THE INFLUENCE OF STATIC EFFORT ON THE RESPIRATION AND ON THE RESPIRATORY EXCHANGE.

By T. BEDFORD, H. M. VERNON and C. G. WARNER.
Investigators of the Industrial Health Research Board.

(With 9 Figures in the Text.)

CONTENTS.

I. INTRODUCTION.

MUSCULAR exertion is conveniently considered to be one of two types, dynamic effort in which there is movement, and static effort in which no movement takes place. In any dynamic effort work is done, and this work is accounted positive or negative according as it is done by or against the body; thus, one does positive work in lifting a weight, and negative work in lowering it.

Purely static effort consists in maintaining tension isometrically, *e.g.* in holding a weight; in such effort, although force is exerted in balancing the body and supporting the load, no external work is performed. This type of muscular activity is commonly referred to in the literature as "static work," but it would seem preferable to use the term "static effort." Any dynamic effort necessarily contains a static component, for, since the movement cannot be made instantaneously, the load must be sustained during the time taken by the action.

The exertion of muscular force is accompanied by expenditure of energy (as will be seen later) whether external work is performed or not. From this it would be expected that the mechanical efficiency of a dynamic effort would decrease with diminishing speed of performance. This is true below a certain speed; at greater speeds the efficiency again decreases owing to the effect of the viscosity of the muscles. The optimum contraction time appears to be about 1 sec. Lupton (1923) found an optimum time of 1·3 sec. for mounting stairs; for crank turning and walking Atzler (1927) gives values of 0·7 sec.; and for pedalling a bicycle Garry and Wishart (1931) give the optimum time as not more than 0·6 sec. At all speeds slower than the optimum the static factor operates, and this fact largely accounts for the low efficiency with which some tasks are performed. Thus, Atzler (1927, p. 183) quotes an efficiency of 8·4 per cent. for weight lifting, while Furusawa, Hill and Parkinson (1927) calculated efficiencies of from 35·0 to 41·1 per cent. for sprint running.

Apart from the question of mechanical efficiency, there is general agreement that static effort is associated with marked fatigue, and involves severe strain. Indeed, Cathcart (1923) has said that it is the static component of the muscular effort which determines *qua* the organism as a whole whether work is severe or not.

Static effort enters very largely into many industrial operations, and an acquaintance with the phenomena accompanying such effort is essential for the full understanding of the effects of many types of work. The present paper describes the results of an investigation of some of these phenomena, and includes a brief summary of the conclusions reached by previous workers.

II. THE ENERGY COST OF STATIC EFFORT.

(1) *Previous work.*

(*a*) *On laboratory animals and on isolated muscle.*

Roaf (1912), working with decerebrate cats, did not find that the abolition of decerebrate rigidity caused any significant reduction in the carbon dioxide output, but he found, later, that in decerebrate rigidity the oxygen intake was slightly (1·2 per cent.) higher than when the muscles were flaccid (Roaf, 1913). Later, Dusser de Barenne and Burger (1924), also using decerebrate cats, found that with these preparations the metabolism in postural contraction was distinctly higher than the resting value, but was much less than the metabolism during rhythmic movements.

Weatherhead (1932) studied the metabolism of prolonged postural contractions of the quadriceps in anaesthetised cats. The oxygen consumption during the period of postural activity was usually about 30 per cent. above the resting value, although in some experiments the cost of maintaining the posture was hardly distinguishable from the resting value. During prolonged postural contractions (2–3 hours) the metabolism showed a slight diminution, but this was possibly due to the general slight fall in metabolism which occurred in 3–4 hour experiments. The metabolism returned to its resting value directly the postural stimulus was stopped. Whereas in the experiments of Dusser de Barenne and Burger the cost of rhythmic movements was much higher than that of postural contractions, Weatherhead found that regular rhythmic movements could be carried out at low metabolic cost, sometimes indistinguishable from the cost of postural contraction.

These results are in agreement in showing that the setting up of the tension necessary for the maintenance of a posture results in the expenditure of energy, even though no external work is done.

For maximal isometric contractions of an isolated frog's muscle, the heat production is accurately described by the well-known equation of Hartree and Hill (1921):

$$H = Tl\,(A + Bt),$$

where H = heat produced in a contraction,
t = duration of contraction,
T = tension developed,
l = length of muscle, and
A and B are constants.

Thus, with tension constant, the energy cost varies directly as the duration of contraction, and with constant time of contraction the cost varies directly as the load.

(*b*) *On man.*

In man, also, any form of static effort is accompanied by increased metabolism. The cost of postural activity may be illustrated by the data of Douglas and Haldane (1912), who found that the oxygen consumption when standing was 38 per cent. greater than that when at rest in bed.

One of the earliest papers on the metabolic cost of static effort appears to be that of Chauveau and Tissot (1896), who maintained loads with the flexed forearm for a period of 2 min. They concluded that with a constant load the excess metabolism due to the effort is proportional to the degree of shortening of the contracting muscles; and with a varying load and a constant degree of contraction the metabolism is proportional to the load. Their results, however, showed considerable variability, and, indeed, they have been interpreted by Bornstein and Poher (1903) and, later, by Atzler (1928) as showing that the metabolism increases, not in proportion to the load, but more rapidly.

Johansson (1901) used the arm muscles for supporting a weight of 10–30 kg., making contractions for periods of 1, 2 or 40 sec. He reached the conclusion that in static effort the carbon dioxide output grows proportionally with the load and with the total time of contraction. He also concluded that the carbon dioxide output increases with the number of contractions; that is to say, the setting up of a muscular tension involves energy expenditure, apart from the cost of maintaining the tension.

As the result of further work, Johansson and Koraen (1902) found that in such static effort the carbon dioxide cost grows, up to a known limit, proportionally with the duration, and then ever more quickly. This limiting value of the duration of contraction coincides with the beginning of fatigue, and is reached earlier as the load increases. These workers confirmed the conclusion of Chauveau and Tissot that the carbon dioxide output increases with greater degree of shortening of the contracting muscles.

In a later paper dealing with dynamic work, Johansson and Koraen (1903) expressed the relation between carbon dioxide output and external work as an equation

$$S = w + vA,$$

where S = carbon dioxide output,
v = carbon dioxide per unit of external work,
A = external work, and
w = "no load" value.

This is known as "Johansson's law" and has been widely used, particularly by German writers (S and v now being expressed in terms of oxygen or calories). Atzler (1928) says that this law holds also for static effort, *i.e.* that the total energy consumption increases proportionally to the increase in the load, and that he and his colleagues have often substantiated it. Atzler mentions, however, that the rule holds only until fresh muscles are brought into play with increasing load.

Frumerie (1913) says that the carbon dioxide output (up to 60 sec. at least) is directly proportional to the length of the contraction time.

Different conclusions were arrived at by Bornstein and Poher (1903), who supported a weight by the outstretched arm while in a lying position. They found that the metabolism increased neither proportionally with the load nor the time, but in both cases more rapidly. They explained the difference between their results and those of Johansson (1901) by saying that he included the cost of the initial tension in his metabolic costs, while they claim to have eliminated this error by making movements of the arms, similar to those required in taking up the weight and effecting the tension, during the rest experiments. Thus they claimed that their results gave only the cost of maintaining the contractions, whereas Johansson's data confused the cost of the initial contractions with that of maintenance; in short contractions of only 1 or 2 sec. the cost of the initial contraction was said to overweigh the cost of maintenance. This criticism of Johansson's work appears to be invalid, for if from his data relating to a load of 20 kg. the carbon dioxide output per contraction be calculated and plotted against the duration of the contraction, it will be found that the points fall on a straight line. Extended to cut the ordinate for zero duration, this line gives the carbon dioxide cost of the initial tension. The method used by Bornstein and Poher for correcting for the initial tension could at best give only an approximation.

Passauer (1925) found that in prolonged static effort the energy consumption increased in the latter half of the working period.

The equation of Hartree and Hill describing the energy liberated in isometric contractions of frogs' muscle dealt with maximal contractions. Lupton (1923) argued that for contractions in which a constant sub-maximal number of fibres was stimulated to a maximal degree the equation

$$Q = a + bt$$

would hold, and he determined the constants a and b for the flexors of the elbow in man, taking care to ensure that the contractions were limited to certain groups of muscles.

Müller (1930), also using the arm muscles, found that the cost per second of maintaining a given tension was the same, whether the contraction lasted 7 or 14 sec. Below a certain speed of contraction there was a constant energy consumption for the setting up of a given tension, but if the speed exceeded this limiting value there was a marked increase in the energy cost of the contraction. The optimal contraction time was found to be proportional to the tension set up.

Atzler (1928), referring to observations on the oxygen cost of holding weights with the outstretched arms, concluded that weights due to parts of the body itself are carried more efficiently than weights of objects foreign to the body. He suggested that this is due to the existence of some special form of tonic contraction.

In connection with this theory, Lehmann (1927) studied the cost of supporting weights by the outstretched leg. The weights were so arranged that the leg was subjected to a vertical pull in an upward or a downward direction, the downward pull being reckoned as positive, and the upward as negative. It would be expected that with a certain upward pull the weight of the leg would be exactly counterbalanced, so that the excess energy consumption over the resting value would be zero, and that as the load diverged from this value the energy consumption would increase. Lehmann's curves, which we have re-drawn (Fig. 1), cut the abscissa in two points, at loads of – 3·25 kg. and – 7·45 kg. That is to say, if the leg is balanced by the mean of these upward pulls (5·35 kg.), a load of 2·1 kg. can be supported without extra energy cost. Lehmann assumes the existence of a special contraction mechanism which accounts for this, and calculates from his data that striated muscle can hold a weight of 0·48 kg. per sq. cm. of cross-section without excess energy consumption.

Although the curves drawn by Lehmann suggest that the excess energy cost for loads of $-3{\cdot}25$ kg. to $-7{\cdot}45$ kg. is zero, only one of his observations gives a zero value—that for a load of $-3{\cdot}61$ kg. For the other loads in Lehmann's zero range there was an energy consumption of at least 115 cal. per min. Wachholder (1928) has criticised Lehmann's conclusion, and maintains that the minimal load is borne, not by a special form of tonic contraction, but by a stiffening of the limb. Atzler (1928), replying to Wachholder, admits that there was some stiffening, but maintains that the crux of the investigation is whether the two straight lines cut the abscissa in one or two points.

