1·10	19·4	10				
G. L.	5·84	5·09	0·75	12·8	15	0·20	75	960	18·3
A. K.	5·04	4·28	0·76	15·1	15	0·21	71	1072	21·6
R. E.	4·72	3·72	1·00	21·2	13	0·155	84	1780	23·7
M. N. Tb. XII	4·70	4·02	0·68	14·5	33	0·074	447	6485	23·0
M. N. Tb. XIII	4·73	4·10	0·63	13·3	18	0·080	225	2993	22·7
O. H. Tb. IX	4·79	4·32	0·47	9·8	33	0·072	459	4500	22·0
O. H. Tb. XVI	4·52	4·10	0·42	9·3	49	0·060	818	7600	23·2
O. H. Tb. XVII	4·57	4·15	0·42	9·2	24	0·060	400	3680	23·0
						Sum	2579	29070	

In Table XVIII we have put together the results obtained in all the different series. There is no definite reason to exclude any of these except the first on J. L. (on account of his illness during the fat diet period) but it is evident that as determinations of the waste of energy from fat their value is very different, and a simple average of the figures in column $\frac{100w}{e_F}$ would be very misleading. We have therefore endeavoured to assign a definite "weight" to each series which should represent its relative reliability, but we are aware that our method of doing so is somewhat arbitrary. We have given the series weight in proportion to the number of determinations in each and further in inverse ratio of the dispersion of the determinations. The approximate weights (nearest whole numbers) are given in column $\frac{n}{\sigma}$, and in column $\frac{100wn}{e_F\sigma}$ we have the products of the weights with the percentage waste of energy found in the series. When the sum of these figures is divided by the sum of the weights we have $\frac{29070}{2579} = 11{\cdot}25$ as the average percentage waste of energy from fat for the whole of our experimental material.

When the preliminary experiments are excluded and the waste of energy observed in the third series is reduced to 11 % by taking into account only those determinations showing quotients above 0·78, the remaining series can be given weights simply in proportion to their number of determinations since their standard deviations will be practically equal and the average works out as $\frac{1456}{148} = 9{\cdot}9$ %.

Table XIX.

	Calories per unit work		Difference			
Subject and series	from fat e_F	from carbohydrate e_C	Cal. w	% $\frac{100w}{e_F}$	Number of exp. n	$n \times \frac{100w}{e_F}$
M. N. Tb. XII	4·58	4·08	0·50	10·9	27	294
M. N. Tb. XIII	4·68	4·18	0·50	10·7	15	161
O. H. Tb. IX	4·79	4·32	0·47	9·8	33	324
O. H. Tb. XVI	4·52	4·10	0·42	9·3	49	456
O. H. Tb. XVII	4·57	4·15	0·42	9·2	24	221
					148	1456

3. *Possible systematic errors in the determination of the waste of energy from fat. The work of respiration.*

The total amount of work incidental to the production of 1 Cal. external work includes several items which are expended in the organism itself, as the increased circulation and respiration and the sweat secretion. It has been assumed in the calculation that this work is constant and independent of the respiratory quotient. This assumption cannot be proved in any case, and in the case of the respiration it can be shown to be incorrect. It is necessary therefore to examine this point somewhat closely and to see what influence the systematic error introduced may possibly have upon the result.

If at a quotient of 1·00 the amount of work performed by a subject corresponds to an oxygen absorption of 1070 cc. per minute, which represents fairly the conditions in most of our experiments, the oxygen absorption at a quotient of 0·71 will, according to our result, be 1210 cc. The corresponding CO_2 productions will be 1070 and 860 cc. respectively. The elimination of the surplus of CO_2 at the high quotient $1070 - 860 = 210$ cc. will require an increase in ventilation, and on the assumption that the alveolar CO_2 percentage remained the same in both cases the increase could be calculated. Hasselbalch [1912] has shown however that on a carbohydrate diet the CO_2 percentage in the alveoli is somewhat increased, and the increase might possibly be sufficient to make the ventilation constant throughout the whole range of quotients. In any case it makes it impossible to calculate *a priori* the increase in ventilation.

From the work experiments of Frentzel and Reach [1901] (referred to in detail below) in which the ventilation of the lungs was measured at different quotients, Zuntz [1911] has calculated the increase in ventilation incidental to a definite increase in quotient. At an average quotient of 0·778 he finds the ventilation per minute and per Calorie of metabolism to be 4·875 l. while at a quotient of 0·894 it is 5·135 l. or a difference of 0·26 l. At the quotients 0·71 and 1·00 the difference per Calorie would amount to 0·62 l. and in our experiments with a total metabolism between 6 and 5 Cal. the difference would be 3·5 l.[1]

Zuntz calculates that each litre ventilation corresponds to an oxygen consumption in the respiratory muscles of 5 cc. or 0·025 Cal., but the very careful determinations of the respiration work made by Liljestrand [1917] show that, when the respiration is free to adjust itself, it is much more economically performed, and the probable consumption of energy per litre ventilation is of the order 0·005 to 0·01 Cal. when the ventilation is, as in our experiments, about 25 to 30 l. per minute. The increased cost of eliminating the CO_2 when the quotient rises from 0·71 to 1·00 amounts therefore in our experiments to between 0·02 and 0·03 Cal., or certainly not more than 0·6 % of the total metabolism per Calorie external work. When corrected for the difference in work of breathing the waste of energy from fat is therefore increased by 0·4 to 0·6 %.

The cost of ventilating the lungs is not the same in different individuals, and it is obvious that other activities of the body incidental to the work, *e.g.* the secretion of sweat, need not be the same on carbohydrates as on fat and may vary from one individual to another. The final figure obtained by us for the waste of energy from fat may therefore be influenced by several systematic errors. Seeing that the difference in ventilation, which is very pronounced, causes only an error of about 0·5 % it is very unlikely, however, that the influence of other varying activities can be anything but very slight.

As mentioned on p. 298 we have used the table of caloric values for oxygen at different quotients given by Zuntz in 1913. This table differs somewhat from the table originally computed by Zuntz and Schumburg and shows a higher caloric value for oxygen at low quotients. The difference amounts to 1·7 %, and the waste of energy from fat computed from our experiments will therefore have to be reduced by 1·7 % (from 11·25 to 9·55 %) if the later table is replaced by the earlier. The difference is mainly due to differences in the assumed composition of fat, and it is obvious that so long as the constitution of the fat actually catabolised is unknown the possibility both of a small systematic error and of slight individual differences cannot be avoided.

THE RESULTS OF EARLIER INVESTIGATIONS.

We have compared the result obtained by us with the figures found in earlier investigations to find out how far the actual determinations made—apart from the conclusions drawn—agree or disagree with ours.

A few (5) experiments made on a dog were published in 1894 by Zuntz and Loeb [1894]. They show about the same average metabolism per unit work

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[1] The increase in CO_2 production was found above to be 210 cc. or 6 % of the increase in ventilation. The increase in alveolar CO_2 percentage with increasing quotient must therefore have been very slight during the work.

at the different quotients, but the individual results at about the same quotient differ by about 12 % and no valid conclusions can therefore be drawn.

An extensive series of experiments was performed under the supervision of Zuntz by Newton Heineman [1901] on a labourer who worked each day during a period of several months on an "ergostat" which could be turned by hand. The exchange measured varies enormously from day to day—sometimes by 100 %. There is a distinct decrease throughout the period in the metabolism per unit work, from 4·7 Calories per Cal. technical work in February to 4·38 in May according to a calculation by Zuntz [1901]. The main result was that the average metabolism per unit work was lower on a fat diet (4·0 Cal.) than on a diet consisting chiefly of carbohydrates (4·4 Cal.), but Zuntz points out that the difference is probably due to the increasing training as the fat experiments were carried out later than the carbohydrate experiments. In any case the individual determinations are too discordant to allow any definite conclusion.

