Muscular Exercise, Lactic Acid and the Supply and Utilisation of Oxygen

A. V. Hill, C. N. H. Long and H. Lupton

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Muscular Exercise, Lactic Acid and the Supply and Utilisation of Oxygen.––Parts VII–VIII.

By A. V. Hill, F.R.S., C. N. H. Long,* and H. Lupton.*

PART VII.—MUSCULAR EXERCISE AND OXYGEN INTAKE.

(A) *The relation between oxygen intake and severity of exertion.*—When muscular exercise commences, the ventilation of the lungs, the oxygen intake and the carbon dioxide output rise rapidly, in a period of about $2\frac{1}{2}$ minutes, to values characteristic of the severity of the exercise ; at these values they remain approximately constant. If the exercise be moderate, *i.e.*, if the oxygen intake does not approach the maximum for the subject investigated, then the exercise may be continued for a long time : the body is able, so to speak, to provide the energy required " out of income." If, however, the effort be excessive, the condition of exercise is not stable, the ventilation, the oxygen intake and the carbon dioxide output tend to attain their maximum values, and fatigue and exhaustion gradually or rapidly set in. The relation between these quantities and the magnitude of the effort made is clearly shown in Table I, especially in the series of 14 experiments made on A.V.H. running at speeds from $2\cdot86$ to $4\cdot7$ metres per second. These results are plotted as double circles in fig. 1 ; the other points shown are the results obtained with S., W., and J. (who have approximately the same body-weight and build

as A.V.H.), and with C.N.H.L. and H.L. (who are lighter). The observations on the two latter have been "reduced" to the same body-weight as A.V.H. before plotting. The running was on an open-air grass track, about 90 metres round, the speed being kept constant by an observer calling the times of successive laps. In every case the collection of expired gases was preceded by a sufficient foreperiod of exercise ($2\frac{1}{3}$ minutes or more) to ensure that a steady condition was reached.

Table I.—Oxygen Intake running at Different Speeds.

Subject.	Weight : Kilos.	Speed : Metres per Second.	Oxygen c.c. per Minute.	Carbon dioxide c.c. per Minute.	Respiratory Quotient.	Ventilation : Litres per Minute.
A.V.H.	73	2·86	3,080	2,750	0·89	52
,,	73	3·02	2,655	2,622	0·99	56
,,	73	3·29	3,490	3,340	0·96	65
,,	73	3·34	3,300	3,010	0·91	63
,,	73	3·38	3,012	2,870	0·95	67
,,	73	3·38	3,320	2,990	0·90	67
,,	73	3·41	3,205	2,905	0·91	69
,,	73	3·42	3,140	2,890	0·92	55
,,	73	3·92	3,492	3,552	1·02	79
,,	73	4·05	4,175	4,475	1·07	90
,,	73	4·32	3,870	4,200	1·08	97
,,	73	4·45	3,950	4,360	1·11	109
,,	73	4·52	4,055	4,335	1·07	114
,,	73	4·7	4,080	4,730	1·16	117
S.	75	2·83	2,635	2,415	0·92	39
,,	75	3·38	3,365	3,230	0·96	52
,,	75	4·25	3,985	4,600	1·15	86
W.	72	2·87	2,808	2,540	0·90	49
,,	72	3·38	3,140	2,932	0·93	58
,,	72	4·25	3,995	4,278	1·07	86
J.	73·5	3·38	3,325	3,131	0·94	58
,,	73·5	4·25	4,010	4,000	1·00	72
,,	73·5	4·98	4,440	4,420	1·10	95
C.N.H.L.	68	3·4	3,265	3,670	1·12	80
,,	68	4·18	3,535	4,015	1·14	103
,,	68	4·3	3,745	3,755	1·00	88
Y.	73	—	3,650	4,380	1·20	76
H.L.	58	3·1	2,550	3,160	1·24	80

The following conclusions may be drawn from these observations :—

(1) At low speeds the ventilation is small and the respiratory quotient is low : the oxygen supply is adequate to the needs of the body, lactic acid does not accumulate, and a steady state is soon attained.

(2) At high speeds the ventilation is very rapid and the respiratory quotient is high : the latter must be regarded as a consequence of the former. The rapid ventilation is caused by the action on the respiratory centre of the

accumulation of lactic acid in the muscles and blood, owing to the inadequacy of the contemporary supply of oxygen to complete the removal of the large amounts of lactic acid liberated by the exercise. The oxygen intake attains its maximum value, which in athletic individuals of about 73 kilograms body-weight is strikingly constant (in the case of running) at about 4 litres per minute. The oxygen intake fails to exceed this value, not because more oxygen is not required, but because the limiting capacity of the circulatory-respiratory system has been attained.

The highest speed at which an observation was made was about 5 metres per second. Greater speeds were not comfortable on our small track, and in any case much higher speeds cannot be maintained long enough to allow a sufficient foreperiod and collection interval. The form, however, of the oxygen intake curve of fig. 1, approaching a constant level of 4 litres per
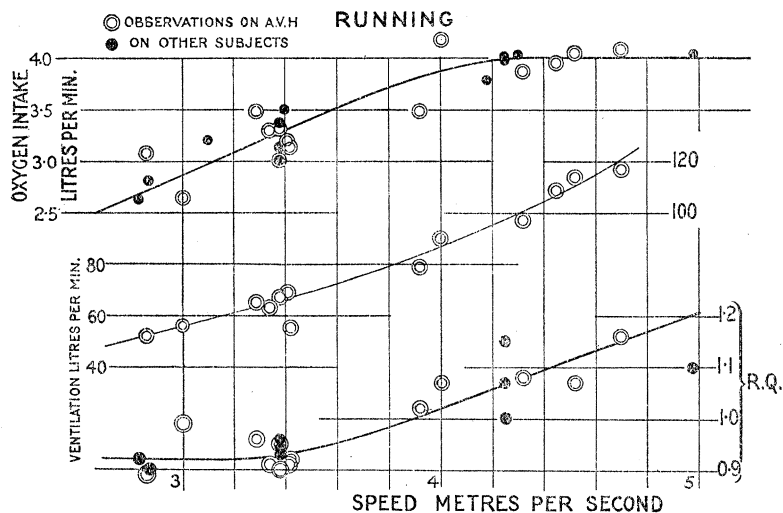

FIG. 1.—Relation between speed of running and (*a*) oxygen intake, (*b*) lung-ventilation and (*c*) respiratory quotient.

minute, makes it obvious that no useful purpose would be served by investigating higher speeds in this way. At higher speeds the method of studying the oxygen *requirement* of exercise, described in the next part, is the one demanded by the conditions.

