PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Respiratory Exchange of Man during and after Muscular Exercise

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PHILOSOPHICAL TRANSACTIONS.

I.—The Respiratory Exchange of Man During and After Muscular Exercise.*

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Contents.

Introduction.

A good deal of attention has been directed of late to the alteration of the respiratory exchange and respiratory quotient during muscular exercise, with a view to elucidating the character of the metabolism and the behaviour of the respiratory centre. Hitherto, it has, as a rule, been the custom to make only a few determinations of the total respiratory exchange in any one experiment at rather long intervals from one another. Such a method, though it may give the general and broader features of the respiratory exchange, especially when experiments are multiplied, is clearly ill adapted to show any rapid variations that may occur. The individual periods during which the respiratory exchange is actually determined may be too long (this length is often essential, in order to render negligible slight errors which would become significant if it were curtailed), and the long intervals between the different determinations are undesirable.

One of us, in conjunction with Haldane, Henderson, and Schneider,† attempted to obtain information on the course of the total respiratory exchange in the period of rest immediately following a short and violent muscular exertion at an altitude of

* The experiments described in this paper were made in 1913, and the method we adopted, and some of our results, were described at the Nineteenth International Physiological Congress at Groningen in that year. Pressure of other work prevented us from publishing our results at that time, and during the war it was impossible for us to deal with our material, as we were on military service.

† Douglas, Haldane, Yandell Henderson, and Schneider, 'Phil. Trans.,' B, vol. 203, p. 185 (1913).

over 14,000 feet on Pike's Peak, using for this purpose the bag method of DOUGLAS.* On this occasion, four determinations of the total respiratory exchange were made in each experiment at different intervals after the cessation of the muscular exertion, and, by making a considerable number of experiments, it was possible to obtain a fairly complete picture of the course of events in the hour-and-a-half immediately succeeding the muscular exertion. The main disadvantage was that, as the experiments had to be made on different days, the initial values for the resting respiratory exchange and respiratory quotient varied considerably in the different experiments. From a consideration of these experiments, it was, however, evident to us that the bag method could easily be adapted to give a practically continuous record of the respiratory exchange in a single experiment, and that the result would be infinitely more satisfactory than that obtained from a few observations made in each of a number of different experiments.

EXPERIMENTAL METHOD.

The general arrangement of the apparatus used by us is shown in fig. 1. The subject sat on a Krogh bicycle ergometer,† and breathed through a mouthpiece

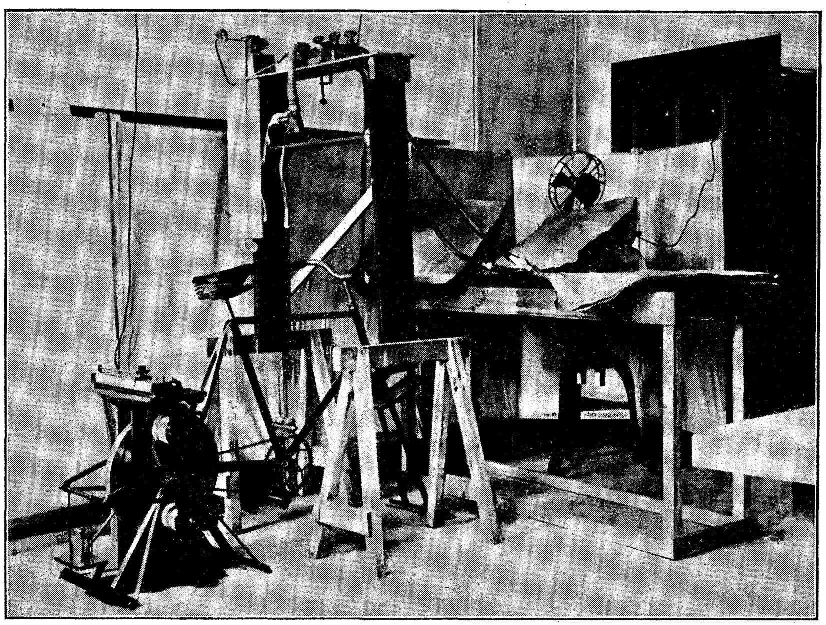

FIG. 1.

connected with inspiratory and expiratory valves. A flexible rubber pipe passed from the expiratory valve to the centre of a piece of brass tubing, into the opposite side, of which were let four short pieces of brass tubing, so that, when the ends of the pipe were included, a six-way distributing system for the expired air was formed.

* 'Journ. Physiol.,' vol. 42; Proc. Physiol. Soc.,' p. xvii (1911).

† 'Skand. Archiv f. Physiol.,' vol. 30, p. 375 (1913).

One end of the main brass tube was closed by a plain rubber stopper, the other by a rubber stopper through which passed a glass tube connected with a tambour writing on a Mackenzie polygraph. The four short pieces of brass tubing were connected to large-bore brass taps, and these in turn by means of lengths of rubber tubing to four gas bags, in which the expired air was collected, the mouth of each gas bag being fitted with a large-bore aluminium tap.* The bore of the rubber and brass tubes was $\frac{3}{4}$ inch. Fig. 2 gives a diagram of the distributing system.

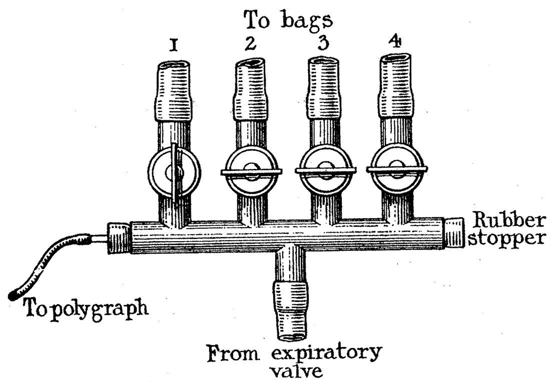

FIG. 2.

Towards the close of the investigations described in this paper, a somewhat different arrangement of the apparatus was devised, and this is shown in fig. 3. In

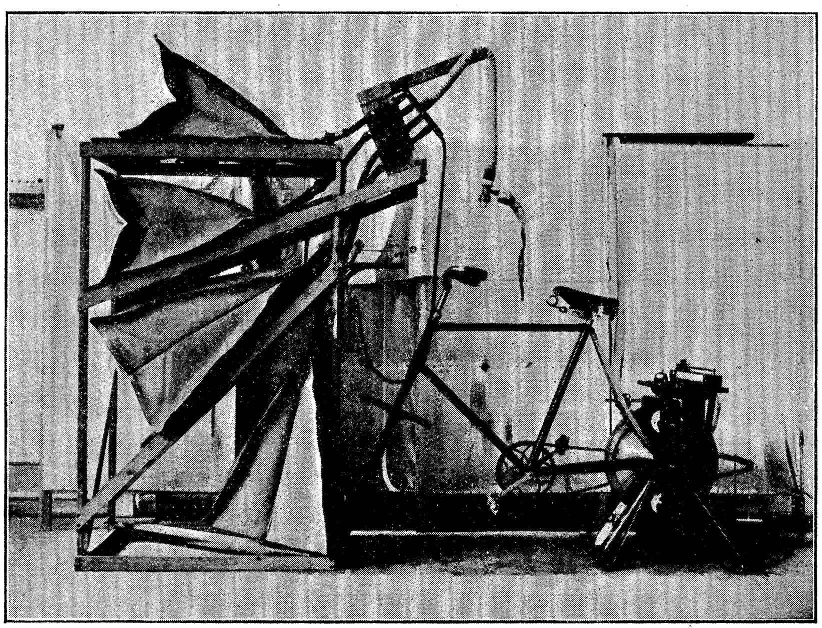

FIG. 3.

* The gas bags, aluminium taps, and valves were made by Messrs. Siebe, Gorman and Co., Westminster Bridge Road, S.E. The valves had been made of specially large bore for us, and offered hardly any appreciable resistance to the passage of even 100 litres of expired air per minute.

this form the bags were mounted one above another in a wooden framework, so that the pipes connecting the distributing system with the bags were reduced considerably in length, and the whole apparatus was rendered far more compact and convenient to work with. All the experiments described in this paper were, however, made with the arrangement shown in fig. 1.

The course of an experiment was as follows: The whole apparatus, including connecting pipes and bags, was first filled with expired air by breathing through the respiration valves. The rubber stopper was then removed from the main brass tube in the distributing system, and the bags emptied in succession by pressing on them and finally rolling them up, the taps on the distributing system being closed directly this was completed. This procedure ensured that any air remaining in the bags and connecting tubes would have approximately the same composition as the expired air entering them during the experiment, and, as the bags were always emptied through the meter in precisely the same way when measuring the volume of expired air collected, any error due to the residual volume of air in the bag was rendered negligible.

The subject then seated himself on the bicycle ergometer with his feet on the foot rests, and maintained himself in as complete a condition of rest as possible, breathing through the valves with a clip on his nose. The expired air passed through the free opening to air in the distributing system. After a preliminary period of 10 or 15 minutes, the rubber stopper was placed in the free opening at the end of an expiration, and one of the taps in the distributing system was turned simultaneously, so that the expired air was diverted into the corresponding bag, the time being noted on a stop-watch. After a sufficient sample had been collected (in about 5–6 minutes), the tap was closed at the end of an expiration and the rubber stopper simultaneously removed, the time being again noted; the subject continued to breathe through the valves to air. The bag, after turning the aluminium tap which closed its mouth, was removed from the tube connecting it with the distributing apparatus and carried to the meter (a wet meter of the Bohr pattern giving 10 litres per revolution), where the volume of expired air collected was measured, after mixing it thoroughly by frequent pressure on the bag, and a small sample was reserved for analysis. After this the empty bag was reattached to the apparatus in readiness for another sample. In some experiments, a second determination of the resting respiratory exchange was made before commencing the muscular work, the total period of rest before starting the work being correspondingly increased. The changes in pressure in the distributing system at each breath were recorded by means of the polygraph, and the tracing therefore gave the number of breaths that were taken while the expired air was being collected.

As soon as the resting respiratory exchange had been determined, the subject commenced to pedal the bicycle against the electric brake. Three different loads were employed in the different experiments, and the muscular work was kept up for either a shorter or a longer period. The subject kept time in pedalling to a metronome placed just in front of him, set at a speed that he found to be convenient (176 revolutions of the back wheel, or 50 complete revolutions of the pedals per minute). The steadiness of the rate of pedalling was further checked by reading the automatic counter on the ergometer at intervals.

While the muscular exercise was in progress, either two or four determinations of the respiratory exchange, depending on the duration of the exercise, were made at intervals, in the same way as that described above. With the last determination of the respiratory exchange during the exercise, the collection of the samples of expired air became continuous. Directly the bag in which the last sample of expired air was collected during the exercise was full, the observer told the subject to stop working, and simultaneously closed the tap on the distributing system connected with the full bag, and opened the tap connected with one of the other bags. The moment this one was filled, he turned the expired air into the third bag, and so on, always turning the taps at the end of an expiration and noting the time on the stop-watch (we used a stop-watch with a split seconds hand, so as to allow us to note the time accurately without disturbing the continuous record of the time). As the bags were filled, they were carried away and their contents measured, reserving samples for analysis, and they were then replaced on the apparatus ready for use again. As soon as the subject received the word to stop, he replaced his feet on the foot rests and resumed his previous condition of rest, and remained thus until the close of the experiment.

In an experiment, one of us (either Douglas or Hobson) acted as subject, the second looked after the distributing taps and noted the times, while the third removed the bags as they were filled and measured their contents, noting the temperature and taking samples for subsequent analysis. Even in the experiments which involved the greatest hyperpnœa, we found that it was possible, when using four bags on the apparatus, to complete the measurement of the sample taken just before stopping the work, and to return the bag to the apparatus in plenty of time for the reception of the fourth sample after the cessation of the work. After this, the hyperpnœa had diminished to such an extent that the bags took a considerable time to fill, and measurement of the different samples became easy.

In order to keep the subject cool during the muscular exercise a current of air was allowed to play on him from an electric fan, and in the severe work experiments, two fans were used for this purpose, the fans being turned off soon after the subject ceased to work.

The general accuracy of the Douglas method for determining the respiratory exchange has been proved by Carpenter* by comparison with different forms of the Benedict apparatus, the Zuntz-Geppert apparatus, and the Tissot apparatus. We

* "A Comparison of Methods for Determining the Respiratory Exchange of Man," 'Publication No. 216, Carnegie Institute of Washington,' 1915.

may note here that we tested the bags we employed to make sure that any diffusion of gas through the walls was negligible. CARPENTER has some distrust of the Siebe Gorman valves, but we took care to test the ones that we used in these experiments, to see whether there was any leakage backwards through the inspiration valve. For this purpose, we did two series of experiments, one at rest, the other at work. In each series determinations of the respiratory exchange were made alternately, firstly with the valves used without any safeguard, and secondly with the addition of a rubber tube 157 cm. long and 2·5 cm. in bore on to the inlet side of the inspiration valve. If there were any material leakage backwards through the valve, the expired air which had leaked out would be held up in the rubber tube, and would be rebreathed at the next breath, and the total respiratory exchange would consequently be found to be greater with the long tube than without it. The results are given in Table I.

TABLE I.

Duration of observation.	Respiratory exchange in c.c. per minute at 0° and 760 mm.		Respiratory quotient.	Breaths per minute.	At 37°, moist, and prevailing barometer.	
	O_2.	CO_2.			Litres breathed per minute.	C.c. per breath.
5′ 47″ rest	297	235	0·791	20·6	10·0	484
*5 7 ,,	297	239	0·805	20·1	10·2	505
5 56 ,,	280	218	0·779	20·2	9·4	465
*6 21 ,,	288	227	0·788	19·8	9·6	485
1 28 work	1605	1538	0·958	25·2	41·7	1654
*1 32 ,,	1600	1506	0·941	25·4	40·8	1606
2 23 ,,	1620	1489	0·919	25·6	40·5	1582
*2 23 ,,	1668	1535	0·920	25·2	41·2	1635

* Samples taken with tube on the inspiration valve.

Rested for 10′, and worked for more than 5′ before beginning to take the samples. Work = 704 kg.m. per minute.

It will be seen that in the rest experiments there are slight differences between the successive results, but there is no definite indication that the results obtained with the addition of the long tube are higher than those without it. In the work experiments the oxygen consumption progressively increases, and the respiratory quotient falls. This, however, is quite characteristic of the respiratory exchange during work in the case of DOUGLAS, who served as the subject in these experiments (see Tables and figures below), and here again there is no distinct indication of any serious loss of the expired air by leakage backwards through the inspiratory valve. We always took care to keep the valves as vertical as possible with the inspiratory valve lowermost—an important point, as the mica discs of the Siebe Gorman valves are closed only by gravity and are not assisted by a spring.

DOUGLAS felt quite comfortable when sitting still on the bicycle, but HOBSON always found the position rather irksome. This may account for the high respiratory exchange shown by Hobson when at rest, for this was more than one would have expected even when one allowed for the fact that Hobson was bigger and of greater muscular development than Douglas. Hobson was in far better muscular condition than Douglas, who was quite out of training.

All our experiments were commenced about two hours after taking a light breakfast. In some respects this is an undesirable feature, but as Benedict and Cathcart's experiments,* which were made on a subject in the post-absorptive state, *i.e.*, when he had taken no food for the previous 12 hours, show the same type of changes as do our experiments, we can feel tolerably certain that though the food may have influenced the degree of the changes of the respiratory exchange caused by the muscular work in our experiments, it has not seriously influenced their general character.

Experimental Results.

1. *Moderate Work of* 704 *kg.m. per minute.*

(*a*) Short period of muscular work, viz., about $\frac{1}{4}$ hour.

The results are given in Table II, and Experiment 4 is shown graphically in fig. 4.

These were our earliest experiments, and the data are not altogether complete, Experiments 2 and 3 lacking determinations of the respiratory exchange in the preliminary period preceding the work. During the work the respiratory exchange per minute was about 1700 c.c. of oxygen and 1500 c.c. of carbon dioxide. Hobson showed higher values than Douglas, but it may be noted that his respiratory exchange at rest was always considerably above that of Douglas. After the stop of the exercise the respiratory exchange falls back extremely rapidly at first, and then more slowly to a value which, so far as can be judged from the available data, corresponds pretty closely with the preliminary resting value obtained just before the exercise commenced.

The respiratory quotient is distinctly raised during the work in Experiment 1 (Douglas), and a similar rise seems probable in Experiment 3; but in Experiment 4 (Hobson) there is little or no evidence of this rise. Both subjects are alike in showing a marked rise of the respiratory quotient to above unity in the first period following the cessation of the exercise. This rise is, however, only temporary, and the respiratory quotient shows a great diminution in the second period after the stop, and soon attains a normal level. In Experiment 4 (Hobson), the respiratory quotient seems eventually to drop back to just the same value that it had before the exercise commenced, but in Experiments 1, 2, and 3 (Douglas) there is perhaps a slight indication of a trifling drop in the respiratory quotient below the preliminary resting value and a subsequent recovery.