At about the same time Frentzel and Reach [1901] published another research carried out in the laboratory of Zuntz. These authors acted as subjects themselves, and the work was performed by walking upwards on an inclined treadmill. Each diet was maintained for a week at a time, during which 3–4 periods of work of about 10 minutes duration each were measured each day. In these series the dispersion of individual experiments was much smaller than in Heineman's series, amounting in the most uniform week to $\sigma = 3{\cdot}4$ % and in the least uniform to $\sigma = 12{\cdot}5$ %. The average for each week should therefore be fairly reliable, but unfortunately the two weeks for each subject on the same diet differ about as much from one another as from those on a different diet.

They obtained the following results:

Table XX.

				Average R.Q.	Cal. per kg. per m.	Average
Frentzel.	Fat diet	first week	31. v.–4. vi.	0·766	2·088	2·07
		second week	28. vi.–3. vii.	0·778	2·049	
	Carbohydrate diet	first week	9. vi.–12. vi.	0·896	1·932	1·98
		second week	5. vii.–10. vii.	0·880	2·031	
Reach.	Fat diet	first week	16. vi.–19. vi.	0·805	2·259	2·15
		second week	12. vii.–17. vii.	0·766	2·034	
	Carbohydrate diet	first week	22. vi.–26. vi.	0·899	2·202	2·10
		second week	19. vii.–24. vii.	0·901	2·005	

In both series the metabolism is lower on "carbohydrates" than on fat and when the corresponding differences are calculated for quotients of 0·71 and 1·00 respectively the percentage waste of energy from fat works out as 11 % in the case of Frentzel and 6 % for Reach. It must be conceded however that these results may be due to training, as the carbohydrate experiments were done after the fat experiments, and in any case the results obtained on the same diet are too discordant to allow any very definite conclusions[1].

Benedict and Cathcart [1913] have made some experiments on the influence of diet in their extensive study of the metabolism during muscular work. They made experiments on a professional bicyclist, who rode on the Atwater-Benedict bicycle ergometer, and determined the respiratory exchange by means of the Benedict "Universal Respiration Apparatus." In the experiments here considered two experimental periods were taken during each ride, and these have been averaged by the authors. Generally the rate of pedalling varied considerably from period to period, and in some cases the respiratory quotients and metabolism per unit work were also very different.

Benedict and Cathcart consider that "the evidence obtained is by no means conclusive" but they have put together such results as are suitable for comparison. In nine experiments the external muscular work was not far from 2 Cal., and in six of these the preceding diet was rich in carbohydrate while in three it was poor in carbohydrate. Comparing the average for the six first-named days with that for the three last they find the same metabolism per unit work (standard metabolism not deducted). When, however, the experiments are arranged according to the quotients actually determined during the work we obtain the following results:

Table XXI.

Date	R.Q.	Cal. per unit work. Gross
Feb. 15	0·95	5·17
Feb. 14	0·93	5·20
Jan. 25	0·92	5·38
Feb. 7	0·91	5·30
Feb. 16	0·88	5·12
Jan. 24	0·87	5·52
Feb. 8	0·86	5·40
Jan. 26	0·83	5·81
Feb. 9	0·82	5·23

It is seen from the plotting given in Fig. 21 that the results are too irregular to admit of any conclusions, but that they are perfectly compatible with our result: that there is a definite waste of energy derived from fat.

In another series of six experiments with a smaller amount of external work there is no apparent difference between the value of carbohydrate and fat, but the discrepancies between the single determinations are even greater than in the series reproduced.

We must mention finally the beautiful experiments made by Anderson and Lusk [1917] on a dog walking horizontally on a treadmill at rates between

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[1] It should be remembered that the problem studied by Zuntz and his collaborators was that raised by Chauveau [1898] whether fat must be converted into carbohydrate before being utilised for muscular work. Zuntz calculated that such a conversion must involve an energy loss of at least 24 % and probably 30 % and it must be admitted that the results found by Frentzel and Reach are not compatible with the assumption of such a loss.

3900 and 4800 m. per hour. When the dog had fasted for 18 hours they found an extra energy production over the standard metabolism corresponding to 0·580 kg.meter per kg. of the dog's weight per meter. The respiratory quotient was in one case 0·74, in another 0·78 (average 0·76). After ingestion of 70–100 g. glucose the resting metabolism was increased some 20 % over the standard metabolism during the absorption, but the extra energy required for walking was nevertheless diminished to 0·550 kg.meter per kg. per meter with a quotient of 0·95 (average of three determinations). The difference is a little over 5 % and when the metabolism per unit work is assumed to be a straight line function of the quotient the waste of energy from fats works out as 8 %, without regard to the increase in resting metabolism due to the absorption of the glucose. As the part played by protein in the metabolism is unknown and may have varied it is not possible to make an exact comparison between the result of Lusk and Anderson and ours, but the essential agreement between them is unmistakable.

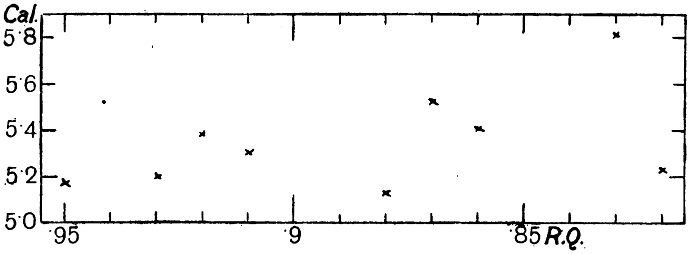

Fig. 21. Experiments from Benedict and Cathcart. Metabolism per unit work, gross.

The foregoing analysis shows that our main numerical result is not at variance with the numerical results of earlier investigations of the same problem and is actually supported by the experiments of Lusk and Anderson and Frentzel and Reach as well as by one series of Benedict and Cathcart's experiments, all of which indicate with more or less probability that the value of fat as a source of muscular energy is lower than that of carbohydrate and that the difference is in the neighbourhood of 10 %.

THE THEORETICAL SIGNIFICANCE OF THE WASTE OF ENERGY FROM FAT.

On the theoretical significance of the difference in value between fat and carbohydrate as a source of energy for the muscular machine, we have very little to say. According to the calculation of Chauveau (quoted by Zuntz) [1911], who assumed that fat was converted into sugar by retaining its hydrogen, splitting of some of the carbon and taking up oxygen to complete the molecule, 30 % of the energy of the fat should become lost by the conversion. It follows therefore from our result—which agrees in so far with the conclusion of Zuntz—that a conversion of this kind does not take place.

Zuntz [1911] has made another calculation, assuming that all the carbon of the fat is retained in the sugar formed. This would correspond to 191·25 g.

sugar formed from 100 g. fat. The fat could yield 950 Cal. and the sugar only 718 Cal.; that is there would be a loss of 24·4 %. This assumption too is incompatible with our determinations.

We are not convinced of the validity of any of these summary methods of calculating the waste of energy incidental to the conversion of fat into sugar or any other substance[1]. We believe that it will be necessary to find out about the stages through which the conversion is actually carried out and the role which may be played by interaction between intermediate products of the fats and other substances which may possibly be derived from carbohydrates.

