THE PHYSIOLOGICAL COST OF NEGATIVE WORK

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In the investigation of muscular work and its cost in terms of oxygen consumed, attention has been concentrated on positive work performed by muscular shortening, while the absorption of work during forcible lengthening has been almost entirely neglected. Yet in the living animal active muscles are regularly stretched, and in the process mechanical work is absorbed in them, e.g. whenever we bend down, or run downstairs, or lower a weight. Throughout the extension the muscles are actually contracting, in contrast, for instance, to the antagonist extensor muscles which, during rapid flexion of a limb, are stretched passively for the greater part of the movement and are not excited to activity until towards the end when they cause deceleration (Wilkie, 1950). The present investigation on human muscles was undertaken as an application of the results of recent studies of the energetics of active isolated muscles during stretch (Abbott, Aubert & Hill, 1951). The cost in oxygen consumption of performing positive work has been compared with that of absorbing the same work, by the same movements and at the same speed, the only difference being that in the one case the muscles shortened, in the other they were forcibly stretched.

When an active muscle exerts a force P and shortens a distance x it does an amount of work Px; on the other hand, if it is stretched a distance x while exerting this force, it absorbs work and is said to do an amount Px of negative work. For example, when a man climbs a vertical ladder, his leg extensors shorten and do positive work against gravity; when he descends, the same muscles are stretched while actively resisting the gravitational pull and may be said to do negative work.

What is the physiological cost of such negative work? It is, of course, common experience that to walk downstairs is easier than to walk upstairs and this can be tested objectively by measuring the oxygen consumption in both tasks. This was done by Chauveau (1901) with a subject walking on a treadmill driven by a motor. According to the direction of its movement the subject

had continually to ascend or descend in order to maintain a constant position and so did positive or negative work. Under the conditions of Chauveau's experiments the oxygen consumption for a given subject doing positive work was about twice that for an equal amount of negative work. Chauveau's concept of the muscle machine was quite different from that held at present, and his physical terms were not clearly defined. He considered that muscle activity was divided between internal and external work; oxygen was equated directly to a number of work units, and variations in oxygen consumption with work under different conditions were discussed in terms of the efficiency of the internal working. It is therefore difficult to obtain an intelligible picture of his conclusions.

In the paper by Levin & Wyman (1927) the experiments on isolated jaw muscles of dogfish (fig. 3 of their paper) showed that the maximum positive work done by a fully active muscle shortening at constant speed may be only one-sixth of the negative work involved when the muscle is stretched at the same speed. From this it can be concluded that in order to obtain equal amounts of positive or negative work from a given isolated muscle the number of fibres activated would need to be up to six times as great for the first as for the second. The ratio, of course, will depend on the type of muscle, the experimental conditions and particularly on the speed. We have assumed that the oxygen consumption associated with equal amounts of positive and negative work must be largely determined by the number of muscle fibres in activity. This assumption is supported by the results of Fischer (1931) which show that a frog sartorius, doing the maximum work possible in an isotonic twitch, consumes only about 20 % more oxygen than in an isometric twitch, although it should be noted that, in an isometric twitch, an unknown amount of work is done which depends on the extensibilities of the tendon, thread and recording system. Our present knowledge of the physical characteristics of muscular contraction calls for a new study of the fuel consumption of human muscles during shortening and imposed stretch.

METHOD

The apparatus is shown in Fig. 1. Two bicycle ergometers were placed back to back and coupled by a chain; when one cyclist (*A*) pedalled in the conventional forward direction, the legs of the other cyclist (*B*) were driven backwards. This is not 'back-pedalling' in the conventional sense, but normal pedalling reversed. During the experiment the forward cyclist pedalled at an agreed ·speed set by a metronome and the other resisted sufficiently to maintain an agreed force read on a gauge. *A* and *B* necessarily exerted the same force, otherwise the system would have accelerated or slowed down.