The least speed investigated was 2·83 metres per second. Unfortunately, still lower speeds of running are not practicable : they would consist of a series either of isolated or of unduly short steps. Running, even at the slowest speed, is a fairly strenuous exertion, at any rate as measured by its oxygen

intake.   In order to study the relation between oxygen intake and severity of exercise at lower levels of the former, we made a number of observations on walking at different speeds, which are given in Table II and fig. 2.   There is already a considerable literature on this subject : see *e.g.*, Benedict and Murschhauser (3), and Douglas, Haldane, Henderson and Schneider (4).   We thought it desirable, however, to re-investigate the matter for ourselves, on our own subjects and by the same technique as we employed in the running experiments.   The walking was continuous, *i.e.*, even at the lowest speeds there was no pause between the stops : it was conducted on the same grass track as the running, in every case with a considerable foreperiod of exercise (usually 6 minutes or more) and a prolonged collection to ensure accuracy. The highest speed of walking in A.V.H. (2·38 metres per second) approaches fairly closely the lowest speed of running (2·86 metres per second) and shows a similar oxygen intake.   Walking is really a much more strenuous exertion than running at the same speed.

Table II.—Oxygen Intake walking at Different Speeds.

Subject.		Weight : Kilos.	Speed : Metres per Minute.	Oxygen c.c. per Minute.	Carbon dioxide c.c. per Minute.	Respiratory Quotient.	Ventilation : Litres per Minute.
A.V.H.	....	73	Standing	350 (mean)			
,,	....	73	36·8	548	442	0·81	10·7
,,	....	73	51·5	664	558	0·84	13·4
,,	....	73	70·7	818	652	0·80	15·8
,,	.... . .	73	91·7	1,058	880	0·83	21·1
,,	....	73	122·1	1,843	1,674	0·91	37·8
,,	....	73	142·8	2,732	2,580	0·94	59·0
C.N.H.L.	....	68	Standing	354	296	0·84	7·3
,,	....	68	37·4	570	496	0·87	11·4
,,	....	68	50·9	644	549	0·85	14·6
,,	....	68	71·5	805	723	0·90	18·8
,,	....	68	94·4	1,048	920	0·88	21·3
,,	....	68	121·1	1,575	1,396	0·89	30·2
,,	....	68	139·8	2,090	2,002	0·96	41·6

The results are similar in certain respects to those on running.   There is a regular increase of ventilation with speed ; a constant respiratory quotient at lower speeds with a tendency to rise at higher ones ; and an oxygen intake steadily increasing with speed.   In the case, however, of walking, the maximum oxygen intake was not attained ; neither of our two subjects was sufficiently practised to be able to walk for several minutes on end at more than 5 to $5\frac{1}{2}$ miles per hour ; consequently the oxygen intake curve goes on rising, apparently

with no tendency to reach a maximum as in fig. 1. A sufficiently practised
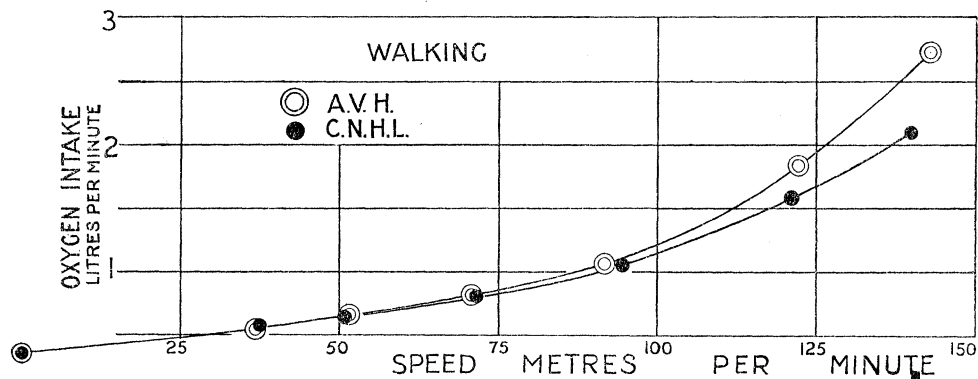" walker," however, would certainly show this maximum.

FIG. 2.—Relation between oxygen intake in man and speed of walking.

The results described are typical of any form of exertion in which the move-
ments of the body are general and continuous ; the oxygen intake per minute
rises with the speed of movement, and (if the conditions allow) the same final
attainment of a maximum occurs, with its accompaniments of an increased
ventilation and an increased respiratory quotient. There is no speed at which
the oxygen intake per minute is a minimum. In some types of exercise,
however, particularly those with a static component in them, such, for example,
as the stair-climbing investigated by Lupton (1), there is a true optimum speed.
The oxygen required to carry out a given task decreases as the speed increases,
up to a certain optimum speed, and then increases again. In the case of
running and walking on the flat there is no such optimum ; the oxygen required
to run, or walk, a given distance increases rapidly with the speed, up to
enormously high values, in the case of running, as will be shown in Part VIII.

(B) *Factors limiting the maximum oxygen intake in man ; the effects of breathing
higher pressures of oxygen.*—In a previous paper (II, p. 153) by two of us, a
table was given containing 26 of the highest values of the oxygen intake in
man, as observed by other workers. Nearly all these values lay between
2,000 and 3,000 c.c. per minute, though six of them lay between 3,000 and
3,700 c.c. It was pointed out there that muscular efforts of the type of running,
skiing and skating tend to take the highest places in the series, since in these
not only vigorous but free and rapid movements occur. We quoted also
experiments of our own in which considerably higher values of the oxygen
intake occurred. We have made further experiments on this subject, in an
attempt to decide what are the factors which limit the oxygen intake ; the

method employed has been that of comparing the results obtained while breathing air with those while breathing higher or lower oxygen pressures. The technique has been that described in Part IV, and owing to the limitations imposed by supplying an artificial gas mixture, the only violent exercise we have investigated is " standing running." Running in the open appears to give rather higher values of the oxygen intake than does standing running, at any rate while breathing air ; probably because of the greater freedom of movement and the easier circulation of the blood. The use of a bicycle ergometer we did not consider ; judging from the small oxygen intakes recorded with it by other workers, even on very athletic subjects, the circulation and respiration are by no means so free as in running or standing running ; and since we wished to study maximum values we thought it advisable to stick to the latter types of exercise. In every case the collection was preceded, not only by a prolonged breathing of the gas mixture, but by a sufficient foreperiod of exercise.

In Table III., as far as possible, we have compared, in each experiment, the *oxygen intake* while breathing air with that while breathing an artificial gas mixture ; and in the last column we give the ratio of the latter to the former. With C.N.H.L. there is a large increase, averaging 35 per cent., while breathing about 50 per cent. oxygen ; with A.V.H. the average increase is smaller, viz., 9 per cent. ; with S.S. it is about 35 per cent. ; with S.H. 32 per cent. ; with T.A.L. 13 per cent. ; with H.L. 20 per cent. The converse effect occurs while breathing low oxygen pressures, with H.L. a 3 per cent. reduction with $17\cdot6$ per cent. oxygen, a 5 per cent. reduction with $13\cdot2$ per cent., and a 32 per cent. reduction with $11\cdot3$ per cent.