On the other hand it is clear that our experiments cannot be used as evidence to prove that fat must be converted into sugar before being utilised for muscular work. The chemical processes actually taking place in muscles, doing work upon a fat diet, must be investigated by studies on the lines so brilliantly initiated by Fletcher, Hopkins, Hill and their collaborators, but it is our hope that the result at which we have arrived—that these processes involve a loss of energy of definite magnitude—may serve as a guide in such studies.

APPENDIX I

Statistical Treatment of the Determinations of Standard Metabolism.

We have regularly each day made two consecutive determinations of about five minutes duration of the standard metabolism of our subjects. A statistical treatment of this material can give some information about the accuracy of the method employed and about the influence of various factors upon the results.

In Table XXII we have arranged the repeated determinations of ventilation, respiratory quotient and metabolism in horizontal lines. For each person we have taken the experimental days in the order of the quotients, beginning with the lowest. The material has been arranged primarily to study the possible influence of variations in the pulmonary ventilation upon the quotient and the metabolism. From our earlier experience, especially with the recording respiration apparatus [Krogh, 1913], we know that in periods of a few minutes duration the ventilation during rest is not quite constant but shows oscillations, and this is borne out also by the present series of determinations.

A priori the oscillations in ventilation must be assumed to influence the quotient observed, which should increase with increasing ventilation and *vice versa* by relative washing out and storing up of carbon dioxide, while the oxygen absorption and the metabolism calculated from it should be practically unaffected.

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[1] As a reason for suspicion against summary methods of calculating the loss of energy in question we would suggest the making up of 1 molecule of fat (tripalmitin) into 12 molecules of sugar by the addition of 21 molecules of CO_2 and 23 of H_2O which would result in a *gain* of energy amounting to about 18 %.

Table XXII.

Subject and date	Ventilation l. per m. × 100				R.Q. × 100				Calories per m. × 100			
	I			II	I			II	I			II
1	2	3	4	5	6	7	8	9	10	11	12	13
J. L.												
1. ii.	403		+ 8	411	77		+ 4	81	106		0	106
2. ii.	399	− 7		392	81	− 1		80	100	0		100
G. L.												
25. i.	517		+12	529	76		0	76	110		+ 1	111
26. i.	480		+ 9	489	76		+ 4	80	104		− 2	102
26. ii.	532	−59		473	80	− 1		79	104	− 8		96
A. K.												
20. ii.	688		+ 3	691	70		+ 3	73	115		+ 3	118
19. ii.	696	−82		614	72	+ 3		75	122	−18		104
1. iii.	618		+ 2	620	83		+ 5	88	110		0	110
12. ii.	650		+10	660	88		− 1	87	104		+ 1	105
13. ii.	651		+17	668	88		+ 6	94	106		− 3	103
R. E.												
25. iii.	609	−48		561	73	− 2		71	140	− 8		132
26. iii.	548			548	74		+ 2	76	124		+ 4	128
20. iii.	559	−15		544	85	− 2		83	115	− 1		114
6. iv.	640	−35		605	93	− 3		90	134	− 4		130
7. iv.	571		+20	591	93		+ 2	95	125		+ 2	127
	Sums	−246	+81			− 6	+25			−39	+ 6	
A. M. N.												
10. ii.	528			528	75		+ 3	78	112		− 4	108
9. ii.	517	−36		481	78	0		78	112	− 4		108
8. ii.	529		+ 4	533	79		− 2	77	112		+ 4	116
16. ii.	516	−22		494	79	+ 2		81	108	− 4		104
17. ii.	510		+28	538	81		− 2	79	104		0	104
30. i.	615		+23	638	82		+ 2	84	113		− 9	104
7. ii.	500		+ 7	507	83		0	83	113		− 3	110
15. ii.	530	−49		481	83	+ 1		84	106	− 6		100
29. i.	679		+51	730	84		+ 2	86	116		− 5	111
1. ii.	641	−21		620	85	+ 1		86	119	+ 1		120
19. ii.	498		+12	510	86		− 1	85	102		+ 1	103
11. ii.	505		+ 5	510	85		+ 2	87	104		− 2	102
31. i.	620	−23		597	87	0		87	109	− 4		105
6. ii.	580		+ 3	583	88		0	88	114		0	114
2. ii.	600	−40		560	90	− 2		88	122	− 6		116
3. ii.	617	− 6		611	90	− 1		89	118	+ 2		120
12. ii.	546	−33		513	94	− 4		90	108	− 2		106
18. ii.	556	−21		535	97	− 5		92	104	− 2		102
5. ii.	561		+40	601	93		+ 8	101	118		− 3	115
13. ii.	616		+ 3	619	97		+ 2	99	108		+ 2	110
4. ii.	620		+35	655	98		+ 1	99	118		+ 4	122
14. ii.	623	−23		600	106	− 3		103	110	− 2		108
	Sums	−274	+211			−11	+15			−27	−15	

Table XXII *continued.*

Subject and date	Ventilation l. per m. ×100				R.Q. ×100				Calories per m. ×100			
	I			II	I			II	I			II
1	2	3	4	5	6	7	8	9	10	11	12	13
O. H. I												
25. v.	561		+17	578	69		+ 3	72	140		+ 6	146
21.	577	- 7		570	71	- 1		70	144	+ 3		147
24.	622		+13	635	71		+ 2	73	155		- 2	153
22.	594		+31	625	71		+ 4	75	140		0	140
10.	605		+39	644	82		- 1	81	142		0	142
11.	597		+38	635	79		+ 5	84	148		- 2	146
8.	593			593	82		0	82	128		- 2	126
18.	595		+11	606	93		- 4	89	138		+ 4	142
14.	634	-13		621	92	+ 4		96	138	- 8		130
15.	624		+ 4	628	94		0	94	146		- 6	140
17.	616		+27	643	92		+ 7	99	140		- 2	138
	Sums	-20	+180			+ 3	+16			- 5	- 4	
O. H. II												
9. iv.	538	-18		520	64	+ 2		66	147	-10		137
8.	513		+54	567	70		+ 2	72	135		+ 3	138
24	646	-55		591	73	- 1		72	132	- 5		127
18.	552		+29	581	77		+ 2	79	126		+ 1	127
3.	571		+79	650	79		+ 7	86	128		0	128
6.	552	- 2		550	78	+ 2		80	128	- 3		125
4.	595	-63		532	82	- 2		80	134	-16		118
16.	578		+ 2	580	83		- 3	80	126		+ 2	128
5.	563	-24		539	84	- 2		82	132	- 2		130
10.	575	-11		564	83	+ 1		84	124	0		124
15.	636	-17		619	84	+ 2		86	128	+ 2		130
26.	603	-44		559	88	- 6		82	126	- 6		120
23.	532		+32	564	84		+ 3	87	104		+ 6	110
27.	584		+21	605	86		+ 1	87	118		+ 8	126
25.	659	-24		635	86	+ 2		88	127	- 7		120
19.	581	-14		567	90	- 2		88	123	- 1		122
20.	654	-11		643	94	+ 1		95	133	- 2		131
13.	649		+14	663	98		- 4	94	125		+ 8	133
21.	643		+ 9	652	98		0	98	125		+ 7	132
12.	647	-14		633	100	- 3		97	129	+ 2		131
11.	623		+15	638	98		+ 2	100	125		+ 3	128
14.	655		+50	705	101		- 1	100	125		+13	138
	Sums	-297	+305			- 6	+ 9			-48	+51	

In columns 3 and 4 we have arranged the differences between the ventilation in the first and second experimental period (II–I) putting the negative differences in column 3 and the positive in column 4. Though there are individual deviations (notably the first series of experiments on O. H.) we find on the whole that increases in ventilation occur to the same extent as decreases. In 30 cases out of 69 the second period shows a decrease in ventilation amounting on an average to 0·28 l. per minute while in 36 cases there is an increase amounting on an average to 0·20 l. per minute. As a grand average we have a decrease in ventilation amounting only to 0·016 l. per minute. This means that the introductory period has been of sufficient duration to insure a practically complete quieting down of the ventilation. In the beginning of a period of rest a steady decrease of the ventilation is the general rule.