Similar muscles were necessarily used by both cyclists; in pedalling the muscles shortened and did work, in resisting they were forcibly stretched and work was done on them. The apparatus was designed to have as little frictional loss as possible in flywheel and transmission chains, so that practically all the work done by *A* was used in stretching the leg muscles of *B*. The platform carrying one bicycle was mounted on roller bearings which allowed free movement along

a smooth steel plate. A sealed waterfilled system of flexible metallic bellows (S, Fig. 1) was placed between the bicycle platforms. During pedalling the tension in the chain C joining the flywheels pulled the bicycles together, compressing S. This compression was registered on a gauge G in front of each subject.

Expired air was collected in Douglas bags and samples were taken from them into 30 c.c. Brodie bottles within a few minutes of collection. The remaining air was expelled through a gas meter for measurement of ventilation rate. The samples were analysed in a Haldane gas analysis apparatus, with sodium hydrosulphite-β-anthraquinone as the oxygen absorber. In all experiments pedalling was preceded by a rest of 30 min on the bicycles, during the last 10 min of which collections of the expired air were taken. Pedalling lasted for about 13 min in all. It was expected that a steady state had been reached after 10 min; expired air was then collected from both subjects for 1–3 min, according to the rate of working. The subjects then changed places, the forward cyclist of the first run now resisting. The pedalling was repeated, with speed and force unchanged.
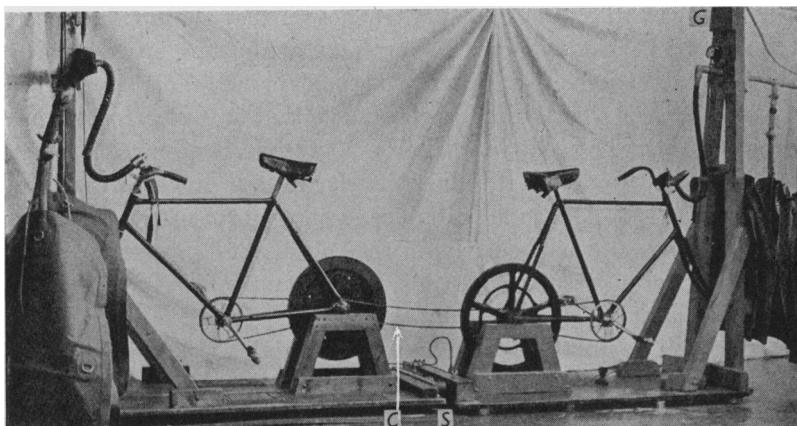

Fig. 1. Two bicycle ergometers coupled together in opposition and separated by a flexible water-filled buffer system S connected to the gauge G. One bicycle is mounted on rollers resting on a smooth metal sheet.

In order to correlate changes in oxygen consumption with muscular activity, a steady state was needed. A maximum sustained effort and a steady state are incompatible, because a continually rising oxygen debt accrues. A compromise was reached using submaximal efforts, by comparing the sum of the two 'forward' oxygen consumptions with the two 'resisting' consumptions. This procedure also tended to eliminate any effect of different muscular efficiencies in the two subjects. Since we were interested only in ratios, gas volumes were not corrected to s.t.p.

Experiments were made at a variety of pedalling speeds and forces. The optimum speed of forward pedalling depends, as would be expected from Hill's characteristic equation for muscle (1938), on the length of the subject's legs and the length of the crank. Dickinson (1929) has shown that on a standard bicycle her highest efficiency was attained with 33 complete rev/min, the efficiency versus speed curve having a flat maximum in this region. Our initial experiments were at about this speed. With very high rates of pedalling, care was taken to use small forces in order to avoid a rising oxygen debt. At low speeds it was difficult to maintain smooth pedalling because of dead points in each rotation.

RESULTS

In all experiments less oxygen was consumed when the subject was resisting than when he was pedalling forward, and the subjective effort was also clearly less.

