CIRCULATORY AND RESPIRATORY CHANGES IN RESPONSE TO MUSCULAR EXERCISE IN MAN.

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INTRODUCTION.

It is well known that if muscular exercise is undertaken at a steady rate of working, some appreciable time elapses before the resultant increases in circulation and respiration attain an approximate equilibrium corresponding to the rise in metabolism. It would seem, therefore, not unlikely that the early stages of muscular work must be performed at a considerable disadvantage owing to this lag in the responses of both systems, even though the ultimate level attained by the circulation and respiration is sufficient to allow the work to be maintained at a steady rate almost indefinitely.

Thus, for example, the initial accumulation of lactic acid in the body might be considerably influenced by the rapidity with which the circulation and respiration respond to the muscular exertion, and if so, it ought to be possible to obtain evidence of this effect either during or after a short period of steady effort. Recently Jervell(1) has found that the lactic acid content of the venous blood in man rises most rapidly in the first few minutes of steady work, and suggests that this is largely due to the fact that the circulation rate is less at the start of exercise than later on.

With a view to testing this hypothesis, a number of pairs of experiments were performed. In each of these pairs the maximum rate of work was identical, but in the one case the subject started from rest with the maximum load, while in the other case the load was increased in several small increments to maximum, with the idea that the accommodation of circulation and respiration would be approaching completion by the time the maximum load was actually applied. Indirect evidence of the relative extents to which lactic acid accumulated was sought by following the course of the total respiratory exchange during preliminary rest and subsequent work, in some experiments; and the changes in the alveolar carbon dioxide percentage after stopping work, in others. In spite of variety in the maximum load and in the type and duration of the preliminary grading chosen for different experiments, no definite evidence could be found by either of these methods that gradual approach to a full rate of working offered any advantage.

In view of this negative evidence it was felt desirable, before proceeding further, to obtain detailed information regarding the rate at which the circulation and respiration respond during the earliest stages of work in the subjects of the foregoing experiments, in the hope that this might throw light on the results which had been obtained. These detailed observations, made upon two subjects, C. G. D. and W. D. P., form the topic of the present paper. Table I shows for comparison some particulars regarding these subjects, as well as their respiratory exchange while at rest and when working on the bicycle ergometer at the rates of work which were usually employed.

TABLE I.

	C. G. D.	W. D. P.
Height	5 ft. 10 in.	5 ft. 8½ in.
Weight	10 st. 4 lbs.	11 st. 1 lb.
Age	45	26
Build	Light	Heavy
Condition	Completely out of training for strenuous exercise	In sufficiently good training to play football

	Total respiratory exchange					
	c.c. per minute at S.T.P.			c.c. per minute at S.T.P.		
	CO_2	O_2	R.Q.	CO_2	O_2	R.Q.
Rest	230	280	0·80	238	282	0·85
Pedalling "no load"	370	440	0·84	507	555	0·91
630 kg.m./min. work	1430	1530	0·94	1420	1630	0·87
840 kg.m./min. work	2000	1950	1·0	1818	1813	1·0

In correspondence with their respective physical conditions W. D. P. was found to be able to maintain steadily a higher rate of work than could C. G. D. (see especially Exps. 5 and 6, Fig. 3), and typical differences between other physiological responses are described throughout the text.

EXPERIMENTAL METHODS.

The muscular exercise was performed on a stationary bicycle ergometer throughout the investigations. In the earlier experiments a Martin ergometer (2) was used, but for reasons described later most of the experiments were done with a Krogh electric brake ergometer (3). A metronome was employed at first to give the rate for pedalling, but as a standard rate of 60 revolutions of the pedal wheel per minute was adopted eventually, an electric bell was connected to a Brodie clock controlling a seconds time-marker. While the subject was working against the brake a current of air was directed on to him by an electric fan.

Pulmonary ventilation was recorded quantitatively on a smoked drum by the spirometer described by Haldane, Meakins and Priestley(4). Pulse rate was obtained from a pulse tracing recorded on the same drum by the use of a Marey tambour connected to a Mackenzie wrist tambour apparatus. The best position of the arm, as found by many tests, was partial flexion at the elbow with the forearm lying on an inclined plane and the elbow supported on a cushioned platform, which was set up at a convenient level close to the ergometer, and protected from vibrations.

Maximal systolic blood-pressure values were ascertained from the tracing given on the same drum as a pulse record by a recording U-tube mercury manometer, connected to a 12 cm. broad pneumatic armlet surrounding the upper arm of the subject. Both the armlet and the manometer were connected to a reservoir of air, under a pressure of about 25 cm. Hg, by means of an inlet tube controlled by a strong spring clip, and the junction was also fitted with a capillary glass outlet closed by another spring clip. By alternate manipulation of these clips it was easy to raise the armlet pressure rapidly to the desired level and then to allow it to fall at a suitable rate, making it possible to repeat complete observations as often as every 10 seconds but usually every 20 seconds, though when diastolic pressure records were taken in addition only two readings of each pressure per minute could be obtained. The reappearance in the pulse tracing of the first wave after complete obliteration was taken as the index of systolic pressure, and was found during rest at least to coincide with the "first sound" heard in auscultation of the brachial artery just below the armlet. In order to identify this reappearance sufficiently clearly to obtain an accurate index on each occasion it was found essential to avoid all but the smallest movements of the forearm causing secondary vibrations in the recording tambour. As it became increasingly difficult to obviate this imperfection as the work became harder, most of the experiments have been limited to a rate of work not above 840 kg.m. per minute to ensure sufficient and consistent accuracy.

Minimal diastolic blood-pressure was approximately determined in the first instance by using a small aneroid manometer ("Tychos") in a shunt from the pressure tubing between the armlet and the mercury manometer. The index of diastolic pressure was taken as the usually definite decrease in amplitude immediately following maximum oscillation of the needle, and the moment when this appeared was recorded on the drum by a hand-operated electric signal, so that a pressure reading could be obtained from the mercury manometer trace superior in several ways to a visual estimate from the aneroid. As this method did not seem altogether satisfactory Pachon's oscillometer and Erlanger's sphygmomanometer were taken into careful consideration and tested in the hope that a better criterion of diastolic pressure might be obtained. However, as in the case of the standard auscultatory method also, these oscillatory methods were found to be even less easy to apply and interpret during muscular exertion, so eventually a simple recording oscillometer, based on Pachon's principle (5), was designed. With this new apparatus it was possible to obtain a *continuous* record, on the same drum as was used for systolic pressure and pulse rate, from which diastolic pressure indices could be secured more accurately and rapidly than previously. A diagram of the instrument is shown in Fig. 1.