In the case of O. H. I the almost constant increase in ventilation from the first to the second period is mainly due to a slight inconvenience, caused by the mouthpiece, which became accentuated towards the end of the period and was repeatedly mentioned by the subject.

In columns 6 and 9 we have recorded the quotients found in the first and second period and in columns 7 and 8 the differences (II–I) between them. In column 7 we have put the differences corresponding to a higher ventilation in period I and in column 8 the differences corresponding to a lower ventilation in period I. As most of the differences in column 7 are negative (16 out of 30) and in column 8 positive (25 out of 37), while their sums are respectively negative (− 0·20) and positive (+ 0·65), it follows that an increase in ventilation is correlated, as was to be expected, with an increase in quotient and *vice versa*, but, as the increases show a decided preponderance over the decreases, the final result is an increase in quotient in the second period amounting to 0·0064 ± 0·0036. This increase is nearly double its mean error and is therefore in all probability real. Since the second quotient is the higher we believe that our determinations have generally been made during that period when the probable initial washing out of carbon dioxide is being made good and take it to mean that the resting quotients as determined by us are on an average probably slightly too low.

In columns 10 to 13 we have treated similarly the determinations of metabolism. Here too we find, contrary to our expectations, a distinct correlation with the ventilation. With a decreasing ventilation there is in the greater number of cases (23 out of 30) a fall in metabolism and an increasing ventilation corresponds in 20 cases out of 37 to an increased metabolism. The average decrease in the 30 cases with decreasing ventilation is 0·040 Cal. and the average increase in the 37 cases is 0·010 Cal. On the whole the metabolism in the second period is lower than in the first by 0·0115 ± 0·0062 Cal., a difference which must be assumed to be real.

The correlation between the ventilation and the metabolism might be considered as physiological, since an increase in metabolism must involve an increase in ventilation and *vice versa*. We do not believe, however, that spontaneous oscillations in the metabolism occur during rest within intervals of a few minutes, and think it safer to ascribe the correlation to the technical error in the taking of samples which we have mentioned on p. 303, and which will have just such an effect when the ventilation is not the same in the two consecutive periods.

That the metabolism is on an average lower in the second period than in the first must probably mean that the preliminary period of rest has not always been long enough for the subject to come down to the true standard metabolism. The difference is very pronounced in the case of A. M. N., where it is on an average 0·019 ± 0·008 Cal., but absent in the case of O. H.: 0·002 ± 0·010 Cal. In future determinations of this kind the preliminary period of rest should be prolonged from ½ to ¾ or a whole hour.

The distribution of the variations considered is wholly independent of the respiratory quotient. It is of importance from the point of view of the relation between the quotient and the standard metabolism, treated in Appendix II, that the investigation of the errors affords no ground for assuming that the determinations made at very low or very high quotients should be less reliable or infested with different systematic errors from those at intermediate quotients[1].

When the two determinations made each day are treated as simple repetitions the mean error of their averages which can be called their technical error is determined by $\tau = \frac{1}{2}\sqrt{\frac{\Sigma d^2}{n-1}}$, where d is the difference between each pair of determinations.

We find

Table XXIII.

	R.Q. τ	Cal. per min. τ
I. L.-R. E.	0·016	0·031
A. M. N.	0·014	0·020
O. H. I	0·019	0·021
O. H. II	0·015	0·033
All experiments	0·015	0·027

The technical error of a double determination of the quotient is therefore $\tau = 0{\cdot}015$ and of the metabolism $\tau = 0{\cdot}027$ Cal. or about 2 % of the standard metabolism of our subjects.

APPENDIX II

THE CORRELATION BETWEEN THE RESPIRATORY QUOTIENT AND THE STANDARD METABOLISM.

In discussing the different series of experiments the standard metabolism has been treated for each subject separately and it has been shown that at very low quotients there is a slight increase in metabolism, while in some experiments a tendency towards an increase at high quotients is also apparent.

In order to obtain more definite information upon this point we have compared all our available data concerning the standard metabolism at

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[1] The ventilation shows as might be expected a distinct increase with increasing quotient corresponding to the increasing elimination of carbon dioxide. As we have not counted the respirations and cannot therefore calculate the average depth of respiration or the alveolar ventilation a detailed study of the relation between the ventilation of the lungs and the elimination of carbon dioxide is scarcely worth attempting.

varying quotients. As the metabolism varies with the subject a direct comparison cannot be instituted, but we have calculated the average standard metabolism for each person and determined the percentage deviation from this average for each experimental day. In the case of A. M. N., whose standard metabolism showed a steady decline throughout the three weeks' experiments, we have taken the curve, Fig. 12, as our unit and determined the percentage deviation of each day's result from this curve.

All the figures thus obtained have been plotted in Fig. 22 with the respiratory quotient as abscissa and using different symbols for the different subjects as indicated. In drawing the curve representing the determinations the two lowest values at the quotients 0·82 and 0·845 have been disregarded as probably erroneous.

The curve shows unmistakably and without any apparent difference between the different subjects that the standard metabolism in subjects with a very low protein metabolism, when calculated on the basis of the caloric values for oxygen given by Zuntz, is not independent of the quotient. It has a minimum value between the quotients 0·8 and 0·94, increases by about 5 % when the quotient falls from 0·8 to 0·71 and increases also by about 3 % when the quotient rises from 0·94 to unity. Even between 0·8 and 0·94 it does not appear to be quite constant, but the variation found is only 1 % and is within the limits of error. The dispersion of the single determinations about the curve is $\sigma = 3{\cdot}0\ \%$. As the mean technical error of a double determination is according to Appendix I $\tau = 2\ \%$ the individual day to day variations of each subject's standard metabolism (ϕ), which is found from the equation $\tau^2 + \phi^2 = \sigma^2$, works out as $\phi = 2{\cdot}2\ \%$.

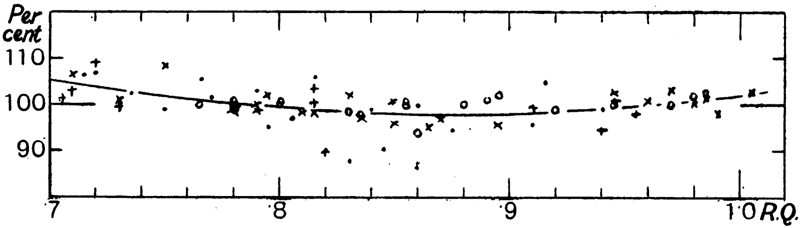

Fig. 22. Percentage variation of standard metabolism with respiratory quotient. Subjects: • J. L., G. L., A. K., R. E., o A. M. N., + O. H. 1917, × O. H. 1918.

A definite explanation of the influence of the materials catabolised upon the standard metabolism, cannot at present be given. It is conceivable, though in our opinion very improbable, that it may be unreal and due to imperfections in the indirect calorimetry employed by us. To settle this point it would be very desirable to have a sufficient number of direct calorimetric determinations of the standard metabolism of human subjects over the whole practicable range of quotients.