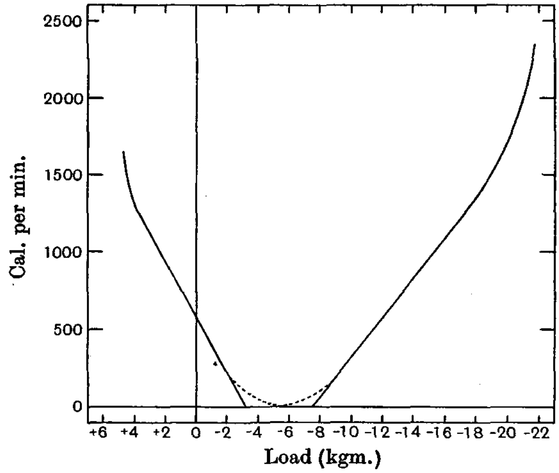

Fig. 1. Energy cost of supporting load with outstretched leg. (After Lehmann (1927).)

(2) *The present observations.*

(*a*) *Introductory.*

The work of other investigators leads to the conclusion that the energy cost of maintaining a given tension varies directly as the duration of the contraction, provided no new muscles are brought into play as the result of fatigue or local strain.

In isolated muscle the cost also varies directly as the tension, but in man the relation of metabolic cost to variation in load is not so clear. Some workers find that the cost varies directly as the load, but others give results which show that as the load increases the cost rises more rapidly.

It has been mentioned that Lupton (1923) and Müller (1930) found that the oxygen cost of maintaining contractions of the arm muscle varied directly as the duration of the contraction. In determining the time coefficient of his equation, Lupton caused his subject to maintain the contraction for a fore-period of $2\frac{1}{2}$ min. before the collection of the gases began. Hence, if in the first $2\frac{1}{2}$ min. of contraction there was any change in the time coefficient it could not be discovered by his method.

The present section describes experiments undertaken to ascertain the rate of variation of oxygen consumption with respect to tension and duration of effort.

(*b*) *Apparatus and method.*

The spring balance dynamometer which was used in these experiments has already been described by Vernon (1922 and 1924). The balance is fixed to a frame lying on the floor, and the handle is connected to the spring by means of a length of bicycle chain passing over a pulley. The subject stands practically erect in front of the dynamometer and holds the handle with both hands. In pulling against this spring the contractions are virtually isometric, as the hands only move through about 6 mm. in pulling from 0 to 100 lb.

In each experiment the subject lay down quietly for half an hour, and then stood still in the working position for 20 min., his expired air being collected during the last 5 min. of this period. He then started pulling at the dynamometer, the contractions being timed by the ticking of a metronome. Each contraction was followed by a rest of at least equal duration, and the frequency of pulling was so arranged that a steady state was reached after about 5 min. of work. After work had proceeded for 10 min. the expired air was collected for two consecutive 5-min. periods. The analyses were done in duplicate and the mean of the two results taken, and the oxygen consumption during the period of effort was taken as the mean of the results obtained from the two 5-min. collections. The oxygen cost per minute of the working period was reckoned as the excess above the cost of "standing resting," and from this the oxygen cost per contraction was ascertained.

The results to be described were all obtained on the same subject. Half the experiments were carried out in the forenoon, and half in the afternoon, so as to equalise any fatigue effects. Throughout the experiments, particular care was taken to ensure that a standard posture was maintained.

(*c*) *Oxygen consumption in relation to duration of contraction.*

The first series of 47 experiments was made with a constant tension of 100 lb., the duration of contraction varying from ½ to 30 sec. The mean oxygen cost for each duration of pull is shown in Fig. 2 (middle curve), and a regression line has been fitted by the method of least squares. It is quite clear that there is a linear relation between time and oxygen cost. The equation to the regression line is

$$Q = 6{\cdot}13 + 5{\cdot}78t \qquad \text{......(i)},$$

where Q = excess oxygen consumption per contraction in c.c.; and
t = duration of contraction in seconds.

The constant, 6·13, represents the cost of effecting the contraction. The results of the individual experiments, which are given in Table I, have been compared with the appropriate values calculated from equation (i). The root-mean-square deviation of the observed from the calculated values is 11·0 per

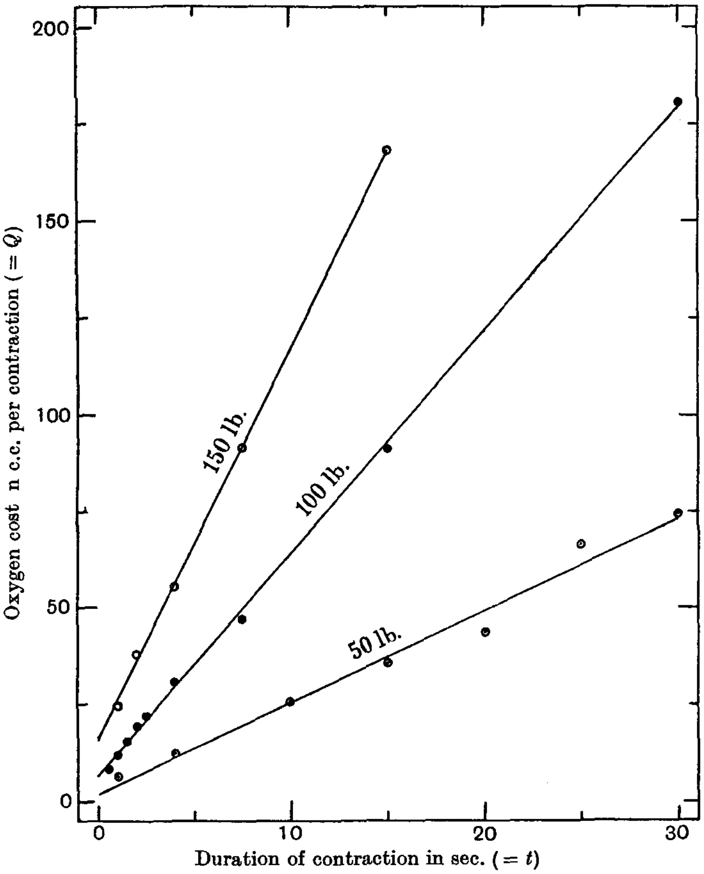

Fig. 2. Oxygen cost in relation to duration of contraction, with tensions of 50 lb., 100 lb. and 150 lb.

Table I. *Oxygen cost per contraction, tension constant at 100 lb.; time varying.*

Duration of contraction (sec.)	No. of exps.	Excess oxygen cost per contraction, in c.c.	
½	9	7·0, 8·3, 8·0, 8·8, 7·5, 8·3, 9·0, 8·7, 6·7	= 8·0
1	8	11·5, 11·3, 9·9, 11·6, 12·9, 11·8, 12·2, 12·2	= 11·7
1½	5	10·8, 18·8, 15·7, 15·0, 16·3	= 15·3
2	4	18·6, 19·9, 18·9, 18·5	= 19·0
2½	5	21·0, 24·0, 19·3, 23·8, 22·8	= 22·2
4	4	28·6, 31·0, 30·6, 31·2	= 30·4
7½	4	53·8, 41·0, 47·5, 47·0	= 47·3
15	4	94·5, 82·0, 89·5, 101·0	= 91·8
30	4	172·0, 194·0, 168·0, 187·4	= 180·4

cent. of the mean calculated value. This degree of variability is very similar to that recorded by Greenwood and Newbold (1923) in their analysis of the data of Benedict and Cathcart (1913). The partial coefficient of variation of oxygen consumption of the trained subject M.A.M. at constant rate of working was 12·2 per cent., and with both rate of working and speed constant the variability was still 8·8 per cent.

Further series of observations with varying contraction times were made with tensions of 150 lb. and 50 lb. The results of these experiments are given in Tables II and III, and the mean values are plotted in Fig. 2. In these series also the relation between oxygen consumption and duration of contraction is a linear one. The equations to the regression lines which have been fitted to the observations are, for the 150 lb. series (12 experiments),

Table II. *Oxygen cost per contraction, tension constant at 50 lb.; time varying.*

Duration of contraction (sec.)	No. of exps.	Excess oxygen cost per contraction, in c.c.
1	2	6·8, 6·0 = 6·4
4	4	15·1, 12·4, 11·1, 9·7 = 12·1
10	3	27·7, 25·5, 24·7 = 26·0
15	4	43·7, 30·8, 33·4, 34·5 = 35·6
20	3	39·8, 46·8, 44·3 = 43·6
25	2	61·3, 72·1 = 66·7
30	3	68·5, 79·5, 76·5 = 74·8

Table III. *Oxygen cost per contraction, tension constant at 150 lb.; time varying.*

Duration of contraction (sec.)	No. of exps.	Excess oxygen cost per contraction, in c.c.
1	3	24·4, 25·3, 23·9 = 24·5
2	2	35·3, 40·2 = 37·8
4	2	57·4, 53·8 = 55·6
7½	2	92·3, 91·3 = 91·8
15	3	178·0, 171·6, 155·5 = 168·4

$$Q = 15{\cdot}35 + 10{\cdot}20t \qquad \text{......(ii)},$$

and for the 50 lb. series (21 experiments)

$$Q = 1{\cdot}83 + 2{\cdot}375t \qquad \text{......(iii)}.$$

The variability of the observed values of Q from the calculated values is 7·2 per cent. for the 150 lb. series, and 12·7 per cent. for the 50 lb. series. With the smaller tensions it was found to be more difficult to hit off the exact strength of pull required, and this probably accounts for the greater variability in the lower tension series.

(*d*) *Oxygen consumption in relation to tension.*

Inspection of the coefficients in equations (i) to (iii) is sufficient to show that the energy expenditure increased more rapidly than the tension, and it was thought desirable that further determinations of the oxygen consumption should be made, keeping the duration of contraction constant and varying the tension. Three series of such determinations were made, with contractions lasting 1, 4 and 15 sec. The individual results are set out in Tables IV–VI, and the mean values are plotted in Fig. 3.

Table IV. *Oxygen cost per contraction, time constant at 1 sec.; varying tension.*

Tension in lb.	No. of exps.	Excess oxygen cost per contraction, in c.c.	
50	2	6·8, 6·0	= 6·4
75	2	9·9, 7·6	= 8·8
100	8	12·9, 11·8, 12·2, 12·2, 11·5, 11·3, 9·9, 11·6	= 11·7
125	2	16·4, 16·9	= 16·7
150	3	24·4, 25·3, 23·9	= 24·5
165	2	35·8, 30·3	= 33·1

Table V. *Oxygen cost per contraction, time constant at 4 sec.; varying tension.*

Tension in lb.	No. of exps.	Excess oxygen cost per contraction, in c.c.	
30	2	6·2, 8·8	= 7·5
50	4	15·1, 12·4, 11·1, 9·7	= 12·1
75	2	22·2, 20·6	= 21·4
100	4	28·6, 31·0, 30·6, 31·2	= 30·4
125	2	40·5, 45·8	= 43·2
150	2	57·4, 53·8	= 55·6
165	2	61·5, 68·8	= 65·2

Table VI. *Oxygen cost per contraction, time constant at 15 sec.; varying tension.*

Tension in lb.	No. of exps.	Excess oxygen cost per contraction, in c.c.	
50	4	43·7, 30·8, 33·4, 34·5	= 35·6
100	4	94·5, 82·0, 89·5, 101·0	= 91·8
150	3	178·0, 171·6, 155·5	= 168·4
165	3	223·4, 167·0, 217·0	= 202·5

In each of the three series of observations the oxygen cost per contraction increased more rapidly than the tension (T), the equations to the curves, fitted by least squares being, for the 1-sec. series (19 experiments)

$$Q = 0{\cdot}02456T^{1{\cdot}364} \qquad \text{......(iv),}$$

for the 4-sec. series (18 experiments)

$$Q = 0{\cdot}0755T^{1{\cdot}309} \qquad \text{......(v),}$$

and for the 15-sec. series (14 experiments)

$$Q = 0{\cdot}1240T^{1{\cdot}441} \qquad \text{......(vi).}$$

The root-mean-square variation of the observed values of Q from the calculated values in the 1-sec. series was 18·8 per cent., in the 4-sec. series 9·2 per cent., and in the 15-sec. series 12·1 per cent. The higher variability of the 1-sec. values is probably due to the proportionately greater influence of small errors in timing.