* Benedict and Cathcart, "Muscular Work," 'Publication No. 187, Carnegie Institute of Washington,' 1913.

TABLE II.

Successive periods of experiment.	Respiratory exchange in c.c. per minute at 0° and 760 mm.		Respiratory quotient.	Breaths per minute.	At 37°, moist, and prevailing barometer.		CO_2 per cent. in expired air.
	O_2.	CO_2.			Litres breathed per minute.	C.c. per breath.	
Experiment 1.—DOUGLAS. Bar. 764 mm., room temp. 15° C. Work = 704 kg.m. per minute for 14¾ minutes. No artificial cooling.							
10′ 0″ rest	—	—	—	—	—	—	—
4 42 ,,	286	227	0·793	15·3	7·6	499	3·70
12 0 work	—	—	—	—	—	—	—
2 50 ,,	1665	1502	0·902	25·1	39·6	1578	4·71
2 8 rest	788	855	1·085	21·6	25·8	1195	4·12
4 0 ,,	—	—	—	—	—	—	—
5 33 ,,	—*	—*	0·849	17·5	—*	—*	3·23
7 8 ,,	328	270	0·823	19·3	10·4	646	3·25
6 11 ,,	311	248	0·797	15·7	9·7	616	3·20
4 0 ,,	—	—	—	—	—	—	—
6 0 ,,	332	254	0·765	—	10·0	—	3·14
6 0 ,,	299	235	0·786	—	9·6	—	3·07
6 0 ,,	301	241	0·800	—	9·6	—	3·12
Experiment 2.—DOUGLAS. Bar. 755 mm., room temp. 15·5° C. Work = 704 kg.m. per minute for 17 minutes. No artificial cooling.							
14′ 45″ rest	—	—	—	—	—	—	—
17 0 work	—	—	—	—	—	—	—
2 32 rest	728	772	1·060	20·1	24·3	1210	3·91
2 32 ,,	403	364	0·903	17·0	12·5	735	3·58
2 25 ,,	356	322	0·905	17·4	11·4	652	3·49
6 10 ,,	319	264	0·828	16·4	10·2	619	3·20
7 23 ,,	316	246	0·779	14·8	9·2	624	3·28
7 0 ,,	299	226	0·756	15·0	8·9	590	3·15
7 4 ,,	296	223	0·754	14·9	8·8	590	3·13
6 53 ,,	303	239	0·789	14·2	9·1	644	3·21
7 1 ,,	289	228	0·789	16·0	9·2	575	3·05
5 39 ,,	299	235	0·786	15·2	9·3	611	3·12
Experiment 3.—DOUGLAS. Bar. 753 mm., room temp. 16° C. Work = 704 kg.m. per minute for 14 minutes. Cooled by one fan during work.							
15′ 0″ rest	—	—	—	—	—	—	—
12 0 work	—	—	—	—	—	—	—
2 4 ,,	1652	1441	0·872	22·7	37·9	1670	4·68
2 0 rest	752	818	1·087	18·0	24·4	1356	4·12
2 2 ,,	416	356	0·856	11·8	11·6	983	3·78
2 3 ,,	388	293	0·755	11·7	9·8	834	3·70
5 58 ,,	319	261	0·819	12·0	9·3	776	3·46
6 0 ,,	322	253	0·786	11·3	8·9	787	3·50
6 7 ,,	307	236	0·769	11·6	8·4	723	3·47
6 2 ,,	309	239	0·773	11·4	8·6	756	3·42
7 0 ,,	295	230	0·780	12·1	8·6	706	3·32
7 9 ,,	296	235	0·794	12·6	8·6	681	3·38
7 13 ,,	284	229	0·807	12·6	8·6	683	3·28

No lactic acid found in either the urine collected immediately before the experiment or in that collected during the experiment.

* Mistake made in measurement of expired air sample.

TABLE II—*continued.*

Successive periods of experiment.	Respiratory exchange in c.c. per minute at 0° and 760 mm.		Respiratory quotient.	Breaths per minute.	At 37°, moist, and prevailing barometer.		CO_2 per cent. in expired air.
	O_2.	CO_2.			Litres breathed per minute.	C.c. per breath.	
Experiment 4.—HOBSON. Bar. 768 mm., room temp. 16·5° C. Work = 704 kg.m. per minute for 15 minutes. Cooled by one fan during work.							
5′ 0″ rest	—	—	—	—	—	—	—
5 1 ,,	385	331	0·860	17·5	10·9	620	3·68
5 3 ,,	350	308	0·880	16·6	10·1	611	3·66
5 0 work	—	—	—	—	—	—	—
2 33 ,,	1750	1571	0·898	23·9	36·2	1515	5·22
5 0 ,,	—	—	—	—	—	—	—
2 33 ,,	1714	1540	0·899	24·3	36·7	1510	5·05
3 3 rest	595	630	1·059	20·7	18·8	909	4·04
2 32 ,,	354	322	0·910	20·5	11·4	555	3·42
2 28 ,,	399	350	0·877	19·1	11·7	613	3·62
7 2 ,,	370	332	0·898	20·5	11·6	567	3·45
5 30 ,,	383	344	0·898	19·8	11·5	583	3·60
7 34 ,,	344	304	0·884	18·6	10·5	565	3·50
6 3 ,,	335	293	0·875	18·8	10·4	554	3·40
8 18 ,,	344	301	0·875	18·4	10·6	575	3·44

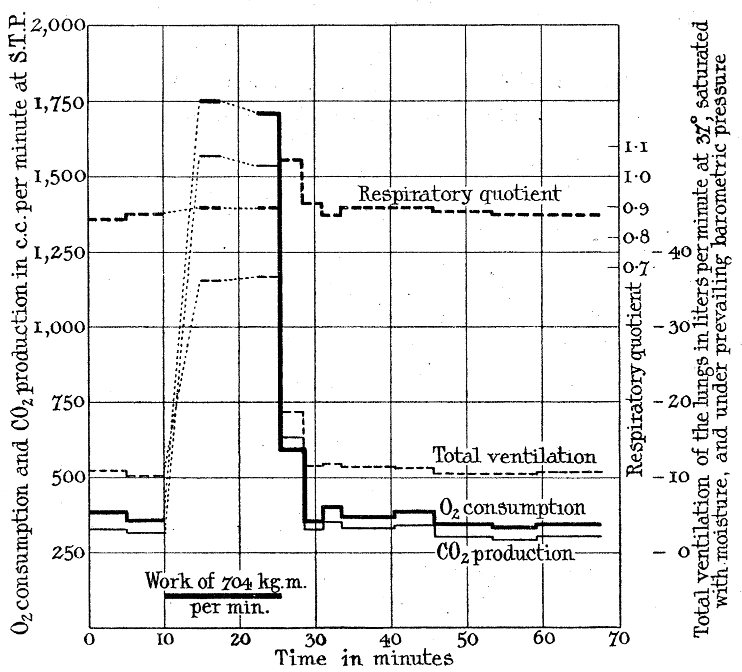

FIG. 4.

(*b*) Long period of muscular work, viz., $\frac{3}{4}$–1 hour.

The results are given in Table III, and Experiment 6 is shown graphically in fig. 5.

TABLE III.

Successive periods of experiment.	Respiratory exchange in c.c. per minute at 0° and 760 mm.		Respiratory quotient.	Breaths per minute.	At 37°, moist, and prevailing barometer.		CO_2 per cent. in expired air.
	O_2.	CO_2.			Litres breathed per minute.	C.c. per breath.	
Experiment 5.—DOUGLAS. Bar. 764 mm., room temp. 17° C. Work = 704 kg.m. per minute for 45 minutes. Cooled by one fan during work.							
5′ 0″ rest	—	—	—	—	—	—	—
5 1 ,,	294	239	0·813	11·6	8·2	707	3·53
5 0 ,,	—	—	—	—	—	—	—
5 1 ,,	293	231	0·788	10·8	7·8	724	3·58
5 0 work	—	—	—	—	—	—	—
2 15 ,,	1611	1504	0·934	18·2	37·0	2030	4·93
10 0 ,,	—	—	—	—	—	—	—
2 33 ,,	1619	1470	0·908	20·8	37·3	1794	4·77
10 0 ,,	—	—	—	—	—	—	—
2 32 ,,	1664	1480	0·890	20·1	37·6	1871	4·76
10 0 ,,	—	—	—	—	—	—	—
2 34 ,,	1747	1504	0·861	17·5	37·8	2160	4·82
2 30 rest	717	725	1·011	16·0	21·4	1338	4·10
2 30 ,,	330	316	0·957	11·6	10·5	905	3·65
2 30 ,,	302	262	0·867	10·0	8·7	870	3·65
4 0 ,,	321	276	0·860	10·0	9·3	933	3·59
Experiment 6.—DOUGLAS. Bar. 758 mm., room temp. 15·5° C. Work = 704 kg.m. per minute for 57½ minutes. Cooled by one fan during work.							
10′ 0″ rest	—	—	—	—	—	—	—
5 0 ,,	263	213	0·808	9·4	7·1	754	3·67
5 0 work	—	—	—	—	—	—	—
2 31 ,,	1624	1534	0·945	16·3	37·6	2310	4·98
22 30 ,,	—	—	—	—	—	—	—
2 31 ,,	1695	1520	0·897	17·1	37·8	2210	4·92
22 30 ,,	—	—	—	—	—	—	—
2 33 ,,	1732	1486	0·858	17·2	36·9	2145	4·92
2 31 rest	721	720	0·998	13·9	20·8	1496	4·23
3 3 ,,	—*	—*	0·846	—	—*	—*	3·71
3 1 ,,	325	278	0·855	10·9	9·1	830	3·76
5 31 ,,	286	232	0·812	11·6	8·4	727	3·41
6 58 ,,	283	220	0·778	10·3	8·0	776	3·38
7 5 ,,	279	221	0·792	9·7	7·7	793	3·52
7 0 ,,	277	214	0·772	9·3	7·3	783	3·59
7 8 ,,	267	209	0·783	9·5	7·5	784	3·43
6 51 ,,	265	208	0·785	9·1	7·4	815	3·43
7 6 ,,	268	211	0·787	9·9	7·6	766	3·41
In one hour preceding experiment 47 c.c. urine, sp. gr. 1016. During whole experiment 265 c.c. urine, sp. gr. 1008. Lactic acid test negative in both samples.							

* Mistake made in measurement of expired air sample.

TABLE III—*continued.*

Successive periods of experiment.	Respiratory exchange in c.c. per minute at 0° and 760 mm. O_2.	Respiratory exchange in c.c. per minute at 0° and 760 mm. CO_2.	Respiratory quotient.	Breaths per minute.	At 37°, moist, and prevailing barometer. Litres breathed per minute.	At 37°, moist, and prevailing barometer. C.c. per breath.	CO_2 per cent. in expired air.
Experiment 7.—HOBSON. Bar. 773 mm., room temp. 15° C. Work = 704 kg.m. per minute for 53 minutes. Cooled by one fan during work.							
10′ 0″ rest	—	—	—	—	—	—	—
4 43 ,,	—*	—*	0·866	18·7	—*	—*	3·19
5 0 work	—	—	—	—	—	—	—
2 31 ,,	1664	1512	0·909	20·3	36·8	1814	4·91
15 0 ,,	—	—	—	—	—	—	—
2 36 ,,	1738	1507	0·867	24·6	37·8	1536	4·77
13 0 ,,	—	—	—	—	—	—	—
2 34 ,,	1687	1487	0·882	24·9	37·9	1521	4·69
10 0 ,,	—	—	—	—	—	—	—
2 33 ,,	1676	1481	0·885	24·7	37·8	1531	4·69
2 20 rest	836	863	1·031	24·4	28·4	1164	3·64
2 19 ,,	384	339	0·883	19·9	12·8	642	3·18
2 6 ,,	396	311	0·785	19·5	11·7	601	3·18

* Mistake made in measurement of expired air sample.

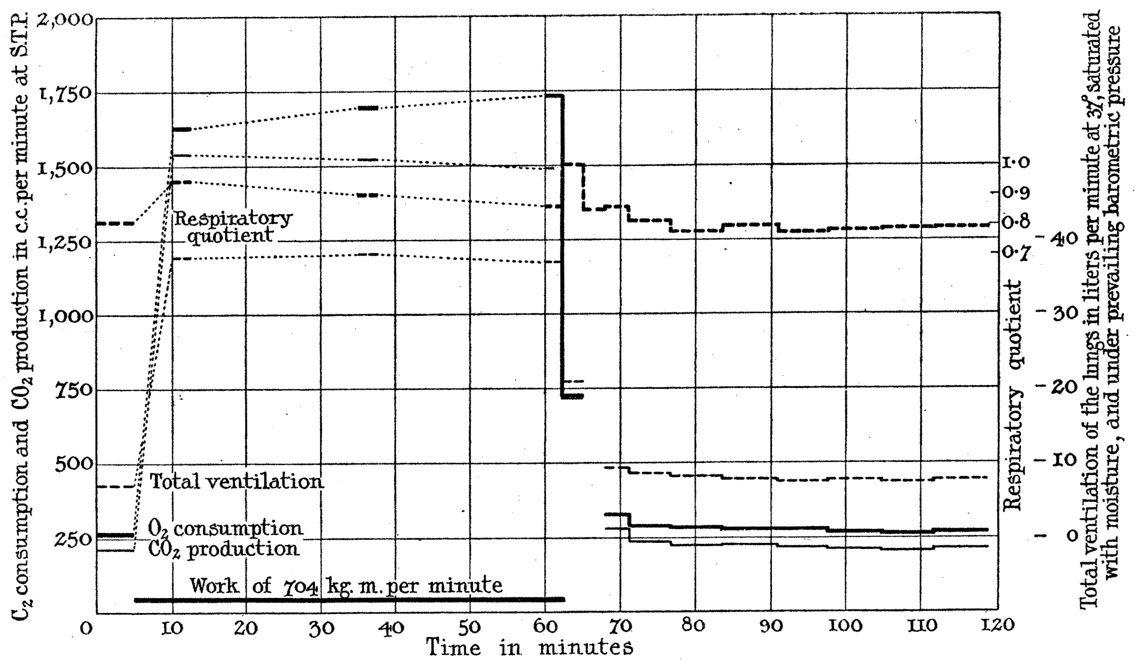

FIG. 5.

The average respiratory exchange during the exercise is practically the same as in the experiments with the shorter period of work, and there is the same rapid fall in the respiratory exchange on cessation of the exercise, and the same temporary sharp rise of the respiratory quotient immediately after the stop.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

In Experiment 7 (Hobson) the respiratory exchange remains tolerably steady throughout the whole period of work, the respiratory quotient being perhaps raised a trifle during this period, but the case is different in Experiments 5 and 6 (Douglas). In these two experiments, while CO_2 output remains pretty constant during the whole period of exercise, or even falls slightly, the oxygen intake rises steadily throughout the work, until in the last determination made in the work period the oxygen consumption is over 100 c.c. per minute higher than in the first. The respiratory quotient which was markedly raised in the first determination during work in these two experiments on Douglas, falls therefore steadily during the work period, though the final value of this quotient just before stopping the work is still very definitely above the resting value.

The respiratory exchange after the stop of the exercise was only followed for a considerable time in Experiment 6, and in this case there is apparently a slight diminution of the respiratory quotient below the initial resting value after the transitory high quotient immediately following the stop of the work has disappeared, and it is dubious whether there is any tendency to recovery of the original value during the period that the observations were kept up.

The volume of air breathed per minute in these experiments varies in a similar manner to the respiratory exchange, though the oxygen consumption shows a more rapid drop after the stop of the exercise than does either the CO_2 output or the hyperpnœa. During the work the total ventilation of the lungs remains pretty steady, and the increase in the ventilation of the lungs is brought about more by increasing the depth of the respirations than by increasing their rate, for the volume of each breath is increased to about thrice the initial resting value in the case of Douglas (Experiments 1, 5, and 6), and the rate is less than doubled; while in the case of Hobson (Experiment 4) these values are respectively $2\frac{1}{2}$ times and $1\frac{1}{2}$ times the resting values. An increase of depth of the breathing is, of course, a more economical method of increasing the alveolar ventilation than is an increase of rate, owing to the greater proportional influence of the dead space in shallow breathing, and one finds therefore in these experiments that though the metabolism, as judged by the oxygen consumption has about six times the resting value in the case of Douglas, and $4\frac{1}{2}$ times the resting value in the case of Hobson, the total ventilation of the lungs is only increased to five times and $3\frac{1}{2}$ times the resting values respectively.