As regards ventilation nothing very definite can be said. On some occasions, and in some subjects, the breathing of 50 per cent. oxygen seems definitely to decrease the ventilation (*e.g.*, A.V.H., experiments 4 and 5) ; on other occasions and with other subjects to increase it (S.S., experiments 7 and 8). There appears to be no consistent effect. On the respiratory quotient, however, the consequence of breathing rich oxygen mixtures is large and unequivocal ; there may be a 30 per cent. or more reduction in the respiratory quotient on substituting 50 per cent. oxygen for air. This is due mainly to the large increase in the oxygen intake, which sometimes occurs, in the denominator of the fraction CO_2/O_2 ; it may, however, on occasions, be due partly to a diminished output of carbon dioxide, as in experiments 4 and 5, or experiments 7 and 8. In experiments 4 and 5 the diminished carbon dioxide is due, presumably, to the diminished ventilation ; in experiments 7 and 8 it

occurs in spite of an increased ventilation, and must be attributed in that case to a diminution in the pressure of carbon dioxide in the blood, owing to the smaller escape of lactic acid into it. The chief factor, however, in the decrease of the respiratory quotient is undoubtedly the large increase in the oxygen intake, which is the one characteristic feature of severe exercise while breathing gas mixtures rich in oxygen.

This increase in the oxygen intake is often too large to be explained simply by an increased saturation of the blood. An oxygen intake (experiment 3) of $5\cdot1$ litres per minute by a subject who has never exceeded $3\cdot7$ in air (*i.e.*, 27 per cent. less), one of $5\cdot9$ litres per minute (experiment 9) by another who has never exceeded $3\cdot8$ in air (35 per cent. less), and one of $3\cdot2$ litres (experiment 10) in place of $2\cdot4$ (24 per cent. less), require too large a degree of unsaturation of the arterial blood during exercise in air to be readily explained in that way. If the blood (to take the extreme case) were 35 per cent. unsaturated after passing through the lungs, we ought certainly to be able to detect that unsaturation from a cyanotic condition of the subject; 24 per cent. and 27 per cent. unsaturation also should be readily detectable. Moreover, if the blood were, say, 25 per cent. unsaturated after passing through the lungs, while breathing air, it would certainly not be as much as 100 per cent. saturated while breathing 50 per cent. oxygen, consequently a difference of 25 per cent. between the two cases would imply a degree of unsaturation considerably greater than 25 per cent. in the former case. This possibility is prohibited by the appearance of our subjects, who have never, even in the severest exercise, shown any signs of cyanosis.

It is necessary, however, to assume that a rich oxygen mixture works primarily by increasing the saturation of the blood with oxygen; there is no other way in which it could work; this increased saturation must, therefore, in some manner increase the rate of circulation of the blood, otherwise our large increases in the oxygen intake cannot be accounted for. It would seem probable, and although we have no direct evidence, the indirect evidence which we are adducing makes it very probable indeed, that the heart is able to regulate its output, to some extent, in accordance with the degree of saturation of the arterial blood, either of that which reaches it through the coronary vessels or by some reflex in other organs produced by a deficient oxygen supply. From the point of view of a well co-ordinated mechanism, some such arrangement is eminently desirable; it would clearly be useless for the heart to make an excessive effort if by so doing it merely produced a far lower degree of saturation of the arterial blood; and we suggest that, in the body (either in the

Table III.—Comparison of Oxygen Intakes, Respiratory Quotients, and Ventilations, while Breathing Air and Oxygen Mixtures.

No.	Subject.	Exercise.	Fore-period of Exercise: Minutes.	Duration of Collection, Exercise.	Gas Mixture.	Oxygen c.c./min.	Carbon Dioxide c.c./min.	Respiratory Quotient.	Ventilation, l.p.m.	Percentage Increase in Oxygen Intake.
1	C.N.H.L.	S.R., "all out"	$2\frac{1}{2}$ $2\frac{1}{2}$	60 sec. 60 sec.	Air .... 50 % O_2	3,466 4,570	4,460 4,120	1·29 0·90	109 107	— 32
2	C.N.H.L.	S.R., 276 steps per minute	2 $2\frac{1}{2}$	62 sec. 62 sec.	Air .... 51·5% O_2	3,240 4,050	3,670 3,905	1·13 0·96	85 92	— 25
3	C.N.H.L.	S.R., "all out." *Cf.* Exp. 1	2	61 sec.	52% O_2	5,110	4,545	0·89	107	48
4	A.V.H.	S.R., 237 steps per minute	3 3	61 sec. 63 sec.	Air .... 55% O_2	3,415 3,715	4,140 2,950	1·21 0·79	115 68	— 9
5	A.V.H.	S.R., 264 steps per minute	3 3	62 sec. 62 sec.	Air .... 55% O_2	3,592 4,080	4,135 3,330	1·15 0·82	121 78	— 14
6	A.V.H.	Running, 243 metres per minute S.R., 300 steps per minute	4 3	1 min. 61 sec.	Air .... 55% O_2	4,175 4,350	4,475 4,700	1·07 1·08	90 124	— 4
7	S.S.	S.R., 276 steps per minute	2 $2\frac{1}{2}$	62 sec. 62 sec.	Air .... 51·5% O_2	3,465 4,675	4,250 3,645	1·23 0·78	107 133	— 35
8	S.S.	S.R., 237 steps per minute Ditto	$2\frac{1}{2}$ 4	$3\frac{1}{4}$ min. 3 min.	Air .... 49% O_2	3,752 4,735	4,385 4,226	1·17 0·89	102 115	— 26
9	S.S.	S.R., "all out" Ditto	2 $2\frac{1}{2}$	76 sec. 2 min.	45·5% O_2 49% O_2	5,520 5,910	5,100 5,445	0·92 0·92	136 134	32 42
10	S.H.	S.R., "all out" Ditto	$2\frac{1}{2}$ $2\frac{1}{2}$	71 sec. 71 sec.	Air .... 50% O_2	2,410 3,170	3,435 3,350	1·43 1·06	75 74	— 32
11	T.A.L.	S.R., "all out" Ditto	$2\frac{1}{2}$ $2\frac{1}{2}$	62 sec. 63 sec.	Air .... 52% O_2	2,715 3,075	3,345 2,975	1·23 0·91	68 63	— 13
12	H.L.	Running in corridor S.R., 276 steps per minute	$3\frac{1}{2}$ $5\frac{1}{4}$	$1\frac{1}{4}$ min. 64 sec.	Air .... 47% O_2	2,550 3,260	3,160 2,730	1·24 0·84	79·5 66	— 28