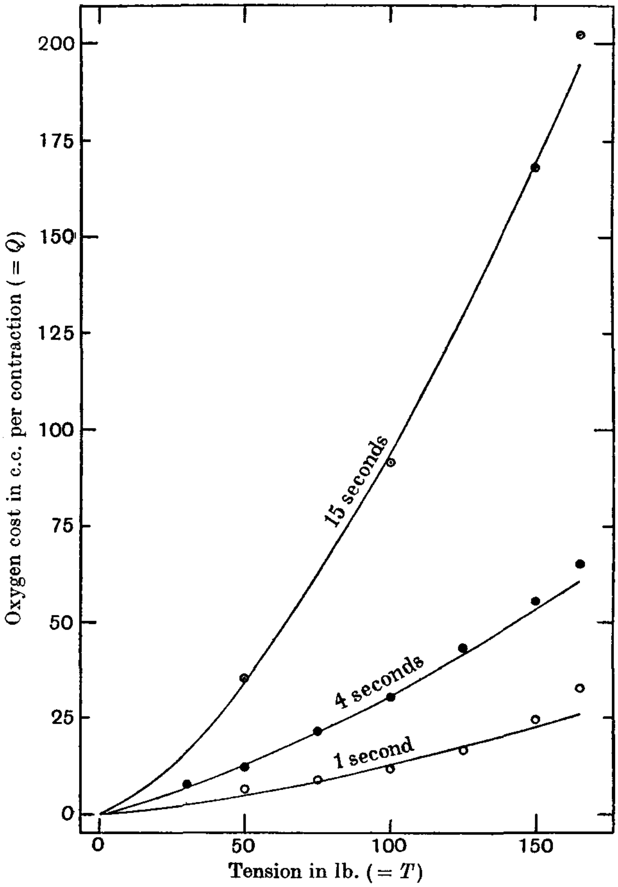

Fig. 3. Oxygen cost in relation to tension, with contractions of 1 sec., 4 sec. and 15 sec. duration.

(*e*) *Discussion.*

Consideration of the indices of T in equations (iv) to (vi), and of their standard errors, shows that there is no significant difference between the indices; for further examination of our data, therefore, we have taken the mean value of these (1·37) as the index of T. Using this power of T, the whole of our 97 observations can be fitted by the equation

$$Q = T^{1\cdot 37}\,(0\cdot 0117 + 0\cdot 0109t) \qquad \ldots\ldots\text{(vii)},$$

the variability of the observed values of Q from the calculated values being 14·7 per cent. On the assumption that the relation between energy cost and tension is linear, the best-fitting equation is

$$Q = T\,(0\cdot 0886 + 0\cdot 0525t) \qquad \ldots\ldots\text{(viii)}.$$

The variation in this case is 34·1 per cent., or nearly $2\frac{1}{2}$ times as great as with the equation using $T^{1\cdot 37}$, so that the relation between Q and T clearly is not linear over the whole range.

Lehmann's (1927) diagram (Fig. 1) is based on the assumption that up to a limiting value the relation between energy cost and load is linear, and that beyond this value the cost increases more rapidly than the load. This assumption is accepted by Atzler (1928). In order to see if our data agree with such a hypothesis, we have taken the results of the 74 experiments in which the tension did not exceed 100 lb. (which was not an excessive load for contractions of short duration), and have calculated an equation assuming a linear relation between Q and T. Using this equation, (ix),

$$Q = T\,(0{\cdot}0607 + 0{\cdot}0511t) \qquad \text{......(ix),}$$

we find that the variability of the observed oxygen cost per contraction from the calculated values was 21·0 per cent., as compared with a variability of 12·5 per cent. of the same data from the values given by equation (vii).

We therefore conclude that, even with comparatively light loads, a linear relation between oxygen cost and tension does not hold.

That equation (vii) gives a good fit over the whole range of our observations is shown by comparing the variability of the observed values of the different series (*a*) from the values given by the appropriate equations to those series, and (*b*) from the values given by equation (vii).

Table VII. *Variability of observed values of oxygen cost from calculated values.*

Series	Percentage variation of observed values of Q from values calculated from	
	(*a*) Equation to series	(*b*) Equation (vii)
150 lb. tension; varying time	7·2	7·6
100 lb. ,, ,,	11·0	12·0
50 lb. ,, ,,	12·7	12·8
1 sec. contraction; varying tension	18·8	22·5
4 sec. ,, ,,	9·2	9·7
15 sec. ,, ,,	12·1	12·6

From such a comparison (Table VII) it is clear that the general equation (vii) adequately describes the energy cost per contraction over the whole range of time and tension covered by the experiments. When, as is the case in effort of this type, the contraction is not strictly limited to one small group of muscles, the energy cost varies as a power of the tension greater than unity.

It appears to us that Lehmann's data show a similar relation between tension and energy consumption. It has been mentioned that the excess energy consumption was zero for a load of $-3{\cdot}61$ kg., so we have taken this value as zero load, and have calculated equations of the form

$$H = aT^n,$$

where H = energy consumption, in calories,
T = load, in kg., and
a and n are constants.

For one side of the zero value the equation is

$$H = 11{\cdot}04T^{1{\cdot}825},$$

and for the other

$$H = 90{\cdot}16T^{1{\cdot}375}.$$

In Fig. 4 we have fitted these curves (in broken lines) to Lehmann's data, and have also included Lehmann's curves (in firm lines). It will be noticed that with the lighter loads the energy consumption was still rather high, suggesting undue stiffening of the limb, but the curves based on our equations give a reasonably good fit over the whole range. Similar curves can be calculated taking Lehmann's mean value of $-5{\cdot}35$ kg. as zero, and an equally good fit is obtained. It seems, therefore, that the data agree well with the view that even with lighter loads the energy consumption increases not directly as the tension, but more rapidly. There would appear to be no need *to postulate the existence of a special form of tonic contraction to account for these results.*

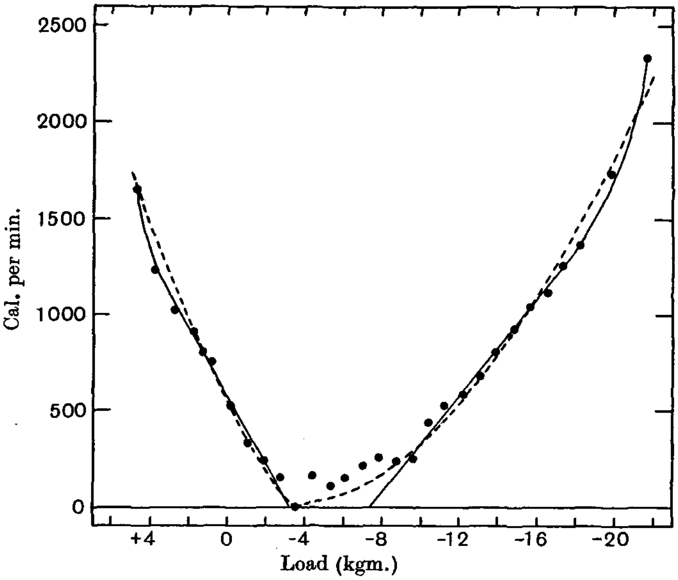

Fig. 4. Energy cost of supporting loads with outstretched leg, showing new curves fitted to Lehmann's data.

III. THE EFFECT OF STATIC EFFORT ON RESPIRATION AND ON THE CIRCULATION.

(1) *Previous work.*

It was shown by Lindhard (1920) that, in the static effort of hanging by the hands from a horizontal bar, the oxygen intake was increased during the effort to a strikingly small extent, while immediately after the end of the effort there was a considerable increase. In one case, where the total energy cost of the effort (which lasted 0·9 min.) was at least 1123 c.c. oxygen, only 168 c.c. were taken in during the period of exertion, and 955 c.c. in the next 6 min. Respirations were most frequent during the effort, but the alveolar ventilation was greatest in the after-period. Six other sorts of gymnastic exercise, in which static effort predominated, were dealt with later, and similar results were obtained. In the exercises in which there was least fixation of the chest the post-work rise of oxygen intake was least marked. In all cases the respiratory quotient increased during work. When the respiration during effort was abdominal the R.Q. increased still more afterwards, but with thoracic breathing the R.Q. fell on the cessation of the effort. The utilisation of oxygen from the blood was less during the effort than when at rest. There was a sharp rise in utilisation immediately after the end of the effort, followed by a fall to sub-normal in 2 or 3 min. Lindhard concluded that the static contraction of muscles causes mechanical hindrance to the circulation and, hence, that static effort is to a great extent anaerobic.

Marschak (1931) confirmed Lindhard's finding, that, in hanging with arms bent, the oxygen consumption is always increased after work. He states that the maximum oxygen consumption occurs, not immediately after the effort, but after an interval of 20 sec. The lactic acid concentration in the blood showed the sharpest rise immediately after the effort, and reached its maximum about 5 min. afterwards.

Dusser de Barenne and Burger (1928) found that, after a "knees bend" posture had been maintained for 3 min., there was a transient but very marked rise in the R.Q. (as high as 1·5). This rise was attributed to the steep decrease in the oxygen consumption immediately after the effort, and the hyperventilation which occurred simultaneously. In rhythmic work (walking at 84 steps per minute) which entailed similar energy expenditure this rise in the R.Q. did not occur.

The effects of holding a load by the outstretched arm were studied by Kektscheew and Braitzewa (1930). Pneumographic records showed considerable chest fixation in static effort. Such effort increased the lung ventilation and the oxygen consumption. It was concluded that the increase in oxygen consumption and ventilation immediately after the cessation of the effort depended on the degree of chest fixation during the effort. The R.Q. increased during the period of exertion and remained high during the first minute of the recovery period, but no rise to 1·5 was observed in the first minute after the effort, as was reported by Dusser de Barenne and Burger.