When the variation of the metabolism with the quotient must be accepted as real it might be thought to be due at low quotients to incomplete oxidations with excretion of keto-substances. We have repeatedly tested the urine of

Table XXIV.

Date and subject	R.Q.	Cal.	Deviation from average		Deviation from curve
			Cal.	%	
J. L.					δ
1917					
1. ii.	·79	1·055	+0·03	+ 3	+3
2. ii.	·805	·995	−0·03	− 3	−2
	Average	1·025			
G. L.					
25. i.	·765	1·105	+0·06	+ 5·5	+4·5
26. i.	·78	1·035	−0·01	− 1	−1
26. ii.	·795	·995	−0·05	− 5	−4·5
	Average	1·045			
A. K.					
20. ii.	·715	1·17	+0·07	+ 6·5	+2·5
19. ii.	·735	1·13	+0·03	+ 2·5	0
5. ii.	·77	1·115	+0·015	+ 1·5	+1
1. iii.	·86	1·10	±0	0	+2
12. ii.	·875	1·04	−0·06	− 5·5	−3
13. ii.	·91	1·05	−0·05	− 4·5	−2·5
	Average	1·10			
R. E.					
25. iii.	·72	1·36	+0·09	+ 7	+3
26. iii.	·75	1·26	−0·01	− 1	−2·5
20. iii.	·845	1·145	−0·125	−10	−8
6. iv.	·915	1·325	+0·055	+ 4·5	+6·5
7. iv.	·94	1·26	−0·01	− 1	0
	Average	1·27			
A. M. N.					
1918					
10. ii.	·765	1·105	±0[1]	0	−1
8. ii.	·78	1·14	+0·015	+ 1·5	+1·5
9. ii.	·78	1·105	−0·01	− 1	−1
16. ii.	·80	1·055	+0·005	+ 0·5	+1
17. ii.	·80	1·04	±0	0	+0·5
30. i.	·83	(1·085)	(−0·125)	(−10·5)[2]	
7. ii.	·83	1·115	−0·02	− 2	0
15. ii.	·835	1·035	−0·02	− 2	0
29. i.	·85	(1·135)	(−0·085)	(− 7)[2]	
1. ii.	·855	1·195	+0·005	+ 0·5	+2·5
19. ii.	·855	1·02	±0	0	+2
11. ii.	·86	1·03	−0·065	− 6	−4
31. i.	·87	(1·07)	(−0·13)	(−11)[2]	
6. ii.	·88	1·145	±0	0	+2·5
2. ii.	·89	1·19	+0·01	+ 1	+3
3. ii.	·895	1·19	+0·02	+ 2	+4
12. ii.	·92	1·07	−0·015	− 1·5	+0·5
18. ii.	·945	1·03	±0	0	0
5. ii.	·97	1·16	+0·005	+ 0·5	0
13. ii.	·98	1·095	+0·02	+ 2	+1
4. ii.	·985	1·20	+0·035	+ 3	+2
14. ii.	1·045	1·085	+0·02	+ 2	

[1] Deviations from curve, Fig. 12. [2] Very doubtful. See p. 325.

Table XXIV *continued.*

Date and subject	R.Q.	Cal.	Deviation from average		Deviation from curve
			Cal.	%	
O. H. I					δ
1917					
25. v.	·705	1·43	+0·02	+ 1·5	−3
21.	·71	1·45	+0·04	+ 3	−1
24.	·72	1·54	+0·13	+ 9	+5·5
22.	·73	1·40	−0·01	− 0·5	−3·5
10.	·815	1·42	+0·01	+ 0·5	+1·5
11.	·815	1·465	+0·055	+ 3·5	+4·5
8.	·82	1·27	−0·14	−10	−8·5
18.	·91	1·40	−0·01	− 0·5	+1·5
14.	·94	1·335	−0·075	− 5·5	−4·5
15.	·945	1·425	+0·015	+ 1	+2
17.	·955	1·385	−0·025	− 2	−1·5
	Average	1·41			
O. H. II					
1918					
9. iv.	·65	(1·42)	(+0·14)	(+11)[1]	
8.	·71	1·365	+0·085	+ 6·5	+2·5
24.	·73	1·295	+0·015	+ 1	−2
7.	·75	1·39	+0·11	+ 8·5	+7
18.	·78	1·27	−0·01	− 1	−1
3.	·79	1·28	±0	0	0
6.	·79	1·265	−0·015	− 1	−1
17.	·795	1·31	+0·03	+ 2·5	+3
4.	·81	1·26	−0·02	− 1·5	−0·5
16.	·815	1·265	−0·015	− 1	0
5.	·83	1·31	+0·03	+ 2·5	+4
10.	·835	1·245	−0·035	− 2·5	−1
15.	·85	1·285	+0·005	+ 0·5	+2·5
26.	·85	1·23	−0·05	− 4	−2
23.	·855	(1·07)	(−0·21)	(−16·5)[2]	
27.	·865	1·22	−0·06	− 4·5	−2·5
25.	·87	1·24	−0·04	− 3	−0·5
19.	·895	1·225	−0·055	− 4·5	−2·5
20.	·945	1·32	+0·04	+ 3	+3·5
13.	·96	1·29	+0·01	+ 1	+1
22.	·97	1·32	+0·04	+ 3	+2·5
21.	·98	1·28	±0	0	−1
12.	·985	1·30	+0·02	+ 1·5	+0·5
11.	·99	1·26	−0·02	− 1·5	−2·5
14.	1·005	1·32	+0·04	+ 3	+0·5
	Average	1·28			

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[1] Somewhat doubtful.

[2] Considered as erroneous. See p. 333.

our subjects for aceto-acetic acid and found no evidence of acidosis, and the rise in metabolism begins at quotients which are too high to admit of acidosis.

In our opinion the higher metabolism both at low and at high quotients is most probably due to transformation processes of carbohydrate into fat at high quotients and of fat (and protein) into carbohydrate at low quotients. Such transformations will cause at high quotients an increase in the total respiratory quotient over that of the true catabolic processes and at low quotients a decrease, provided of course that the transformation products are stored, at least provisionally.

It is significant therefore that we have occasionally observed quotients above unity, when the subjects were on a carbohydrate diet, and below 0·71, when the diet consisted chiefly of fat. We have no reason to doubt the reality of these quotients, which must mean that synthetic transformations take place, and it is a natural inference that the same transformations take place, though with diminished intensity, when the quotient is somewhat below 1·00 or above 0·71.

Additional evidence corroborating the view that a transformation of fat into carbohydrate takes place regularly, when the respiratory quotient is below 0·8, and the reverse transformation, when the quotient is above 0·9, will be given in Appendix III.

APPENDIX III

THE CHANGE IN RESPIRATORY QUOTIENT TAKING PLACE ON THE TRANSITION FROM REST TO MUSCULAR WORK.

In Table XXV we have compared the average respiratory quotient found each day during rest with the quotient observed on the same day during the first experimental period of work. The experiments have been arranged as usual in the order of increasing quotients during rest.

