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FORCE GENERATING CAPACITY

OF HUMAN MUSCLE

by

CAROLYN ANNE GREIG

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The proportion of maximum force (% PF max) utilised during cycling exercise was determined within a group of trained and untrained subjects. Maximum forces were determined isokinetically and submaximum forces were measured during continuous progressive exercise tests.

A large individual variation in the proportion of maximum force utilised at equivalent values of power output was demonstrated. The mean value obtained from the group of subjects was 50% (at 70 rpm and 100% of $\dot{V}O_2$ max), although this was much greater in subjects possessing a high aerobic capacity. The data suggest that the limitation to sustained dynamic exercise, which is a balance between 'central' and 'peripheral' factors, may tend towards the latter in certain individuals.

Measurement of % PF max at equivalent values of power output over a range of pedal frequencies (40 - 100 rpm) revealed a systematic reduction (28% at 100% VO_2 max) when fast frequencies were compared to slow. These results suggest the advantage of employing high pedal frequencies during sustained exercise; furthermore, there was no detrimental effect upon exercise efficiency, again, when slow and fast pedal frequencies were compared.

The underlying mechanism of a reduction of % PF max with increasing frequency of contraction was also investigated using surface integrated electromyography (IEMG). Percentage of maximum IEMG activity (% IEMG max) also demonstrated a reduction with increasing frequency of contraction (at equivalent values of power output) in parallel with % PF max. It is suggested that at high contraction frequencies, a selective recruitment of fast twitch motor units may occur which would be capable of maintaining a given power output but with a lower level of force.

Finally, the effect of oral supplementation of L-Carnitine upon maximum and submaximum exercise performance was investigated. The submaximal cardiac frequency response to exercise and pre- and post-exercise plasma metabolite concentrations were unchanged under Carnitine supplemented conditions, implying that Carnitine is of little benefit to exercise performance.

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Appendix 3

A: Reprint of : Greig, C., Rutherford, O., Sargeant, A.J. (1986). Effect of pedalling rate on the muscle force required during cycling exercise in man. J. Physiol. 377 : 109P.

B: Reprint of : Greig, C., Hortobagyi, R., Sargeant, A.J. (1985). Quadriceps surface E.M.G and fatigue during maximal dynamic exercise in man. J. Physiol. 369 : 180P.

C: Reprint of : Greig, C., Sargeant, A.J., Vøllestad, N.K. (1985). Muscle force and fibre recruitment during dynamic exercise in man. J. Physiol. 371 : 176P.

D: Reprint of : Greig, C., Finch, K.M., Jones, D.A., Cooper, M., Sargeant, A.J., Forte, C.A. (1987).
The effect of oral supplenetation with L-carnitine on maximum and submaximum exercise capacity. Eur. J. Appl. Physiol. 56 : 457-460.

CHAPTER 1

INTRODUCTION

INTRODUCTION

Measurement of force-generating capacity

The key to both human and animal movement lies in the ability of skeletal muscle to generate force and the speed with which it is able to do so. Until this century, little was known about the relationship between force generation and speed of contraction within skeletal muscle. The first investigations were conducted by Hill (1922) who reported an inverse relationship between maximum force generation and contraction velocity in human muscle, maximum force generating capacity decreased as velocity of contraction increased. Although the subsequent in vitro studies of Gasser and Hill (1924), Fenn and Marsh (1935) and Hill (1938) demonstrated a similar reduction in force generation with increasing velocity of contraction, a curvilinear relationship was obtained. This apparent discrepancy between in-vivo and in-vitro results could be explained by the fact that in the latter studies force was measured in direct line with the actual tension developed within the muscle, that is, the muscle was isolated and free of the joint, whereas in-vivo, the situation is more complex, with factors such as the angle of pennation of the muscle fibres and the muscle/joint lever system itself influencing the tension developed (Lindahl and Movin, 1967; Alexander and Vernon, 1975). It is interesting to note, however, that there are reports in the literature of in-vivo studies which have demonstrated a curvi-linear force-velocity relationship, for example, Wilkie (1950) investigating the elbow flexor muscles using an isotonic loading technique and more recently Thorstensson, Grimby and Karlsson (1976) investigating the force velocity characteristics of the quadriceps muscle group (although their data does appear to be linear if the value obtained for isometric tension is excluded). More recently studies of the force-velocity relationship of the leg extensor muscles using a specially modified cycle ergometer have reported a linear relationship (Sargeant, Hoinville and Young, 1981; McCartney, Heigenhauser, Sargeant and Jones, 1983; Dolan, 1985). The discrepancy between the results of in-vivo investigations may be explained by the different characteristics of the muscle groups or by differences in the test procedure employed.