Cathcart, Bedale and McCallum (1923) investigated the effects of supporting loads with the outstretched arm whilst lying horizontally. There was no reduction in the oxygen consumption during the effort, and, contrary to the results of Lindhard and of Marschak, no marked increase after the effort, and only slight alteration in the R.Q. was noticed. There was generally a definite rise in the pulse and respiration rates and in the blood pressure during the effort; the increase in the diastolic pressure being more marked than the increase in the systolic. These workers attribute the divergence between their results and those of Lindhard to the strong chest fixation which occurs in such forms of effort as beam hanging.

Passauer (1925) found that static effort was accompanied by a rise in the R.Q. In his experiments the oxygen consumption fell to its resting value in 2–5 min. after the end of the effort.

In her work on postural and rhythmic contraction in cats Weatherhead (1932) found that the R.Q. showed a definite rise above the resting value with rhythmic contraction, and a smaller rise with postural contraction. After prolonged postural contraction the metabolism fell to its resting value within 10 min.; this rapid return to the resting value shows that there could have been no considerable accumulation of lactic acid.

Verzár (1912) showed that during a tetanic contraction of the gastrocnemius of a cat the blood flow was noticeably diminished. Other evidence of the lessened circulation in static effort was supplied by Marschak (1930), who studied the effect of static and dynamic effort on the skin temperature; in dynamic effort the skin temperature increased over the working muscles, and decreased over those muscles not participating in the work, while in static effort there was a fall in skin temperature over the contracting muscles. Marschak (1931) concludes that the accumulation of lactic acid in statically contracting muscles is caused by obstructed circulation and the consequent oxygen lack.

Riabuschinsky (1928) measured the lactic acid content of the blood from both arms when one arm was exerting a static effort. He found that after static effort there was an increased amount of lactic acid in the blood of the arm which had been under load, and states that this increase of lactic acid is chiefly conditioned by the appearance of congestion and insufficient oxygen supply; the amount of lactic acid in the resting arm remains practically unaltered. Later, Riabuschinsky (1931) showed that static work of various types causing complete fatigue can be carried out without any increase in the lactic acid content of the blood, and he says that the production of lactic acid in static effort is probably directly dependent on the degree of dynamic work carried out.

Jervell (1932) determined the lactic acid concentration in the blood from a group of arm muscles before and after static effort, with free circulation and with the circulation artificially hindered. The lactic acid concentration with free circulation was greater after static effort than when at rest, but the concentration was considerably greater after static effort with obstructed circulation. Hence it is concluded that in static effort the rise in the lactic acid concentration is not due to restricted circulation alone.

(2) *The present observations.*

(*a*) *The hyper-ventilation in static effort.*

In the foregoing summary it has been shown that at the end of a static effort some workers have observed an increase in the lung ventilation, in the oxygen consumption, and in the R.Q., while other observers have found these measurements to be changed but little as a result of the effort. It has been suggested that the increase in ventilation, oxygen consumption, and R.Q. after the effort depends on the degree of chest fixation which occurs during the effort.

As an index of hyper-ventilation it is necessary to have some other measure than merely the volume of air breathed; an increase in the metabolism due to work would be expected to raise the ventilation, but if the metabolism were raised considerably a proportionate increase in the ventilation could scarcely be called excessive. Simonson (1926) used an index which he named the "Kalorische Ventilationsquotient" (or K.V.Q.); this is the quotient obtained by dividing the volume of air breathed by the calorific value of the oxygen absorbed. It seems to us that this quotient is not suitable for use in experiments of short duration, since the respiratory quotient, from which the calorific value of the oxygen is estimated, is considerably influenced by excessive or under-ventilation. Instead of using calories as the denominator of the quotient we have used oxygen intake, and have calculated the ratio (ventilation volume)/(oxygen intake), both quantities being measured in the same units. Anthony (1930) has used a similar measure (litres of ventilation per 100 c.c. of oxygen) which he calls the "ventilation equivalent for oxygen," and Bock and Dill (1931, p. 56) have also made use of the (ventilation)/(oxygen) ratio.

Analysis of the data of the experiments described in section II (2) showed that at the highest tension (165 lb.) the ventilation per unit oxygen consumption increased with increasing duration of contraction. Taking the excess ventilation and excess oxygen consumption above the resting values, the mean ratio (excess ventilation)/(excess oxygen intake) was 18·0, 25·1 and 36·9 for contractions of 1, 4 and 15 sec. respectively.

For the further examination of this point experiments were made on two subjects. In one series the subjects maintained a steady tension of 100–125 lb. for 2 min.; and in another series they made contractions lasting for ½ sec. at the rate of 40 per min. for 2 min., with tensions of 160–220 lb. in different experiments. The expired gases were collected for each of the 2 min. of work, and for successive periods of 1, 2 and 3 min. during recovery. The "standing resting" metabolism was determined from 5-min. collections made at the beginning and end of each experiment.

The results of the separate experiments were very consistent, and so only the averages are given in Table VIII. These data are shown graphically in Fig. 5. The oxygen consumption was greatest in the second minute of effort, and after the end of the exertion it rapidly fell towards the resting value.

Table VIII. *The effects of intermittent or continuous static effort for* 2 *min.*

					Period of gas collection						
						Effort		Recovery			
	Subject	Type of effort	No. of exps.	Mean tension during effort (lb.)	Standing resting 5 min.	1st min.	2nd min.	1st min.	2–3 min.	4–6 min.	7–11 min.
Oxygen intake in c.c. per min.	W	Intermittent	4	183	359	661	769	570	395	353	334
		Continuous	5	118	330	587	610	476	402	354	332
	V	Intermittent	4	220	305	615	825	609	388	301	295
		Continuous	5	119	306	432	504	474	358	314	299
Ventilation (l.)/ O_2 intake (l.)	W	Intermittent	4	183	25·3	22·9	21·8	22·7	26·6	25·4	27·6
		Continuous	5	118	24·8	25·6	35·0	37·5	32·4	27·1	26·5
	V	Intermittent	4	220	26·9	26·7	24·7	26·5	30·9	29·8	29·4
		Continuous	5	119	28·9	27·5	31·5	33·0	30·6	29·2	28·7
% CO_2 in expired air	W	Intermittent	4	183	3·44	3·69	3·82	3·76	3·59	3·34	3·24
		Continuous	5	118	3·38	3·50	3·06	3·05	3·06	3·06	3·06
	V	Intermittent	4	220	3·18	3·41	3·64	3·57	3·17	3·02	3·02
		Continuous	5	119	3·08	3·30	2·94	3·05	3·10	2·93	3·02
Respiratory quotient	W	Intermittent	4	183	0·860	0·839	0·829	0·852	0·953	0·846	0·892
		Continuous	5	118	0·840	0·958	1·078	1·142	1·017	0·835	0·825
	V	Intermittent	4	220	0·858	0·909	0·898	0·943	0·976	0·901	0·888
		Continuous	5	119	0·888	0·907	0·918	1·003	0·951	0·854	0·864

Note. In this and subsequent tables all gas volumes are quoted dry and at N.T.P.

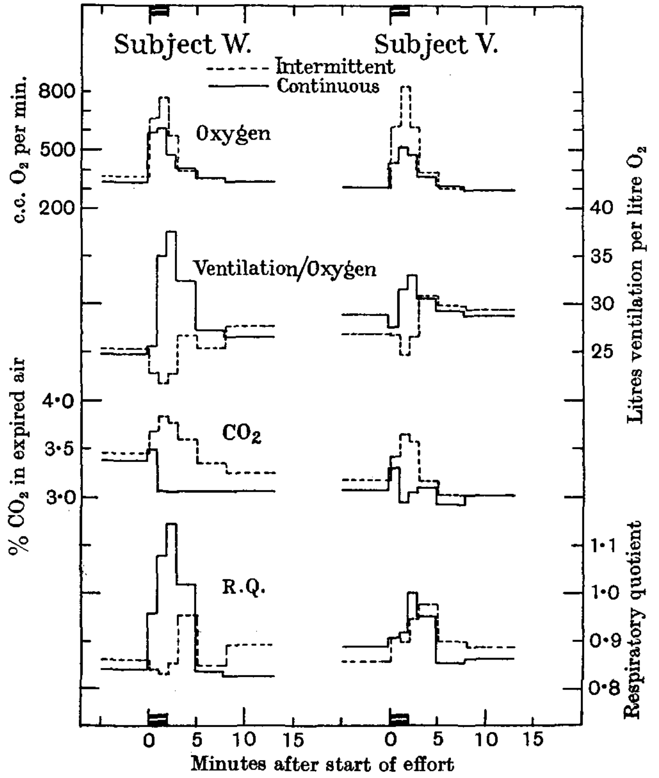

Fig. 5. Comparison of the effects of continuous and intermittent static effort for 2 minutes.

The typical effect of static effort is seen in the diagrams of the ventilation per unit oxygen consumption. The curves for the intermittent pulling experiments show that during the period of effort this ratio diminished, and after the cessation of the effort it rose rapidly to or above the pre-work value. On the other hand, the curves for continuous effort lasting 2 min. show a rise of the ventilation/oxygen ratio above the resting value in the first or second minute of exertion, with a further rise in the first minute of recovery. The influence of this increased ventilation in continuous effort is reflected in the percentage of carbon dioxide in the expired air, and in the R.Q. During intermittent effort, the contractions being only momentary, there was a marked rise in the percentage of carbon dioxide in the air expired during work, followed by a fall during recovery to well below the pre-work value. In continuous effort there was a marked fall in the percentage of carbon dioxide during the second minute of work. The continuous effort had more marked effects on subject W than on subject V.

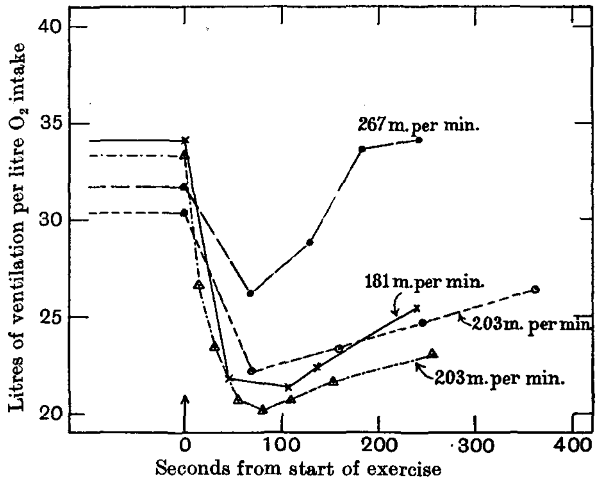

Fig. 6. Litres of ventilation per litre of oxygen intake in running, calculated from data of Hill and Lupton (1923).