2. *Hard Work of* 1056 *kg.m. per Minute.*

(*a*) Short period of muscular work, viz., 15 minutes.

The results of experiment on Douglas are given in Table IV.

In this case the CO_2 production during the work remains steady, but the oxygen consumption is considerably higher in the second determination than in the first. Though the respiratory exchange falls after the stop of the exercise with a rapidity comparable with that in the previous experiments, there are some significant alterations in the respiratory quotient. In the first place, there is the abnormally high respiratory quotient of unity in the first observation made in the work period, and in the second, the respiratory quotient, after the transitory sharp rise immediately after the stop of the exercise has passed away, falls to a value which is definitely below that which it had before the work was begun, and this value remains practically steady during the last four or five periods of the experiment. The respiratory exchange reaches a steady value 18 minutes after the stop of the exercise, and it will be seen that though the CO_2 output during the remaining 25 minutes of the experiment (a period that corresponds with the persistent low respiratory quotient), is below the value obtained during the preliminary rest period, the oxygen consumption is on the average somewhat above the initial resting value.

TABLE IV.

Successive periods of experiment.	Respiratory exchange in c.c. per minute at 0° and 760 mm.		Respiratory quotient.	Breaths per minute.	At 37°, moist, and prevailing barometer.		CO_2 per cent. in expired air.
	O_2.	CO_2.			Litres breathed per minute.	C.c. per breath.	
Experiment 8.—DOUGLAS. Bar. 764 mm., room temp. 12° C. Work = 1056 kg.m. per minute for 15 minutes. Cooled by two fans during work.							
10′ 0″ rest	—	—	—	—	—	—	—
5 45 ,,	281	233	0·829	10·4	8·1	776	3·50
5 0 work	—	—	—	—	—	—	—
1 45 ,,	2240	2245	1·002	24·6	59·3	2410	4·58
7 0 ,,	—	—	—	—	—	—	—
1 34 ,,	2350	2250	0·957	23·3	59·7	2460	4·57
5 5 rest	631	738	1·170	16·7	25·9	1551	3·45
2 58 ,,	364	324	0·891	14·2	12·4	874	3·17
5 9 ,,	350	301	0·860	13·4	11·5	857	3·18
4 46 ,,	331	267	0·806	12·6	10·1	803	3·20
5 2 ,,	291	229	0·787	11·7	9·1	775	3·07
4 47 ,,	290	222	0·765	10·9	8·6	789	3·13
5 1 ,,	275	211	0·767	10·2	8·1	792	3·17
4 52 ,,	298	225	0·755	12·1	8·9	731	3·09
5 24 ,,	283	225	0·788	11·1	9·0	807	3·02

In one hour preceding experiment 106 c.c. urine, sp. gr. 1011 ; lactic acid negative.
During whole experiment 245 c.c. urine, sp. gr. 1004, containing 0·10 grm. lactic acid.

It will be noted that in this case the first resting period after the stop of the exercise is much longer than in the other experiments. As a matter of fact there were two periods, but on switching the expired air from the first bag into the second the watch was by accident not stopped, though the approximate position of the hand was noted, and on this occasion it was impossible to distinguish the transition from the first to the second bag on the polygraph tracing of the respirations. In order to reckon the respiratory exchange accurately, the two periods had therefore to be taken together. The first sample took approximately 1½ minutes to collect, and accepting this figure the respiratory exchange averaged in the first $1\frac{1}{2}$ minutes after the stop of the exercise 1369 c.c. O_2 and 1714 c.c. CO_2 per minute, with R.Q. = 1·254, and in the succeeding 3′ 35″ 324 c.c. O_2 and 329 c.c. CO_2 per minute, with R.Q. = 1·016.

(*b*) Long period of muscular work, viz., 29–38 minutes.

The results are given in Table V, and Experiment 9 is shown graphically in fig. 6.

TABLE V.

Successive periods of experiment.	Respiratory exchange in c.c. per minute at 0° and 760 mm.		Respiratory quotient.	Breaths per minute.	At 37°, moist, and prevailing barometer.		CO_2 per cent. in expired air.
	O_2.	CO_2.			Litres breathed per minute.	C.c. per breath.	
Experiment 9.—DOUGLAS. Bar. 763 mm., room temp. 12° C. Work = 1056 kg.m. per minute for 37 minutes. Cooled by two fans during work.							
10′ 0″ rest	—	—	—	—	—	—	—
5 0 ,,	308	266	0·863	11·8	9·0	761	3·60
3 0 work	—	—	—	—	—	—	—
1 42 ,,	2234	2446	1·095	25·3	65·6	2595	4·52
9 0 ,,	—	—	—	—	—	—	—
1 56 ,,	2380	2260	0·950	23·8	59·5	2500	4·61
9 0 ,,	—	—	—	—	—	—	—
1 45 ,,	2395	2270	0·948	26·0	63·1	2430	4·36
9 0 ,,	—	—	—	—	—	—	—
1 54 ,,	2420	2220	0·917	24·7	59·6	2415	4·52
2 1 rest	1070	1258	1·175	30·3	44·5	1470	3·44
3 8 ,,	396	367	0·927	16·0	14·2	889	3·14
5 47 ,,	358	301	0·841	13·1	11·4	872	3·20
10 15 ,,	321	249	0·776	12·1	9·8	808	3·10
11 57 ,,	324	248	0·765	12·0	9·2	768	3·27
10 52 ,,	335	253	0·755	12·7	9·4	743	3·26
11 5 ,,	324	241	0·744	12·8	9·1	707	3·24
10 31 ,,	334	254	0·760	11·4	9·2	808	3·35
3 0 ,,	—	—	—	—	—	—	—
10 57 ,,	330	243	0·736	10·0	8·5	850	3·47
In $1\frac{1}{4}$ hours preceding experiment 302 c.c. urine, sp. gr. 1004; lactic acid negative. During whole experiment 193 c.c. urine, sp. gr. 1011, containing 0·05 grm. lactic acid.							
Experiment 10.—HOBSON. Bar. 755 mm., room temp. 16° C. Work = 1056 kg.m. per minute for $28\frac{3}{4}$ minutes. Cooled by two fans during work.							
5′ 0″ rest	—	—	—	—	—	—	—
5 21 ,,	394	349	0·885	19·3	12·7	658	3·38
7 0 ,,	—	—	—	—	—	—	—
5 11 ,,	423	373	0·881	19·1	12·9	677	3·55
4 0 work	—	—	—	—	—	—	—
1 49 ,,	2490	2490	1·000	25·3	59·0	2330	5·17
7 0 ,,	—	—	—	—	—	—	—
1 59 ,,	2580	2270	0·880	25·7	55·7	2170	5·00
12 0 ,,	—	—	—	—	—	—	—
1 52 ,,	2680	2325	0·868	25·7	54·9	2140	5·20
3 12 rest	832	917	1·102	23·8	28·9	1214	3·90
4 15 ,,	487	395	0·811	21·7	14·6	624	3·32
4 37 ,,	464	405	0·872	20·6	14·6	707	3·42
Bicycle saddle too low and subject very uncomfortable throughout the work.							

TABLE V—*continued.*

Successive periods of experiment.	Respiratory exchange in c.c. per minute at 0° and 760 mm.		Respiratory quotient.	Breaths per minute.	At 37°, moist, and prevailing barometer.		CO_2 per cent. in expired air.
	O_2.	CO_2.			Litres breathed per minute.	C.c. per breath.	
Experiment 11.—HOBSON. Bar. 765 mm., room temp. 15° C. Work = 1056 kg.m. per minute for 38 minutes. Cooled by two fans during work.							
10′ 0″ rest	—	—	—	—	—	—	—
6 33 ,,	375	323	0·860	16·9	11·3	671	3·45
3 6 work	—	—	—	—	—	—	—
1 55 ,,	2310	2230	0·966	25·0	53·9	2125	5·01
9 10 ,,	—	—	—	—	—	—	—
1 50 ,,	2435	2250	0·925	25·1	56·5	2250	4·82
9 0 ,,	—	—	—	—	—	—	—
1 46 ,,	2400	2240	0·934	24·9	56·7	2280	4·78
9 26 ,,	—	—	—	—	—	—	—
1 47 ,,	2360	2140	0·907	24·7	54·2	2190	4·78
2 39 rest	819	852	1·041	23·4	26·7	1141	3·87
3 7 ,,	426	389	0·913	22·8	14·3	629	3·29
3 22 ,,	376	337	0·896	22·0	12·8	582	3·20
7 29 ,,	395	331	0·838	21·4	12·4	579	3·24
7 53 ,,	371	305	0·822	20·7	11·7	567	3·15
8 19 ,,	355	293	0·826	19·7	11·2	569	3·17
8 46 ,,	358	295	0·824	20·1	11·1	550	3·24
7 40 ,,	334	269	0·805	18·9	10·3	542	3·18
8 10 ,,	350	283	0·809	19·5	10·6	541	3·26

During the whole of the experiment and in the hour preceding it 95 c.c. urine, sp. gr. 1023, which showed only a trace of lactic acid.

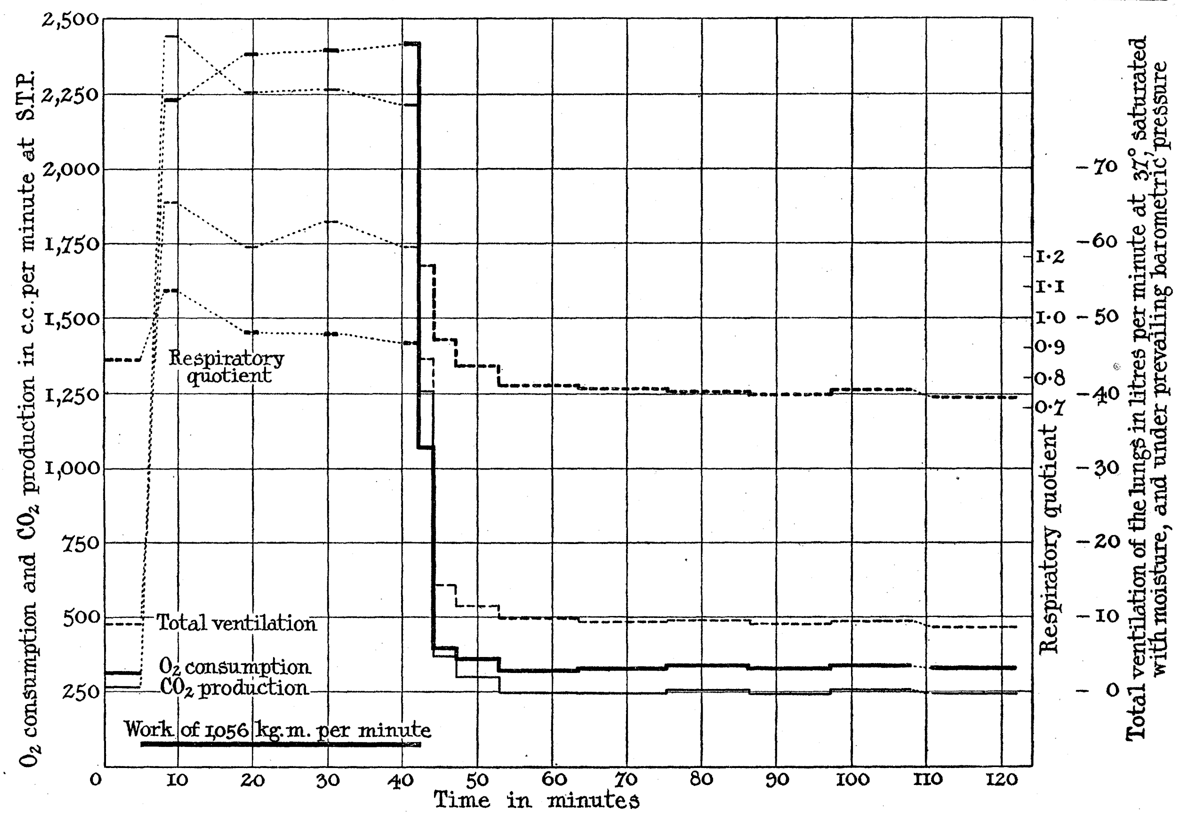

FIG. 6.

To deal first with Experiment 9 (DOUGLAS). The oxygen consumption in the first two determinations during the work period agrees closely with that found in Experiment 8. It shows a marked rise during the course of the work, and this rise is greater than was the case in Experiments 5 and 6, the oxygen consumption being 186 c.c. per minute higher in the last determination made during the work period than it was during the first. The CO_2 output is 112 c.c. per minute above the oxygen intake in the first work period, and the respiratory quotient well above unity at this time (it should be noted that the sample was taken at an earlier stage of the work period than in Experiment 8). The CO_2 output has dropped below the oxygen consumption by the time of the second observation during the work and remains fairly steady, or even diminishes slightly, during the remainder of the exercise, the respiratory quotient, which had fallen to 0·95 in the second observation, diminishing further as the oxygen consumption increases, though it is still well above the preliminary resting value in the last period of work.

After the stop of the exercise there is the usual immediate rise of the respiratory quotient followed by a rapid drop. The respiratory exchange falls rapidly, and at the end of 11 minutes has reached a value which remains practically constant for the subsequent 68½ minutes of the experiment. During this last 68½ minutes the respiratory quotient remains pretty steady at a figure considerably below the initial resting value shown at the commencement of the experiment, the diminution of the respiratory quotient being proportionally greater than in Experiment 8. The low respiratory quotient is due to the fact that the CO_2 output is on the average 18 c.c. per minute below the initial resting value as well as to the fact that the oxygen consumption is 20 c.c. per minute above the initial resting value. It will, moreover, be seen that the average oxygen consumption of 328 c.c. per minute during this period is considerably above what was found in the previous experiments on DOUGLAS either during the preliminary rest period or in the later stages of rest subsequent to muscular work when the respiratory exchange has reached a steady value.

To allow of comparison with Experiment 8, the first and second periods after the stop of the work may be added together. If this is done the oxygen consumption averaged 660 c.c. per minute, and the CO_2 output 716 c.c. per minute, with respiratory quotient 1·085, during the first 5′ 9″ after stopping the work.

In this experiment DOUGLAS was quite comfortable throughout the work, and though he felt a little tired at the end he could have continued the work for a good deal longer without serious discomfort.

Experiment 10 (HOBSON) gives a picture very similar to Experiment 9. There is the same steady rise in the oxygen consumption during the work period, the oxygen consumption being 200 c.c. per minute higher in the third determination than in the first, while the CO_2 output is 220 c.c. per minute lower in the second determination during the work, and 155 c.c. per minute in the third, than it was in the first. The respiratory quotient is 1·0 in the first determination during the work, but in the second and third determinations it falls to a value identical with the initial resting figure. In this experiment HOBSON forgot to raise the bicycle saddle to the proper height, and in consequence found the work extremely uncomfortable. We were therefore compelled to terminate the work earlier than we had intended.

The experiment was therefore repeated on HOBSON some days later (Experiment 11), with the bicycle saddle at the correct height. This time he was pretty comfortable throughout the work, though he sweated a good deal notwithstanding the two fans. The picture presented in this experiment is somewhat different from that in the preceding one. The average respiratory exchange during the work is a good deal lower, as indeed one might expect since he was not subject to the disadvantage of a cramped position. Though the oxygen consumption in the three later observations during the work is higher than in the first, the rise is neither so marked as in Experiment 10 nor is it progressive. The CO_2 output remains constant for the greater part of the work period, but diminishes somewhat in the last determination. The respiratory quotient is only 0·966 in the first observation during the work, and shows a diminution during the course of the work, though in the last observation during the work it is still a good deal above the initial resting value. The whole course of events during the muscular work is, in fact, remarkably like that found in the case of DOUGLAS in the long experiments with lighter work (Experiments 5 and 6, Table III). Nine minutes after the work ceased, however, the respiratory quotient falls below the initial resting value, and a further fall occurs in subsequent periods, and even when the experiment terminated 48 minutes later there was no sign of recovery.