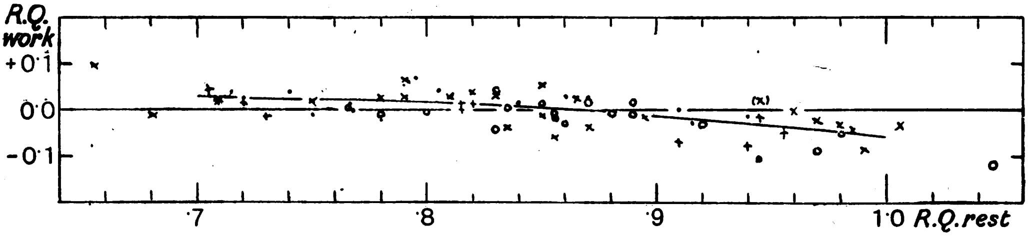

Fig. 23. Change in respiratory quotient on transition from rest to work.
Subjects: • J. L., G. L., A. K., R. E., o A. M. N., + O. H. 1917, × O. H. 1918.

The results have been plotted in Fig. 23 with the quotient during rest as abscissa and the differences in quotient between rest and work as ordinates. When the quotient during work is increased over that during rest the difference has been denoted as positive. Though the individual results are somewhat irregular it is unmistakable that at low quotients there is on the whole an increase in the quotient on the transition from rest to work, but at high (above 0·9) there is a very decided decrease, amounting, when the quotient during rest approaches unity, to about 0·05.

The dispersion of the individual results about the curve drawn is $\sigma = \pm 0{\cdot}028$ which is partly explained by the technical errors of the determinations involved. The technical error on the difference between resting and working quotient here considered is about $\tau = \pm 0{\cdot}016$. Those variations from the curve, which are due to the subjects, are therefore $\phi = \pm 0{\cdot}023$.

There are two known sources of systematic error in the comparison here given between the respiratory quotients during rest and work. The first is that we have compared the quotient during rest, not with the quotient at the beginning of the work, but with the quotient found during a period extending from 30 to 50 (or 60) minutes after the beginning of work. According to the results given in Appendix IV we must assume that the quotient at the beginning of the work was generally a little higher and by making a somewhat uncertain extrapolation we find it to be about 0·01 higher. A correction of this magnitude would shift the curve slightly to the right so that we should have the zero point at 0·91 instead of at 0·87.

Another systematic error is that the quotients determined during rest are (as shown in Appendix I) probably on an average slightly too low, which may possibly compensate the error on the quotients during work.

Whether the curve shall finally be shifted slightly to the right or slightly to the left the essential result remains unchanged: that on the transition from rest to constant work of moderate intensity a rise in quotient takes place only when the quotient was low beforehand, but a fall when it was high, while at intermediate quotients the average change is very slight.

Our result as here summarised agrees with the findings of Zuntz and his school, but is strikingly at variance with the results reported by Benedict and Cathcart [1913], who found that the quotients during work were generally higher than in a preceding period of rest and were increased more or less in proportion to the severity of the work performed. The quotients determined by Benedict and Cathcart during work have been adversely criticised by Lindhard [1915] on the ground that some of them are undoubtedly influenced by forced respiration and that there is good reason to think that they are generally so influenced on account of the inconvenience of breathing through a mouthpiece and into a respiration apparatus. We would point out further, that since it can be deduced from the experiments of Carpenter [1915], referred to above (p. 293), that the "unit" apparatus employed gives quotients during rest which are on an average 0·03 too high, it is quite possible that during work there is an even greater systematic error.

To explain the increase in standard metabolism both at low and at high quotients we have in Appendix II offered the hypothesis that synthetic processes take place, resulting respectively in the formation of carbohydrate or

Table XXV.

Date	R.Q. rest	R.Q. work	Diff.	Deviation from curve 100 δ
J. L.		●		
1. ii.	·79	·846	+·055	+ 4
2. ii.	·805	·846	+·04	+2·5
G. L.		●		
25. i.	·765	·766	0	- 2
26. i.	·78	·762	-·02	-3·5
26. ii.	·795	·863	+·07	+5·5
A. K.		●		
20. ii.	·715	·757	+·04	+ 1
19. ii.	·74	·781	+·04	+1·5
1. iii.	·86	·891	+·03	+2·5
12. ii.	·87	·896	+·025	+2·5
13. ii.	·91	·909	0	+ 1
R. E.		●		
25. iii.	·72	·747	+·025	0
26. iii.	·75	·742	-·01	- 3
20. iii.	·84	·854	+·015	+0·5
6. iv.	·915	·891	-·025	- 1
7. iv.	·94	·932	-·01	+ 1
A. M. N.		o		
10. ii.	·765	·770	+·005	-1·5
9. ii.	·78	(·768)	-·01[1]	- 3
8. ii.	·78	·770	-·01	-2·5
16. ii.	·80	·793	-·005	- 2
30. i.	·83	·873	+·045	+3·5
7. ii.	·83	·787	-·045	-5·5
15. ii.	·835	·841	+·005	-0·5
29. i.	·85	·866	+·015	+ 1
1. ii.	·855	·850	-·005	- 1
19. ii.	·855	·844	-·01	-1·5
11. ii.	·86	·829	-·03	-3·5
31. i.	·87	·890	+·02	+ 2
6. ii.	·88	·876	-·005	-0·5
2. ii.	·89	·886	-·005	0
3. ii.	·89	·910	+·02	+2·5
12. ii.	·92	·889	-·03	-1·5
18. ii.	·945	·843	-·10[2]	- 7
5. ii.	·97	·882	-·09	-5·5
13. ii.	·98	·930	-·05	- 1
14. ii.	1·045	·926	-·12	
O. H. I		+		
25. v.	·705	·744	+·04	+ 1
21.	·71	·731	+·02	- 1
24.	·72	·735	+·015	- 1
22.	·73	·717	-·015	- 4
10.	·815	·814	0	- 1
11.	·815	·830	+·015	+0·5
8.	·82	·836	+·015	+0·5
18.	·91	·839	-·07	- 6
14.	·94	·864	-·075	- 5
15.	·945	·929	-·015	+ 1
17.	·955	·904	-·05	- 2
O. H. II		×		
9. iv.	·655	·751	+·095	
8.	·71	·728	+·02	- 1
7.	·75	·768	+·02	0
18.	·78	·808	+·03	+1·5
3.	·79	·855	+·065	+ 5
6.	·79	·819	+·03	+1·5
4.	·81	·840	+·03	+ 2
16.	·82	·862	+·04	+ 3
5.	·83	·858	+·03	+ 2
10.	·835	·797	-·04	- 5
15.	·85	·904	+·055	+ 5
26.	·85	·838	-·01	-1·5
23.	·855	·796	-·06	-6·5
27.	·865	·890	+·025	+2·5
25.	·87	·832	-·04	- 4
19.	·895	·880	-·015	- 1
20.	·945	(·966)	(+·02)[3]	
13.	·96	·961	0	+ 3
22.	·97	·951	-·02	+1·5
21.	·98	·950	-·03	+ 1
12.	·985	·944	-·04	0
11.	·99	·904	-·085	- 4
14.	1·005	·974	-·03	+ 2
			Sum	- 25

[1] Slightly uncertain. [2] Slightly uncertain.

[3] Doubtful.

fat with consequent lowering or raising of the respiratory quotient. The quotient of the catabolic processes alone would, according to this view, be higher when the total quotient is low and lower when it is high. When work is being performed the anabolic processes may continue unaltered or may possibly become reduced, because the necessary blood supply is deflected to the working muscles, but there is no reason to think that they should be intensified in proportion to the work. If we assume with Zuntz that the proportion between the catabolism of carbohydrate and fat remains on the whole unchanged on the transition from rest to work, while the anabolic processes going on at the time are continued without any increase proportional to the increased catabolism, their influence upon the total quotient becomes diminished, and we shall consequently obtain a rise in total quotient when it was low before the work and a fall when it was high—or just what we have found.