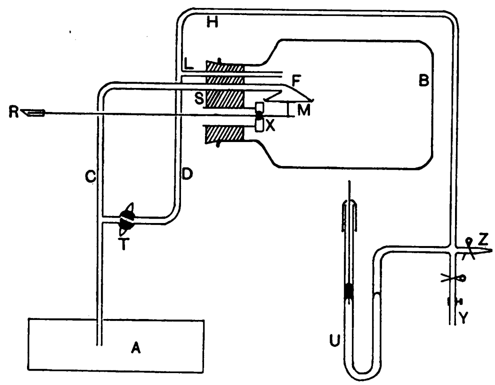


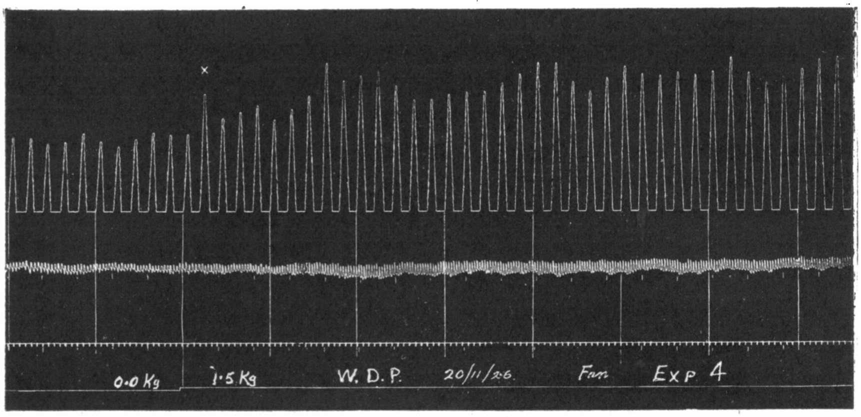
Fig. 1. Diagram of recording oscillometer.

B represents a stout-walled glass bottle of about 600 c.c. capacity acting as a transparent pressure chamber, which is closed by a large rubber stopper *S*, through which pass three glass tubes. *M* is an elastic membrane made of dental rubber dam 2 cm. in diameter and attached to the rim of a small glass funnel *F*, leading directly from the armlet *A via* as short a length of rubber pressure tubing, *C*, as possible. *R* is the writing pen of a light aluminium lever pivoted in a small spindle *X*, lubricated with thin vaseline in a bearing which is carefully ground in a brass plate firmly cemented to the inner end of a wide glass tube passing through the stopper. The particular arrangement of this lever was designed to overcome the difficulty of accurately transmitting the movements of the thin rubber membrane from the interior of the pressure chamber to the outside without any leakage of air. It will be evident from the diagram that the membrane operates not only in an atmosphere always subjected to a higher pressure than that of the air outside the apparatus, but that this pressure alters considerably in correspondence with changes in armlet pressure. Tests proved that no appreciable leak of air occurred even at 300 mm. Hg pressure and that the lubrication of the pivot was sufficiently good to allow of small variations in the armlet pressure oscillations to be recorded very sensitively. *D* is a shunt airway from the armlet with an adjustable tap, *T*, near its connection with airway *C* and opening by a glass T-tube *L*, into *B*, and also by a longer tube *H* to the mercury manometer *U* with its associated compressed air inlet *Y* and outlet *Z*. As in Pachon's oscillometer the average pressure in the armlet and on both sides of the membrane must be equal at any pressure level if tap *T* be open, even during a change in pressure throughout the whole system. Closure of tap *T* at any steady average pressure not too far above the systolic value of the blood-pressure being investigated, results in oscillations in pressure from the armlet (due to alterations in calibre of the underlying brachial artery) being transmitted entirely to *M* and therefore indicated by *R*.

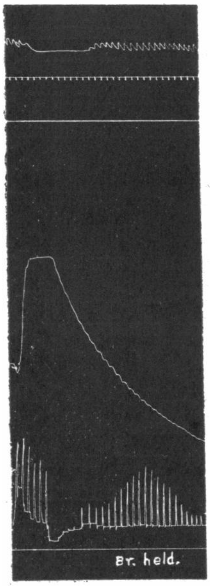
Before the extent of the oscillations, often called the "oscillation range," can be determined for any other armlet pressure, tap *T* has to be opened so as to allow renewed equalisation of average pressure on both sides of the membrane. It was discovered by experiment that if tap *T* was slightly opened and a high average pressure allowed to fall sufficiently slowly, that the membrane remained motionless until about 30 mm. Hg or so above the systolic pressure level, when there began to appear a series of oscillations rising from an almost straight horizontal base-line. As the pressure continued to fall these oscillations steadily increased in amplitude to a definite maximum after which they showed a rapid decrease in amplitude followed by a slower diminution. Tap *T* evidently functions as a selective leak allowing a continuous slow escape of air from the armlet and inner side of membrane, but effectually resisting the passage of all but a small fraction of the rapid air pressure fluctuations set up in the armlet by the underlying pulsation of the brachial artery. By repeated comparison of this continuous record or "oscillogram" with the auscultatory method, it was found during rest at least that the index of diastolic pressure as estimated by "change of sound" ("point 4" between the third and fourth phases of Ettinger(6)) occurs very soon after the last maximal oscillation, *i.e.* during the usual short phase of rapid decrease in the oscillations. The diastolic pressure index in this investigation has therefore been taken as the point in the oscillogram at which the oscillations begin definitely to diminish after reaching a maximum. After varnishing the tracings the blood-pressure and other values were ascertained by drawing fine vertical lines through the appropriate points with a sharp instrument.