Table III—*continued.*

No.	Subject.	Exercise.	Fore-period of Exercise: Minutes.	Duration of Collection, Exercise.	Gas Mixture.	Oxygen c.c./min.	Carbon Dioxide c.c./min.	Respiratory Quotient.	Ventilation, l.p.m.	Percentage increase in Oxygen Intake.
13	H.L.	S.R., 276 steps per minute	2	62 sec.	Air	2,400	3,080	1·29	72	—
			$2\frac{1}{2}$	62 sec.	51·5% O_2	2,738	3,195	1·17	74	14
14	H.L.	S.R., 237 steps per minute	$6\frac{3}{4}$	—	Air	2,443	3,018	1·23	76	—
			$2\frac{1}{2}$	2 min.	11·3% O_2	1,669	2,158	1·29	74	−32
			$2\frac{1}{2}$	3 min.	13·2% O_2	2,325	2,560	1·10	78	− 5
			$2\frac{1}{2}$	$3\frac{1}{2}$ min.	17·6% O_2	2,374	2,888	1·22	72	− 3
			3	5 min.	31% O_2	2,648	2,609	0·99	64	+ 8
			$3\frac{3}{4}$	3 min.	33% O_2	2,669	3,105	1·15	81	9
			$9\frac{1}{4}$	—	43% O_2	2,645	2,852	1·07	75	8
			3	5 min.	48·5% O_2	2,900	2,580	0·89	60	19
			9	5 min.	ditto	3,105	2,500	0·81	61	27
			$2\frac{1}{2}$	2 min.	49·5% O_2	3,010	3,005	1·00	58	23
			11	2 min.	ditto	2,895	2,500	0·86	58	18
			5	5 min.	52·5% O_2	2,820	2,610	0·93	63	15

Remarks.

Experiment 1.—Pulse rate 184.

Experiment 6.—Highest value ever recorded in air. The increase is really greater than 4 per cent., since a higher oxygen intake is attainable while running than while standing running.

Experiment 9.—Compared with the highest value for air ever recorded for any subject (No. 6). Highest value ever recorded.

Experiment 12.—Highest value recorded in air for H.L. Highest value recorded in oxygen for H.L.

heart muscle itself or in the nervous system), there is some mechanism which causes a slowing of the circulation as soon as a serious degree of unsaturation occurs, and *vice versa.* This mechanism would tend, to some degree, to act as a " governor," maintaining a reasonably high degree of saturation of the blood ; the breathing of a gas mixture rich in oxygen would produce a greater degree of saturation of the blood and so allow the output to increase until the " governor " stopped it again. We realise the danger of a hypothesis partly suggested by teleological reasoning ; in this case, however, we can see no other explanation of our experimental results.

(C) *Factors determining the maximum oxygen intake ; the output of the heart.*— The amount of oxygen passing into the blood and carried to, and utilised by, the active muscles depends upon a variety of circumstances :—

(*a*) on the degree of saturation of the arterial blood ;

(*b*) on the degree of saturation of the mixed venous blood ;

(*c*) on the oxygen capacity of the blood ; and

(*d*) on the circulation rate.

Of these, unfortunately, only (c) is directly determinable in our experiments. In a man at rest, or undertaking moderate exercise, methods are available of finding (a) and (b). These methods, however, implicitly assume an equilibrium to exist between the arterial blood and the gases in the lung alveoli, an assumption which is certainly untrue in the case of the very severe exercise which we have investigated. Moreover, an examination of the alveolar air, and the taking of special samples of gas into the lungs, of a subject breathing twice his own volume of air per minute is quite out of the question. It might be possible to obtain a sample of the arterial blood during exercise, though in the case of the most severe exercise undertaken by our subjects this would appear to be a difficult and dangerous operation, especially since the exercise would have to continue unabated up to the moment of the puncture. In any case this would still leave the most important factor of all, the degree of saturation of the mixed venous blood, unmeasured. The matter might be investigated in an animal, but an animal cannot readily be induced to take such severe exercise as a man, at any rate under controlled conditions. No course, therefore, would seem to be open at present except to make an approximate estimate of the several factors.

(i) *The case of air.*—An oxygen intake of approximately 4 litres per minute has been attained by several of our subjects (fig. 1). Let us assume (a) their arterial blood to be 90 per cent. saturated, (b) their mixed venous blood to be 30 per cent. saturated, (c) the oxygen capacity to be 18·5 c.c. per 100 c.c. of blood, and let us then calculate their circulation rate. We have

$$4 = 0 \cdot 185 \, (0 \cdot 90 - 0 \cdot 30) \, x$$

where x is circulation rate in litres per minute. This gives $x = 36$; apparently, therefore, some 36 litres of blood are passing through the heart per minute, during exercise of the severity investigated. Even if we assume the mixed venous blood to be only 10 per cent. saturated, an almost impossibly low figure, the circulation rate still comes out as 27 litres per minute. The effect of high pressures of oxygen, in increasing the oxygen intake, cannot well be explained by an arterial saturation, while breathing air, of more than 90 per cent. It would appear, therefore, that probably about 36 litres of blood per minute is the circulation rate during fast running by an athletic subject of 73 kilograms body-weight, *i.e.*, the output of the heart per minute reaches a value of about half the body-weight. A minimum value would seem to be 27 litres per minute, about one-third of the body-weight.

(ii) *The case of oxygen mixtures.*—Even more astonishing results emerge

from a similar consideration of the oxygen experiments.   C.N.H.L. (68 kilograms) attained oxygen intakes of 4·6 and 5·1 litres per minute, while S.S. (70 kilograms) reached values of 4·7, 5·5 and 5·9 litres per minute. Assuming in this case for both subjects a degree of saturation of the arterial blood of 100 per cent. and of the mixed venous blood of 30 per cent., for C.N.H.L. an oxygen capacity of 18·5 volumes per cent., for S.S. one of 20·5 volumes (observed), we may calculate the circulation rates as under :

| C.N.H.L. | .. | .. | .. | .. | 36 and 40 litres per minute. |
| S.S. .. | .. | .. | .. | .. | 33, 38 and 41 litres per minute. |

Even if we assumed a complete unsaturation of the mixed venous blood (quite an impossible assumption) we should get 7/10 of these values.   It is clear, therefore, that the output of the heart, in a man of 70 kilograms, may exceed 30 litres and possibly even 40 litres per minute.   In our experiments on severe exercise, the pulse rate, whenever recorded by the electrocardiograph, was about 180 beats per minute.   This implies an output of 170 to 220 c.c. per beat.

(D) *The work of the heart.*—The chief determining factor, therefore, in the oxygen intake is the rate of circulation of the blood.   Large differences probably exist between different individuals in respect of the outputs of their hearts.   Some individuals can naturally run, or walk up hill, for long periods without distress ; others, able-bodied with no obvious physical or nervous defect, soon suffer from dyspnœa when they attempt to do so.   This may be partly a matter of the diffusion constant of the lungs for oxygen ; largely, however, it is probably one of the capacity of the heart itself.   Characteristic differences in individual maxima may be found in our records of oxygen intake.   Now the hearts of different individuals may differ in varying ways : in the rhythm and adjustment of their beats, in their venous filling as determined partly by the size of the pericardium, in the effectiveness of their coronary supply.   We do not propose to discuss the matter more fully otherwise than by giving a short calculation which emphasises the importance of the supply of oxygen to the cardiac muscle itself, and, therefore, of the coronary blood supply of the heart.