The intermittent static effort with which we are concerned here is closely akin to dynamic work, since the contractions were of so short duration. The decrease in the ventilation/oxygen ratio which was found to occur during the intermittent effort is characteristic of dynamic exertion. This can be seen from Fig. 6, which shows the total ventilation per unit oxygen consumption in running, calculated from data given by Hill and Lupton (1923). The ventilation volumes refer to moist air at 37° C. and at the actual atmospheric pressure, and the oxygen volumes are for the dry gas at N.T.P. Since the atmospheric pressures are not recorded, it is not possible to render the two measurements strictly comparable, but for any one experiment the fluctuations are relatively the same. In each of the four curves shown there was a marked diminution in the ratio (that is, an increase in the utilisation of ventilation) immediately after the beginning of exercise. As the exercise was prolonged the ratio increased, but at speeds of 181 and 203 metres per minute the ratio rose to above the pre-work value after about 3 min. This increase in the ventilation/oxygen ratio was probably due to the increasing lactic acid concentration.

Although in the foregoing experiments the period of effort was only 2 min., the experiments are sufficient to show the typical static effects on the ventilation. It was thought desirable, however, to study the effects of more prolonged effort, and further experiments were made in which the subject continued the prescribed effort almost to the limit of his endurance.

The maximum time for which subject W could maintain a continuous tension of 100 lb. on the dynamometer was 5–6 min. The results of a typical experiment, in which this tension was maintained for 5 min., are recorded in Table IX. The frequency and depth of respiration increased throughout the period of tension. In the first 2 min. of effort the ventilation/oxygen ratio diminished, but it rose later, and reached its maximum in the first minute of recovery, remaining high in the next 2 min. The influence of this excessive ventilation is seen in the high R.Q. of 0·96–1·04 during this period. A later consequence is the low R.Q. of 0·67 in the ninth to thirteenth minutes of recovery. The result of prolonging the effort was to intensify the effects previously described.

Table IX. *Effects of maintaining tension of* 100 *lb. continuously for* 5 *min.* (*subject W*).

	Standing resting 5 min.	Tension of 100 lb.			Recovery			
		1–2nd min.	3–4th min.	5th min.	1st min.	2–3rd min.	4–8th min.	9–13th min.
Ventilation per min. (litres)	8·51	13·44	22·84	29·46	30·20	15·33	8·82	6·89
O_2 intake per min. (litres)	0·253	0·460	0·589	0·745	0·686	0·359	0·273	0·237
Ventilation/oxygen intake	33·6	29·2	38·8	39·5	44·0	42·7	32·3	29·5
Respiratory quotient	0·933	0·842	1·043	0·964	0·996	1·004	0·803	0·674
% CO_2 in expired air	2·77	2·88	2·69	2·44	2·26	2·35	2·49	2·32
Respirations per min.	11·6	14·5	13·5	17	16	12·0	11·0	12·2
Depth of respiration (c.c.)	734	927	1692	1733	1888	1278	802	565

A tension of 100 lb. is a heavy load, and the subject very soon felt considerable strain. The results of a sample experiment in which the subject held a lighter load (40 lb.) for 15 min. are given in Table X. The ventilation per

Table X. *Effects of maintaining tension of* 40 *lb. continuously for* 15 *min.* (*subject W*).

	Standing resting 4 min.	Tension of 40 lb.					Recovery	
		1–3rd min.	4–6th min.	7–9th min.	10–12th min.	13–15th min.	1–3rd min.	4–8th min.
Ventilation per min. (litres)	7·83	6·83	6·83	7·75	9·16	16·04	12·83	6·19
O_2 intake per min. (litres)	0·278	0·312	0·327	0·330	0·409	0·475	0·367	0·267
Ventilation/oxygen intake	28·2	21·9	20·9	23·5	22·4	33·8	35·0	23·2
Respiratory quotient	0·848	0·665	0·699	0·793	0·740	1·044	0·899	0·641
% CO_2 in expired air	3·01	3·04	3·35	3·38	3·34	3·09	2·57	2·77
Respirations per min.	10·0	10·0	10·7	10·3	10·0	11·3	10·7	9·4
Depth of respiration (c.c.)	783	683	638	752	916	1419	1199	59

unit oxygen intake fell at the beginning of the period of tension in the manner typical of dynamic work, and remained low until the twelfth minute of the effort. In the last 3 min., however, it rose to well above the pre-work level, and rose still higher in the first recovery period. In consequence of the reduced ventilation, the R.Q. fell to the low value of 0·665 in the first 3 min. of effort. In the last 3 min. the hyper-ventilation brought the R.Q. up to 1·044, and then in the last recovery period, with its low ventilation, the R.Q. fell again to 0·641. Further experiments with the same tension were made by this and another subject, but as the results were very similar to those quoted they are not reproduced.

These data show that what we have called the typical static effect of hyper-ventilation can be evoked by supporting a comparatively small load provided the tension is maintained continuously for some time. On the other hand, intermittent static effort, even when quite severe, fails to elicit such a response. Table XI shows the results of an experiment in which ½ sec. pulls of 200 lb. were made at the rate of 40 per min. for 8 min. The initial resting value of the ratio (ventilation)/(oxygen intake) was rather low, but there was no sign of the static hyper-ventilation effect during the period of effort.

Table XI. *Effects of intermittent static effort for* 8 *min.* (*tension* 200 *lb.*, ½ *sec. contractions*, 40 *per min.*, *subject W*).

		Intermittent pulls of 200 lb.				Recovery		
	Standing resting 5 min.	1–2nd min.	3–4th min.	5–6th min.	7–8th min.	1–2nd min.	3–5th min.	6–10th min.
ntilation per min. (litres)	5·11	12·74	17·35	21·84	24·80	13·84	10·96	8·71
intake per min. (litres)	0·230	0·562	0·836	0·948	1·089	0·527	0·345	0·307
ntilation/oxygen intake	22·2	22·7	20·8	23·0	22·8	26·3	31·8	28·4
spiratory quotient	0·787	0·882	0·867	0·919	0·870	0·963	0·997	0·810
CO_2 in expired air	3·54	3·89	4·18	3·99	3·82	3·67	3·14	2·86
spirations per min.	10·6	15·5	16·0	20·5	18·5	10·5	9·0	10·0
pth of respiration (c.c.)	482	822	1084	1065	1341	1318	1218	871

Although it is generally stated that static effort is accompanied by hyper-ventilation, so far as we are aware attention has not been drawn previously to the effect of such effort on the ratio of the ventilation to the oxygen intake; it can be found in the literature, however, that this ratio generally rises during such effort. We have observed this rise in data published by Lindhard (1920), Cathcart, Bedale and McCallum (1923), Kektscheew and Braitzewa (1930) and Marschak (1931).

(*b*) *Chest fixation.*

Lindhard (1920) found that when the respiration during effort was abdominal, the R.Q. increased afterwards, but with thoracic breathing the R.Q. fell on the cessation of effort, and Kektscheew and Braitzewa (1930) attributed the rise in ventilation after the effort to chest fixation. In both the prolonged continuous effort experiments recorded in Tables IX and X the ratio (ventilation)/(oxygen intake) increased after the effort, and in the experiment with 100 lb. tension (Table IX) the R.Q. also rose in the immediate recovery period;

yet it does not appear that there was a sufficient degree of chest fixation to account for these rises. Fig. 7 reproduces pneumograph tracings taken during the experiment recorded in Table IX; the upper tracing is of the thoracic breathing, and the lower of the abdominal. At the beginning of the period of effort there was undoubtedly some chest fixation, but in the latter part of the period the chest movement was considerable. From Table XI it will be observed that with intermittent effort, in which the low (ventilation)/(oxygen intake) ratio typical of dynamic work was found, there was a rise in this ratio after the cessation of effort, and the R.Q. also rose to its highest value in recovery, but it is clear from the pneumograph tracings of this experiment (Fig. 8) that there was no chest fiation.

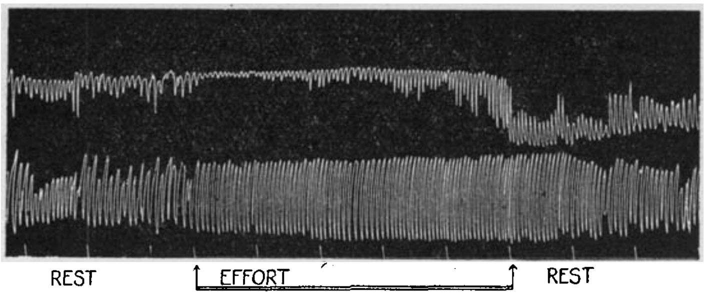

Fig. 7. Pneumograph tracings for continuous pull of 100 lb. for 5 min. Top tracing is of thoracic breathing, and middle one of abdominal. Lowest trace shows time in minutes.

Table XII. *Effects of holding leg extended for* 4 *min. while in lying position* (*subject W*).

	Lying resting 5 min.	Right leg extended				Recovery			
		1st min.	2nd min.	3rd min.	4th min.	1st min.	2–3rd min.	4–13th min.	14–18th min.
Ventilation per min. (litres)	6·63	10·77	14·45	20·35	34·72	27·45	15·25	3·73	4·83
O_2 intake per min. (litres)	0·285	0·423	0·506	0·592	0·812	0·554	0·369	0·229	0·298
Ventilation/oxygen intake	23·3	25·5	28·6	34·4	42·8	49·5	41·3	16·3	16·2
Respiratory quotient	0·865	0·827	0·943	1·082	1·081	1·248	1·000	0·543	0·658
% CO_2 in expired air	3·72	3·25	3·30	3·15	2·53	2·52	2·42	3·34	4·06
Respirations per min.	10·8	11	11	14	24	21	19·5	8·6	11·0
Depth of respiration (c.c.)	614	979	1314	1454	1447	1307	782	434	439

Further experiments were made in which there was definitely no chest fixation. The subject lay on his back in a reclining chair so that he was supported from the head to the buttocks, and both feet rested on the floor. With this as the basal position, the static effort consisted in extending the right leg horizontally and maintaining it in that position. Owing to the intense feelings of strain which were experienced, the leg could not be supported thus for more than 4 or 5 min. Table XII shows the results of such an experiment in which subject W held his leg extended for 4 min., and in Fig. 9 the pneumographic record of the same experiment is reproduced. From the tracing it is evident that there was no suggestion of chest fixation, yet the R.Q. reached its maximum value in the first minute of recovery, and,

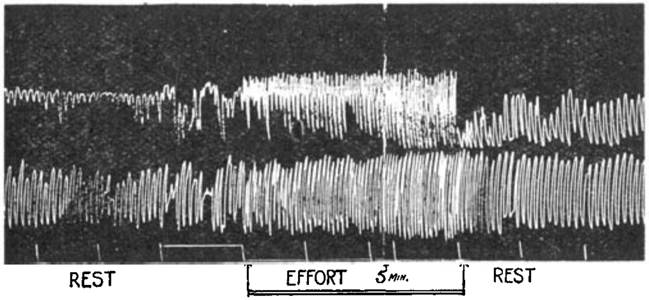

Fig. 8. Pneumograph tracings for experiment in which intermittent pulls of 200 lb. were made at rate of 40 per min. for 8 min. Only the records for the 1st, 2nd and 8th minutes of effort are shown.