The theoretical conception to which our experiments appear to lead up is therefore the following, which is meant not as a proved theory but as a definite formulation of a working hypothesis.

The proportion of carbohydrate to fat catabolised is a function of the relative available quantities of the two substances, and substantially the same during rest and during muscular work.

Fat is formed from carbohydrate and stored up when the available supply of carbohydrate is in excess of the supply of fat. The formation becomes distinct at quotients above 0·9. When the total quotient during rest has reached unity the catabolic quotient is only about 0·95. The conversion of carbohydrate into fat takes place with a loss of energy and a consequent increase of a few per cent. in the total standard metabolism at high quotients.

Sugar (or substances allied to carbohydrates) is formed from fat (and protein) and stored up when the available supply of fat is in excess of the supply of carbohydrate. The formation becomes distinct at quotients below 0·8. When the total quotient during rest has reached 0·71 the catabolic quotient is about 0·74. The conversion of fat takes place with a loss of energy and a consequent increase in the standard metabolism at decreasing quotients.

It is a consequence of this hypothesis that neither fats alone nor carbohydrates alone are suitable for the supply of the energy requirements of the body, but that the catabolic disintegration of either of these substances requires the presence and the simultaneous catabolisation of the other.

While it has long been concluded from the acidosis and excretion of keto-substances in severe diabetes and during starvation that carbohydrates are necessary for the complete catabolisation of fat and our results only lend support to this view, it is, so far as we are aware, a new hypothesis that fats are likewise necessary for the catabolisation of carbohydrate.

APPENDIX IV

THE VARIATION OF THE RESPIRATORY QUOTIENT AND THE METABOLISM DURING ONE HOUR OF CONSTANT WORK.

In Table XXVI we have arranged the three work determinations of each day in horizontal lines and figured out the differences in respiratory quotient and total metabolism between the three periods. For each subject we have taken the days in the order of increasing quotients. For the sake of convenience we have multiplied the quotients by 1000 and the Calories per minute

Table XXVI.

Date	R.Q. during work × 1000					Metabolism during work Cal. × 100				
	I	Diff. II–I	II	Diff. III–II	III	I	Diff. II–I	II	Diff. III–II	III
J. L.										
16. i.	767	+ 4	771	+20	791	608	− 3	605	+11	616
15. i.	772	−16	756	+ 4	760	592	+15	607	+39	646
1. ii.	846	+27	873	− 5	868	568	0	568	+ 6	574
2. ii.	846	− 3	843	− 7	836	584	+ 3	587	− 5	582
G. L.										
26. i.	762	− 5	757	+ 5	762	479	+ 2	481	+ 7	488
25. i.	766	+11	777	−26	751	463	+ 8	471	+19	490
26. ii.	863	− 6	857	−24	833	459	+19	478	−10	468
18. i.	906	−21	885	−18	867	428	+17	445	0	445
19. i.	927	−14	913	−13	900	472	− 6	466	−18	448
A. K.										
20. ii.	757	+ 5	762	− 5	757	590	+ 9	599	+ 8	607
19. ii.	781	− 7	774	−19	755	531	+19	550	− 1	549
1. iii.	891	−21	870	−24	846	530	+24	554	+ 9	563
12. ii.	896	−29	867	− 6	861	522	+ 6	528	+ 8	536
13. ii.	909	−16	893	−10	883	538	+ 3	541	+19	560
R. E.										
26. iii.	742	−12	730	+ 8	738	576	+11	587	+15	602
25. iii.	747	− 5	742	+ 9	751					
20. iii.	854	−18	836	−19	817	538	0	538	+ 6	544
6. iv.	891	+ 4	895	−16	879	523	− 1	522	+ 1	523
7. iv.	932	−14	918	−21	897	532	+ 9	541	+25	566
A. M. N.										
9. ii.	(768)	− 4	764	− 4	760	(512)	+25	537	− 1	536
8. ii.	770	− 9	761	+ 3	764	536	+ 2	538	0	538
10. ii.	770	− 7	763	− 2	761	527	+ 2	529	+ 9	538
7. ii.	787	− 5	782	+23	805	514	+11	525	− 6	519
16. ii.	793	−14	779	+23	802	516	+11	527	−14	513
11. ii.	829	+ 1	830	− 5	825	511	+ 1	512	+10	522
15. ii.	841	− 3	838	+ 4	842	499	+ 7	506	+ 5	511
18. ii.	(843)	−14	829	+ 4	833	(491)	+ 5	496	+10	506
19. ii.	844	+ 2	846	− 6	840	495	+ 6	501	+ 1	502
1. ii.	850	− 4	846	0	846	529	+ 7	536	+11	547
29. i.	866	− 6	860	−12	848	612	−14	598	+ 9	607
30. i.	873	−11	862	− 7	855	533	− 3	530	+13	543
6. ii.	876	0	876	− 8	868	511	− 2	509	+11	520
5. ii.	882	+25	907	−31	876	519	− 3	516	+10	526
2. ii.	886	−16	870	+ 2	872	520	+ 7	527	+ 6	533
12. ii.	889	− 5	884	− 8	876	496	− 1	495	+12	507
31. i.	890	− 2	888	− 5	883	520	+ 4	524	+ 8	532
3. ii.	910	−14	896	− 4	892	568	− 5	563	+ 5	568
14. ii.	926	− 2	924	+16	940	514	− 4	510	+ 5	515
13. ii.	930	− 5	925	+ 3	928	493	+ 3	496	+13	509

Table XXVI *continued.*

	R.Q. during work × 1000					Metabolism during work Cal. × 100				
Date	I	Diff. II–I	II	Diff. III–II	III	I	Diff. II–I	II	Diff. III–II	III
O. H. I										
22. v.	717	− 8	709	+10	719	671	− 1	670	+ 8	678
21.	731	−16	715	− 1	714	682	+ 3	685	+ 3	688
24.	735	− 1	734	+31	765	656	+ 7	663	−21	642
25.	744	−13	731	+15	746	668	0	668	0	668
10.	814	−11	803	+ 7	810	682	− 1	681	+ 1	682
11.	830	+ 5	835	−21	814	669	− 8	661	+11	672
8.	836	− 7	829	−11	818	686	− 3	683	+ 4	687
18.	839	−22	817	−18	799	656	+12	668	+ 2	670
14.	864	+ 6	870	+ 6	876	668	− 8	660	− 7	653
17.	904	− 8	896	−15	881	634	+11	645	+ 5	650
15.	929	− 7	922	− 3	919	650	+ 4	654	− 3	651
O. H. II										
8. iv.	728	+12	740	− 8	732	664	− 8	656	+11	667
9.	751	−14	737	+11	748	644	+14	658	− 7	651
7.	768	− 2	766	− 3	763	649	+ 3	652	+ 4	656
23.	796	− 8	788	−10	778	611	+10	621	+ 8	629
10.	797	+ 7	804	0	804	650	− 6	644	+13	657
18.	808	0	808	− 8	800	627	+ 1	628	+11	639
17.	816	− 5	811	−20	791	627	+ 3	630	+21	651
6.	819	+20	839	− 9	830	636	−10	626	+11	637
25.	832	−10	822	+ 7	829	614	+ 3	617	+ 3	620
26.	838	+ 8	846	+ 2	848	613	+ 4	617	− 4	613
4.	840	− 1	839	− 8	831	662	− 7	655	− 5	650
3.	855	−12	843	+ 2	845	642	+ 5	647	0	647
5.	858	−12	846	−20	826	636	− 5	631	+16	647
16.	862	−11	851	− 2	849	618	+ 6	624	0	624
19.	880	+ 4	884	−14	870	622	− 4	618	+ 6	624
27.	890	+17	907	−15	892	608	− 5	603	+ 8	611
11.	904	− 1	903	− 1	902	631	+ 1	632	+ 4	636
15.	904	− 9	895	−13	882	607	+ 6	613	+ 5	618
12.	944	+ 1	945	−28	917	622	− 6	616	+12	628
21.	950	−11	939	+31	970	605	− 3	602	− 2	600
22.	951	−16	935	+14	949	598	− 2	596	+10	606
13.	961	+ 6	967	−23	944	616	− 4	612	+14	626
20.	(966)	−31	935	+ 2	937	(594)	+18	612	+ 6	618
14.	974	−36	938	+ 2	940	610	+17	627	− 9	618