If the output of the heart of S.S. or of C.N.H.L. was actually 40 litres per minute, we may make a rough estimate of the work done by it and of the oxygen requirement of that work.   Let us assume that the arterial blood pressure, averaged over the output of a beat, is 100 mm. ; then the work of the *left* heart is $40 \times 100/760$ litre-atmospheres $= 530 \times 10^7$ ergs $= 128$ calories.

Assuming a mechanical efficiency of 20 per cent., this would imply a total expenditure of 640 cals. of energy per minute. Adding 1/4 for the energy expenditure of the right side of the heart, we obtain a total expenditure of energy, by the whole heart, of about 800 cals. per minute. This would require some 160 c.c. of oxygen per minute, or (assuming a 60 per cent. utilisation coefficient and an oxygen capacity of $0 \cdot 185$) the passage of $1 \cdot 4$ litres of blood through the coronary vessels per minute. Thus the coronary blood supply to an active heart, if the latter is to continue in a steady state of exertion, must be two to three times its own volume per minute : a value which is probably considerably greater than the actual blood supply to any skeletal muscle.

This calculation, though admittedly approximate, does emphasise, therefore, the importance of the blood supply to the heart muscle itself during severe exercise. A heart, adequate in every other way, might fail to allow its owner to undertake severe continued effort, simply because of the imperfect arrangements of its own supply of blood.

Summary of Part VII.

1. The relations existing between severity of exertion on the one hand and (a) the final oxygen intake attained, (b) the ventilation of the lungs and (c) the respiratory quotient, on the other hand, are described for the two cases of running and walking. The oxygen intake rises steadily as the speed is increased, attaining a maximum, however, beyond which no bodily effort can drive it. This maximum is conditioned, not by the absence of need for more oxygen at higher speeds, but by the limitations of the circulatory-respiratory system.

2. The use of gas mixtures containing a high pressure of oxygen enables a considerably higher oxygen intake to be attained. The increase is often so large that it cannot be due simply to more complete saturation of the blood in its passage through the lungs. It is suggested that a " governor " mechanism exists, either in the heart muscle itself, or elsewhere, which tends to co-ordinate the output of the heart with the degree of saturation of the blood leaving it.

3. The high values of the oxygen intake attained, especially while breathing oxygen mixtures, allow an approximate calculation of the maximum output of the heart. Apparently, under some circumstances of severe exercise, the output in man may reach 170 to 220 c.c. per beat, or 30 to 40 litres per minute.

4. Assuming these high values, a further approximate calculation of the work done by the heart emphasises the great importance, in muscular exercise,

of an adequate coronary blood supply to the heart muscle itself. In order to do the work required of it, during severe exercise, the heart muscle must be supplied with at least twice its own volume of blood per minute.

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PART VIII.—MUSCULAR EXERCISE AND OXYGEN REQUIREMENT. By K. FURUSAWA, A. V. HILL, F.R.S., C. N. H. LONG,* and H. LUPTON.*

The oxygen requirement of a given effort is defined as the total oxygen used during the exercise and in complete recovery from it, reckoned from the resting level of oxygen intake. Fig. 1 expresses the conception of oxygen
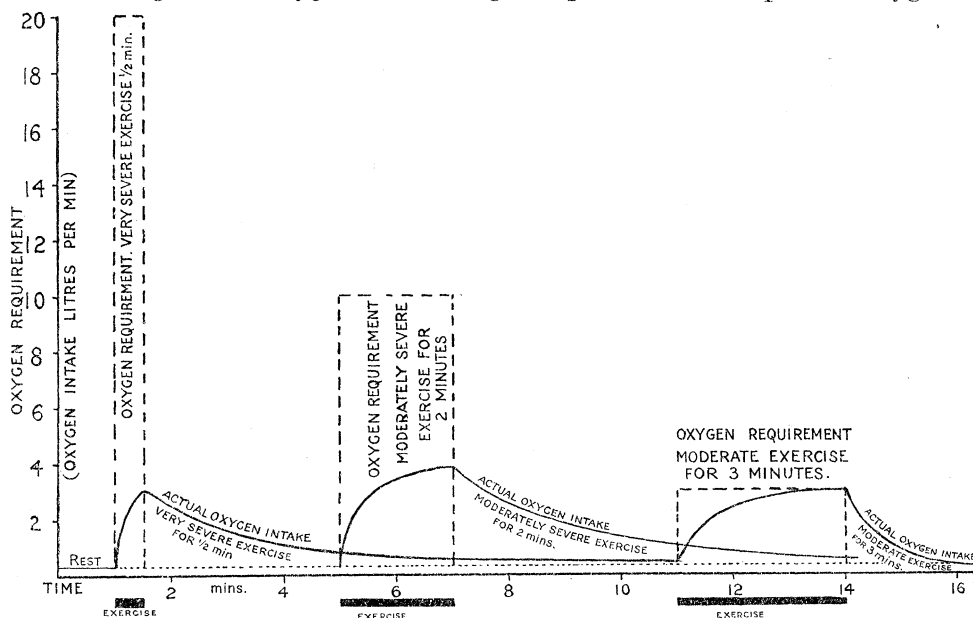

FIG. 1. Diagram to illustrate the meaning of " oxygen requirement," and the distinction between " oxygen requirement " and " oxygen intake." The area of an oxygen require-ment rectangle is, by definition, the same as that of the complete oxygen-intake curve, each being measured from the level of the resting oxygen intake (shown dotted). Three periods of exercise of different severity.

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requirement in diagrammatic form.   The *area* of the rectangle shown in broken lines over any period of exercise represents the *total* oxygen requirement of that exercise ; the oxygen requirement per minute is represented by the height of the rectangle.   The actual oxygen intake differs from the oxygen require-ment most widely in the case of the severest exercise.   The total oxygen intake (in excess of resting), during the exercise and in complete recovery from it, *i.e.*, the area of the oxygen-intake curve, is equal to the total oxygen requirement, *i.e.*, to the area of the rectangle.