In Experiments 9 and 10 it will be seen that the hyperpnœa during the work is at a maximum in the first determination, *i.e.*, at a time corresponding to the abnormally high respiratory quotient, and CO_2 output, and that there is a decided drop in the amount of air breathed per minute in the subsequent observations during the exercise. This definite variation in the hyperpnœa is, however, absent in Experiment 11 in which the respiratory quotient during the work is always well below unity. If we disregard for the moment the observations which show an abnormally high respiratory quotient of 1·0 or over during the work in these experiments, since these are evidently influenced by some disturbing factor, and confine ourselves to the period during which the hyperpnœa remains fairly steady, it will be seen that in DOUGLAS's case the oxygen consumption is increased about eight-fold during the work, while the amount of air breathed per minute is only about seven times the resting value, the rate of breathing being rather more than doubled, and the depth of the breathing rather more than trebled. HOBSON's oxygen consumption rises during the work to rather more than six times the preliminary resting value, but the total ventilation of the lungs is barely five times the resting value, the rate of breathing being about $1\frac{1}{2}$ times as great, and the depth of breathing more than three times as great, as during rest. The hyperpnœa is therefore being brought about, just as was the case with the lighter work, more by increasing the depth than by increasing the rate of the respiration. That the hyperpnœa in the later stages of the work in these experiments is not excessive in comparison with that observed in the case of lighter work, is shown by the fact that the average volume of expired air per 1 c.c. of CO_2 given off is in DOUGLAS's case, 25·2 c.c. in the experiments with work of 704 kg.m. per minute, and 26·9 c.c. in the experiments at 1056 kg.m. per minute, HOBSON giving values of 24·6 c.c. and 24·7 c.c. respectively (observations which show an abnormally high respiratory quotient being excluded as before).

3. *Severe Muscular Work of* 1232 *kg.m. per Minute.*

The results of this experiment (No. 12) are given in Table VI, and are shown graphically in fig. 7.

TABLE VI.

Successive periods of experiment.	Respiratory exchange in c.c. per minute at 0° and 760 mm.		Respiratory quotient.	Breaths per minute.	At 37°, moist, and prevailing barometer.		CO_2 per cent. in expired air.
	O_2.	CO_2.			Litres breathed per minute.	C.c. per breath.	
Experiment 12.—DOUGLAS. Bar. 762 mm., room temp. 16° C. Work = 1232 kg.m. per minute for 7¾ minutes. Cooled by two fans during work.							
21′ 27″ rest	—	—	—	—	—	—	—
4 0 work	—	—	—	—	—	—	—
4 0 rest	—	—	—	—	—	—	—
3 0 work	—	—	—	—	—	—	—
0 45 "	2795	2880	1·030	48·0	114·8	2390	3·06
0 51 rest	2110	2390	1·132	56·5	105·1	1862	2·77
1 37 "	806	1011	1·255	33·4	44·4	1330	2·78
3 13 "	469	485	1·033	20·8	20·6	991	2·87
7 2 "	379	359	0·947	19·5	16·1	826	2·72
9 4 "	334	268	0·802	18·2	12·7	699	2·58
6 40 "	325	240	0·739	19·5	11·6	596	2·53
9 24 "	292	199	0·684	17·7	9·7	550	2·50
11 31 "	276	178	0·645	18·7	9·1	489	2·38
10 2 "	318	207	0·651	18·7	10·0	534	2·53
4 42 "	—	—	—	—	—	—	—
10 31 "	330	214	0·648	18·0	9·8	545	2·67
10 54 "	323	221	0·684	19·0	9·9	521	2·62
In one hour preceding experiment 34 c.c. urine, sp. gr. 1026; lactic acid negative. During whole experiment 92 c.c. urine, sp. gr. 1022, containing 0·57 grm. lactic acid.							

This amount of work proved too severe for the subject (DOUGLAS) to keep it up for more than a few minutes. The initial rest period lasted for 21½ minutes, but, owing to an error, we did not succeed in determining the respiratory exchange during this time. We had intended that the work should be kept up for five minutes before collecting the first sample of expired air, but, at the end of four minutes, the hyperpnœa and distress were so great that the subject could no longer tolerate breathing into the apparatus, and he was forced to stop working. After an interval of four minutes' rest, at the end of which time the hyperpnœa had greatly diminished, though it had by no means ceased, the work was begun again. Three minutes later the respiratory exchange was determined over a period of 45 seconds, and then the subject stopped work. The after-effect of the work was followed for 85½ minutes.

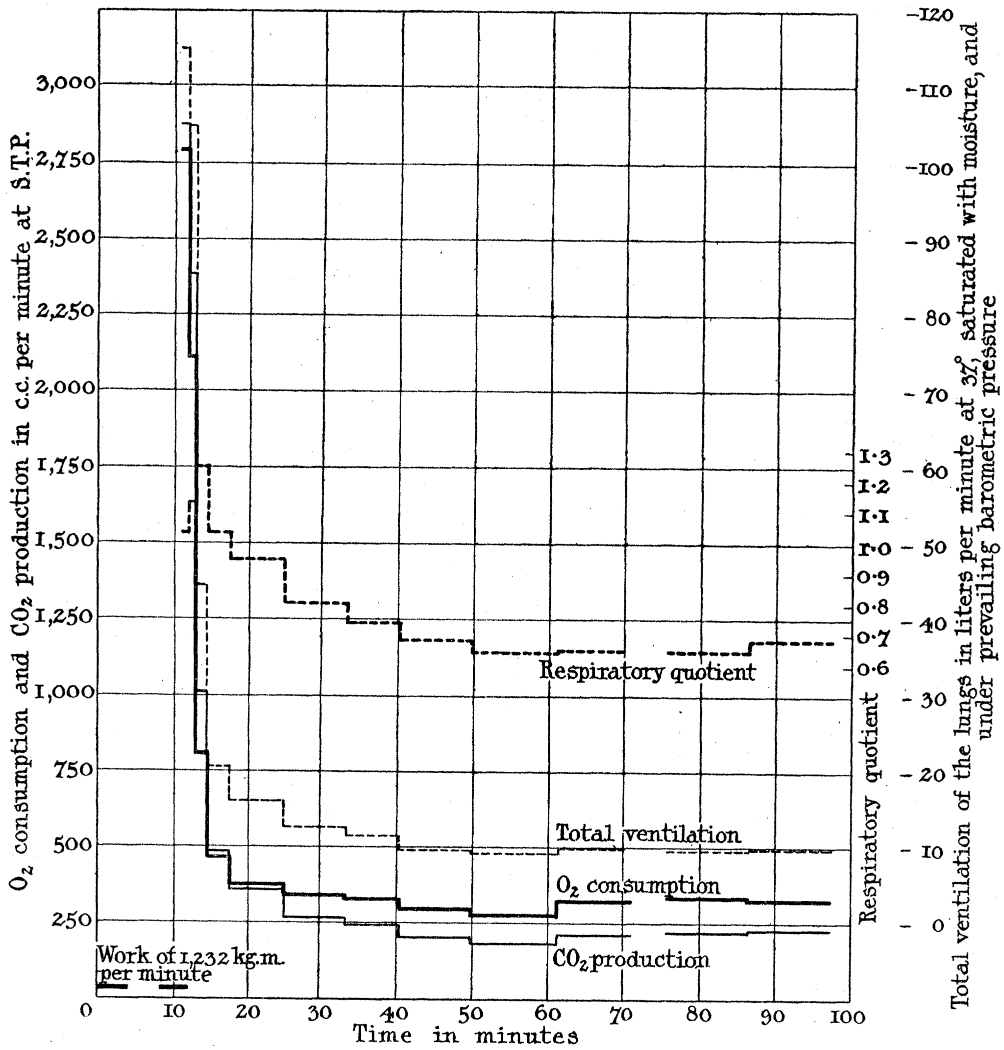

Fig. 7.

It will be seen that, in spite of the fact that the work had already lasted for a total of seven minutes, and that there had been, in addition, an interval of four minutes between the two periods of work, the CO_2 output is still above the oxygen consumption, and the respiratory quotient above unity, when the determination of the respiratory exchange was made just before stopping the work.

In the first minute after the stop of the work, there is only a comparatively small drop in the respiratory exchange, though there is a big diminution in the succeeding minute and a-half, and a considerable further fall in the next three minutes. The figures show clearly how greatly the fall in the CO_2 output lags behind the fall in the oxygen consumption during these three periods. The respiratory exchange and respiratory quotient fall to a minimum in the eighth period after the stop (*i.e.*, between the 38th and 49th minutes), and subsequently rise again to some extent. It is possible that the lowness of the figures in the eighth period is due to some chance error, though we were unable to identify any fallacy in our measurements, and one may note that as low, or even lower, figures for oxygen consumption are recorded in Experiments 6 and 8. Taking the last 57 minutes of the experiment (seventh period after the stop of the work onwards), as a whole, the striking features are the great depression of the respiratory quotient, which lies well below 0·7, and the height of the oxygen consumption, in comparison with the lowness of the CO_2 output. Lower figures for CO_2 output in individual periods after the work are recorded during this time than in any of the other experiments on Douglas, though the average CO_2 output for the whole period is approached in the later stages of Experiment 6.

The extreme hyperpnœa during the muscular work is obvious. Though the metabolism, as judged by the oxygen consumption, is only about ten times the average preliminary resting value, as opposed to the eight-fold increase shown in Experiments 8 and 9, the volume of air breathed per minute is practically double what it was in these experiments. What is more, this additional increase is brought about entirely by increasing the rate of the respiration, for the depth of the breathing is actually somewhat less than in Experiments 8 and 9. The excessive character of the breathing is well brought out by the extremely low percentage of CO_2 in the expired air (3 per cent., as opposed to $4\frac{1}{2}$ per cent. or more in the previous experiments), as well as by the fact that the volume of expired air per 1 c.c. of CO_2 given off is 39·8 c.c., instead of the 26·9 c.c. observed in the experiments with work of 1056 kg.m. per minute; had the latter ratio held good in Experiment 12, the volume of air breathed per minute would have been only 77·5 litres instead of 114·8. The volume of air breathed per minute remains about as great during the first minute after the stop of the work as it was during the work. It then drops slowly, and attains a fairly steady value $28\frac{1}{2}$ minutes after the cessation of the work. It will be noticed that the rate of the breathing during the later stages of the after-period remains much higher than in the other experiments on Douglas, and that there is a corresponding reduction in the depth; a rate of 18 breaths a minute during rest has, however, often been observed in Douglas under other circumstances.

Discussion of the Results.

(1) *The "Efficiency" during the Work.*

Though these experiments were not undertaken with the idea of determining accurately the mechanical efficiency of the body during the performance of muscular work, *i.e.*, the relationship between the heat equivalent of the work done and the amount of heat actually liberated in the body in the performance of that work, it is of interest to calculate this value in order to compare the results with those obtained in the recent careful experiments of BENEDICT and CATHCART (*loc. cit.*), in which the muscular work was done by a trained subject in the post-absorptive state on a bicycle ergometer, and the energy output was calculated from the respiratory exchange. This may be done by using ZUNTZ and SCHUMBURG's figures* for the calorie value of oxygen at different respiratory quotients, though this method does not, of course, take into account the metabolism of protein.

In order to calculate the efficiency, one must subtract from the total heat output during the work a quantity corresponding to the "basal metabolism," on which the actual heat output corresponding to the work may be assumed to be superimposed. BENEDICT and CATHCART have discussed in detail the different values which may be selected to represent the basal metabolism. We give in Table VII the efficiency values for our experiments, using as "basal metabolism" the energy output in the preliminary rest period when sitting still on the bicycle.

TABLE VII.

	Respiratory exchange in c.c. per minute at 0° and 760 mm.		Respiratory quotient.	Calories produced per minute.	Extra calories per minute during work.	Calorie equivalent of work.	Efficiency.
	O_2.	CO_2.					
DOUGLAS.							per cent.
Preliminary rest . .	288	235	0·816	1·39			
704 kg.m. per minute	1668	1493	0·896	8·21	6·82	1·65	24·2
1056 " "	2386	2250	0·943	11·91	10·52	2·47	23·5
HOBSON.							
Preliminary rest . .	385	337	0·873	1·88			
704 kg.m. per minute	1705	1516	0·890	8·38	6·50	1·65	25·4
1056 " "	2398	2210	0·922	11·87	9·99	2·47	24·7

In this Table, the respiratory exchange at rest of each subject is the average of all the values obtained on that subject before starting the work. The figures given with work of 704 kg.m. per minute are the average of all the observations made on the subject in question while this work was in progress. In the case of the work of 1056 kg.m. per minute, the figures only give the average value for the second observation during work in Experiment 8, and the last three observations during work in Experiment 9 on DOUGLAS, and the average value for the last three observations in Experiment 11 on HOBSON. Owing to the liability of the respiratory

* ZUNTZ und SCHUMBURG, 'Physiologie des Marsches,' Berlin, 1901, p. 361.

quotient to be abnormally high in the early stages with this degree of work, we must clearly discard at least the first observations during work in these experiments. We have not included Experiment 10 on HOBSON in the above Table, for it is not strictly comparable with the other experiments, because of the discomfort during the work, owing to the low position of the saddle, but this experiment shows an appreciably lower value for the efficiency than does Experiment 11, the heat equivalent of the oxygen consumption in the last two determinations during work being 12·87 calories.

In the case of DOUGLAS, previous determinations of the respiratory exchange at rest in bed immediately after waking in the morning,* have shown an oxygen consumption per minute of 237 c.c. and a CO_2 production of 197 c.c., with a respiratory quotient of 0·829, corresponding to a heat output of 1·15 calories per minute. Using this value for the "basal metabolism," the efficiency at 704 kg.m. per minute becomes 23·4 per cent., and at 1056 kg.m. per minute 23·0 per cent.

We made two determinations on DOUGLAS on the bicycle ergometer, when he was pedalling at the same speed as during the work, but with no load on the brake, and found an oxygen consumption per minute of 494 c.c. and a CO_2 production of 409 c.c., with a respiratory quotient of 0·828, corresponding to a heat production of 2·39 calories per minute. With this "basal value," which has the advantage of including the heat production involved in merely rotating the pedals, so that any extra heat production during the work corresponds more nearly simply with the output of energy entailed by putting the load on the brake, the efficiency at 704 kg.m. per minute becomes 28·4 per cent., and at 1056 kg.m. 25·9 per cent.

In whichever of these three ways the efficiency is calculated, the results are of much the same order of magnitude as those obtained by BENEDICT and CATHCART when using similar values for the "basal metabolism." If, however, the efficiency is calculated from the difference between the data obtained for each subject at the two different degrees of work, *i.e.*, for the external work of 352 kg.m. per minute, when this is superimposed on external work of 704 kg.m. per minute, the efficiency has the rather low value of 22·2 per cent. for DOUGLAS and 23·5 per cent. for HOBSON.

In those experiments in which the oxygen consumption rises progressively during the work, there is a corresponding increase in the heat production, *i.e.*, a falling off of efficiency, though the fall of efficiency is not quite proportional to the rise of oxygen consumption owing to the alteration of the respiratory quotient. For instance, in Experiment 6 on DOUGLAS, the heat production per minute during the work is 8·10 calories at the first observation, 8·35 at the second, and 8·45 at the third, and there is the same type of alteration in Experiment 5. This effect suggests the influence of fatigue, the more so, as HOBSON, who was in better muscular condition than DOUGLAS, only showed this phenomenon in Experiment 10, in which he was considerably hampered by the low position of the bicycle saddle, and had in

* DOUGLAS, HALDANE, HENDERSON, and SCHNEIDER, *loc. cit.*

consequence an exceptionally high rate of metabolism. A similar slight rise of heat production during the course of muscular work is shown in a few of BENEDICT and CATHCART's experiments, but it is noticeably absent in the majority, especially in an experiment in which a trained cyclist rode the bicycle ergometer continuously for a period of 4 hours and 22 minutes, during the whole of which time his oxygen consumption per minute was close on 2000 c.c. One may note, too, that the heat production was practically constant in Experiment 9 on DOUGLAS in the last three observations during the work, a period of 23½ minutes, though the oxygen consumption rose considerably between the first and second observations. ZUNTZ and SCHUMBURG* have found a decreased efficiency during walking, as the result of a long march, which they ascribe to the effects of fatigue, but BENEDICT and MURSCHHAUSER† have not been able to find definite evidence of this, though the distance walked reached as much as 14 miles; the pace, however, in their longest experiments was only about 3 miles per hour.

(2) *The Respiratory Exchange during the Work.*

We made no attempt to determine the respiratory exchange during the very early stages of the work, though it would naturally have been of great interest to follow the transition from rest to work as well as from work to rest. We felt, however, that as it takes a brief time for the subject to pick up the rate of the metronome and to steady down to the work, the results would be somewhat difficult to compare with those obtained at a later stage, and we preferred therefore to allow from three to five minutes to elapse after starting pedalling before we took our first samples, so as to allow the subject to get into reasonable equilibrium with the work.

(i) *Work of* 704 *kg.m. per minute.*

While DOUGLAS invariably shows a definite rise of the respiratory quotient throughout the period of work, HOBSON's respiratory quotient remains practically steady at the same level as in the preliminary resting period. DOUGLAS's respiratory quotient is highest in the earliest period of work, and diminishes slowly and steadily as the work is continued, though it is considerably above the preliminary resting value even when the work has been kept up continuously for ¾–1 hour.