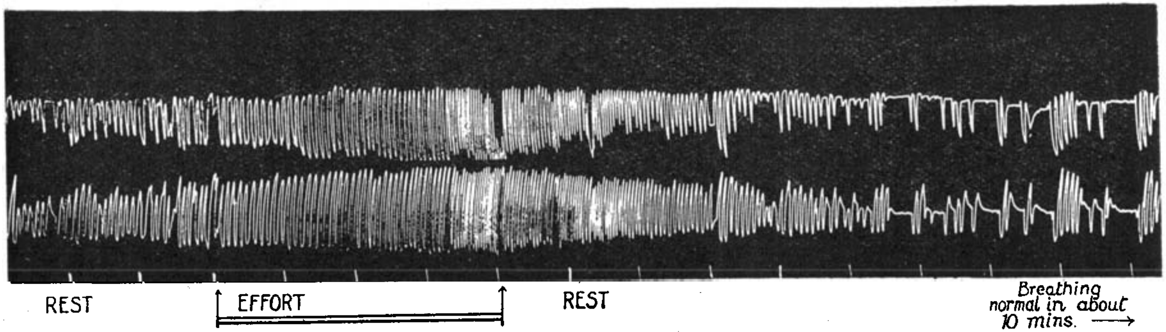

Fig. 9. Pneumograph tracings of experiment in which subject held leg extended for 4 min. while lying in chair.

although the actual volume of ventilation decreased immediately after the effort, the ventilation per unit oxygen consumption steadily increased during the effort and attained its highest value in the first minute of recovery. The effect of the hyper-ventilation during the period of effort and the first 3 min. of recovery is shown in the pneumograph record of the later recovery period; intermittent breathing commenced in the sixth minute after effort and persisted for several minutes. Another experiment on the same subject gave similar pneumograph tracings, intermittent breathing again occurring in the recovery period. In the first minute of recovery the R.Q. fell somewhat (0·92 as compared with 1·15 in the last minute of effort), but the hyper-ventilation was more marked than in the experiment already described; the ventilation per unit oxygen consumption during the first minute of recovery was 74·3, as compared with values of 36·5, 43·3, 53·8 and 52·7 for the 4 min. of work. Similar experiments repeated on another subject also showed a progressive increase in the (ventilation)/(oxygen intake) ratio during the period of effort, with a further increase in the first minute of recovery, but the R.Q. for the immediate recovery period was rather less than for the last minute of effort. The pneumograph tracings for this subject also showed no sign of chest fixation.

The data which have been presented are sufficient to show that the hyper-ventilation which so generally occurs in static effort, together with its effects on the R.Q. and the percentage of carbon dioxide in the expired air, cannot be attributed to the influence of chest fixation. The probable cause of this excessive breathing is discussed in the next section.

IV. THE FATIGUE ARISING FROM STATIC EFFORT.

(1) *Fatigue and energy exchange.*

Johansson (1901) reported that static effort involving a relatively small increase in energy expenditure gave rise to a marked feeling of fatigue. Later, Johansson and Koraen (1902) found that beyond a certain limit the carbon dioxide cost of such effort increased more rapidly than the duration of the contraction. This limiting value coincided with the beginning of fatigue and was reached sooner at the greater loads.

Other workers also have been cited as having found that the ratio (energy exchange)/(duration of contraction) increases as the effort is prolonged, and in our own data (cf. Tables IX to XII) this increase is apparent. This fact does not contradict the conclusions reached in section II of this paper concerning the linear relation between oxygen consumption and duration of contraction. In the experiments there described particular care was taken to ensure that the standard posture was maintained, whereas towards the end of the more prolonged efforts to which Tables IX–XII refer considerable distress occurred, and in those circumstances it was not possible to adhere rigidly to a standard posture. The increase in energy exchange with prolongation of the effort is probably due to extra muscles being called into action.

Frumerie (1913) stated that provided no new muscles were brought into play the sensation of fatigue did not influence the carbon dioxide output; and Loewy (1891), in a study of dynamic work, found that the oxygen cost per unit of work was increased by fatigue. He attributed the increase to a change in the type of movement consequent on other muscles being called in to assist.

Frumerie (1913) and Passauer (1925) found that the subjective sensations of fatigue have no relation to the energy exchange, but (Passauer) were parallel with the duration of contraction and size of load.

Bedale (1924) mentions local strain as one of the factors influencing the mechanical efficiency in load carrying.

(2) *The cause of the fatigue in static effort.*

(*a*) *Previous work.*

Lindhard (1920) concluded that the great fatigue resulting from static effort was caused by the accumulation of lactic acid in the contracting muscles.

Cathcart, Bedale and McCallum (1923) also found that fatigue, associated with pain, was a pronounced feature in their experiments. They found also that tremor of the muscles came on very rapidly and lasted after the conclusion of the effort. The smallness of the alteration in R.Q. in their experiments showed that the feeling of fatigue could not be due to the accumulation of lactic acid. The subjective sensations of strain were accompanied by more or less convulsive breathing.

The sensation of fatigue in static effort was ascribed by Frumerie (1913) to mechanical pressure on the nerve endings in muscles, tendons and joints, and von Frey and Meyer (1918) showed that any long continued pull on tendons causes painful sensations.

Dusser de Barenne and Burger (1928) state that the lactic acid concentration in static effort was never sufficient to account for the feeling of fatigue which was experienced. Instead, they attribute the feeling of fatigue to the pull and pressure on nerve endings in muscle and skin. This, they say, accounts for the lack of signs of fatigue in the static effort of catalepsy and hypnosis.

Marschak (1931) disagrees with the conclusion of Dusser de Barenne and Burger, and supports Lindhard in believing that the symptoms of fatigue are due to the accumulation of lactic acid caused by obstructed circulation.

According to Riabuschinsky (1931) static effort causing complete fatigue can be carried out without any increase in the lactic acid content of the blood. He concludes that the production and accumulation of lactic acid in muscles are not causally related to the phenomena of fatigue.

Jervell (1932) found no relation between symptoms of fatigue and the lactic acid content of the blood.

All authors agree that static effort is accompanied by marked fatigue which is out of all proportion to the energy expenditure involved. Some workers attribute this fatigue to the accumulation of lactic acid in the contracting muscles, while others dispute this view and ascribe the symptoms of fatigue to the pull and pressure on nerve endings in muscle and skin. The preponderance of opinion appears to be in favour of the latter view.

(b) *The present observations.*

In our own experiments we have found that static effort is attended by sensations of strain in the tendons and muscles ranging from discomfort, in the lighter and shorter experiments, to considerable pain in the prolonged experiments. For instance, in maintaining a tension of 40 lb. no discomfort was felt for the first 4 or 5 min., but after that time feelings of strain appeared, and by the end of 12 min. the strain was distinctly painful; but with a load of 100 lb. painful sensations appeared after 3 or 4 min. In these prolonged experiments marked tremor of the muscles of the hands, arms and legs occurred; and after the cessation of effort a prickling sensation ("pins and needles") was usually experienced in these parts.

(c) *Pain as the cause of hyper-ventilation.*

We have already shown that the typical effect of static effort is an increase in the ratio of the ventilation to the oxygen intake. In the course of the experiments it was evident that increase in this ratio ran parallel with the increasing feelings of strain due to the load, and there appears to us to be no doubt that the hyper-ventilation as measured by this ratio is provoked by the painful sensation which attend such effort.

It is already known that pain gives rise to increased ventilation. Meyer (1914) caused pain by placing a clamp on the end of the little finger, and found that the pain caused an increase in the ventilation of 10–56 per cent. above the resting value. The oxygen consumption was greater during pain than when at rest, probably on account of the general tension which often accompanies pain, but it can be calculated that the ratio of ventilation to oxygen intake was always greater during pain than during the corresponding rest period. Y. Henderson (1909) says that pain, ether excitement, sorrow, fear, and other conditions inducing shock, involve excessive ventilation. Knipping and Moncrieff (1932) mention that the ventilation per unit oxygen intake is increased by emotion.

We caused pain in ourselves by applying a strong faradaic stimulus to the legs, while lying, with feet supported, in a reclining chair. So long as the stimulus caused only slight discomfort the (ventilation)/(oxygen intake) ratio was practically unaltered, but when the stimulus became very painful the ratio increased. The results of the experiment in which this increase was most marked are given in Table XIII. In the first 3 min. of stimulation a certain amount of discomfort was felt, and the ratio of the ventilation to the oxygen intake rose slightly. In the next period of 3 min. the strength of the stimulus was increased, and the subject experienced intense pain. The result of this painful stimulation is seen in the hyper-ventilation which it provoked; the ratio of ventilation to oxygen intake was more than twice the resting value, and the R.Q. rose to 1·368. In the third to seventh minutes of recovery the R.Q. fell to 0·476, the percentage of carbon dioxide in the expired air was still very low, the breathing was shallow, and the ventilation was only two-thirds of the initial resting value.

These experiments, together with the findings of previous workers, would appear to confirm our conclusion that the hyper-ventilation, together with the consequent fluctuations of R.Q., and percentage of carbon dioxide in the expired air, which accompanies static effort, is attributable to the painful feelings of strain to which such effort gives rise.

Table XIII. *Effects of painful faradaic stimulus to legs (subject B).*

	Lying resting 5 min.	Stimulus		Lying resting	
		Initial 1–3rd min.	Increased 4–6th min.	1–2nd min.	3–7th min.
Ventilation per min. (litres)	6·58	13·95	25·63	8·58	4·33
O_2 intake per min. (litres)	0·267	0·538	0·487	0·268	0·236
Ventilation/oxygen intake	24·6	25·9	52·6	32·0	18·3
Respiratory quotient	0·845	0·928	1·368	0·779	0·476
% CO_2 in expired air	3·43	3·58	2·60	2·43	2·60
Respirations per min.	13·2	13·7	16·3	16·5	14·0
Depth of respiration (c.c.)	498	1018	1572	520	309

The limit of endurance in our longer experiments on static effort appeared to be governed by the painful sensations which arose or, in some cases, by the feeling of faintness which came on as a result of over-ventilation. Thus, directly or indirectly, the endurable limit depended on the intensity of the painful sensations aroused by the effort.