In the case of moderate exercise the oxygen intake gradually rises, as the exercise is continued, until in two or three minutes it equals the oxygen requirement : the recovery oxygen in this case is simply equal to the initial lag in the oxygen intake.   In the case, however, of more severe exercise, the oxygen intake can never catch up the oxygen requirement, and a large oxygen debt is incurred which is paid off during recovery.   We have made a variety of experiments on the oxygen requirement of running and walking, of which the most instructive are given in Table I and plotted in fig. 2.   These
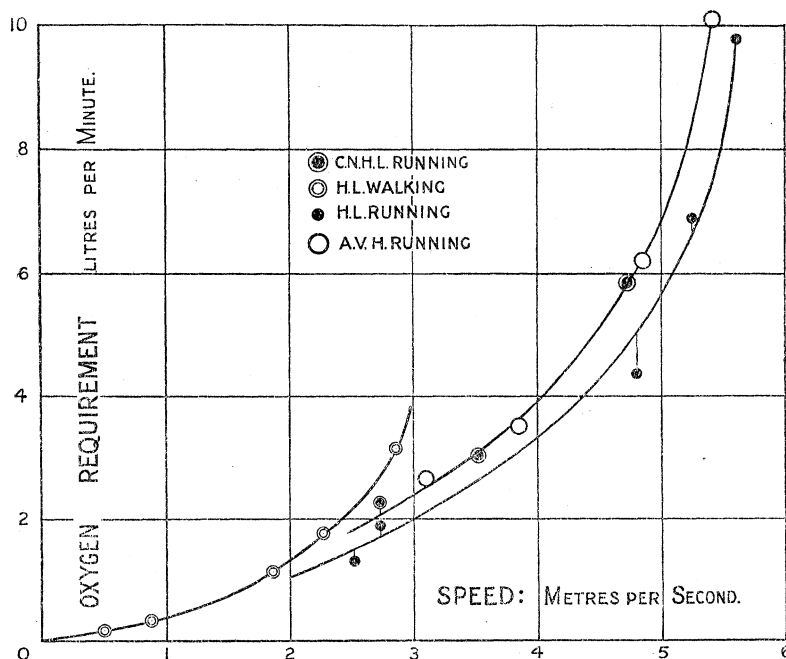

FIG. 2.   Oxygen requirement of walking and running ; earlier experiments ; Table I.

are among our earlier experiments ; they were made before we fully realised the considerable duration of the recovery process after severe exercise : in

Table I.—Oxygen Requirement of Exercise.

Subject.	Exercise.			Rest : CO_2/O_2, c.c. per Minute.	Exercise and Recovery.			Oxygen require- ment per minute, c.c.	Note.
	Type.		Duration. Seconds.		Duration. Minutes.	Total CO_2/O_2, c.c.	Excess CO_2/O_2, c.c.		
A.V.H.	Running : 3·1 m.p.s.		82·0	277/346 (standing)	8·1	5120/6430	2880/3630	2660	
,,	Ditto 3·85 m.p.s.		44·0	,,	8·1	4650/5380	2410/2580	3520	A.
,,	Ditto 4·85 m.p.s.		30·5	,,	8·1	5325/5950	3085/3150	6200	
,,	Ditto 5·42 m.p.s.		19·5	,,	6·2	5390/5765	4055/3280	10100	
C.N.H.L.	Running 2·73 m.p.s.		64·0	299/339 (standing)	8·0	4550/5140	2165/2435	2280	
,,	Ditto 3·52 m.p.s.		49·0	,,	8·0	4440/5195	2050/2485	3040	B.
,,	Ditto 4·72 m.p.s.		26·8	,,	8·05	5600/5340	3190/2610	5850	
H.L.	Running 2·52 m.p.s.		36·3	187/220 (standing)	8·1	2079/2574	565/794	1310	
,, ...	Ditto 5·25 m.p.s.		17·4	,,	9·1	4950/4075	3250/2075	6900	C.
,, ...	Ditto 5·61 m.p.s.		16·3	,,	10·3	5760/4930	3830/2660	9800	
H.L.	Walking 0·50 m.p.s.		183·0	225/250 (standing)	8·05	2205/2592	395/580	190	
,, ...	Ditto 0·88 m.p.s.		104·0	,,	10·05	2630/3105	370/590	340	
,, ...	Ditto 1·86 m.p.s.		49·2	,,	10·1	3400/3465	1125/940	1150	D.
,, ...	Ditto 2·27 m.p.s.		40·0	,,	10·6	3165/3840	775/1190	1780	
,, ...	Ditto 2·86 m.p.s.		32·0	,,	10·1	4340/4205	2065/1680	3150	
H.L.	Running 2·73 m.p.s.		33·5	,,	10·2	3040/3605	750/1060	1900	E.
,, ...	Ditto 4·80 m.p.s.		19·1	,,	10·15	4025/3925	1745/1390	4360	

Notes.

A. (1) This experiment on A.V.H. was followed by a measurement of the oxygen intake running at 4·7 metres per second, foreperiod 2 minutes 3 seconds, collection 51 seconds, CO_2/O_2 per minute, 4730/4080 c.c., respiratory quotient 1·16, ventilation 117 litres per minute.

(2) Oxygen requirement at 5·42 m.p.s. obviously too small ; recovery incomplete (respiratory quotient of excess metabolism 1·24).

B. Oxygen requirement at 4·72 m.p.s. obviously too small ; recovery incomplete ; " excess " respiratory quotient = 1·22.

C. Running 100 yards. Oxygen requirement at the two higher speeds obviously too small ; recovery incomplete.

D. Walking 100 yards.

E. Running 100 yards.

several of them, therefore, recovery is not quite complete and the oxygen requirement as determined is appreciably too small. Other experiments on the oxygen requirement of stair-climbing have been already published by one of us (Lupton (5)). In the latter experiments the recovery period allowed was never very long (seven minutes or more) ; here also, therefore, recovery was not quite complete, and some of the results given may be rather (possibly 10 per cent.) too small. The most accurate experiments in this connection have been made recently and are shown in Tables II and III and fig. 3. In these the exercises investigated were running and standing running, and the period of recovery allowed was about 30 minutes ; the discussion in Part V indicates that, using the initial resting metabolism as base line, this is the most suitable recovery period to employ. The exercise itself lasted for a period varying from a few seconds to about a minute. Collection of the expired gases was made during the exercise itself and for a subsequent half-hour ; the exercise was always preceded by a long period of rest, during which the resting metabolism was estimated.

In Table I are given the oxygen requirements of three different individuals while walking or running at various speeds. The maximum oxygen intake of H.L. in air is about $2 \cdot 6$ litres per minute. Walking at $2 \cdot 86$ metres per second ($6 \cdot 4$ miles per hour) his oxygen requirement is $3 \cdot 15$ litres per minute, appreciably in excess of his maximum intake. The oxygen requirement of running is, for a given speed, considerably less than that of walking : running at $3 \cdot 9$ metres per second is only as expensive as walking at $2 \cdot 86$ metres per second ; running at $2 \cdot 86$ metres per second is only about 60 per cent. as expensive as walking at the same speed. In H.L. running the oxygen requirement soon exceeds the maximum oxygen intake as the speed is increased. Running at $3 \cdot 5$ metres per second ($7 \cdot 8$ miles per hour), his requirement is just equal to his maximum intake ; this, therefore, is the maximum speed which he could hope to maintain for a long period. At higher speeds his oxygen requirement rises rapidly, reaching nearly four times his maximum intake at about $5 \cdot 6$ metres per second.