by 100 so as to have the differences in whole numbers. In the experiments on J. L., G. L., A. K. and R. E. the periods were of about 30 minutes duration; in the first series of experiments on O. H. they were of about 24 minutes and in the remainder of the experiments of 21 minutes duration.

The table shows that the quotient varies irregularly but on the whole very slightly. In most cases there is a slight decrease in quotient from the first to the second and again from the second to the third period but it does not amount to more than about 0·01, and in some cases there is an increase of similar magnitude. The largest difference observed between two periods is 0·035. We have averaged the differences found in all the experiments (74) and those found in the most reliable series with periods of about equal length (series 2–4) with the following results:

Number	R.Q.II–R.Q.I	R.Q.III–R.Q.II	Cal. II–I	Cal. III–II
74	−0·0056	−0·0040	+0·033	+0·054
55	−0·0051±0·0014	−0·0025±0·0018	+0·019±0·010	+0·047±0·010

There is a slight fall in the quotient from the first to the second period and a still smaller from the second to the third. Though the work remains constant the metabolism increases slightly from the first to the second period and somewhat more from the second to the third. As the fall in quotient must cause an increase in the metabolism a correction can be applied to give the change in metabolism from period to period, on the assumption that the quotient remained constant. According to the average result of our determinations a decrease in the quotient of 0·01 will correspond approximately to an increase in the metabolism of 0·02 Cal. In the 55 best experiments the corrected increase in metabolism from the first to the second period will be therefore 0·019 − 0·51 × 0·02 = 0·009 ± 0·010 and from the second to the third 0·047 − 0·25 × 0·02 = 0·042 ± 0·010.

The corrected increase in metabolism from period to period must be taken to show the influence of fatigue, and the calculations show that such an influence is practically absent in the second period but distinct, though small, in the third.

In order to see whether the diet has any influence upon the variation of the quotient during work and upon the onset of fatigue we have averaged the differences in the experiments with initial quotients between 0·7 and 0·85 and compared them with the averages derived from the remaining experiments with quotients between 0·85 and 1·00. The results are as follows:

Number	R.Q.	R.Q.II–R.Q.I	R.Q.III–R.Q.II	Cal. II–I	Cal. III–II
28	0·7 −0·85	−0·0043±0·0017	−0·0001±0·0024	+0·031±0·014	+0·032±0·016
27	0·85 − 1·00	−0·0059±0·0023	−0·0049±0·0025	+0·007±0·014	+0·062±0·012

Caloric difference corrected for decrease in quotient

R.Q.	Cal. II–I	Cal. III–II
0·7 −0·85	+0·022±0·018	+0·032±0·021
0·85 − 1·00	−0·005±0·017	+0·052±0·017

The fall in quotient during a one hour period of constant work is slightly larger at high quotients than at low, and the influence of fatigue upon the economy of the work appears to be very nearly the same at all quotients. All the changes observed are scarcely outside the limits of error.

In our experiments work has been performed at the same rate for 30 minutes before the beginning of the first period. An extrapolation shows that at the beginning of work the respiratory quotient has probably on an average been about 0·01 higher than in the first experimental period.

The results here given show that the organism maintains during work a remarkably constant proportion between the amounts of carbohydrate and fat catabolised. This proportion is evidently a function of the available supplies of the two sources of energy, and the change in quotient shows that the balance between carbohydrate and fat is very slowly altered as the work progresses in favour of the latter.

SUMMARY.

1. Methods are described for determining in 20 minute periods the respiratory exchange of human subjects doing constant work on an ergometer placed in a Jaquet respiration chamber.

2. The technical error on determinations of total metabolism made by these methods is below 1 % and the respiratory quotient can be determined with a maximum error of 0·005.

3. Four series of experiments (about 220 determinations) on six different subjects, living during the experiments on a diet poor in protein, have been made to study the relative value of fat and carbohydrate as a source of muscular energy. All the series agree in showing that work is more economically performed on carbohydrate than on fat. When the work was sufficiently severe the subjects performed it with greater difficulty on fat than on carbohydrate and became much more tired.

4. The net expenditure of energy (standard metabolism deducted) necessary to perform one Calorie technical work on the ergometer has varied between about 5·5 and 4 Cal. At a constant quotient it varies with the subject and for the same subject it decreases with increasing training. During one hour of work it generally rises slightly from fatigue.

5. For the single subject and on a constant level of training the relation between the respiratory quotient and the net expenditure of energy per unit work can be expressed graphically as a straight line. Since the proportion of fat to carbohydrate catabolised is also a straight line function of the quotient the difference in value for muscular work between fat and carbohydrate can be expressed by a single figure: the waste of energy from fat. In the three best series of experiments the net expenditure of energy per Cal. technical work varies from about 4·6 Cal. when fat alone is catabolised (R.Q. = 0·71) to about 4·1 Cal. when carbohydrate alone is catabolised (R.Q. = 1·00). The waste of energy from fat is 0·5 Cal. or 11 % of the heat of combustion of the fat.

6. The standard metabolism (during rest, in the postabsorptive state) of a human subject is not independent of the preceding diet. When the diets are poor in protein it is lowest at intermediate quotients and increases about 5 % when the quotient falls to about 0·71 and about 3 % when the quotient rises to about unity.

7. On the transition from rest to moderate muscular work the respiratory quotient is generally altered. On an average it is increased when the quotient was low and diminished when it was high before the work. The fall at high quotients is greater (0·05) than the increase at low (0·03). At quotients between 0·8 and 0·9 the average change on the transition to work is very slight.

8. It is suggested as a working hypothesis:

that both during rest and during work the proportion of fat to carbohydrate catabolised is a function of the available supplies of these substances;

that carbohydrate is formed from fat and provisionally stored when the quotient is below 0·8 while a corresponding transformation of carbohydrate to fat takes place when the quotient is above 0·9;

that these anabolic processes make the total respiratory quotient lower than the catabolic when this is low and higher when it is high and that they give rise to an extra expenditure of energy during rest;

and finally that during work the anabolic processes (combined with storage) are not increased in proportion to the catabolic, whereby the total quotient is lowered when it was high and raised when it was low beforehand.

9. During one hour of constant work of moderate intensity the respiratory quotient decreases on an average only 0·008; slightly more at high quotients and less at low. The metabolism per Cal. technical work increases a little (0·065 Cal.). Part of the increase is due to the fall in quotient (0·01 Cal.) and the rest to fatigue. The effect of fatigue upon the economy of the work appears to show itself earlier when the quotient is low than when it is high.

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