(3) *Fatigue and capacity for effort: the influence of postural change.*

(*a*) *Previous work.*

In order to determine the influence of postural changes, Vernon (1924) made maximal isometric contractions lasting ½ sec. when pulling against a powerful spring. With rest intervals of 2–60 sec., suitably arranged during experiments lasting 10 min., a slight change of posture (gentle movements of shoulders and arms) during the rest interval caused an increase in the capacity for effort. In the fifth to tenth minutes of the posture-changed experiments the mean tension effected was 18–38 per cent. greater than in the corresponding unchanged posture experiments. This difference was attributed to the beneficial effect of the postural changes on the circulation.

In another series of experiments, Vernon and another subject (W) made maximal ½ sec. contractions for 20 min. (*a*) when standing, (*b*) when sitting, and (*c*) when standing and sitting alternately. The changes of posture were made every 40 to 300 sec., and as they necessitated a temporary cessation of work, rest pauses of equal duration were taken in all series of experiments. The average tensions reached by the two subjects in the posture-changed experiments were respectively 12 and 7 per cent. more than the averages of the corresponding experiments with the posture unchanged.

(*b*) *The present observations.*

In the present investigation two subjects made parallel series of intermittent and continuous contractions, over periods of 10 min. In the intermittent experiments a maximal ½ sec. contraction was made every 1½ sec. for 37½ sec.; this was followed by a rest interval of 2½ sec., after which the effort was continued for a further 37½ sec., and so on. During the rest intervals the subject either stood or sat quietly, or he changed from one position to the other according to the character of the experiment. In those experiments in which the posture alternated between sitting and standing, similar changes of posture were made every 40 sec. during the 30 min. preceding the effort, and during the recovery period. In the continuous effort experiments a maximum pull was maintained for periods of 37½ sec., alternating with the 2½ sec. rest intervals. Tables XIV–XVI show the effects of these experiments on the ratio of the ventilation to oxygen intake, the percentage of carbon dioxide in the expired air, and the R.Q.: each line in the tables is the mean of five or six experiments.

In both the standing and the sitting experiments continuous static effort provoked in both subjects that hyper-ventilation which we have found so typical of static effort which is at all prolonged. In both subjects the hyperventilation was more marked in the sitting experiments than in the standing. Subject W showed a rise in the ventilation ratio in the first 5 min. of the effort, and the ratio continued to rise in the second 5 min. On the other hand, in subject V the ratio fell slightly in the first 5 min., and then showed a marked rise in the latter half of the period of effort. The data for the experiments in which the posture alternated every 40 sec. between sitting and standing show quite a different picture. In neither subject did the ventilation ratio show the usual rise, but remained very near the initial resting value.

The results of the intermittent effort experiments show the fall in the ventilation ratio which we have found to be associated with dynamic work, or exertion in which the contractions are made rapidly and are of short duration. Change of posture appears to have had no definite influence, for in the case of each subject the values in the three series of observations are practically the same.

From Tables XV and XVI it can be seen that the percentage of carbon dioxide in the expired air, and the R.Q., followed closely the fluctuations in the ventilation ratios given in Table XIV. We have seen that the highest ratios in both subjects were observed in the sitting continuous effort experiments, and accordingly we find that in these experiments the lowest carbon dioxide percentages and the highest respiratory quotients were observed. In the static effort experiments with alternate standing and sitting the ventilation ratio was practically unchanged; here, too, we find least alteration in the percentage of carbon dioxide in the expired air, and in the respiratory quotient.

Table XIV. *Effects of postural change on the ratio of ventilation to oxygen intake.*

		Continuous effort					Intermittent effort				
			Pulling		Recovery			Pulling		Recovery	
ubject	Posture	Rest 5 min.	1–5th min.	6–10th min.	1–5th min.	6–10th min.	Rest 5 min.	1–5th min.	6–10th min.	1–5th min.	6–10th min.
V	Standing only	27·5	26·2	33·6	28·2	27·2	27·4	24·3	23·8	28·4	27·1
	Sitting only	27·0	25·8	40·5	27·3	25·0	27·0	24·9	24·7	27·3	27·4
	Standing and sitting alternately	26·0	25·0	26·4	25·3	25·2	26·5	23·6	23·3	26·6	26·7
W	Standing only	24·8	29·7	33·2	26·3	23·3	26·6	20·4	22·1	25·5	27·5
	Sitting only	26·7	32·7	36·9	30·1	27·0	28·4	20·2	21·2	26·3	26·3
	Standing and sitting alternately	25·2	25·0	26·5	21·3	23·6	24·0	20·0	20·6	24·9	24·6

Table XV. *Effects of postural change on the percentage of CO_2 in the expired air.*

		Continuous effort					Intermittent effort				
			Pulling		Recovery			Pulling		Recovery	
ubject	Posture	Rest 5 min.	1–5th min.	6–10th min.	1–5th min.	6–10th min.	Rest 5 min.	1–5th min.	6–10th min.	1–5th min.	6–10th min.
V	Standing only	3·26	3·28	2·81	3·04	3·03	3·20	3·72	3·82	3·22	3·22
	Sitting only	3·22	3·46	2·60	2·98	3·13	3·24	3·65	3·73	3·41	3·15
	Standing and sitting alternately	3·30	3·55	3·24	3·33	3·33	3·33	3·77	3·87	3·41	3·25
W	Standing only	3·46	3·30	2·88	3·14	3·33	3·53	4·09	4·07	3·68	3·27
	Sitting only	3·37	3·22	2·83	2·95	3·02	3·45	4·13	4·08	3·72	3·50
	Standing and sitting alternately	3·68	3·70	3·45	3·51	3·49	3·59	4·24	4·17	3·86	3·63

Table XVI. *Effects of postural change on the respiratory quotient.*

		Continuous effort					Intermittent effort				
			Pulling		Recovery			Pulling		Recovery	
ubject	Posture	Rest 5 min.	1–5th min.	6–10th min.	1–5th min.	6–10th min.	Rest 5 min.	1–5th min.	6–10th min.	1–5th min.	6–10th min.
V	Standing only	0·898	0·862	0·932	0·854	0·824	0·880	0·901	0·906	0·913	0·871
	Sitting only	0·875	0·890	1·042	0·815	0·784	0·876	0·909	0·920	0·930	0·862
	Standing and sitting alternately	0·862	0·884	0·853	0·843	0·840	0·887	0·891	0·900	0·905	0·871
W	Standing only	0·852	0·949	0·914	0·811	0·767	0·939	0·834	0·901	0·935	0·897
	Sitting only	0·896	1·034	0·999	0·883	0·813	0·978	0·837	0·865	0·972	0·906
	Standing and sitting alternately	0·918	0·913	0·898	0·825	0·818	0·867	0·855	0·863	0·961	0·894

From data recorded in an earlier section (*e.g.* Tables IX and X, p. 136) it was noticed that the hyper-ventilation is not apparent at the beginning of the static effort but takes some time to develop, and that the rise in the ventilation ratio runs parallel with the increasing sensations of strain. In the alternate standing and sitting experiments the posture was changed every

40 sec., and the strain thus differently distributed; because of this frequent changing of the muscle groups subjected to tension the strain never made itself felt to the same extent as in the experiments in which the posture remained unchanged. We suggest that this reduction in the strain experienced accounts for the fact that in these experiments there was no sensible rise in the ventilation ratio.

Table XVII. *The influence of postural change on strength of pull.*

	Continuous effort						Intermittent effort					
	Subject V			Subject W			Subject V			Subject W		
Posture	No. of obs.	Mean pull (lb.)		No. of obs.	Mean pull (lb.)		No. of obs.	Mean pull (lb.)		No. of obs.	Mean pull (lb.)	
Standing only	6	80	84	6	73	83·5	6	152	175	5	154	172·5
Sitting only	6	88		6	94		6	198		5	191	
Standing and sitting alternately	6	89		6	97		6	185		6	189	
Per cent. difference		+6			+16			+6			+10	

Table XVII shows the mean strength of pull attained in these experiments. In the "standing and sitting" experiments the mean pull was 6–16 per cent. greater than the average for the corresponding standing only and sitting only experiments. Thus the postural change had the effect of increasing the maximum effort which could be exerted.

V. THE STATIC FACTOR IN DYNAMIC EFFORT.

(1) *The assessment of the static factor.*

It has been shown that static effort enters in greater or less degree into all kinds of work. On account of the particularly fatiguing character of such effort it is a matter of some importance, in the application of physiology to industry, to be able to assess the extent to which the static factor enters into a particular piece of work.

Atzler (1927 and 1928) estimates the static component of a task by calculating partial efficiencies. Thus, he shows (1928) that in dragging a load of 16 kg. over 1 metre the energy cost was 155·2 cal. The no-load movement accounted for 39 cal., and the static element for only 2 cal. In carrying a load of 9·1 kg. on a level road the total cost was 49 cal. per metre, and the static effort of balancing cost 8·3 cal. per metre. The larger proportion of the cost due to static effort illustrates the tiring character of carrying work. In a study of bricklaying, Baader and Lehmann (1928) used this partial efficiency method of estimating the static factor, in order to arrive at the most convenient size of brick.

In a paper dealing with the recovery after work, Simonson (1927) calculated a "recovery constant,"

$$RK = \frac{1}{t} \log \left(\frac{\text{cal. } A}{\text{cal. } t} \right),$$

where RK = "recovery constant,"

t = period over which the initial recovery metabolism is determined, say 3 min.,

cal. A = total recovery metabolism, and

cal. t = arrears of recovery metabolism after time t.

Thus, the higher the value of RK the more rapid is the recovery. As the static element in work predominates, the value of RK diminishes, *i.e.* recovery is less rapid (Simonson, 1929).

(2) *Examples of the influence of the static factor.*

One of the commonest tasks involving a large static factor is that of carrying loads. Bedale (1924) found that the efficiency of carrying a load was influenced by local strain, posture, gait and chest freedom. For a given load, carrying with a shoulder yoke, which allowed the retention of erect carriage and normal gait, caused the least energy expenditure of any of the methods investigated; while carrying on the hip, involving all the disadvantages named, was the most expensive.

From mechanical considerations it appears evident that the static effort of supporting a given load will be greater as the moment of the load about the body's centre of gravity increases. It is a commonplace that more effort is required to hold a weight with the arm stretched sideways than with the arm by the side. The extra energy cost of such holding is shown in the data of Atzler and Herbst (1928, p. 72). Holding a load of 9·1 kg. with the arm by the side cost 76·36 cal. per min., while it cost 5440 cal. per min. to hold the same load with the arm stretched horizontally. Atzler (1928) calculates that (until the arm assumes a horizontal position) the energy consumption entailed by the effort varies as the tangent of the angle between the arm and the trunk, and it can be calculated from the data of Atzler and Herbst that this relation approximately holds.

Examples of the influence of the static factor of postural maintenance on energy costs could be multiplied, but it will suffice to give one other example. Kommerell (1929), in a study of shovelling while in a stooping position, found that a reduction of height from floor to ceiling from 1·2 to 1·0 metre caused a loss of 10 per cent. in working efficiency.