The same type of relation is shown with A.V.H. running. His maximum recorded oxygen intake is $4 \cdot 175$ litres per minute. This falls on his oxygen requirement curve at $4 \cdot 1$ metres per second. This, therefore ($9 \cdot 2$ miles per hour), is the highest speed which he could hope to maintain over a long period without accumulating a large oxygen debt. In the same way C.N.H.L., whose oxygen requirement curve appears to be identical with that of A.V.H., over the range investigated, has a maximum oxygen intake of about $3 \cdot 75$ litres per

minute. This falls on his oxygen requirement curve at 3·9 metres per second (8·7 miles per hour). Both A.V.H. and C.N.H.L. are capable of running considerably faster than the maximum speed shown in fig. 2. The higher range, however, of oxygen requirements was not touched in these earlier experiments : for this we must refer to the experiments on K.F., recorded in Tables II and III and fig. 3. Arguing from the case of K.F., both A.V.H. and C.N.H.L., running at top speed, should have maximum oxygen requirements exceeding 25 litres per minute.

In Tables II and III and fig. 3 are recorded experiments made on, and by,
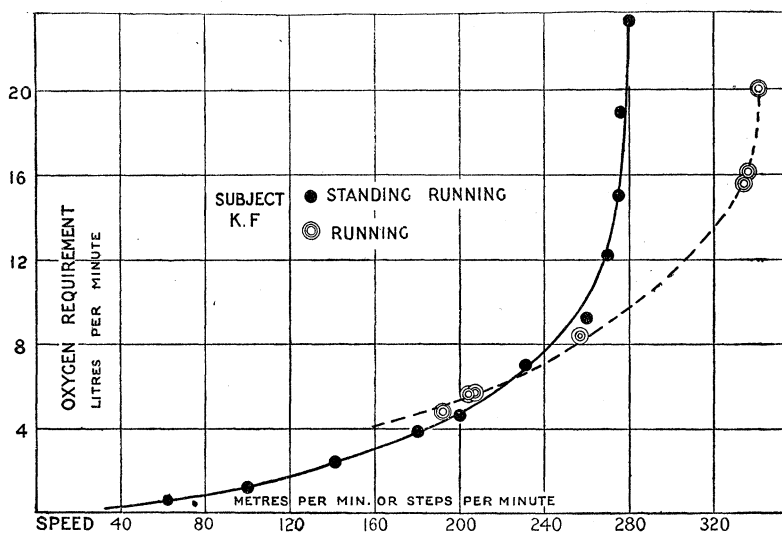

Fig. 3. Oxygen requirement of K.F., Tables II and III, (1) running at various speeds up to his maximum, and (2) standing running at various speeds up to his maximum.

K.F., with all the precautions now known to be necessary in measuring the oxygen requirement of exercise. These experiments, moreover, cover the whole range of speeds, going to the highest of which K.F. is capable.

Details of K.F. are as follows : *Nationality*, Japanese ; *height* (standing). 155½ cm. (5 ft. 1 in.), (sitting) 83½ cm. (2 ft. 9 in.) ; *weight*, 51 kilos. (8 stones) ; *age*, 24 years.

Table II and fig. 3 show the relation between oxygen requirement and speed for the case of running. In order to hinder the subject as little as possible, a large bag was not worn on the back during the run ; instead of it a small bag of 30 litres capacity was carried in one hand, and as soon as possible after the completion of the run (92 metres == 100·8 yards) the outlet pipe was connected to a large bag in which the expired air was collected for the rest of the period.

Finally, the contents of the small bag were mixed with those of the large one before a sample was taken and the volume measured.   Even this arrangement, however, of the small bag was an appreciable hindrance to K.F. running at his highest speeds.   The maximum speed at which he could perform the experiment (5·7 metres per second) is low, partly because K.F., although powerful and well-built, has very short legs, to some degree, however, because of carrying the bag.

Unfortunately in Tables II and III some of the intermediate data have been lost, only the final results remaining.   The observations extended over several weeks and were made in a random order; the missing data were together in one note-book.   The results, however, are just as reliable as those of the other experiments.

Table II.—Oxygen Requirement of Flat Running (92 metres).

Exercise.		Rest. CO_2/O_2 c.c. per Minute.	Exercise and Recovery.			Oxygen require-ment per minute. Litres.
Speed : metres per second.	Duration. Seconds.		Duration. Minutes.	Total CO_2/O_2 c.c.	Excess CO_2/O_2 c.c.	
3·20	27·7	186/205	22·5	6390/6740	2210/2130	4·8
3·40	25·8	216/264	25·0	7680/8920	2280/2320	5·65
3·45	—	—	—	—	—	5·75
4·28	21·0	197/232	30·0	8560/9810	2655/2849	8·4
5·57	16·2	201/246	30·0	10610/11500	4580/4117	15·6
5·60	—	—	—	—	—	16·1
5·68	15·8	197/242	30·0	11360/12460	5450/5200	20·0

The experiments on the oxygen requirement of running, shown in the broken line of fig. 3, emphasise how far the oxygen requirement may exceed the oxygen intake in the case of really strenuous exertion.   The highest recorded oxygen intake of K.F. is about 2·3 litres per minute; running at 341 metres per minute his oxygen requirement is 20 litres per minute.

The experiments on the oxygen requirement of standing running, shown in the full line of fig. 3, demonstrate the same fact even more emphatically.   These observations fall on a very smooth curve.   At first it was found impossible to obtain consistent results with standing running; this was ascertained to be due to the fact that the exercise was not standardised; it could be rendered more or less strenuous by raising the knees higher or less high.   As soon as every experiment was made with the knees raised to the same height, viz., to the horizontal, consistent results were at once obtained.   Carried out in this way " standing running " becomes an extremely violent type of exercise at high

Table III.—Oxygen Requirement of Standing Running.

Exercise.		Rest. CO_2/O_2 c.c. per Minute.	Exercise and Recovery.			Oxygen requirement per minute. Litres.
Steps per minute.	Duration. Seconds.		Duration. Minutes.	Total CO_2/O_2 c.c.	Excess CO_2/O_2 c.c.	
62	210	165/218	42	8470/10630	1541/1470	0·62
100	—	—	—	—	—	1·25
141	—	—	—	—	—	2·45
180	210	148/212	11	15800/15230	13840/12900	3·90
200	—	—	—	—	—	4·67
231	44	206/240	39	13890/14540	5860/5180	7·0
260	—	—	—	—	—	9·2
270	24	—	20	8310/6980	—	12·2
275	13	237/285	20	7830/8900	3090/3200	15·0
276	20	160/199	40	12600/14210	6200/6250	18·9
280	15	155/200	30	10480/11750	5800/5750	23·2

speeds ; and the oxygen requirement curve becomes practically asymptotic to a speed slightly exceeding 280 steps per minute. The highest recorded oxygen intake of K.F. is exceeded 10 times by his oxygen requirement in the last experiment of Table III. His maximum oxygen intake (about 2·3 litres per minute) comes on his curve at about 137 steps per minute ; this, therefore, is the maximum speed at which he could hope to maintain this exercise for a long time. The smoothness of the curve is a tribute to the general effectiveness of the method used ; it contains all the observations made once the need of standardising the exercise had been appreciated.