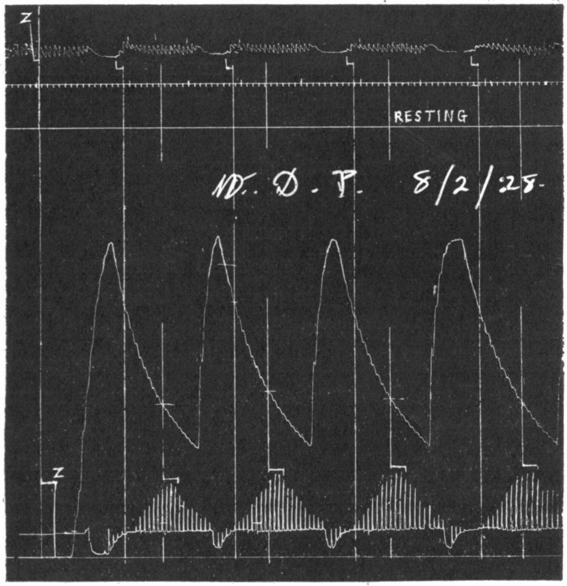
It was found impossible to record blood-pressure as well as pulmonary ventilation and pulse rate on the same drum owing to the limited width of paper. Accordingly one series of records was confined to pulmonary ventilation and pulse rate, while the other, which was taken under identical conditions, recorded pulse rate and blood-pressures, the record of pulse rate being common to both tracings. Typical specimens of the two types of record taken are shown in Fig. 2. *A* shows a continuous spirometer record uppermost, below this a pulse tracing, then a time-marker record of seconds, and lowest an electric signal trace denoting the start of work. *B* shows a record of pulse tracing uppermost, then time-marker and signal records, a manometer record of armlet pressure, below this an oscillogram showing the index of diastolic pressure, and lowest of all the manometer zero pressure line. In this portion of record taken during rest the breath was held subsequent to a short period of deep breathing so that the fundamental outline of the oscillogram would be evident. The series of records in *C* show in addition the vertical lines, corrected for zero errors, drawn from their respective pressure indices, from which it can be seen that the readings for both pressure values can be obtained about every 30 seconds or so.

Respiration even during rest produced a periodic variation in the amplitude of the oscillations derived from the brachial artery as shown by a small decrease over several beats during inspiration followed by a somewhat slower increase during expiration, superposed on the general outline of the oscillogram and most clearly shown with a steady average pressure or a very slow pressure fall. During work this variation became more marked, but as the pulse rate had increased it was possible to select the diastolic pressure index at the same phase of respiration on each occasion. The systolic pressure readings derived from the radial pulse index were necessarily taken at random, but their consistency showed that respiratory variation, though just detectable in the records, was unimportant, as might have been expected with such a small artery.



A





B *C*

Fig. 2. Reproductions of typical tracings.

Experimental results.

While many observations on pulmonary ventilation, pulse rate and blood-pressure changes have been made after exercise of different kinds, few continuous records during the transition from rest to work and from work to rest have been published. Krogh and Lindhard(7, 8), however, have produced much evidence regarding the nature of the respiratory and circulatory changes during both transitions; while Bowen(9) has charted and described the general alterations in pulse rate and systolic pressure during a period of cycling exercise lasting about half an hour and for about the same time thereafter. Masing(10), Lowsley(11), Barringer(12), Gillespie, Gibson and Murray(13), Liljestrand and Zander(14) and others have made somewhat infrequent observations of pulse rate and of one or both blood-pressures in man during work on some form of stationary ergometer. McCurdy(15) obtained high values, over 200 mm. Hg for systolic pressure during maximum effort in weight lifting as early as 1901, and was one of the first to emphasise the need for obtaining blood-pressure readings during work.

(*a*) *Pulmonary ventilation and pulse rate.* The first experiments described in this paper were made on pulmonary ventilation and pulse rate in the manner adopted by Krogh and Lindhard(7). The subject sat at rest on a Martin ergometer with his feet on the pedals and at the word of command started work with the full load on the brake. Typical examples of the results obtained are shown in the graphs of Exps. 1 and 3 in the upper portions of Figs. 3 and 4.

The abscissæ indicate time in minutes from the moment the work started while the ordinates show the pulse rate and pulmonary ventilation. The commencement of work also is indicated for clarity by a vertical line drawn from zero on the time scale.

In W. D. P. there is a very rapid rise in pulse rate, from 90 to 140 beats per minute by the end of 15 seconds, maintained during most of the working period. Pulmonary ventilation increases very rapidly within the same time interval, from 12 to 28 litres per minute, and then less rapidly till the end of the first minute after which it more slowly approaches a maximum level of about 40 litres per minute during the following two minutes. In C. G. D. also the pulse rate shows an initial but much smaller rise from the same resting value of 90 to 115 beats per minute in 15 seconds, with a distinctly gradual rise during the following 2¼ minutes towards an almost steady value of 140 beats per minute. Pulmonary ventilation rises rapidly within the first 15 seconds, from

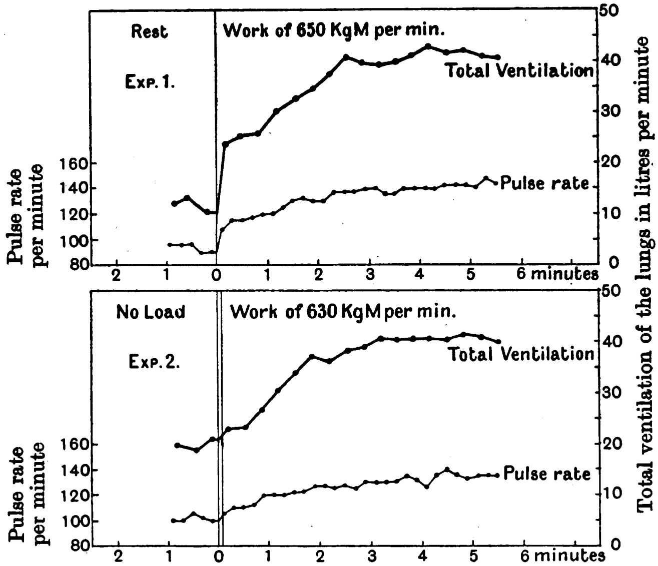


Fig. 3. C. G. D. Respiratory rate per minute 15.

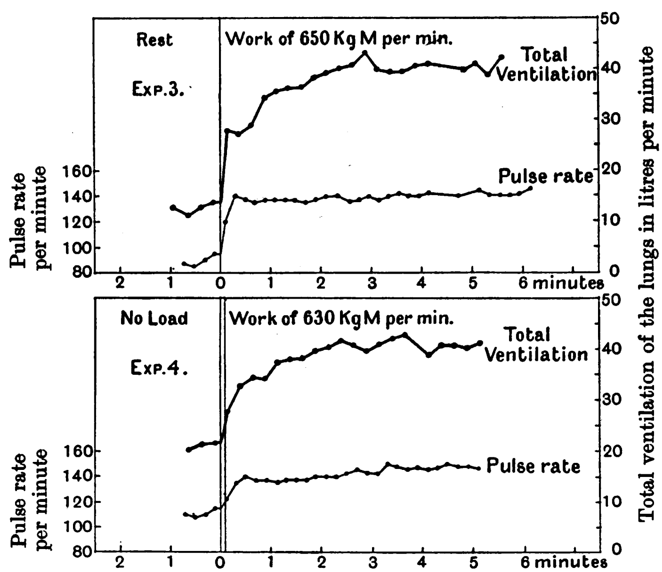


Fig. 4. W. D. P. Respiratory rate per minute 20.