Three speeds of pedalling were used in the experiment summarized in Table 1. With 35·4 complete revolutions of the pedals per minute, subject *A*, doing positive work, used 0·70 l. O_2/min in excess of his resting rate, compared with 0·19 l./min by the resisting subject *B* doing the same amount of negative work. When their positions were reversed the oxygen consumptions were

TABLE 1. Oxygen consumptions in forward pedalling and in resisting

Subject	Pedalling speed (revs/min)	Oxygen consumption (l./min)			Ratio of excess oxygen consumptions above resting value
		Resting	Positive work	Negative work	
B.C.A.	25·0	0·33	1·16	0·64 ⎫	2·4
J.M.R.	25·0	0·37	1·28	0·80 ⎭	
B.C.A.	35·4	—	1·03	0·52 ⎫	3·7
J.M.R.	35·4	—	1·06	0·56 ⎭	
B.C.A.	52·0	—	1·71	0·61 ⎫	5·2
J.M.R.	52·0	—	2·14	0·69 ⎭	

0·69 l. O_2/min by *B* doing positive work and 0·19 l. O_2/min by *A* resisting. Thus at this speed the positive work cost, in oxygen, 3·7 times as much as
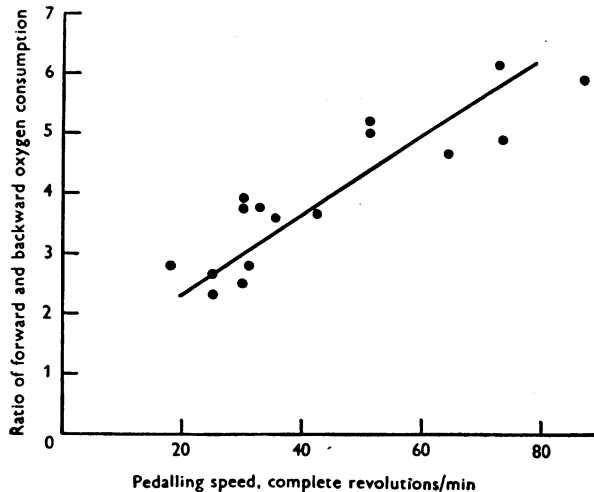

Fig. 2. The ratio of oxygen consumption in forward pedalling to oxygen consumption in resisting, for equal amounts of positive and negative work, plotted against frequency of pedalling. The oxygen consumptions are in excess of the resting value.

did an equal amount of negative work. This figure is the ratio of the sums of the oxygen usages for positive and negative work respectively.

The ratio varied with speed: it fell to 2·4 at 25·0 rev/min and rose to 5·2 at 52 rev/min. In Fig. 2 the ratios obtained from all experiments are plotted against speed of pedalling. Although there is considerable scatter in the

points there is no doubt about the main trend: the relative cost of negative work decreases as speed increases.

The gauge in front of each subject gave an indication of the mean force exerted. This force was maintained constant during each experiment so that, the speed of pedalling being known, the rate of doing work could be calculated. In Fig. 3 the rate of oxygen consumption for one subject B.C.A. is plotted against rate of working for both positive and negative work. The rate of oxygen uptake increases with work for positive working, but, as can be seen from the figure, there is little change with negative work: from 150 to
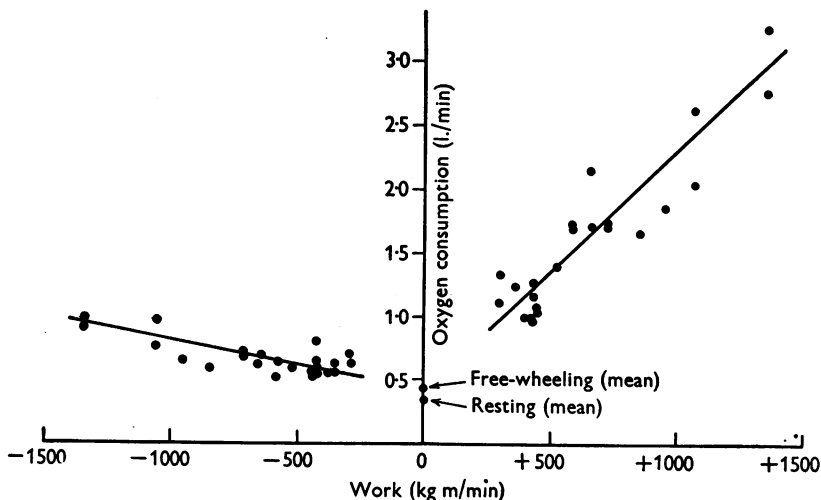

Fig. 3. Variation in the rate of oxygen consumption with the rate of work in pedalling for both positive and negative work.