Into the reasons why the oxygen requirement rises so rapidly with the speed we need not enter very fully. If the oxygen requirement per step, or per metre, were constant, then the oxygen requirement per minute would increase in a linear manner with the speed. It increases much more rapidly than that. One cause of this is the diminution of work done with speed of movement, as described by A. V. Hill (1), Lupton (2), and Gasser and Hill (3). In order to secure the same result a greater effort must be made at higher speeds. A second cause lies in the fact that at high speeds the momentum of the moving limbs themselves becomes large, and this momentum has alternately to be created and destroyed by active muscular effort. In any case the curves show the extremely uneconomical nature of very rapid and violent movement.

This method of determining experimentally the relation between oxygen requirement and speed is applicable to any kind of muscular effort ; whereas the measurement of the oxygen intake is practicable only in the case of exercise

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which can be maintained for some time, since it takes 2 to 3 minutes for the intake characteristic of the exercise to be attained. Moreover, the oxygen requirement of a muscular effort is always a measure of the energy used in it, the oxygen intake often is not. For these reasons a careful investigation of the oxygen requirement of different types of effort, and of different speeds and manners of working, may prove valuable in a scientific study of human muscular activity.

The results given above allow some striking calculations of the lactic acid liberated in severe muscular activity. An oxygen requirement of $23 \cdot 2$ litres per minute would imply the liberation of lactic acid at the rate of about $23 \cdot 2 \times 7 = 162$ gms. per minute, assuming (see Part V) that 1 litre of oxygen is used in recovery in removing 7 gms. of lactic acid. This is $2 \cdot 7$ gms. per second. Assuming the active muscles in K.F.'s body to weigh about 20 kilos., it would take about 21 seconds to attain a concentration of $0 \cdot 3$ per cent. in them ; *the lactic acid maximum would be reached in something of the order of half a minute.* The limiting duration of a really maximal effort in a vigorous man is actually rather less than half a minute, as is shown by the fact that the speed for a 200 metres race is just as high as that for 100 metres, while all greater distances show a lower speed. It is not possible for K.F. to maintain the highest speed of standing running for more than about 20 seconds. All of which is strong confirmation of the view that lactic acid is the real and fundamental basis, as we have taken it to be, of muscular exercise and fatigue.

One aspect only of the results of Tables II and III remains for discussion. In the last column but one are given both the excess carbon dioxide and the excess oxygen due to the exercise. The ratio of these two may be called the "respiratory quotient of recovery." In successive experiments the ratio has the following values: Table II, $1 \cdot 04$, $0 \cdot 98$, $0 \cdot 93$, $1 \cdot 10$, $1 \cdot 05$, *mean* $1 \cdot 02$; Table III, $1 \cdot 05$, $1 \cdot 07$, $1 \cdot 13$, $0 \cdot 97$, $0 \cdot 99$, $1 \cdot 01$, *mean* $1 \cdot 04$. The interval allowed is admittedly not long enough for an absolutely complete recovery; the exercise, however, was generally of short duration, though sometimes very severe, and the recovery should not be very protracted. The effect of a collection of insufficient length would be to raise the respiratory quotient, since in the later stages of recovery there is a *retention* of carbon dioxide. It is tempting, therefore, to conclude that the mean values found, $1 \cdot 02$ and $1 \cdot 04$, are really approximations to unity, but rather too high owing to too short a period of collection during recovery. If this be so, we may conclude that the energy for severe exercise of this type, maintained for a short period only, is supplied by the oxidation of carbohydrate.

In the isolated muscle Meyerhof (4) found that during the recovery period the mean respiratory quotient is about unity; he concluded that in the recovery process the substance oxidised is carbohydrate. In man, however, undergoing prolonged exertion, the respiratory quotient certainly is not unity; this has been proved, not only by our own observations, but by those of many other workers. It would seem possible, however, that in man an *element* of muscular exercise, of such short duration that it does not seriously affect the general metabolism of the body, may be paid for primarily by the oxidisation of carbohydrate; and that if the effort be prolonged the carbohydrate so oxidised must be restored at the expense of other substances; which means, from the point of view of the total balance of metabolism, that it is those other substances which are, in effect, being oxidised. Certainly it is difficult to believe that an observed respiratory quotient of 1·03 (mean of 11 recovery experiments of fair duration) is really 0·81 (mean of the corresponding 11 resting experiments) with an allowance for the incompleteness of the recovery process. We are inclined rather to regard the high respiratory quotient of the recovery process after these short-lived efforts as a genuine effect, in which case it proves that the primary process of recovery in the muscle of the intact animal is carried out through the oxidation of carbohydrate. This conclusion, however, if correct, is so important from the standpoint of carbohydrate metabolism that we intend to devote much more careful work, especially with longer recovery periods, to its confirmation or otherwise. At present the conclusion must be regarded as tentative.*

Summary.

1. The oxygen requirement per minute has been determined for walking, running, and standing running, carried out at various speeds; it rises continually as the speed increases, attaining enormous values (up to ten times the maximum oxygen intake) at the highest speeds.

2. The oxygen requirement of walking is, as was to be expected, considerably greater than that of running at the same speed.

3. The oxygen requirement is a measure, under all conditions and at all speeds, of the energy needed to carry out a given series of muscular movements,

[*Added in proof*.—Further experiments have entirely confirmed this conclusion. Even on a diet of fat and protein (R.Q. 0·75) the complete cycle of exercise and recovery has a respiratory quotient of unity, provided that the exercise be not too long. As the duration of the exercise is increased the R.Q. falls from unity at short durations to the low value characteristic of prolonged exercise at long durations.]

whether continuous or otherwise. It is a valuable quantitative criterion, therefore, of the effort made. The study, however, simply of the oxygen intake affords no such criterion, except in the case of moderate exertion, since no account is taken in it of the recovery process. Moreover, the measurement of the oxygen intake characteristic of any exercise requires that the exercise should be continued at the same speed for at least three minutes. In the case of many types of movement the latter condition is prohibitive.

4. In very severe exercise the rate of lactic acid formation in a man of 51 kilos. (8 stone), as measured by the oxygen requirement of the exercise, attained a value of $2 \cdot 7$ gms. per second. In such exercise a concentration of $0 \cdot 3$ per cent. of lactic acid in the active muscles would be attained in just over 20 seconds, and the lactic acid maximum within half a minute. This is in keeping with what is known about the limiting duration of the maximal muscular effort in athletes.

5. The respiratory quotient of the total excess metabolism caused by short-lived muscular effort appears to be unity. This is in keeping with the observation of Meyerhof that the recovery process in isolated muscle has a respiratory quotient of unity, but is apparently opposed to the well-known and accepted fact that in prolonged muscular exertion the respiratory quotient is considerably less than unity. We conclude tentatively that, after a short element of muscular exertion, not prolonged enough to affect the general metabolism, the recovery process involves the oxidation simply of lactic acid or carbohydrate ; but that in the intact animal, once the exercise and recovery are prolonged, other chemical processes and organs come into play (*e.g.,* a restoration of the carbohydrate stores) which, in the balance of the body as a whole, produce a lower respiratory quotient, and cause, in effect, the oxidation of other substances.

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