VI. SUMMARY.

(1) *The energy cost of static effort.*

From previous work it appears that the metabolic cost of maintaining a given tension varies directly as the load, provided no new muscles are brought into play as the result of fatigue or local strain. There is conflict of opinion as to the relation of cost to tension; some workers find a linear relation, while others find a non-linear one.

In the present observations contractions, which were virtually isometric, were made against a powerful spring, while in a standing position.

With constant tension the oxygen cost per contraction varied directly as the duration of the contraction. With constant time and increasing tension the oxygen cost increased more rapidly than the tension.

The duration of contraction varied from $\frac{1}{2}$ to 30 sec., and the tension from 30 to 165 lb. Over the whole range the oxygen cost per contraction is adequately described by the equation

$$Q = T^{1\cdot 37}(0\cdot 0117 + 0\cdot 0109t),$$

where Q is the oxygen cost per contraction, T is the tension, and t is the duration of contraction.

(2) *The effect of static effort on the respiration.*

As a measure of hyper-ventilation the ratio of ventilation to oxygen intake is used. It is shown that in dynamic work this ratio falls below the resting value, whereas in static effort of whatever severity the ratio increases considerably above the resting value if the effort is sufficiently prolonged. The rise in the ventilation ratio runs parallel with the feelings of strain which are associated with static effort. Pain causes such a rise in the ratio, and the rise which occurs in static effort is ascribed to the influence of painful sensations of strain.

Observations were made in which the posture alternated between sitting and standing every 40 sec. The change of posture altered the distribution of the strain, and thus the subjective sensations were not so marked as in the experiments with posture unchanged. In consequence of the postural change the ventilation ratio did not rise sensibly above the resting value, and the maximum strength of pull was increased by 6–16 per cent.

ACKNOWLEDGEMENTS.

This investigation was carried out in the Department of Industrial Physiology at the London School of Hygiene and Tropical Medicine. We wish to express our indebtedness to the authorities of the school, and especially to Dr G. P. Crowden, for the facilities offered to us in our work.

REFERENCES.

ANTHONY, A. J. (1930). Untersuchungen über Lungenvolumina und Lungenventilation. *Deutsches Arch. f. klin. Med.* **167**, 129.

ATZLER, E. (1927). *Körper und Arbeit.* Leipzig: Georg Thieme.

—— (1928). Probleme und Aufgaben der Arbeitsphysiologie. *Ergebn. Physiol.* **27**, 709.

ATZLER, E. and HERBST, R. (1928). Die Ökonomie des Lasttragens über eine ebene Strecke. *Arbeitsphysiol.* **1**, 54.

BAADER E. and LEHMANN, G. (1928). Über die Ökonomie der Maurerarbeit. *Ibid.* **1**, 41.

BEDALE, E. M. (1924). Comparison of the energy expenditure of a woman carrying loads in eight different positions. *Ind. Fat. Res. Bd.* Rep. No. **29**.

BENEDICT, F. G. and CATHCART, E. P. (1913). Muscular work. *Carnegie Inst. of Washington*, Publ. No. **187**.

BOCK, A. V. and DILL, D. B. (1931). In Bainbridge's *The Physiology of Muscular Exercise.* London: Longmans, Green and Co.

BORNSTEIN, A. and POHER, E. (1903). Ueber den respiratorischen Stoffwechsel bei statischer Arbeit. *Arch. ges. Physiol.* **95**, 146.

CATHCART, E. P. (1923). The efficiency of man and the factors which influence it. *Brit. Assoc. Reports* for 1922, p. 164.

CATHCART, E. P., BEDALE, E. M. and McCALLUM, G. (1923). Studies in muscle activity. I. The static effort. *J. Physiol.* **57**, 161.

CHAUVEAU, A. and TISSOT, J. (1896). L'énergie dépensée par le muscle en contraction statique pour le soutien d'une charge d'après les échanges respiratoires. *C.R. Acad. Sci. Paris*, **123**, 1236.

DOUGLAS, C. G. and HALDANE, J. S. (1912). The capacity of the air passages under varying physiological conditions. *J. Physiol.* **45**, 235.

DUSSER DE BARENNE, J. G. and BURGER, G. C. E. (1924). A method for the graphic registration of oxygen consumption and carbon dioxide output; the respiratory exchange in decerebrate rigidity. *Ibid.* **59**, 17.

—— —— (1928). Untersuchungen über den Gaswechsel des Menschen bei statischer Arbeit. *Pflüger's Arch.* **218**, 239.

v. FREY, M. and MEYER, O. B. (1918). Versuche über die Wahrnehmung geführter Bewegungen. *Z. Biol.* **68**, 301.

FRUMERIE, K. (1913). Über das Verhältnis des Ermüdungsgefühls zur CO_2-Abgabe bei statischer Muskelarbeit. *Skand. Arch. Physiol.* **30**, 409.

FURUSAWA, K., HILL, A. V. and PARKINSON, J. L. (1927). The energy used in "sprint" running. *Proc. Roy. Soc.* B, **102**, 43.

GARRY, R. C. and WISHART, G. M. (1931). On the existence of a most efficient speed in bicycle pedalling, and the problem of determining human muscular efficiency. *J. Physiol.* **72**, 425.

GREENWOOD, M. and NEWBOLD, E. M. (1923). On the estimation of metabolism from determinations of carbon dioxide production and on the estimation of external work from the respiratory metabolism. *J. Hyg.* **21**, 440.

HARTREE, W. and HILL, A. V. (1921). Regulation of the supply of energy in muscular contraction. *J. Physiol.* **55**, 133.

HENDERSON, Y. (1909). Acapnia and shock. IV. Fatal apnoea after excessive respiration. *Amer. J. Physiol.* **25**, 310.

HILL, A. V. and LUPTON, H. (1923). Muscular exercise, lactic acid, and the supply and utilisation of oxygen. *Quart. J. Med.* **16**, 135.

JERVELL, O. (1932). Die Milchsäurebildung bei statischer Muskelarbeit und bei lokaler Asphyxie. *Arbeitsphysiol.* **5**, 150.

JOHANNSON, J. E. (1901). Untersuchungen über die Kohlensäurabgabe bei Muskelthätigkeit. *Skand. Arch. Physiol.* **11**, 273.

JOHANSSON, J. E. and KORAEN, G. (1902). Untersuchungen über die Kohlensäurabgabe bei statischer und negativer Muskelthätigkeit. *Ibid.* **13**, 229.

—— —— (1903). Die Einwirkung verschiedener Variabelen auf die Kohlensäurabgabe bei positiver Muskelthätigkeit. *Ibid.* **14**, 60.

KEKTSCHEEW, K. and BRAITZEWA, L. (1930). Material zur physiologischen Untersuchung der statischen Arbeit. *Arbeitsphysiol.* **2**, 526.

Knipping, H. W. and Moncrieff, A. (1932). The ventilation equivalent for oxygen. *Quart. J. Med.* n.s. **1**, 17.

Kommerell, B. (1929). Die Schaufelarbeit in gebückter Haltung. *Arbeitsphysiol.* **1**, 278.

Lehmann, G. (1927). Zur Frage der Sperrung des Skelettmuskels. *Pflüger's Arch.* **216**, 353.

Lindhard, J. (1920). Untersuchungen über statische Muskelarbeit. *Skand. Arch. Physiol.* **40**, 145 and 196.

Loewy, A. (1891). Die Wirkung ermüdender Muskelarbeit auf den respiratorischen Stoffwechsel. *Pflüger's Arch.* **49**, 405.

Lupton, H. (1923). An analysis of the effects of speed on the mechanical efficiency of human muscular movement. *J. Physiol.* **57**, 337.

Marschak, M. E. (1930). Hauttemperatur bei dynamischer und statischer Arbeit. *Arbeitsphysiol.* **3**, 168.

Marschak, M. (1931). Eine Untersuchung über den Gaswechsel und über die Milchsäure und Alkalireserve im Blut bei statischer Arbeit. *Ibid.* **4**, 1.

Meyer, A. L. (1914). Hyperpnoea as a result of pain and ether in man. *J. Physiol.* **48**, 47.

Müller, E. A. (1930). Der Einfluss der Kontraktionsgeschwindigkeit auf den Energieverbrauch bei einer statischen Arbeit. *Arbeitsphysiol.* **3**, 298.

Passauer (1925). Über den Einfluss statischer Arbeit auf Ermüdung und Stoffwechsel. *Z. Hyg. Infektkr.* **104**, 33.

Riabuschinsky, N. P. (1928). Besteht eine Proportionalität zwischen der Arbeitsleistung und der Milchsäure-Phosphor- und Zuckermenge im Blute? *Biochem. Z.* **193**, 161.

—— (1931). Zur Frage über Beziehung zwischen der Milchsäure im Blut und der Ermüdung. *Pflüger's Arch.* **226**, 79.

Roaf, H. E. (1912). The influence of muscular rigidity on the carbon dioxide output of decerebrate cats. *Quart. J. Exp. Physiol.* **5**, 31.

—— (1913). The influence of muscular rigidity on the oxygen intake of decerebrate cats. *Ibid.* **6**, 393.

Simonson, E. (1926). Zur Physiologie des Energieumsatzes beim Menschen. I. Beiträge zur Physiologie der Arbeit, der Restitution und der Atmung. *Pflüger's Arch.* **214**, 380.

—— (1927). Zur Physiologie des Energieumsatzes beim Menschen. III. Weitere Beiträge zur Physiologie der Erholung bei körperlicher Arbeit. *Ibid.* **215**, 716.

—— (1929). Rationalisierung industrieller Arbeit nach physiologischen Gesichtspunkten. II. Über die Erholung während und nach beendeter Arbeit und das Verhalten des calorischen Ventilationsquotienten und des respiratorischen Quotienten beim Formen und seinen Elementen. *Arbeitsphysiol.* **1**, 540.

Vernon, H. M. (1922). The influence of rest pauses and changes of posture on the capacity for muscular work. *J. Physiol.* **56**, *Proc.* xlvii.

—— (1924). The influence of rest pauses and changes of posture on the capacity for muscular work. *Ind. Fat. Res. Bd.* Rep. No. **29**.

Verzár, F. (1912). The gaseous metabolism of striated muscle in warm-blooded animals. *J. Physiol.* **44**, 243.

Wachholder, K. (1928). Willkürliche Haltung und Bewegung insbesondere im Lichte elektrophysiologischer Untersuchungen. *Ergebn. Physiol.* **26**, 568.

Weatherhead, E. L. (1932). The metabolism of postural and phasic contractions of the quadriceps of the cat. *J. Physiol.* **74**, 163.

(*MS. received for publication* 28. x. 1932.—Ed.)