1300 kg m/min of negative work the rate of oxygen consumption hardly changes. In these experiments the rate of working was varied mainly by changes in speed. Some changes in force were unavoidable, however, and a further more detailed study of this small variation in oxygen consumption with speed, at constant force, is desirable.

Because oxygen consumption rather than oxygen requirement was measured, the results depend on the existence of a steady state at the time of collection. The total ventilation rate of one subject, B.C.A., for positive work in the whole series of experiments is plotted in Fig. 4 against his oxygen consumption. The smoothness of the curve is an indication that the subject was in nearly the same condition from day to day, and from its linearity it might be expected that before and during the collection period a steady state had been reached; for, if an O_2 debt were accruing, the points at high ventilation rate would lie above the line.

In one experiment, at a high pedalling speed and high rate of working, the

oxygen debt was determined approximately. After the usual experimental procedure a further collection of expired air was taken for a period of 10 min after cessation of the exercise. Although the oxygen consumption was high, about 2·5 l./min in positive working, the oxygen debt was small, about 2 l. in 10 min of exercise. This oxygen debt probably accrued during the first few minutes, but it would be too small to have much effect on the results even if spread over the whole period.
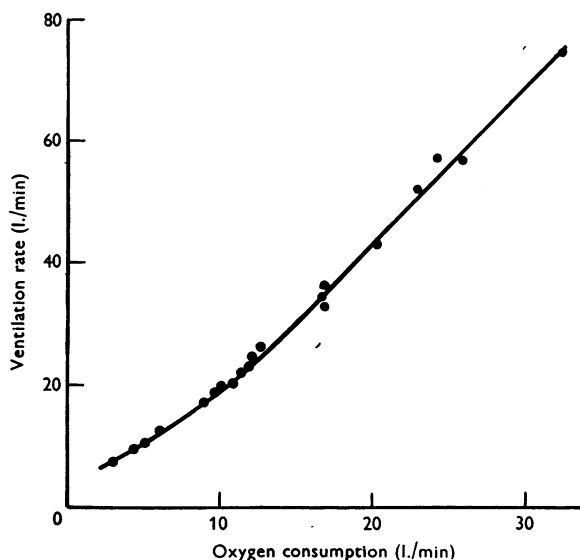

Fig. 4. Ventilation rate plotted against total rate of oxygen consumption of one subject (B.C.A.) obtained from all experiments when he was doing positive work.

DISCUSSION

It is clear to the cyclist that he exerts more effort when pedalling forward than when resisting, and this is confirmed by the difference in oxygen consumption. The difference can be explained with the help of Fig. 5: the solid line is the force-velocity curve for human arm muscles during shortening as obtained by Wilkie (1950) on one of the subjects of the present experiments (J.M.R.). The force-velocity line can be extrapolated backwards with a discontinuity of slope as shown diagrammatically in Fig. 5 (cf. Katz's (1939) experiments with maximally stimulated frog muscle). The faster a muscle shortens the less force it can exert: in imposed lengthening, however, the force exerted by the muscle increases with the speed up to a certain limit. Consider a single fibre shortening with velocity v_1: it exerts a force P_1. A similar fibre being stretched at velocity v_1 resists with a larger force f_1. The total force exerted by a muscle is determined by the product of the force in a single fibre and the number of

fibres active. In our experiments both subjects exerted the same force, and the forward cyclist must have had f_1/P_1 times as many fibres in action as the resisting cyclist, provided that the frequency of excitation was the same in both cases. This difference in the number of fibres used for the two motions must necessarily be reflected in the oxygen consumption, and the ratio of these consumptions has been taken as an index of the fibre activity.