12 to 24 litres per minute, but not so much as in the case of W. D. P. This is followed by a more rapid secondary rise than in W. D. P., but the same level of about 40 litres per minute is reached in about the same time, 2½ minutes, from the start of work. Thus from both records it is evident that the general response of C. G. D. is slower than that of W. D. P. within the first three minutes taken by both subjects to approach an equilibrium. Within the first half-minute of the work in preliminary experiments there was often a rapid temporary rise in the respiratory rate accompanied by an appreciable but inconstant fluctuation of the pulmonary ventilation above the continuous increase. In each subject the breathing tended involuntarily to pick up and maintain during the work a rate in accordance with the natural rhythm of the pedalling, and it was found easy to maintain the same rate voluntarily when pedalling with no load on the brake. In these circumstances the actual rate of the breathing remained unchanged during the entire experiment and increased hyperpnœa involved merely a change in the depth of the breathing. It was only in experiments dealing with the heaviest loads that it was found impossible to avoid an increase of rate of breathing as well as of depth. The striking changes in respiratory rate for heavy work are shown in Exps. 5 and 6, Fig. 5, but the particular constant rates in each of the other experiments is given in the legend below each pair. Curiously enough, as can be observed, the two subjects chose different respiratory rates even for a light load undertaken at the same pedalling rate.

A number of experiments performed in the manner just described showed that there were still appreciable variations in the earliest portions of the records on different occasions, though they were supposed to be obtained under exactly the same conditions. In some instances W. D. P. actually had a very rapid initial rise in pulse rate which was followed by a definite fall before a subsequent slower rise to the level of the early maximum took place; while the large initial increase in ventilation was followed by a definite decrease preliminary to the usual steady increase to maximum. C. G. D. showed less rapid initial rises without a temporary fall in pulse rate and a smaller transient decrease in ventilation. These results are in close accordance with the findings of Krogh and Lindhard(7, 8) for trained and untrained subjects respectively undertaking work from a condition of rest. It seemed not unlikely that these effects were largely due to the heavy initial exertion required to overcome the inertia of the flywheel when it was necessary to raise its rate of revolution from zero to 175 per minute in the shortest time possible. Thus it became clear that two uncertain factors were probably involved in the initial response of the respiration and circulation at the start of work undertaken from rest: (1) a nervous or psychic factor, (2) the sudden large momentary effort required to overcome the inertia of the flywheel.

With a view to avoiding this extra inertial factor and with the idea that the nervous or psychic factor might at the same time be reduced, it was decided to alter the method of applying the load. Instead of sitting at rest, the subject pedalled on the Krogh ergometer for several minutes with no load on the brake, and then the load was applied very rapidly by quickly adjusting the rheostat. The advantages of this method were (1) that the pedalling rate was maintained steadily throughout the entire experiment, (2) that the flywheel was already rotating at its proper speed when the load was applied, (3) that the subject required no verbal or other warning, but had merely to watch the metronome and maintain the steady pedalling rate, so that he had no idea of the precise moment when the load would be applied. While this method shows the changes which occur when the work done is considerably increased from a very low value, though the type and rate of muscular movement remain unaltered throughout, it does not afford an accurate picture of the changes which result on the transition from complete rest to considerable muscular exertion, and must therefore be carefully distinguished from Krogh and Lindhard's standard method. In actual practice the new method was found to be very satisfactory as repetition of experiments under circumstances intended to be identical effected the same responses, typical for the particular subject, on each occasion, so the method was adopted as a standard.

Exps. 2 and 4 graphed in the lower portions of Figs. 3 and 4 give examples of the results obtained in this way. These may be readily compared with the changes occurring on the transition from rest to the same rate of work. The distance between the lines in each vertical pair in this and subsequent diagrams represents the short time interval taken to apply or remove the load by rapid adjustment of the rheostat. It can be seen that the subjects still show typical differences between their initial responses. W. D. P. again exhibits the largest increase in ventilation at the very start, and pulse rate has increased rapidly enough within half a minute nearly to reach the maximum level attained. In the case of C. G. D. the pulmonary ventilation shows no sudden initial rise, but mounts fairly steadily and rapidly towards maximum, while pulse rate also increases gradually and reaches a nearly steady value in about 3 minutes. Similar but more marked changes occur with a rate of 840 kg.m. per minute work as can be seen from Exps. 11 and 13 in Figs. 8 and 9 below.

In the case of very heavy work, 1260 kg.m. per minute, these typical differences become accentuated (see Exps. 5 and 6, Fig. 5). Under such

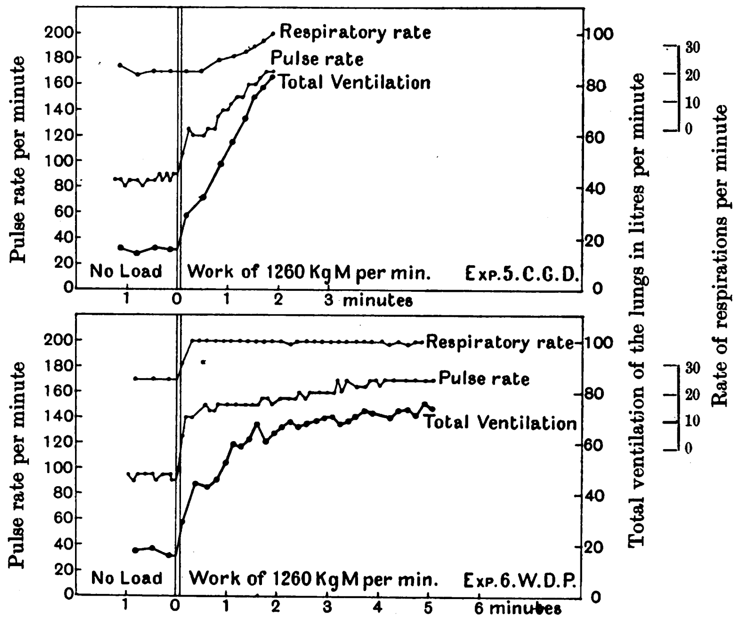


Fig. 5.

conditions for W. D. P. the initial rises in pulmonary ventilation, pulse and respiratory rates are very rapid. About 50 p.c. of the final increase in ventilation rate above "no-load" value is reached within 20 seconds after the start of work, while about 60 p.c. of the final increase in pulse rate is attained in 10 seconds, and thereafter there is a very gradual rise in both without a true equilibrium ever being struck. The respiratory rate actually rose from 15 per minute to the final steady value of 30 per minute in 18 seconds. C. G. D. showed a much less rapid initial response in all three values, but the rise continued steadily and fairly rapidly in each case until the hyperpnœa was so great that the experiment had to be stopped at the end of only two minutes' work, owing to an insufficient supply of air from the spirometer. In any case the subject could not have maintained this high rate of work much longer.