Such a rise of the respiratory quotient might be determined by one or more of several causes. Thus it might be an indication of a real alteration in the character of the metabolism, and imply that during work a greater proportion of the necessary energy is derived from carbohydrate than during rest. On the other hand, the explanation might be found in some cause which leads to an expulsion of CO_2 from the store held in combination in the body (the so-called "preformed" CO_2) without

* *Loc. cit.*, p. 259.

† BENEDICT and MURSCHHAUSER, "Energy Transformations during Horizontal Walking," 'Publication No. 231, Carnegie Institute of Washington,' 1915.

any corresponding variation in oxygen consumption, or necessary alteration in the character of the metabolic processes in the tissues.

Two factors at least which might be responsible for the latter effect suggest themselves at once, namely, (*a*) shortage of oxygen arising from the increased oxygen requirements of the body, and (*b*) general rise of body temperature due to the muscular exertion.

In recent years the phenomena of deficiency of oxygen which may arise during muscular work have been ascribed, at least during severe exertion, to the action of lactic acid liberated in the active muscles in consequence of the metabolism of these muscles out-running the available oxygen supply that can be furnished by the blood stream,* and RYFFEL has, in fact, shown the presence of lactic acid in blood and urine as a result of hard muscular work.†

Lactic acid arising in this way will give rise to several effects. It will lower the alkalinity of the blood, and, since the activity of the respiratory centre is dependent on the hydrogen ion concentration in the blood, thus aid carbonic acid to excite the respiratory centre, a lower partial pressure of CO_2 being required to stimulate the centre to a given degree than would be the case in the absence of lactic acid. As lactic acid which has reached the blood stream is extremely slowly eliminated or destroyed (see Ryffel's data), it will tend to accumulate, and the hyperpnœa will, consequently, become much greater than one would expect from the CO_2 stimulus alone. If the excessive hyperpnœa caused in this way is sufficiently great, the alveolar CO_2 pressure may actually be reduced below the normal resting threshold value, in spite of the greatly increased production of CO_2 due to the muscular work, and directly this happens preformed CO_2 must be washed out of the body, the expulsion of this preformed CO_2 being unaccompanied by any corresponding increase in the oxygen absorption.

What is more, lowering of the alkalinity of the blood in severe muscular work is associated with a decrease in the absorption power of blood for CO_2,‡ and this decrease may be enormous with very severe work. A sudden diminution in the absorption power of blood for CO_2 must be accompanied by a great rise in the partial pressure of CO_2 in the blood, with, of course, an increase of the hydrogen ion concentration in correspondence, and consequently, if the muscular work is sufficiently severe to lead to the formation of lactic acid, the hyperpnœa must be still more exaggerated at the start until the redundant preformed CO_2 can be eliminated.

Were lactic acid to continue to accumulate, there is little doubt that the subject would find the work too severe for him, and he would soon be forced to stop; but

* DOUGLAS and HALDANE, 'Journ. Physiol.,' vol. 38, p. 420 (1909). See also DOUGLAS, HALDANE, HENDERSON, and SCHNEIDER, *loc. cit.*; and DOUGLAS, 'Ergebnisse der Physiol.,' 1914, p. 391.

† RYFFEL, 'Journ. Physiol.,' vol. 39, p. xxix, Proc. (1910).

‡ CHRISTIANSEN, DOUGLAS, and HALDANE, 'Journ. Physiol.,' vol. 48, p. 244 (1914); MORAWITZ and WALKER, 'Biochem. Zschr.,' vol. 60, p. 395 (1914).

there is some evidence to suggest that if lactic acid production is not very great and the work can be kept up for a considerable time, the rate of production of lactic acid will presently be balanced by the rate of its elimination or destruction, and a condition of equilibrium will be reached in which the threshold stimulating value of CO_2 on the respiratory centre will remain constant at some point which is below the normal and dependent on the steady amount of lactic acid present, and the ventilation of the lungs will now be determined, in the absence of other disturbing factors, by the height of the CO_2 pressure in the arterial blood above the new threshold stimulating value, not above the normal threshold value.

So long as expulsion of preformed CO_2 is occurring without corresponding increase in the absorption of oxygen, the respiratory quotient must be abnormally high, and muscular work of sufficient severity to give rise to lactic acid will therefore be characterisd both by excessive hyperpnœa and output of CO_2 and by an abnormal rise in the respiratory quotient. These changes will presumably be most marked at the commencement of the muscular exertion when the body is, so to speak, suddenly flooded with lactic acid, and there has not yet been time for any material reduction in the amount of preformed CO_2 in the body. Should, however, a balance be struck between production of lactic acid and its elimination, the abnormal hyperpnœa and respiratory quotient of the early stages will gradually diminish as the excess of preformed CO_2 is got rid of, till finally a condition of equilibrium will be reached in which the ventilation of the lungs will again become proportional to the mass of CO_2 given off, just as is the case in the absence of lactic acid or other disturbing factors, and the respiratory quotient will once more afford a true index of the character of the metabolism in the tissues. At this stage, even though the initial hyperpnœa has shut down to some extent, it of course remains in excess of what one would expect from the CO_2 stimulus alone, since there is also the constant action of lactic acid to be reckoned with.

If lactic acid is still present when the muscular work stops, the lowering of the threshold exciting value of CO_2 on the respiratory centre will become evident as the hyperpnœa dies away, since a considerable time elapses before the excess of lactic acid disappears, and a minute or two after the stop, the resting alveolar CO_2 pressure falls below the normal value. As the lactic acid disappears, a quantity of CO_2 must be retained to make up for the amount of preformed CO_2 originally expelled, and this will be accompanied by a gradual rise in the threshold stimulating value of CO_2 on the respiratory centre (*i.e.*, on the resting alveolar CO_2 pressure), as was shown by DOUGLAS and HALDANE, the normal threshold value being regained when the whole of the lactic acid has been eliminated. While CO_2 retention is occurring in this way, the respiratory quotient will be abnormally low, since there will be no corresponding reduction in oxygen consumption. If lactic acid production is limited only to the early period of the work, we should expect to find evidence of this compensatory CO_2 retention at a later stage of the work, and possibly no indication of the presence of lactic acid when the work stops.

Lactic acid has so far only been definitely recognised in severe muscular work. It is, however, possible to imagine another method by which want of oxygen might exert its effect, and this might come into play with milder degrees of work. Thus supposing the arterial blood is not quite fully saturated with oxygen during the work, owing to the rate of passage of oxygen through the pulmonary epithelium being insufficient, and that this slight depression of the arterial oxygen pressure is in itself capable of exerting an effect on the respiratory centre, the threshold stimulating value of CO_2 on the respiratory centre will be lowered. Such an effect of want of oxygen will, however, presumably remain constant when the body has settled down to the work and be limited to the time during which the muscular work is actually in progress, for it should vanish with the reduction in the oxygen consumption on the cessation of the work. If this effect is sufficiently great to cause the alveolar CO_2 pressure to fall below the normal threshold value during the work, it should lead to temporary exaggerated hyperpnœa and expulsion of preformed CO_2 with an abnormally high respiratory quotient, just as does the accumulation of lactic acid. In this case, however, one would expect that apnœa would ensue when the oxygen want is relieved on the stop of the work and compensatory retention of CO_2 is taking place, for the threshold stimulating pressure of CO_2 on the respiratory centre should at once return to its old normal value, unless of course the deficiency of oxygen has led (in the absence of lactic acid) to some more lasting alteration of the threshold CO_2 pressure by a change in the "fixed alkalinity" of the blood, a condition which appears to come into force during prolonged exposure to atmospheres in which the oxygen pressure is reduced, *e.g.*, at high altitudes.

With a less degree of oxygen want of this type the effect should be of a different character. All that will happen will be that throughout the work the hyperpnœa will be somewhat greater, and the alveolar CO_2 pressure somewhat lower than would be expected if CO_2 alone afforded the stimulus to the respiratory centre; yet here again the correlation of the activity of the respiratory centre with the varying metabolism of the tissues will depend on CO_2, since the want of oxygen may be regarded merely as exerting a constant action during the work and causing the respiratory centre to respond to a greater degree than normal for a given rise of CO_2 pressure. So long as the alveolar CO_2 pressure during the work does not fall below the normal threshold value there will be no expulsion of preformed CO_2. Consequently, a determination of the total respiratory exchange ought under these circumstances to afford evidence neither of excessive output of CO_2 nor of temporary great exaggeration of the hyperpnœa, while the respiratory quotient should continue to afford a true indication of the character of the metabolism of the tissues. The effect of such a want of oxygen will only be rendered apparent during the work by studying the relationship of the hyperpnœa to the alveolar CO_2 pressure at the time.

A "direct" effect of want of oxygen on the respiratory centre of this nature might of course be superimposed on the effects due to accumulating lactic acid in the case of severe work.

In DOUGLAS'S case the behaviour of the CO_2 output and of the hyperpnœa do not appear to conform with what is required by the "lactic acid" or gross want of oxygen theories as stated above, for these values remain practically constant throughout the whole period of work, in spite of the slow steady rise in the oxygen consumption and corresponding fall in the respiratory quotient. No support is therefore given to the lactic acid hypothesis in this case.

In Experiments 3 and 6 we analysed the urine passed just before the experiment began, and that passed just after it terminated, for lactic acid by RYFFEL'S method,* and found in the second sample no more lactic acid than the trace found in the first. Our determinations of lactic acid were not made with the greatest care in these experiments, and the results given in Tables II–VI should be regarded as approximate: the trace of lactic acid found in the normal resting urine is referred to as negative in these Tables.

The actual identification of lactic acid in the urine is, however, probably too coarse a method to adopt if the production of lactic acid is small, for lactic acid might get destroyed in whole or part before it could be excreted by the kidneys, and RYFFEL shows in fact that after severe exercise, excess of lactic acid in the urine disappears more rapidly than does that in the blood.

Far the most delicate test for the lowering of the alkalinity of the blood owing to deficiency of oxygen or production of lactic acid is to be found in the reaction of the respiratory centre. DOUGLAS and HALDANE (*loc. cit.*) showed that if the alveolar CO_2 pressure is determined at intervals whilst resting after the stop of some severe muscular work, it shows a characteristic fall to a value much below normal, followed by a slow recovery, indicating that the threshold stimulating value of CO_2 on the respiratory centre has been temporarily lowered by the exercise. This reaction is, however, absent after gentle or moderate exercise, the threshold value after the exercise being the same as it was before.

We made three experiments on DOUGLAS by this method, using the HALDANE-PRIESTLEY method of obtaining alveolar air samples and employing the same degree of work as in the determinations of the respiratory exchange. The results are given in Table VIII.

The figures show that there was a definite, though small, temporary lowering of the alveolar CO_2 pressure after the exercise in the first only of these experiments, but it should be noted that the subject was not cooled by the fan in this experiment.

It is known that rise of body temperature in an otherwise normal person is associated with a degree of hyperpnœa out of proportion to the CO_2 production at

* 'Journ. Physiol.,' vol. 39, p. v, Proc. (1909).

TABLE VIII.

	Percentage of CO_2 in dry alveolar air.	Pressure of CO_2 in mm. Hg in alveolar air at 37° saturated with moisture.	Rectal temperature, degrees Fahrenheit.
(1) Work of 704 kg.m. per minute for 12 minutes. No cooling by fan. Bar. 765 mm.			
Normal before start	5·58	40·0	
3½′ after stop	5·25	37·7	
12 ,,	5·29	38·0	
25½ ,,	5·23	37·6	
45 ,,	5·52	39·6	
63½ ,,	5·46	39·2	
(2) Work of 704 kg.m. per minute for 21 minutes. Cooled by one fan during work. Bar. 764 mm.			
Normal before start	5·29	38·0	99·6
3½′ after stop	5·31	38·1	
11 ,,	5·14	36·9	
15 ,,	—	—	99·8
23½ ,,	5·39	38·7	
37 ,,	5·31	38·1	
52 ,,	5·32	38·2	
(3) Work of 704 kg.m. per minute for 20¼ minutes. Cooled by one fan during work. Bar. 742 mm.			
Normal before start	5·61	39·0	98·8
3½′ after stop	5·74	39·9	
10¾ ,,	5·68	39·5	
17 ,,	—	—	99·8
22 ,,	5·47	38·0	
34 ,,	—	—	99·2
37 ,,	5·58	38·8	

the time.* As HALDANE pointed out to us, the temperature which really matters in this connection is that of the blood reaching the respiratory centre. This, unfortunately, is practically impossible to estimate, since the blood coming from parts of the body which are abnormally warm owing to heightened metabolism is mixed in the heart with cooled blood coming from the skin. It is clear that a temporary rise in temperature of the blood reaching the respiratory centre during muscular work might give rise to alterations in the hyperpnœa, CO_2 output and respiratory quotient of the same sense as those caused by the development and disappearance of lactic acid. We recognised the difficulties of the question of temperature, but the best we could do was to try by means of fans to keep the general body temperature within reasonable limits during the work, for we were afraid that it might otherwise rise unduly in the still air of the laboratory. One fan was sufficient to keep the subject cool and comfortable in experiments at work of 704 kg.m. per minute, though two were necessary in

* HALDANE, 'Journ. of Hygiene,' vol. 5, p. 503 (1905); HILL and FLACK, 'Journ. Physiol.,' vol. 38, p. lvii, Proc. (1907).

the experiments with harder work. In each case the sweat evaporated almost as fast as it was formed, and the subject did not therefore get chilled in the long period of rest that followed the muscular exertion. From the data given in Table VIII, where a few determinations of the rectal temperature before and after the muscular work are recorded, we should judge that our efforts to prevent undue rise of temperature had been tolerably successful, though it is quite possible that in the first of these experiments the distinct fall in the alveolar CO_2 pressure after the work is dependent more on rise of temperature than on anything else, as no fan was used.

The lactic acid theory and temperature changes therefore appear inadequate to explain the rise of the respiratory quotient during the work in DOUGLAS's case in this series of experiments, and, as we have pointed out above, a slight "direct" action of deficiency of oxygen on the respiratory centre, if limited to the period of work, would not be appreciable in a record of the total respiratory exchange, though it might become evident from a consideration of the volume of air breathed during the work and the prevailing alveolar CO_2 pressure. We suggest, therefore, that this alteration is, in the main at least, due to the fact that the energy output during the work involves the metabolism of a greater proportion of carbohydrate to fat than is the case during rest.

This idea is strengthened by the earlier experiments on DOUGLAS during walking exercise,* in which it was shown that rise of respiratory quotient could be detected at rates of exercise so low as to demand only double the resting metabolism, though the rise became greater as the rate of walking and the total metabolism increased, and that moderate prolongation of the exercise did not lead to any striking alteration of the respiratory quotient. It was tentatively suggested on these grounds, as well as on the fact that examination of the alveolar air gave no indication of a persistent lowered threshold value of CO_2 unless the pace of walking was very fast, that the most probable explanation lay in the increased proportion of carbohydrate to fat consumed during the work. AMAR,† using a bicycle ergometer, had previously obtained very similar results and had reached the same conclusion. A number of BENEDICT and CATHCART's experiments show a fairly considerable rise of respiratory quotient during the work, with in some cases a tendency to diminution with prolongation of the exercise, though in a good many instances the respiratory quotient remains just about the same during the work as it was during the preliminary resting period, as was the case with HOBSON in our experiments. The average of their experiments shows that there is a distinct, though slight, rise of respiratory quotient during the work, and in a full discussion of the significance of this change they incline strongly to the view that it indicates an increase in the proportion of carbohydrate consumed. BENEDICT and MURSCHHAUSER's experiments on trained athletes during walking exercise afford many examples of a rise of respiratory quotient during the exercise, and

* DOUGLAS, HALDANE, HENDERSON, and SCHNEIDER, *loc. cit.*

† AMAR, 'Le Rendement de la Machine Humaine,' Paris, 1910.

though this change is most marked when the subject had had food shortly before the commencement of the experiment, it also occurs to a less degree when he was in the post-absorptive state. The diminution of respiratory quotient during long periods of exercise is also shown in these experiments. Apparently, therefore, our experiments are not vitiated by the fact that the subjects had had breakfast about two hours before the commencement, though no doubt the degree of alteration that we observed was exaggerated by the fact that the subjects were not in the post-absorptive state.

If the view is right that carbohydrate may be used in greater proportion during work than during rest, a diminution of respiratory quotient during the work would seem by no means improbable, since the degree of rise will no doubt be to some extent dependent on the availability of carbohydrate, and this will quite likely be lessened as the stores of carbohydrate in the muscles or in the body at large are depleted in consequence of the heightened metabolism. It is clear from all these experiments that there is a good deal of difference between different individuals, and between the same individual at different times, as regards the character of their metabolism. Some, like HOBSON, seem to have much the same type of metabolism during work as during rest, at least under circumstances when the work is not very hard, while others like DOUGLAS appear to consume an increased proportion of carbohydrate, as indicated by a definite rise of respiratory quotient, even when the work is quite light. It is, of course, possible that the degree of physical fitness for the work in question may be of importance in this connection.