It can be seen from Fig. 4 that at a higher speed v_2, the ratio f/P will also have risen since f is increased and P is diminished—and the ratio of the oxygen consumptions will be correspondingly greater. The conformity of our results
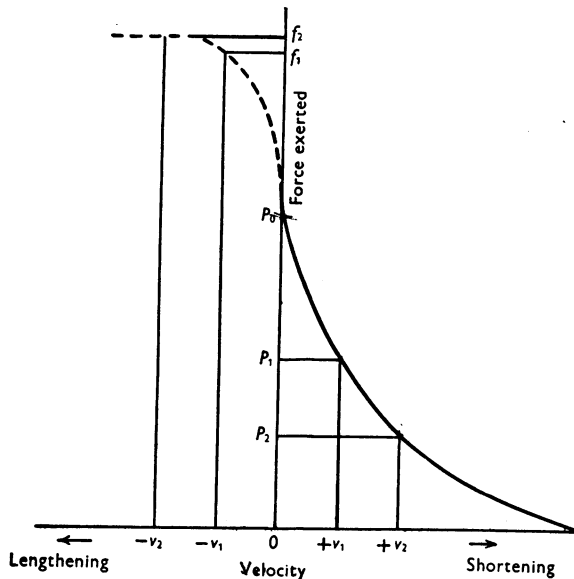

Fig. 5. A diagram of the relationship between force and velocity of shortening for human muscle: P_1 and P_2 are the forces exerted by a single fibre shortening at velocities v_1 and v_2; f_1 and f_2 are the forces when the fibre is being stretched at the same velocities v_1 and v_2; P_0 represents the isometric tension of that fibre.

with the theoretical conceptions is evident from inspection of Fig. 2. Although at zero speed a ratio of unity must occur, it was not possible to approach this experimentally; at very low speeds the motion could not be made uniform because of dead-points when the cranks were vertical.

We have considered so far, for simplicity, the case in which all the muscle fibres involved are excited at the same frequency, giving a more or less complete tetanus; even at frequencies where the individual fibre responses are unfused, the total response can be smooth if groups of fibres are stimulated out of phase from each other. Oxygen consumption will then be proportional to the number of active fibres and can be used as a measure of the muscular effort. In the living animal, however, a tension below the maximum is

characterized by the asynchronous excitation of many motor units at frequencies below that for a completely fused tetanus and is varied by altering the frequency of excitation as well as the number of motor units employed (Creed, Denny-Brown, Eccles, Liddell & Sherrington, 1932). The oxygen consumption of the muscle increases with tension exerted, but not necessarily in a simple manner. Bronk (1930) measured the economy of isolated muscles at different frequencies of stimulation, defining economy as the ratio between the area under the tension-time curve and the total heat liberated during a contraction. Since total heat production is related to oxygen consumption and provides the most accurate available method for measuring that consumption, Bronk's results enable us to correlate tension exerted with oxygen consumed. At stimulus frequencies below that for a completely fused tetanus and extending into the range where the responses of the muscle are discrete with no sign of summation, the economy of contraction increases with frequency. Thus, in any fibre, the heat liberated and hence the oxygen consumed in maintaining the contraction increases less rapidly with frequency of stimulation than does the mean tension exerted.

Therefore, for the cyclist pedalling at constant speed in the conventional forward direction, oxygen consumption increases with rate of working as more fibres are recruited, but not in a simple manner since the economy of the fibres also increases. When the speed of pedalling is raised, further recruitment and a higher oxygen consumption will occur. A measure of the subject's effort and of the activity of his muscles (when well below maximal) is thus supplied by the rate of oxygen consumption, although the correlation is not as direct as our first simplified example would suggest.

The cyclist resisting the movement had stretches imposed on his muscles. An active muscle resists stretch with a tension greater than the isometric value under the same conditions of excitation: the area under the tension-time curve is increased by imposed lengthening both for fused and for unfused tetani (Abbott, unpublished). The cyclist therefore can resist with a force equal to that exerted by the 'forward cyclist' (whose muscles are shortening) with less fibres and/or with a lower frequency of excitation of the fibres. One other factor helps to reduce the effort when resisting. The forces used during these experiments were well below maximal, and most of the responses of the motor units were probably unfused. Each imposed stretch would extend over many twitches of the active units and so would overlap both active and relaxation phases. Some of the work done during the rising phase of a twitch may be absorbed (Abbott *et al.* 1951) by the contractile mechanism so diminishing the oxygen consumption, but all the work done during relaxation would be degraded into heat and cannot be expected to influence the oxygen consumption. Over the range of speeds used the oxygen consumption needed for resisting did not vary much with speed (Fig. 3).