Pulmonary ventilation during recovery after moderate exertion, 630 kg.m. per minute, shows less striking differences between C. G. D.

and W. D. P. (see Exps. 7 *a* and 9 *a*, Figs. 6 and 7). The time intervals taken to return to equilibrium values are respectively 3 and 2 minutes, in close accordance with the periods required for the rise to maximum level at the start of work in each case. In addition the total deficit in ventilation below maximum during the early stage of the work period is almost as great as the total excess ventilation after the work is over. In the case of C. G. D. the pulse rate fell rapidly during the first minute and then very slowly thereafter, taking 5½ minutes to reach an equilibrium. W. D. P. showed an equally rapid preliminary fall with a distinct temporary rise during the second minute of recovery, soon followed by very steady values. A very similar comparison, but with even sharper contrasts for the complete sequence of events during work and recovery, can be drawn from Exps. 11 and 11 *a*, Fig. 8, for C. G. D., and Exps. 13 and 13 *a*, Fig. 9, for W. D. P., in which the rate of work was 840 kg.m. per minute (see below).

(*b*) *Blood-pressure and pulse rate.* The changes in blood-pressure due to quite moderate exertion are considerable, as can be seen from the graphs of Exps. 8 and 8 *a*, Fig. 6, and Exps. 10 and 10 *a*, Fig. 7, for 630 kg.m. per minute; also Exps. 12 and 12 *a*, Fig. 8, and Exps. 14 and 14 *a*, Fig. 9, for 840 kg.m. per minute.

During pedalling with no load the systolic pressure is higher for W. D. P. than for C. G. D., 134 mm. Hg as compared with 112 mm. Hg, but in both subjects the value finally obtained during effort is about the same for a given load. Whereas in the case of W. D. P. for 630 kg.m. per minute a value of 164 mm. is reached in 1⅓ minutes and thereafter there is very little increase in systolic pressure, C. G. D. takes 2½ minutes to attain 160 mm. after which the increase is likewise very gradual. With 840 kg.m. per minute the main rise to 170 mm. has occurred with 1 minute in W. D. P. and the gradual approach to the highest value of 180 mm. is not completed till after the third minute. In C. G. D. the rise in systolic pressure is gradual from the start though the final value of 200 mm. reached in 4 minutes is distinctly higher than that attained by W. D. P. in the same time. The diastolic pressure, as determined by the oscillometer, remained almost constant both during and after work of 630 kg.m. per minute in W. D. P., but there was an appreciable rise of about 20 mm. during the work followed by a corresponding fall after the load was removed in the case of C. G. D. With the heavier work of 840 kg.m. per minute W. D. P. also showed a distinct rise in diastolic pressure, which is apparent during the first minute after application of the load (see Exps. 14 and 14 *a*, Fig. 9). Unfortunately the corresponding

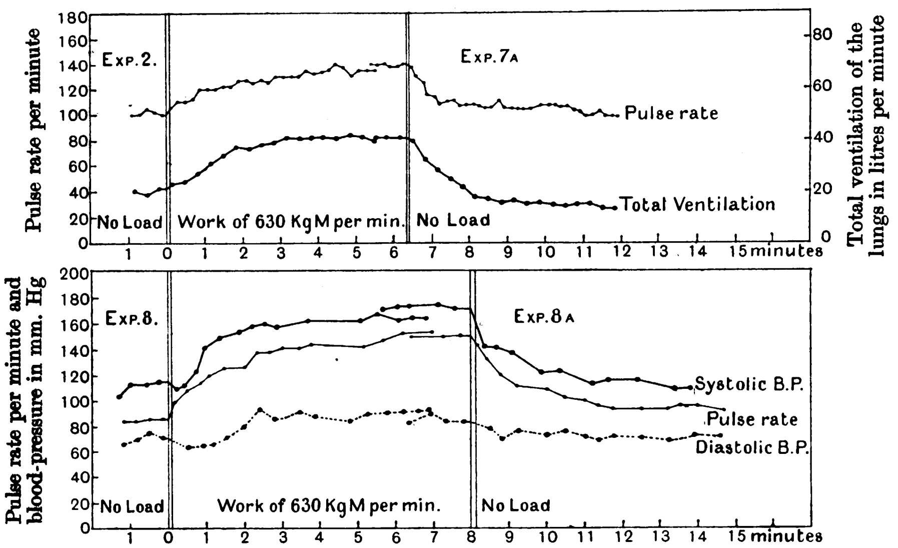


Fig. 6. C. G. D. Respiratory rate per minute 15.

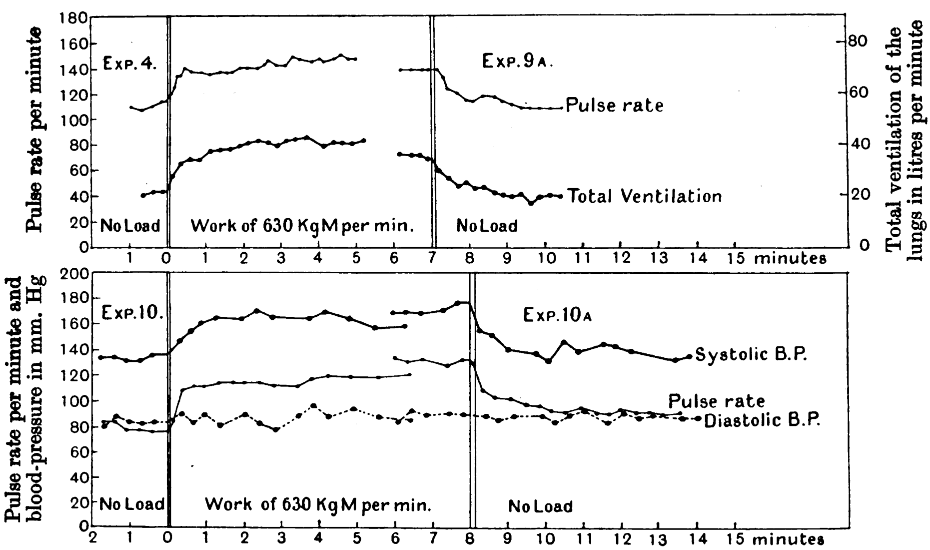


Fig. 7. W. D. P. Respiratory rate per minute 20.