It is of interest to consider whether it is possible in these experiments to explain the hyperpnœa merely by a rise of CO_2 pressure in the arterial blood along the lines originally suggested by HALDANE and PRIESTLEY.* KROGH and LINDHARD† have raised a valid objection to direct determinations by the HALDANE–PRIESTLEY method of the alveolar CO_2 pressure (with which the arterial blood must be nearly in equilibrium) during muscular work, and one must therefore use an indirect method, though the direct method is applicable during rest.

The average normal alveolar CO_2 percentage during rest was about 5·5 per cent. in DOUGLAS (Tables VIII and IX). Taking an average of all the observations during the period of rest before commencing the work (Tables II to VI), the volume of each breath was 703 c.c. and the CO_2 percentage in the expired air 3·6 per cent. Calculation from these figures gives an effective dead space at rest of 244 c.c. (this includes the dead space of 60 c.c. in the valves and mouthpiece). An average of all the observations on DOUGLAS during work of 704 kg.m. per minute shows a volume for each breath of 1974 c.c. and an expired CO_2 percentage of 4·83 per cent. If we assume that the dead space during the hyperpnœa caused by the work has the same value as during rest, the calculated alveolar CO_2 percentage during the work is

* HALDANE and PRIESTLEY, 'Journ. Physiol.,' vol. 32, p. 225 (1905).

† KROGH and LINDHARD, 'Journ. Physiol.,' vol. 47, p. 30 (1913); *ibid.*, p. 431.

5·51 per cent., *i.e.*, a value identical with the resting normal. Any increase in the dead space during the work above the normal resting value would, of course, imply an increase in the alveolar CO_2 percentage.

We have previously shown* that the effective dead space shows a considerable increase during the hyperpnœa, caused by breathing air containing CO_2 when the oxygen consumption and CO_2 production are practically the same as during rest, and HALDANE† and YANDELL HENDERSON, CHILLINGWORTH and WHITNEY,‡ have shown that the effective dead space increases rapidly with the depth of the breaths in experiments in which the depth of the breathing was altered voluntarily. KROGH and LINDHARD,§ on the contrary, maintain that the effective dead space is hardly altered at all, no matter whether the breathing is deep or shallow. While it seems to us possible that the method of investigation adopted by KROGH and LINDHARD may give information regarding the volume of air contained in the respiratory passages, including trachea, bronchi and bronchioles, and its variations, we are not convinced by their argument that this anatomical dead space is identical with the true effective dead space, which is a purely conventional though very convenient expression, by which we assume the expired air to be composed of a mixture of average "alveolar air" with pure air contained in the "dead space."

Our previous experiments on DOUGLAS have shown that, during a hyperpnœa, caused by breathing air containing CO_2, a rise of 0·28 per cent. in the alveolar CO_2 percentage at normal barometric pressure (*i.e.*, of 2 mm. pressure of CO_2) is sufficient to cause a rise of 10 litres in the total ventilation of the lungs. If we suppose in our present experiments that, during work of 704 kg.m. per minute, the threshold stimulating value of CO_2 on the respiratory centre remained the same as during rest, corresponding to 5·5 per cent. of CO_2 in the alveolar air, the average rise during the hyperpnœa of about 30 litres above the normal total ventilation of the lungs at rest would have required a rise of about 0·84 per cent. above the resting alveolar CO_2 percentage to account for it. With the average volume of each breath at 1974 c.c., and expired CO_2 percentage of 4·83 per cent., the required percentage of CO_2 in the alveolar air (viz., 6·34 per cent.) would have been obtained if the effective dead space (including valves) had been 472 c.c. So far as we can judge from the experiments by ourselves, by HALDANE, and by HENDERSON and his colleagues, this value for the dead space is quite reasonable, having regard to the depth of the breathing. At the same time, it should be remembered that the rise of alveolar CO_2 pressure, that we should otherwise expect to find to account for the hyperpnœa, would be proportionally lowered if there were any "direct" action of slight deficiency of oxygen on the respiratory centre during the period of muscular work.

* CAMPBELL, DOUGLAS, and HOBSON, 'Journ. Physiol.,' vol. 48, p. 303 (1914).

† 'Amer. Journ. Physiol.,' vol. 38, p. 20 (1915).

‡ 'Amer. Journ. Physiol.,' vol. 38, p. 1 (1915).

§ 'Journ. Physiol.,' vol. 51, p. 59 (1917).

In the case of Hobson, we have only two earlier determinations of the normal alveolar CO_2 percentage at rest,* and these give an average value of 5·2 per cent. If we accept this value, his resting dead space in our experiments was about 205 c.c., and, if this had remained unchanged during the muscular work, his alveolar CO_2 percentage during the work would have been about 5·6 per cent., *i.e.*, above the resting value.

(ii) *Work of* 1056 *kg.m. per Minute.*

Experiments 8 and 9 on Douglas, and Experiment 10 on Hobson, show a quite abnormal rise of the respiratory quotient to unity or beyond in the early period of the work. This large rise is, however, quite shortlived, for, by the time the second observation is made, the respiratory quotient has fallen to about 0·95 in Douglas's case and to 0·88 in Hobson's. After the temporary sharp rise of the respiratory quotient has passed away, the picture presented for the remainder of the period of muscular work is very similar to that shown in the experiments at 704 kg.m. per minute, *i.e.*, Douglas's respiratory quotient remains at a level considerably above the resting value, with a tendency to fall as the work is prolonged and the oxygen consumption rises, while Hobson's returns to about its preliminary resting value. It will be noted in Experiments 9 and 10 that the CO_2 output during the first work period is markedly in excess of what it is subsequently, and that the hyperpnœa is definitely at a maximum during the same period. In the later work periods, both CO_2 output and hyperpnœa have dropped back to fairly steady values.

These changes shown in the early period of the exercise can be explained quite simply on the "lactic acid" hypothesis, coupled, it may be, with a more direct action of want of oxygen on the respiratory centre, for there is clear evidence of excessive hyperpnœa and washing out of pre-formed CO_2 at this time. Moreover, 0·1 grm. of lactic acid was recovered from the urine passed at the end of Experiment 8, and 0·05 grm. at the end of Experiment 9.

In addition to this, we obtained definite evidence in Douglas' case of a persistent, though not very great, lowering of the threshold stimulating value of CO_2 on the respiratory centre by following the alveolar air changes after the cessation of work at 1056 kg.m. per minute. The figures are given in Table IX.

It will be seen that the resting alveolar CO_2 percentage fell from the normal of about 5·5 per cent. to about 5·1 per cent. between roughly the fourth and twentieth minutes after the stop (*i.e.*, a fall of about $2\frac{1}{2}$ mm. below the normal alveolar CO_2 pressure). The general rise of body temperature seems in this instance again to have been fairly effectively controlled by the arrangements we adopted for cooling the subject.

The shortness of the period during which the abnormally high respiratory quotient and excessive hyperpnœa are shown in these experiments, and the slightness of the

* Campbell, Douglas, Haldane, and Hobson, 'Journ. Physiol.,' vol. 46, p. 301 (1913).

TABLE IX.

	Percentage of CO_2 in dry alveolar air.	Pressure of CO_2 in mm. Hg in alveolar air at 37° saturated with moisture.	Rectal temperature, degrees Fahrenheit.
(1) Work of 1056 kg.m. per minute for 21 minutes. Bar. 757 mm.		Cooled by two fans during work.	
Normal before start	5·37	38·2	99·5
4′ after stop	5·23	37·2	
11 ,,	5·23	37·2	
18 ,,	—	—	100·3
$22\frac{3}{4}$,,	5·13	36·4	
$31\frac{1}{2}$,,	5·28	37·5	
47 ,,	5·33	37·8	
58 ,,	—	—	98·9
$61\frac{1}{2}$,,	5·50	39·1	
71 ,,	—	—	98·7
$77\frac{1}{2}$,,	5·46	38·8	
(2) Work of 1056 kg.m. per minute for 20 minutes. Bar. 761 mm.		Cooled by two fans during work.	
Normal before start	5·52	39·4	99·2
$4\frac{3}{4}$′ after stop	4·87	34·8	
$11\frac{3}{4}$,,	5·07	36·2	
18 ,,	—	—	99·9
$21\frac{3}{4}$,,	5·30	37·8	
32 ,,	—	—	99·4
$35\frac{3}{4}$,,	5·24	37·4	
46 ,,	—	—	99·0
50 ,,	5·48	39·1	

after-effect on the alveolar CO_2 pressure, may tempt one at first sight to suggest that the lactic acid was mainly produced in the early period of the exercise, at a time, perhaps, when the circulation had not yet become fully adapted to meet the demand made on it owing to the sudden increase in the metabolism of the active muscles. This may be so, but it will be evident from what we have said previously that the figures as they stand do not justify this interpretation, for we might get a result of the same character if lactic acid were produced at a slow rate throughout the muscular work and elimination or destruction of lactic acid were gradually to balance its production. Under these circumstances, as the initial disturbance caused by the production of lactic acid dies away, a change in the respiratory quotient, due to an alteration in the character of the metabolism in the tissues, should gradually be unmasked, and, in the later periods of work in these experiments, any persistent increase of the respiratory quotient may well have the same explanation as the one we have already put forward in the case of lighter work, viz., an increase in the proportion of carbohydrate to fat metabolised. In order to settle the point clearly, the simplest plan would appear to be to eliminate so far as practicable any possibility of want of oxygen, and this could be done by working in an atmosphere containing a higher percentage of oxygen than normal. Unfortunately, we have not yet had the opportunity of making these experiments.

Experiment 11 on HOBSON differs from the other experiments with this degree of work, as it resembles closely the result we got on DOUGLAS with work of 704 kg.m. per minute. The work leads to a rise of respiratory quotient, which diminishes progressively during the course of the work, but there is no definite evidence pointing to excessive hyperpnœa and washing out of pre-formed CO_2 in the early stages. Only a trace of lactic acid could be found in the urine at the end of the experiment, and this was probably not in excess of what is shown by normal urine. Apparently, therefore, HOBSON was not affected by any gross want of oxygen in this experiment, though, in Experiment 10, the additional demand of 200 c.c. of oxygen per minute, entailed by the disadvantageous conditions under which he was working, sufficed to put him in difficulties from this cause. Owing to HOBSON'S better physical condition, one would naturally expect him not to show want of oxygen effects as soon as DOUGLAS.

If we discard in the experiments on DOUGLAS the early periods in which the respiratory quotients are clearly abnormally high, and confine ourselves to the last observation during work in Experiment 8, and the last three in Experiment 9, the average volume of each breath during the work is 2451 c.c., and the CO_2 percentage in the expired air 4·52 per cent. Assuming the resting effective dead space of 244 c.c. to hold good during the work, the calculated alveolar CO_2 percentage during the work becomes 5·01 per cent., a value which is considerably below the normal found at rest, but approximately the same as the temporary low value found shortly after the cessation of the work (Table IX). The average total ventilation of the lungs is 60·5 litres per minute, *i.e.*, about 52·5 litres above the resting value. In the case of hyperpnœa caused by breathing air containing CO_2, this increase would have been caused in DOUGLAS'S case by a rise of 1·47 per cent. above the normal alveolar CO_2 percentage. If we assume in the experiments on DOUGLAS, with work of 1056 kg.m. per minute, that the hyperpnœa, when it has steadied down after the preliminary disturbance due to lactic acid production, is proportional to the mass of CO_2 produced, and the respiratory centre reacts to the same degree to changes of CO_2 pressure as during rest, we should expect to find an average rise in the alveolar CO_2 percentage of 1·47 per cent., not above the resting normal value of 5·5 per cent., but above the lowered threshold value maintained during the work owing to the effects of want of oxygen. The only index of this latter figure is furnished by the low value of about 5·1 per cent., to which the alveolar CO_2 falls after the stop of the exercise, though very likely this is not so low as that which prevailed during the work. Supposing the real average alveolar CO_2 percentage during the work had been 5·1+1·47, viz., 6·57 per cent., the effective dead space calculated from this figure, the average volume of a breath, and the average CO_2 percentage in the expired air would become 761 c.c., a large figure admittedly, but still by no means out of the way in comparison with the observations of ourselves, of HALDANE, and of HENDERSON and his colleagues, which we have quoted previously. Here, again, the anticipated rise of alveolar CO_2 pressure and the calculated volume of the dead space would have been considerably reduced during the work if a "direct" effect of oxygen deficiency on the respiratory centre had been superimposed upon the effects caused by lactic acid accumulation.

In HOBSON'S case, if we assume the resting dead space to remain constant during the work, his alveolar CO_2 percentage during the work (Experiments 10 and 11) would be about 5·48 per cent., *i.e.*, a little above his resting normal and a little below the alveolar CO_2 percentage calculated during the work of 704 kg.m. per minute.

(iii) *Work of* 1232 *kg.m. per Minute.*

The results obtained in the single determination made during the work are evidently an exaggeration of those observed in the earlier period of work in Experiments 8, 9, and 10. No less than 0·57 grm. of lactic acid was recovered from the urine passed at the end of the experiment. Though the hyperpnœa was still very excessive, the respiratory quotient was only 1·03 when it was determined just before the stop, but it is evident that it must have had a much higher value at an earlier stage of the work before a great part of the excess of preformed CO_2 had been blown off. It is most unfortunate that we were prevented from determining the respiratory exchange at the end of the first 4 minutes of the work, but we can get some idea of what might have been happening in the earlier stages from some previously unpublished observations of DOUGLAS, HALDANE, and BOOTHBY. These are shown in Table X.

TABLE X.

Body weight in lbs.	Pace in miles per hour.	Kg.m. of lifting work per minute.	Respiratory exchange in c.c. per minute at 0° and 760 mm.		Respiratory quotient.	Breaths per minute.	At 37°, moist, and prevailing barometer.		CO_2 per cent. in expired air.
			O_2.	CO_2.			Litres breathed per minute.	C.c. per breath.	
DOUGLAS. 150	2·8	1132	2870	3490	1·22	41·4	109·4	2670	3·95
—	2·7	1095	2940	3420	1·16	45·5	104·8	2300	4·04
HALDANE. 183	2·5	1125	2790	3015	1·08	39·0	80·3	2060	4·64
BOOTHBY. 113	1·6	570	2750	3300	1·20	39·0	96·1	2465	4·25

The work in this instance consisted in pushing a motor bicycle weighing about 150 lb. up an average gradient of 10·8 per cent., and the muscular work was continued for three minutes only before the sample of expired air was collected in a bag carried on the back of the subject, the collection of the sample taking rather over one minute. The walk was begun at a point where the gradient was far less steep and about one minute elapsed before the gradient of 10·8 per cent. was reached. The second experiment on DOUGLAS was made 1½ hours after the first. BOOTHBY started walking at too fast a pace to keep it up, and as he was slowing up very rapidly towards the end of the period of sampling owing to exhaustion, the average pace of 1·6 miles an hour does not give a real indication of the rate of work that he really reached during the observation.

These experiments were originally made simply to get some idea as to how far the respiratory exchange could be increased in really severe muscular work. The subjects were absolutely untrained, but BENEDICT and CATHCART'S observations show that a trained athlete can keep up work entailing an oxygen consumption of 3000 c.c. per minute, or even more, for some time. Judging by the oxygen consumption in DOUGLAS'S case the metabolism was perhaps a little higher than in Experiment 12, but the hyperpnœa and distress seemed to be much the same in the two cases. Respiratory quotients as high as 1·2 were reached, the volume of CO_2 produced per minute being in excess of the volume of oxygen absorbed by amounts varying in the different experiments from 225 c.c. in HALDANE'S case to 620 c.c. in the first observation on DOUGLAS. These figures give some idea what an enormous volume of preformed CO_2 may be expelled in very severe work. The excessive hyperpnœa and the lowness of the CO_2 percentage in the expired air are particularly marked in the experiments on DOUGLAS and BOOTHBY.

Further evidence regarding the cause of the very violent hyperpnœa, and the amount of preformed CO_2 that may have to be got rid of in short experiments when the work is extremely severe, is afforded by the observations of CHRISTIANSEN, DOUGLAS, and HALDANE (*loc. cit.*), in which it was shown that muscular work of this character led to an enormous temporary alteration in the CO_2 absorption power of the blood, the volume of CO_2 that can be held in combination in the blood at any given partial pressure of CO_2 being greatly reduced, as well as to a very great lowering of the threshold stimulating value of CO_2 on the respiratory centre, recovery of the normal absorption curve and normal threshold value of CO_2 not being attained till an hour or more after the stop of the muscular work.