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In all experiments in which oxygen usage is related to exercise the oxygen in excess of some reference level is required. We have used as our baseline the oxygen consumption of a subject when seated at rest on the bicycle. During a bout of pedalling some extra energy is used in placing the limbs and maintaining balance. For our purpose the magnitude of this effect was small, as seen from one experiment in which the pedalling forces were kept small enough to involve negligible work. The oxygen consumption of both subjects, whether free-wheeling backwards or forwards, increased above the resting value of 0·35 l. O_2/min by only about 0·1 l./min. when the pedals revolved at 33 rev./min. Taking a higher baseline would only serve to increase the ratio of forward to backward oxygen consumption.

The physiological cost of negative work is considerably less than that of positive work, and the difference increases with speed of movement. For the investigation of this cost, other types of exercise could have been used, such as climbing up and down a rope; in descending, fewer fibres would be required to bear the subject's weight than during ascent—or a lower frequency of motor-neurone discharge. It is important, however, to employ muscle movements which are truly comparable in the two directions, 'mirror images' both in placing the limbs concerned and in the time sequence of activity. The obvious example of walking up and down stairs fails to satisfy this criterion, for the procedures are quite dissimilar. In going downstairs, the muscles are tensed only towards the end of each step, and provide a controlled deceleration. The only permissible mode of descent in such experiments would be to walk backwards down the stairs (not an easy habit to acquire) when all the leg movements would correspond to those in ascent. In the experiments of Chauveau (1901) great care was taken to ensure this symmetry of movement, but the recent ones by Orsini & Passmore (1951) ignore the requirement.

It is known from work on isolated muscles (Abbott et al. 1951) that when an active muscle is stretched some of the work done on it disappears. Since this work does not reappear either as heat or as mechanical energy, it might have been used to stop or reverse some chemical process normally providing energy in the muscle. This, in turn, might reduce the oxygen required by the system to maintain the muscle activity. We originally expected that this might provide an appreciable contribution to the decreased cost of negative work, but the observed decrease proved to be much too large for this contribution to be the chief factor. The work absorbed by a muscle cannot be expressed directly in terms of an equivalent decrease in oxygen consumption, as Orsini & Passmore (1951) apparently suggest. They seem to have assumed implicitly that in walking downstairs the oxygen is required merely to maintain posture during the movements, and is decreased by the oxygen equivalent of the work done on the subject by gravity. Such an assumption has no experimental justification.

APPENDIX

The results of these experiments could have been discussed in terms of muscle viscosity, to which much attention has been given in the past. But simple viscosity within a muscle would be expected to result in a linear relationship between force exerted and velocity of shortening. This is not found experimentally as can be seen from Fig. 5 and has been discussed by Fenn & Marsh (1935). Hill's characteristic equation (1938), however, does satisfy the experimental findings and permits analysis of the mechanical properties of muscle without resort to physical models that have no real significance. Some complex form of viscosity could be postulated, but until more is known of the mechanism involved in muscular contraction it would seem more convenient to regard the force-velocity curve as simply one of the properties of muscle.

Simple viscosity does enter into the pedalling movements: bending the various limb joints as well as movements of the skin over the muscles and even relative displacements of the fibres within the muscles introduce viscous resistances. These would all tend to increase the task of the forward cyclist and reduce that of the resisting cyclist. But this contribution is small as can be seen at once from the slight difference in oxygen consumption between rest and free-wheeling shown in Fig. 3.

SUMMARY

1. The physiological cost of negative work has been studied using a pair of subjects on two bicycle ergometers coupled in opposition. The oxygen consumption for positive work was compared with that for the same negative work, the leg muscles exerting the same forces, in similar movements at the same speed.

2. Positive work always costs more than negative work. At a pedalling speed of 35 rev/min the ratio of oxygen consumptions for the two tasks was 3·7. This ratio increased with speed of pedalling.

3. The results are discussed in terms of the characteristic relationship between force and velocity for muscle.

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