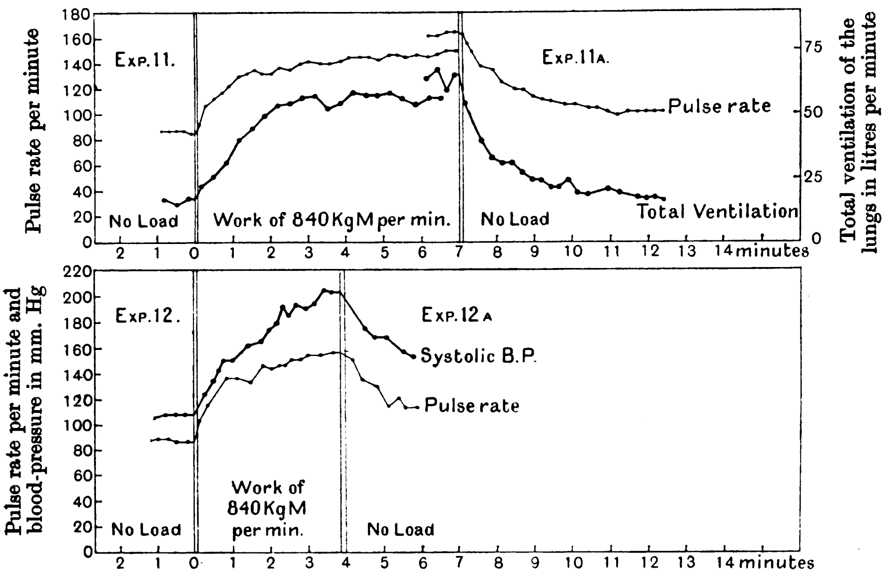


Fig. 8. C. G. D. Respiratory rate per minute 20.

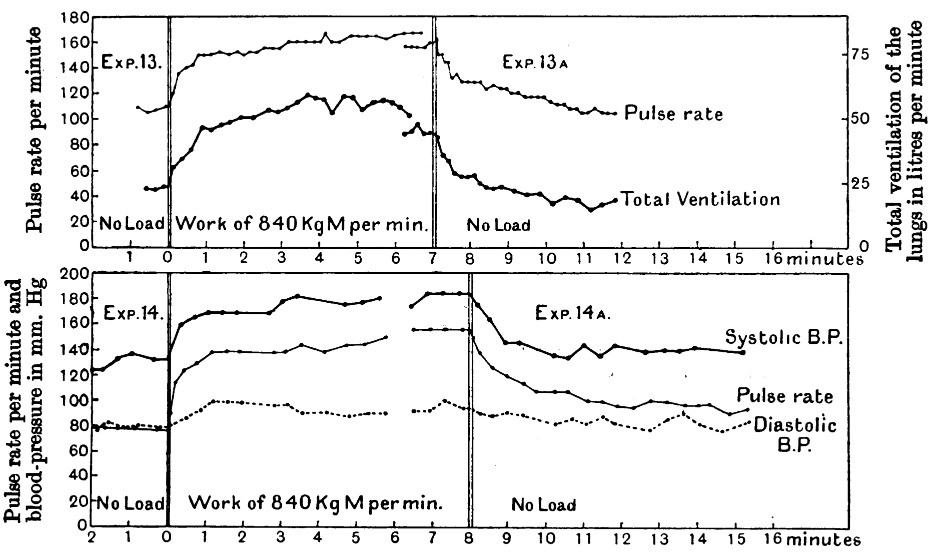


Fig. 9. W. D. P. Respiratory rate per minute 30.

complete graph for C. G. D. could not be obtained, as the load was too heavy in the case of this subject to allow of reliable readings; but from the results available it is clear that with a sufficiently heavy load, which was, however, different for the two subjects, the brachial diastolic pressure rises appreciably with muscular effort.

With the aid of the diastolic pressure readings it is, of course, possible to obtain values for pulse pressure (systolic minus diastolic pressure) and so-called "mean pressure" (half the sum of the systolic and diastolic pressures), which cannot be deduced from systolic readings alone. In C. G. D. the pulse pressure during pedalling "no load" was about 40 mm. (112–72), while during the later stages of work at 630 kg.m. per minute it was 80 mm. (170–90), an increase of 100 p.c. In the case of W. D. P. the corresponding values are 52 mm. (134–82) and 80 mm. (170–90), an increase of only 59 p.c. This difference is largely due to the fact that W. D. P.'s systolic pressure has already risen from 122 mm. during rest to 134 mm. during pedalling "no load" and his diastolic pressure from 72 to 82 mm., whereas C. G. D.'s resting systolic pressure of 104 mm. has only risen to about 112 mm. with only 4 mm. rise in the diastolic value.

Table II gives a summary of the average values of the circulatory data obtained from many experiments during rest and at the two different levels of exertion. These *average* values can only be taken as correct to within ± 4 mm. for blood-pressure, and those of pulse rate to within ± 3 beats per minute, but the figures differ sufficiently in the case of the two subjects to make their comparison with the respiratory values in Table I of interest. For example, the difference between resting and pedalling "no load" as indicated by the circulatory as well as the respiratory values is distinctly greater in the case of W. D. P. than in that of C. G. D.

TABLE II.

	C. G. D.				W. D. P.			
	S.B.P.	D.B.P.	P.P.	P.R.	S.B.P.	D.B.P.	P.P.	P.R.
Rest	104	68	36	85	122	72	50	85
Pedalling "no load"	112	72	40	100	134	82	52	105
630 kg.m./min. work	170	90	80	145	170	90	80	140
840 kg.m./min. work	200	[100]	[100]	150	182	98	84	150

P.P. = pulse pressure in mm. P.R. = pulse rate per minute.