(3) *The Respiratory Exchange during the Period of Rest following the Muscular Work.*

One of the most striking features in our experiments is the exceedingly rapid fall of both the respiratory exchange and the hyperpnœa as soon as the muscular exercise stops. It has, of course, long been recognised experimentally* that such a fall occurs, though it is not till one can plot out the actual values as a continuous record that one fully appreciates its character. It is quite clear from figs. 4–7 that by far the greater part of this fall occurs in the first minute or two after the stop of the work, though a number more minutes elapse before the respiratory exchange and the hypernœa definitely fall to a steady value. The total period elapsing after the stop of the exercise before the respiratory exchange reaches a steady minimum varies in different experiments from 11 to 28½ minutes, with an average of about 20 minutes. We may presumably regard these final steady values as representing truly the more or less lasting effects produced on the resting respiratory exchange by a period of muscular work, and it seems reasonable to look upon the rapidly diminishing respiratory exchange in the period between the stop of the work and the assumption of these steady values as being determined, both in amount and character, by certain temporary causes incidental to the transition from work to rest.

The respiratory exchange after the stop of the muscular work is excessive for a short time in comparison with the figure at which it remains constant in the later stages, and it is of interest to ascertain the magnitude of this "excess respiratory exchange." This can be done in the case of some of our experiments in which the data are sufficiently complete by calculating the total respiratory exchange for the whole period from the stop of the work till the respiratory exchange reaches a reasonably steady value, and subtracting from the figure so obtained the total respiratory exchange calculated for the same period at the final steady rate. The figures are given in Table XI.

By comparison with Tables II–VI it will be seen that the "excess oxygen consumption" after work of 704 and 1056 kg.m. per minute on the average barely amounts to as much as the oxygen consumption during one minute of the muscular work, while the "excess CO_2 production" is considerably higher than the CO_2 production during one minute of the muscular work. In the case of the severe work of 1232 kg.m. per minute the "excess respiratory exchange" is greatly above the respiratory exchange during one minute of the previous muscular work. The values of this "excess respiratory exchange" after the work of 704 and 1056 kg.m. per minute are surprisingly low, especially as regards the oxygen consumption, but agree completely with the conclusions of earlier observers. LOEWY, for instance, states† that after the cessation of muscular work the respiratory exchange remains high for several minutes, though the excess oxygen consumption during the entire period of rest following the exercise scarcely amounts to so much as the oxygen consumption

* SPECK, 'Physiologie d. menschl. Atmens,' p. 56, Leipzig (1892); KATZENSTEIN, 'Pflügers Archiv,' vol. 49, p. 330 (1891); LOEWY, 'Pflügers Archiv,' vol. 49, p. 405 (1891); ZUNTZ und SCHUMBURG, *loc. cit.*, pp. 223, 235; ZUNTZ und HAGEMANN, 'Stoffwechsel des Pferdes,' p. 286, Berlin (1898).

† *Loc. cit.* See also LOEWY, 'Oppenheimer's Handbuch der Biochemie,' vol. 4, Part I, p. 262, Jena (1911).

during a single minute of the work period, and only mounts to a higher value when there is great muscular fatigue or when the work is done under conditions of insufficient supply of oxygen.

TABLE XI.

Experiment.	Work in kg.m. per minute.	Final period after the work in which the respiratory exchange is steady.			Period intervening between the stop of the work and the assumption of the steady respiratory exchange.		
		Length of period.	Average respiratory exchange in c.c. per minute.		Length of period.	Total O_2 consumption and CO_2 production in c.c. in excess of values which would have been obtained if the respiratory exchange during this period has been the same as the steady rate eventually reached.	
			O_2.	CO_2.		O_2.	CO_2.
DOUGLAS.							
2	704	33′ 37″	297	230	21′ 2″	1775	2262
3	704	33 31	298	234	18 3	1598	1807
8	1056	25 6	287	222	17 58	2512	3543
9	1056	68 37	328	248	10 56	1880	2720
12	1232	57 4	308	204	28 27	3708	5981
HOBSON.							
4	704	21 55	342	300	20 35	1363	1650
11	1056	32 55	350	285	24 30	2068	2498

Several different factors must combine to prevent the respiratory exchange from falling to a steady resting value immediately after the work stops, and some of these suggest themselves at once.*

(i) At the moment when the muscular work stops, blood, whose gaseous content has been determined by the last few moments of muscular activity, is in process of passing from the active muscles to the lungs. Clearly there can be no material decrease in the gaseous exchange in the lungs till the last of this blood has passed through the lungs.

(ii) It is improbable that at any given moment in the course of muscular activity the gaseous content of the blood leaving the active muscles corresponds with the actual consumption of oxygen or formation of CO_2 at the same moment in these muscles. The changes in the blood must lag a little behind the changes in the muscles, partly on account of the time required for the passage of gases between the blood and the muscles, and partly perhaps on account of the nature of the processes involved in the absorption of oxygen and production of CO_2 in a muscle.† At the

* In this connection see DURIG und ZUNTZ, 'Skand. Archiv für Physiol.,' vol. 29, p. 133 (1913).

† See FLETCHER and HOPKINS, 'Roy. Soc. Proc.,' B, vol. 89, p. 444.

same time it would appear that a lag of this description must be a pretty small thing under normal conditions of activity with an effective circulation of the blood through the muscles, otherwise it is difficult to see why it would not act prejudicially if the work were to be kept up for more than a short time, though the lag will be somewhat accentuated in the case of CO_2 by the capacity of the blood and tissue fluids for absorbing more CO_2 at higher partial pressures of the gas.

(iii) It is possible that complete rest is not assumed at once on stopping the work, or the "tone" of the muscles may only decrease gradually to a steady value after a period of activity. When determining the resting respiratory exchange it is always necessary to wait for some time before a reasonably steady value can be obtained, even if the preceding activity has been quite slight.

(iv) General rise of body temperature causes an increase of the resting metabolism.* When, therefore, rest is resumed after a period of muscular activity one would expect the metabolism in those parts of the body in which the exercise has caused a rise of temperature to remain unduly high until the temperature falls back to its normal value.

(v) The hyperpnœa after the stop of the muscular exercise decreases in much the same manner as does the respiratory exchange, keeping pace with CO_2 production rather than with oxygen consumption. So long as the hyperpnœa persists it implies some increase in the resting metabolism on account of the heightened activity of the respiratory muscles.

Of these factors, the first, which would have a considerable effect, as well as the second, one would expect to be limited to a brief period after the stop of the work, whereas the last three would be operative for a longer period and would cease more gradually. The excess respiratory exchange per minute in our experiments is far greater in the first period after the stop than in any of the subsequent periods, and after the great primary fall diminishes more and more gradually as the final steady value of the respiratory exchange is approached.

The fact that there is a temporary sharp rise of the respiratory quotient to 1·0 or beyond, *i.e.*, that the CO_2 output is for a brief time actually in excess of the oxygen absorption, immediately after the stop of the exercise has been noticed by other observers (LOEWY, KATZENSTEIN, ZUNTZ and HAGEMANN, ZUNTZ and SCHUMBURG; *loc. cit.*). These authors have suggested that the cause of this is to be found in the fact that in addition to CO_2 other substances derived from the active muscles (*e.g.*, lactic acid) stimulate the respiratory centre, and that on cessation of the work the breathing remains exaggerated until these substances can be oxidised, the exaggeration of the breathing implying, of course, washing out of CO_2 from the body in excess of the oxygen absorbed.

This theory alone seems to us quite insufficient to explain the facts. The sharp rise of the respiratory quotient is shown in our experiments no matter whether the

* SUTTON, 'Journ. Path. and Bact.,' vol. 13, p. 62 (1909).

work is light or heavy, or the period of exercise short or long, though the rise is more marked in the experiments with work of 1056 kg.m. per minute than in those with work of 704 kg.m. per minute. We have shown above that we could get no distinct evidence of the formation of lactic acid in the case of work of 704 kg.m. per minute. In the experiments with work of 1056 kg.m. per minute we got unmistakable evidence of the formation of lactic acid in several cases; the amount, however, did not appear to be very great, while it seemed quite likely that in the later stages of the work production and elimination of lactic acid were balanced. In neither of these cases does there seem to be any reason for supposing that CO_2 would be expelled from the body after the stop of the work out of proportion to the oxygen consumed.

The facts seem to us capable of another interpretation. Whilst admitting that there will no doubt be a tendency during the work to accumulation of CO_2 in the active parts of the body owing to the amount of CO_2 held in the blood and tissue fluids being dependent on the partial pressure of CO_2, and that this excess will be given off directly the work stops, the close similarity both in general character and in rate between the diminution of the hyperpnœa after stopping the work and the diminution of the hyperpnœa when breathing is resumed after holding the breath,* or when fresh air is breathed again after exposure to an atmosphere containing CO_2†, suggests the necessity of a deeper explanation. In the latter two cases the difficulty was pointed out of explaining the gradual subsidence of the hyperpnœa without any signs of marked periodicity of the breathing, unless the assumption was made that the respiratory centre is itself charged up with more CO_2 than normal in consequence of the rise of alveolar CO_2 pressure while the breath is held or air containing CO_2 is breathed, and that the washing out of this excess from the respiratory centre when the breathing recommences or fresh air is again breathed takes an appreciable time.

It appears to us probable, therefore, that the alveolar CO_2 pressure during the work is above the resting threshold stimulating value which holds good just after the exercise stops—this may be the same as the normal threshold value in the case of light work, or lower than the normal in the case of heavy work owing to the effect of lactic acid (and perhaps rise of temperature), and that CO_2 is therefore dammed back in the body at large, including the respiratory centre, during the work. It has been shown above that this condition can only be attained in our experiments if the effective physiological dead space during the hyperpnœa is increased during the work above the normal resting value. Directly the muscular work ceases the alveolar CO_2 pressure will tend to fall as CO_2 production is reduced, and the CO_2 which was dammed back in the body will be expelled, the expulsion being rapid at first while the excess of CO_2 retained in the body is still high, and then becoming slower and slower as the amount of CO_2 retained sinks towards the value corresponding to the prevailing threshold CO_2 pressure. Expulsion of CO_2 dammed back in this manner

* DOUGLAS and HALDANE, *loc. cit.*

† CAMPBELL, DOUGLAS, HALDANE, and HOBSON, *loc. cit.*

would not be accompanied by any corresponding variation in the oxygen consumption. One would expect that the higher CO_2 production in the heavier work experiments would be accompanied by a higher relative increase in the alveolar CO_2 pressure than is the case with the lighter degree of work, and this will help to explain why the sharp rise of the respiratory quotient after the stop of the work is more pronounced with work of 1056 kg.m. per minute than it is with work of 704 kg.m. per minute.

If, however, the body has not attained equilibrium with the lactic acid production by the time the work stops, it is evident that the action of lactic acid must continue during the earlier period of rest following on the muscular exercise, and that its effect will be superimposed on that postulated above. This condition must be present in Experiment 12 at least, for as the respiratory quotient was still above unity in the last period of work it is clear that the expulsion of preformed CO_2 was not by any means complete when the work stopped, and this process must have continued for some time after resuming rest.

The precise height to which the respiratory exchange will rise after the exercise stops will depend in observations of this type on the length of the period of observation, for the longer the period the lower must be the apparent rise. At the same time one would expect the rise to be most evident not in the first few moments after the stop of the work, when the gaseous content of the blood reaching the lungs is still largely determined by the gaseous exchange of the muscles in the final stage of of the work, but at a slightly later period when the respiratory exchange has dropped considerably. This seems to be the case in Experiment 12, where the highest respiratory quotient was observed not in the first 51 seconds after the subject resumed rest, but in the succeeding period of 1 min. 37 secs.

It would be of very great interest to ascertain the amount of surplus CO_2 which is expelled without corresponding intake of oxygen in the early period after the stop of the exercise, but our data are insufficient for this purpose, though it is possible to get some idea as to the order of magnitude of this quantity. It would no doubt be right to regard the volume of CO_2 produced in excess of the total volume of oxygen absorbed whilst the respiratory quotient is above unity as derived from CO_2 dammed back or preformed in the body, and to take this as the minimal value. During this time, as well as in the subsequent two or three periods, there is, however, nothing to indicate the true respiratory quotient significant of the character of the metabolism in the tissues as distinct from the observed respiratory quotient, which must differ from the former in a degree depending on the amount of surplus or preformed CO_2 expelled or on the amount of CO_2 retained to make up for a deficiency previously created. It would seem to us that a still fairer approximation would be obtained by taking the whole period following the stop of the muscular work in which the respiratory quotient is above the value found in the last work period, and reckoning as surplus CO_2 expelled from the body the volume of CO_2 in excess of what is required by the oxygen intake if one allows a respiratory quotient identical with that shown in the last work period. The real metabolic respiratory quotient directly after the work can hardly exceed that shown during the last stages of the work; in fact, the general course of events would suggest that it begins to fall very soon after the exercise stops. We can obtain a limiting value for this surplus CO_2 discharge by assuming that the real metabolic respiratory quotient falls immediately after the stop of the work to its final steady value, and calculating the excess CO_2 on this assumption for the whole period which elapses before the respiratory exchange and observed respiratory quotient become steady, for such a value must be in excess of the true one since the respiratory exchange and metabolic respiratory quotient are bound to approximate in the first few moments after the stop to the values shown during the last stages of the work, while no account is taken of the possibility that the fall of the respiratory quotient may be in part attributable to retention of CO_2. The values calculated by these three methods are given in Table XII, and it will be seen that with the exception of Experiment 11 the apparent surplus of CO_2 expelled is greater after the heavier work than after the lighter.

TABLE XII.

Experiment.	Work in kg.m. per minute.	Surplus CO_2 production after the stop of the work in c.c., reckoned on the assumption that it indicated so long as the respiratory quotient is above :—		
		1·00	Value shown in last period of work.	Final steady value shown in later periods of rest.
DOUGLAS.				
2	704	114	—	882
3	704	132	322	557
5	704	20	354	—
6	704	—	253	—
8	1056	540	678	1598
9	1056	380	570	1290
12	1232	620	—	3531
HOBSON.				
4	704	106	296	445
7	704	63	287	—
10	1056	272	620	—
11	1056	90	·302	818

One slight source of error in our results may be alluded to here, since it is likely to be most evident just after the work stops. The bag method can only give a perfectly correct result provided that the composition of the air left in the lungs at the end of the period of sampling is identical with that at the beginning. This condition is fulfilled in the normal resting condition or when the subject is in equilibrium with the work. If, however, the composition of the air in the lungs alters while the expired air is collected an error is introduced in the calculation of the CO_2 output and oxygen absorption. Thus if the CO_2 percentage in the air in the lungs is lower at the end of the period than it was at the beginning, a change which is likely to occur when rest is resumed after a period of work, the contents of the bag will indicate a rather higher CO_2 production and oxygen consumption than the true respiratory exchange of the body at the time. Our periods of sampling were, however, so long, and the total CO_2 production and oxygen consumption during the period so large, that any error due to this cause becomes negligible, the more so as the chest is in the expiratory position when the period begins and when it ends, and the volume of air contained in it is therefore small. Change of respiratory quotient in the air in the lungs might also cause a slight error in the observed respiratory quotient, but having regard to the general rate at which the respiratory quotient alters in our experiments this error would be quite trivial.

It will be seen in Tables II and III that the respiratory exchange and respiratory quotient eventually fall back after the stop of the work of 704 kg.m. per minute to just about the same values as were shown during the preliminary rest (see also Table XIII below). In DOUGLAS's case there is some evidence that the respiratory quotient falls to a minimal value, which is slightly below the original resting value, about 20–30 minutes after the stop of the exercise, and may then rise again to the

TABLE XIII.

Experiment.	Work in kg.m. per minute.	Preliminary resting period. Respiratory exchange in c.c. per minute. O_2.	Preliminary resting period. Respiratory exchange in c.c. per minute. CO_2.	Preliminary resting period. Respiratory quotient.	Final steady period after the work. Respiratory exchange in c.c. per minute. O_2.	Final steady period after the work. Respiratory exchange in c.c. per minute. CO_2.	Final steady period after the work. Respiratory quotient.
DOUGLAS.							
1	704	286	227	0·793	—	—	—
2	704	—	—	—	297	230	0·775
3	704	—	—	—	298	234	0·785
5	704	{ 294 293	239 231	0·813 0·788 }	—	—	—
6	704	263	213	0·808	269	212	0·788
8	1056	281	233	0·829	287	222	0·773
9	1056	308	266	0·863	328	248	0·756
12	1232	—	—	—	308	204	0·662
HOBSON.							
4	704	{ 385 350	331 308	0·860 0·880 }	342	300	0·877
7	704	—	—	0·866	—	—	—
10	1056	{ 394 423	349 373	0·885 0·881 }	—	—	—
11	1056	375	323	0·860	350	285	0·815

preliminary resting value. This apparent variation in the respiratory quotient depends, however, on such small differences in the observed values of CO_2 output and oxygen consumption that it becomes rather dubious. There is certainly no marked diminution of the respiratory quotient which we should have expected if the rise of the respiratory quotient during the work had been due to expulsion of preformed CO_2, and had been followed after the stop of the work by retention of a corresponding amount of CO_2. The absence of this feature supports the view, therefore, that the rise of the respiratory quotient during the work is in this case due to a relatively greater employment of carbohydrate.