For 840 kg.m. per minute the highest value of pulse pressure recorded for W. D. P. is 92 mm. (184–92), representing an increase of 84 p.c. as compared with pedalling "no load." Though no values of diastolic pressure were obtained from C. G. D. for this load it is reasonable to suppose from the values for the lighter load that the rise was not above 100 mm. If this were so, then the corresponding value would be 104 mm. (204–100), equivalent to an increase of 250 p.c. compared with "no load" value. The "mean pressures" for C. G. D. during pedalling "no load" and during 630 kg.m. per minute work were 92 mm. and 130 mm., an increase of 41 p.c. The corresponding values for W. D. P. were 108 mm. and 130 mm., an increase of only 21 p.c., while for 840 kg.m. per minute the rise to 138 mm. represents an increase of 29 p.c., corresponding to a probable value of 152 mm. or an increase of 65 p.c. in the case of C. G. D. As the rise in diastolic pressure was inconsiderable for the lighter load, it will be evident that the change in "mean pressure" caused by such work is, as a rough approximation, but little more than half the change in systolic pressure. However, it must be emphasised here that this arithmetic mean of two pressures possessing different physical characteristics is empirical, and probably has no simple fundamental interpretation, particularly in relation to relative circulation rates.

The records of pulse rate taken along with those of the blood-pressures were almost identical with those secured during measurement of the pulmonary ventilation, though on different occasions the same subject showed small differences in the maximum value obtained for a given load. This close and consistent correspondence between the values of the common factor in the two series of experiments provided good evidence of equal physiological response for each subject during experiments which, though performed on different occasions, were intended to be identical. The changes in pulse rate follow much the same course as changes in ventilation and systolic pressure, and even more closely those of pulse pressure, C. G. D. showing the typically slower initial response as compared with W. D. P., whose pulse increases very rapidly within the first 20 or 30 seconds and then rises much more slowly to the final value for 630 kg.m. per minute. Indeed in C. G. D. the change is gradual from the very start and shows hardly any indication of sudden increase after the load is undertaken, though the pulse rate eventually reached is practically the same in both subjects. With 840 kg.m. per minute W. D. P. shows a very rapid initial rise with only a very gradual increase after the first minute. C. G. D. has a less rapid initial rise and the pulse rate was still increasing at the end of 5 minutes. W. D. P.'s pulse rose from 80 to 150 per minute; C. G. D.'s from 86 to 156 per minute. Owing to the limits of the apparatus individual records were restricted to a duration of about 9 minutes. It will be seen that during the working period a perfect equilibrium is not reached in the majority of the experiments, though in the later stages of work the changes in pulmonary ventilation, pulse rate and systolic pressure are all very gradual. This phenomenon is considered below, in the discussion.

On removal of the load the ventilation, pulse rate and systolic pressure fall rapidly within the first minute and then more slowly towards the values obtained before the load was applied, while the diastolic pressure falls very little but perceptibly. The changes occurring in all four factors during this recovery period can be readily compared in Figs. 6 to 9 with those shown during application of the load, those in Fig. 9 providing the clearest contrasts.

Discussion of results.

When work was undertaken suddenly from rest, as in the earliest experiments, the results obtained were in close accordance with those described by Krogh and Lindhard(7) for similar conditions. These authors put forward the view that the rapid initial increase in pulmonary ventilation and pulse rate was caused by "irradiation of impulses from the motor cortex" rather than by reflex action, partly because one of their subjects showed a marked increase in ventilation when he anticipated the application of a heavy load but actually started pedalling without any brake load. They also described three phases in the ventilation changes, a sudden initial increase followed by an increasingly slow rise towards an approximate equilibrium, whose level depended on the extent of the change in metabolism.

The experiments described in this paper show that similar but less marked changes occur when, instead of starting from rest, the amount of work per minute is considerably increased from a very low value (that of pedalling "no load"), while the nature and rate of the muscular movement is maintained uniformly. These changes in pulmonary ventilation were pretty closely followed throughout by the simultaneous alterations in pulse rate and blood-pressure. It seems probable that the smaller initial responses shown when the work was undertaken in this new way were due to reduction of the psychic or nervous influences involved in starting from rest and elimination of the considerable initial effort required to overcome the inertia of the flywheel. Thus C. G. D. showed a gradual increase in ventilation and pulse rate from the very start of work when undertaking the lighter load while pedalling, in contrast with the very sharp rise induced by undertaking the same load from rest (see Exps. 1 and 2, Fig. 3). Even so, close inspection of the spirometer records shows that the depth of the first or second inspiration after application of the load was usually greater than those immediately following though the respiratory rate was constant (see *A*, Fig. 2). This effect was even more marked in the case of W. D. P., though in both subjects much less obvious than in some of Krogh and Lindhard's experiments, as would be expected. Whatever the contributory causes in their experiments the effect seems more likely to be due to reflex rather than psychic causes in the standard type of experiment adopted in this investigation.

Another transitory and more variable effect was noticeable in some of the blood-pressure records obtained from C. G. D. and well shown in Exp. 8, Fig. 6. Systolic and sometimes also diastolic blood-pressure readings within the first minute of work either fell below, or scarcely increased above, the average "no load" value. This phenomenon was noticed by Gillespie, Gibson and Murray(13) who suggested that it might possibly be due to deepened inspiration. In view of the frequently repeated observation that systolic pressure always rose rapidly from the start even with a greater initial respiratory increase for W. D. P. as compared with C. G. D., it seems more probable that the cause of this delayed pressure rise is largely due to a less rapid general vasomotor response. In this connection Exps. 5 and 6, Fig. 5, are interesting in that they suggest the importance of the rapidity of the initial response of the circulation and respiration in relation to the capacity of a subject to maintain a high rate of work. As Krogh and Lindhard pointed out, unless the circulation and respiration were able to adapt themselves rapidly to the instantaneous and enormous rise in muscular metabolism coincident with sudden and strenuous exertion, before the vasomotor and respiratory centres were directly influenced by the more gradual increase in metabolites carried to them by the blood stream, then such muscular activity could not possibly be sustained for more than a fraction of a minute. The active muscles would be hopelessly asphyxiated before a fresh supply of oxygen could reach them, and the excess of lactic acid and carbon dioxide be disposed of.

When the records of systolic pressure and pulse rate are compared with those of pulmonary ventilation it can be seen that not only are the initial responses similar, but that the times taken to reach an approximate equilibrium are about the same for all three factors. Thus for 630 kg.m. per minute it takes about 3 minutes for these factors to approach equilibrium, while W. D. P. only requires about 1½ minutes. If one may fairly take the systolic, diastolic and pulse pressure changes together as an index of circulatory alteration, it is evident that the accommodation of the circulation requires about the same time as that of the pulmonary ventilation to meet the needs imposed by the rise in metabolism, and that all this is largely effected within 3 or 4 minutes in the case of even the heavier load chosen for either subject.

With regard to the actual systolic pressure values attained during the moderate rates of work employed in these experiments, it seems advisable to point out that they are much higher than those suggested even very recently by Norris (16) and others for dumb-bell exercise above 1000 kg.m. per minute, partly on the basis of Cotton, Rapport and Lewis' (17) graphs obtained entirely after effort had ceased. On the other hand the high systolic pressure and pulse rate values obtained by Hill and Flack (23) in athletes and by Pembrey and Todd (24) in trained and untrained men very soon after running up and down stairs are very similar to those shown in the earliest portions of the recovery curves graphed in this paper. As their readings fall just as rapidly during rest immediately following exertion it seems reasonable to suppose that the values during the exertion were at least as high as those actually measured during the ergometer exercise. The results of these and other types of muscular exertion and even of identical exercise followed by rest must be carefully distinguished from the particular experiments cited in this paper. Also the fallacious assumptions involved in attempting to deduce blood-pressure values during exertion from readings taken even a fraction of a minute after removal of the load must now be apparent from the graphs in Figs. 6 to 9. The contrast between the rises in systolic pressure for different increments of work per minute relative to "no load" value was greater and more constant in each subject than that between the corresponding increases in pulse rate, which did not always start from the same "no load" value as did the pressure. This result is in accordance with the observations of other investigators (13, 14, 17, 18) for a constant rate of limb movement with different loads. Unfortunately no values are available for similar amounts of work per minute performed at different pedalling rates for comparison of the relative efficiencies (18), and the corresponding effects on pulse rate and blood-pressure. The fact that pulse rate and pulmonary ventilation continued to increase slowly even several minutes after the main rises had occurred suggests that possibly there was a slight temperature effect, only making itself noticeable some time after the actual start of work, though it was hoped to minimise this complication by the measures described previously.

Neither blood-pressures nor pulse rate can in themselves afford a true index of the output of the heart, but many attempts have been made to deduce alteration in circulation rate from simultaneous changes in these factors. The most recent suggestion due to Liljestrand and Zander (14) is that changes in circulation rate can be inferred from the formula $\left[\frac{\text{P.P.} \times \text{P.R.}}{\text{M.P.}}\right]$, in which P.P. represents pulse pressure, P.R. pulse rate, and M.P. "mean pressure," in the brachial artery. Using this method of calculation it would appear that the relative figures for circulation rate in the case of C. G. D. are: at rest 100, pedalling "no load" 130, later stages of 630 kg.m. per minute work 270; while for W. D. P. the corresponding figures are 100, 111, 193, and 237 for 840 kg.m. per minute. However, as the universal validity of this and similar formulæ can by no means be regarded as definitely established, no attempt has been made in this paper to apply such a method of calculation in detail throughout the experiments. Indeed the relation of brachial artery pressure values, obtained by the armlet method, to aortic pressures may be even less direct during a period of muscular exertion than seems probable for the resting condition (see Dawson (25)). Though every care was taken to protect the upper limb carrying the armlet from strain of any sort, it cannot have been entirely immune from some increased reflex tone due to the considerable activity of muscles in other parts of the body, and may therefore have required extra armlet pressure for its necessary distortion by compression over the region of the brachial artery and underlying bone.

Perhaps more important might be the hypertonus, presumably induced in the whole arterial system of the upper limbs for compensatory restriction of blood flow in an inactive region of the body whose aortic supply had greatly increased in pressure as well as in output, and possibly extending from the smaller vessels so as to be appreciable even in the brachial artery. The only direct evidence obtained for the existence of such a hypertonus was similar to that described, for example by Stacey Wilson (19), for pathological hypertonus in subjects at rest, namely, a much more rapid approach to a more prolonged plateau in the "oscillation range" outline during work as compared with what was obtained previous to or sometime after the working period. Whatever the extent of these two types of increased tonus the total effect would be to make compression and distortion of the brachial artery require an armlet pressure greater than that necessitated by the lateral blood-pressure alone. Armlet pressure readings derived from quite critical indices would thus tend to be too high for estimations made while the subject was working. Now the actual pressures obtained seem very high for an artery in an inactive limb and may not at all accurately represent even the relative increase in the lateral blood-pressure, as would be measured by a manometer and canula. It is interesting to note in passing that Russell (20) insisted on the importance of this discrepancy in cases of marked and often palpable hypertonus (as distinct from arterio-sclerosis) of the brachial artery in pathological conditions with subjects at rest, and it is at least probable that considerable muscular activity may produce a transient example of a similar phenomenon.

Lindhard (26), also Lythgoe and Pereira (21), have shown that the rate of O_2 intake falls much more rapidly than pulse rate after strenuous exercise, and suggested that circulation rate and therefore cardiac output per beat probably decrease more rapidly than pulse rate, at least in the earliest stages of recovery. However, the important factor of change in the percentage utilisation of oxygen, as described, for example, by Douglas and Haldane (22), must also be taken into account during most of a large and rapid alteration in circulation and respiration. In any case, from the close harmony which has been shown to exist in the experiments described between the changes in ventilation pulse rate and blood-pressure, both at the start and end of undertaking a steady rate of work per minute, it is reasonable to suppose that the respiration and circulation adapt themselves to muscular activity at all stages in a closely coordinated fashion. Moreover, this coordination shows a characteristic difference between different individuals in accordance with their respective physical conditions.

Conclusions.

1. Observations have been made at frequent intervals on pulmonary ventilation, pulse rate and blood-pressure at the commencement and cessation of steady muscular work in two subjects of different age and physical training.

2. A simple form of recording oscillometer has been designed for determination of the diastolic blood-pressure.

3. The initial changes in respiration and circulation, which occur during the earlier stages of work at a steady rate, show variations depending on the way in which the load is undertaken.

4. Comparison of the changes in pulmonary ventilation, pulse rate and blood-pressure suggests that the rate of accommodation of the cir-

culation follows a very similar course to that of the respiration when the metabolism is altered on account of change in muscular activity.

5. The rises in total ventilation, systolic and pulse pressures and to a lesser extent pulse rate were roughly proportional to the relative increments in the amount of work per minute, and therefore to the corresponding metabolic increases.

6. The times taken by all factors to attain an approximate equilibrium were dependent not only on the load but on the particular subject.

7. There is a definite difference between all the corresponding responses of the two subjects in accordance with their respective physical conditions.

The writer's sincere thanks are gratefully acknowledged to Dr C. Gordon Douglas for his assistance and encouragement, especially during the earlier part of this investigation.

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