After work of 1056 kg.m. per minute, the respiratory quotient falls quite definitely below the preliminary resting value. In DOUGLAS'S case this fall is more obvious in Experiment 9 than in Experiment 8, in which the work lasted for a much shorter period; it is also more marked than in Experiment 11 on HOBSON, notwithstanding the long period of work in this case. This is shown in Table XIII, which gives the preliminary resting respiratory exchange and the average respiratory exchange during the later period after the stop of the work when a fairly steady value is reached in the different experiments.

In Experiment 8 the oxygen consumption during the final steady period is on the whole slightly above, and the CO_2 production slightly below, corresponding values in the preliminary resting period. In Experiment 9 the alteration is in the same sense, but much more marked. In Experiment 11, however, both oxygen consumption and CO_2 production are lower than in the preliminary resting period, though the diminution of CO_2 production is proportionally greater than that of oxygen consumption. In Experiments 8 and 9 there was definite evidence of lactic acid formation and expulsion of preformed CO_2 during the work, and one might therefore expect that gradual retention of CO_2 after the work would account either in whole or part for the lowering of the respiratory quotient.

In our observations on the alveolar air changes, after this degree of work, we found (Table IX) that the aveolar CO_2 pressure reached the lowest point between the 4th and the 20th minutes after the stop of the work, and that recovery of the normal alveolar CO_2 pressure occurred within $\frac{3}{4}$ to 1 hour. As observations were only kept up for 43 minutes after the stop of the work in Experiment 8, retention of CO_2 might easily be sufficient to account for the lowering of the respiratory quotient. In Experiment 9, however, there is no definite indication of a gradual rise in the respiratory quotient, though observations were kept up for 79 minutes after the stop of the work, nor does Experiment 11 differ in this respect, though in this instance there were no variations in either the hyperpnœa or CO_2 output during the work, significant of lactic acid production. In BENEDICT and CATHCART'S experiments a low respiratory quotient was also observed after exercise, and this was in some cases found to persist for as much as several hours.

It is therefore far from probable that the sole cause of the low respiratory quotient after work in these last two experiments is CO_2 retention, and what appears to us more likely is that some at least of the diminution is due to the fact that when rest is resumed proportionally less carbohydrate than fat is metabolised than in the preliminary resting period owing to the depletion of carbohydrate during the work, a suggestion which is in consonance with the views expressed by the Zuntz school and by Benedict and Cathcart. It is, however, rather a remarkable feature that the fall of respiratory quotient after the stop of the work only becomes obvious in the experiments with work of 1056 kg.m. per minute, though Experiment 6 with work of 704 kg.m. per minute actually led to a greater total output of energy, owing to the longer duration of the work. In the experiments at 1056 kg.m. per minute, however, the work was done at a greater rate, and the average respiratory quotient was at a higher level during the work, so the actual effect on carbohydrate metabolism may have been greater. At first sight, one is liable to suggest that the high oxygen consumption in the final steady period of Experiment 9 may indicate some transformation of fat into carbohydrate to make up for the depleted stores of the latter, for this would entail some oxygen consumption without corresponding CO_2 production. Against this is the fact that in our experiments the energy output (calculated by the Zuntz-Schumburg Tables) is practically identical in the preliminary resting period and in the final stages of the rest following the work: *e.g.*, in Experiment 9 the calorie output per minute during the preliminary rest is 1·50 calories, and during the final steady period after work 1·55 calories, and in Experiment 8 these figures are 1·36 and 1·37 respectively.

In Experiment 12 with very severe work of 1232 kg.m. per minute the respiratory quotient falls to a very low value in the later stages of rest following the exertion, and for the last 57 minutes of the experiment is well below 0·7. The CO_2 output during the whole of this period is extremely low, especially if one considers it in relation to the oxygen consumption, and there seems little doubt that this is mainly determined by retention of CO_2 to make up for the large quantity of preformed CO_2 expelled at an earlier stage of the experiment. The average oxygen consumption during this period is rather higher than in the majority of the experiments, but this is mainly due to the high values in the last two determinations, and it is possible that these indicate a rise in the general metabolism owing to some accidental cause, *e.g.*, the subject may have got rather cold from sitting still so long (the period of rest after the work lasts in this case for almost an hour and a half). That CO_2 retention should continue for so long after the stop of the exertion is not in itself surprising, considering the severity of the work and the magnitude of the lactic acid effect, for, after exertion of similar severity (due to running up and down stairs repeatedly), Christiansen, Douglas, and Haldane found (*loc. cit.*) that the alveolar CO_2 pressure was in one case still distinctly below the normal value 70 minutes after the work stopped, and the absorption power of the blood for CO_2 still depressed. The whole course of events in this experiment is very much like that observed by

DOUGLAS, HALDANE, HENDERSON, and SCHNEIDER (*loc. cit.*) in the Pikes' Peak expedition after ascending a quarter of a mile of a 1 : 4 gradient in 5 minutes at an altitude of 14,000 feet. This led to a great lowering of the respiratory quotient after the stop, the diminution being due to reduction of CO_2 output rather than to alteration in oxygen consumption. The respiratory quotient reached its minimum on this occasion half to three-quarters of an hour after the stop, and then rose slowly again, though a normal respiratory quotient was reached within an hour and a half in only one experiment.

It will be seen from Tables II–VI that in Experiments 4 and 6 the CO_2 percentage in the expired air and the depth of the breathing are about the same both in the preliminary resting period and in the last steady period after the stop, and that in Experiment 11 lowering of the expired CO_2 percentage in the later periods of the experiment is accompanied by a diminution in the depth of the breathing. In none of these cases does there seem to be any material alteration in either the dead space or the alveolar CO_2 percentage. In Experiment 9, and especially in Experiment 8, there is, however, a marked diminution in the expired CO_2 percentage in the final steady period after the stop below the value shown in the preliminary resting period, though the depth of the breathing remains much the same. This must indicate either an increase in the dead space or a lowering of the alveolar CO_2 pressure below their preliminary resting values. From the observations given in Table IX, one would not have expected a lowering of the alveolar CO_2 pressure to have lasted so long, or to have been of such magnitude, as to have made so great and lasting a difference in the expired CO_2 percentage, though it is true that the minimum percentage of CO_2 in the expired air is reached in Experiment 9 during the period when we might have expected the alveolar CO_2 pressure to be at its minimum. In Experiment 12 again the fall in the expired CO_2 percentage is more than can be accounted for by the small depth of the breathing, though in this case there is every reason to suppose that the alveolar CO_2 pressure was a good deal below the normal value. We feel, however, that further investigations are necessary on this point before a definite opinion can be formed.

A good deal more work is obviously necessary before we can get a clear picture of the course of events in these comparatively short periods of muscular work. The problem which appears to need most urgent solution is the part played by want of oxygen, for our present knowledge is still very inexact in this respect. It is evident that caution must be used in reckoning the energy output during short periods of hard muscular work, as well as during the earlier stages of rest following on the work, since the respiratory quotient is liable to show large temporary alterations which are dependent on other factors than an alteration in the proportion of carbohydrate to fat metabolised, such alterations involving great variations in CO_2 output without corresponding variations in oxygen consumption.

Conclusions.

(1) A simple method is described which enables a practically continuous record to be obtained of the respiratory exchange and hyperpnœa during and after muscular work on a stationary ergometer. It is possible by this means to get a considerable amount of information regarding rapid and transitory variations in the respiratory exchange.

(2) The efficiency of the body determined by this method agrees closely with the results obtained by other observers.

(3) Evidence is given in favour of the view that muscular work not infrequently involves the metabolism of a higher proportion of carbohydrate to fat than is the case during rest.

(4) With the harder degrees of work the course of events is liable to be influenced by the effects of serious shortage of oxygen as indicated by the production of lactic acid, which leads to a temporary great exaggeration of the hyperpnœa, accompanied by washing out of preformed CO_2 from the body and an abnormally high respiratory quotient. Our experimental data are not sufficient to exclude the possibility of the action of a slight degree of oxygen deficiency (possibly a "direct" action on the respiratory centre) in the lighter degrees of work in which there is no definite evidence of the production of lactic acid.

(5) After the stop of the work the respiratory exchange and hyperpnœa diminish with great rapidity. The respiratory quotient shows an immediate, but quite temporary, sharp rise, and it is suggested that this is largely due to the expulsion of CO_2 dammed back in the body during the muscular work owing to the alveolar CO_2 pressure being above the threshold stimulating value for the respiratory centre which prevails just after the cessation of the work, though this effect may be exaggerated by the simultaneous action of lactic acid. After this the respiratory quotient may return to the same value that it had previous to the muscular work, or it may show a marked diminution indicative of retention of CO_2 to make up for the preformed CO_2 washed out of the body at an earlier stage, or of a true change in the tissue metabolism dependent on the depletion of carbohydrate during the work.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

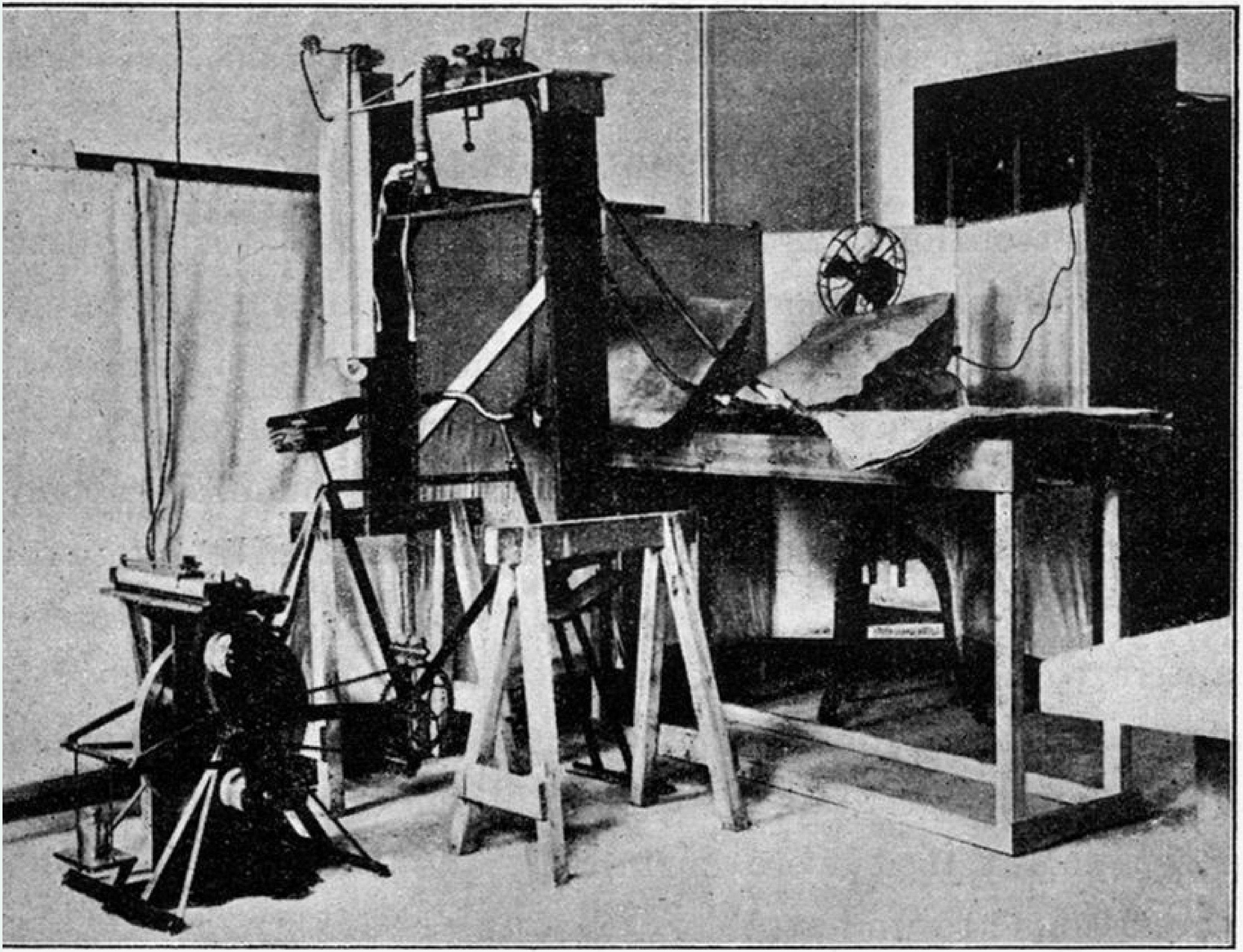

Fig. 1.

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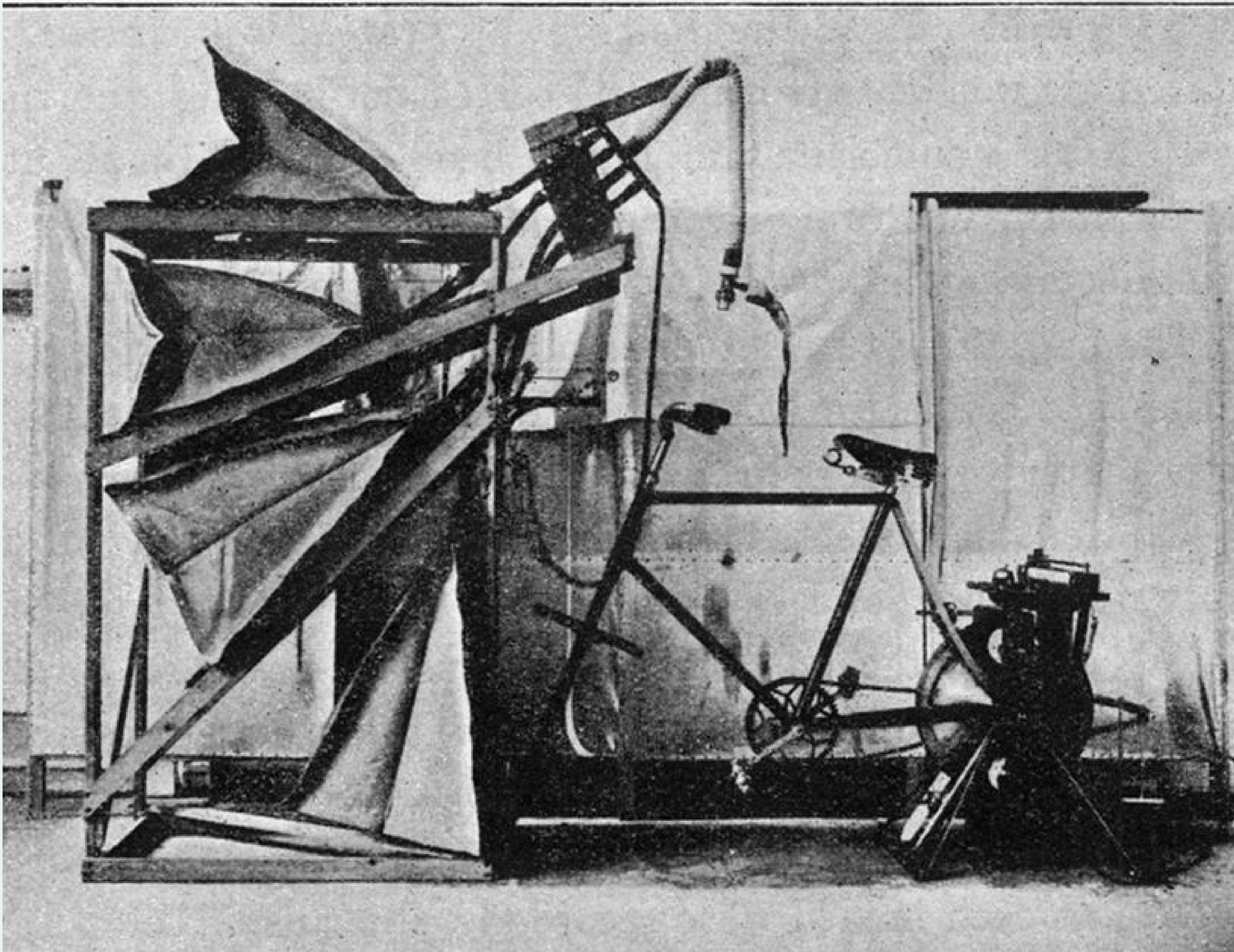

Fig. 3.

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