Although the important relationship between force-generation and velocity of contraction has received more attention in recent years, the majority of relevant studies have been concerned with the measurement of maximum force-generating capacity at a given velocity of contraction. It is clear that during normal daily activities maximum muscle function is rarely used. Indeed, it is impossible to sustain maximum values of force generation since muscle fatigue will occur after only a few seconds.

It would be more appropriate to measure how much of an individual's maximum force generating capacity is utilised during more moderate, sustained dynamic exercise, in an attempt to represent normal daily activity, than to confine measurements of force generation to brief maximal bursts of activity. This functional (and non-invasive) measurement could also yield useful information concerning the level of peripheral stress experienced by the individual during dynamic activity.

Measuring the proportion of maximum force generating capacity utilised during dynamic exercise is not without problems, since the measurement of maximum force is obviously still required and this is dependent upon the velocity of contraction. Wilkie's study of the elbow flexors (1950), employed the use of afterload as the controlled variable. An alternative approach would be to use an isokinetic technique, that is, a technique in which the velocity of contraction is controlled and the external forces generated are measured. Recently, apparatus based upon this principle (such as the Cybex dynamometer) have become commercially available. However, measurements of maximum force at high velocities are not reliable using this device, since the muscle under investigation may be unable to develop its maximum tension before passing the optimum joint angle. According to Thorstensson (1976), isokinetic devices such as the Cybex are only reliable at velocities below 25% of the maximum voluntary contraction velocity.

Another approach which has attempted to overcome this problem employs the use of a specially modified motor driven cycle ergometer which allows force to be generated during a brief maximum test but does not allow the subject to alter the frequency of contraction (Sargeant, Hoinville and Young, 1981). Thus maximum forces are generated under isokinetic conditions and over a large range of contraction velocities.

Having established the maximum force generating capacity of a muscle or muscle group at a particular velocity of contraction, submaximum forces recorded during more moderate sustained exercise may then be expressed as a proportion of the maximum available force generating capacity.

There are several reports in the literature concerning the measurement of submaximum forces during sustained dynamic exercise, particularly cycling, (Hoes, Binkhorst, Smeekes-Kuyl and Vissers, 1968; Bigland-Ritchie and Woods, 1976; Sargeant and Davies, 1977). Forces exerted upon either the cranks or pedals of a cycle ergometer were measured and found to increase linearly with increments in exercise intensity. The force data obtained from these studies, however, was not expressed as a proportion of maximum force generating capacity - probably due to the methodological difficulties in measuring maximum forces under identical conditions, particularly contraction frequency which has previously been mentioned. One of the few attempts to measure proportional force utilisation, or relative force generating capacity, has been made by Sjøgaard, (1978), during dynamic cycling exercise. The proportion of maximum force utilised by a group of untrained individuals at values of power output requiring 70% and 100% respectively of maximum oxygen uptake ($\dot{V}O_2$ max) was measured over a range of pedal frequencies and was shown to increase with increments in exercise intensity up to a mean value which did not exceed 49% (SD $\pm$ 9.7%) at 100% of $\dot{V}O_2$ max. The results of this study indicate the presence of a large reserve of force generating capacity, even when the subjects had achieved maximum aerobic power.

If one were to use the proportion of maximum force-generating capacity as an index of the peripheral 'stress' experienced by the individual, it would appear from the data obtained by Sjøgaard, that under the conditions described in the study the major limitation to sustained dynamic exercise is not peripheral in origin. This observation is consistent with several previous studies performed under similar conditions, in which the major limitation to sustained dynamic exercise has been shown to be determined by the maximum capacity of the oxygen transport system (Bevegard and Shepherd, 1967; Davies and Sargeant, 1974; Gollnick, Armstrong, Saubert, Piehl and Saltin, 1972), that is, a limitation of 'central' origin rather than peripheral. It would appear, nevertheless, that the major limitation to sustained dynamic exercise is a balance between central and peripheral factors; the former being predominant under the conditions mentioned above, with a large reserve of force-generating capacity available even at $\dot{V}O_2$ max. It is conceivable however that this situation may alter under certain conditions, such as supra-maximal exercise and also within trained individuals.

Sjøgaard (1978) did not measure proportional force utilisation in groups of trained subjects, and therefore it was not known whether a 'similar' situation (that is, a large reserve of force-generating capacity available, even at $\dot{V}O_2$ max) existed in individuals whose muscles had undergone specific adaptation as a result of physical training. Physical training may result in changes in muscle fibre cross-sectional area, enzyme activity and production and clearance of muscle metabolites which may be expected to influence force generating capacity. Therefore, would the level of peripheral stress during sustained dynamic exercise, as assessed by measurement of proportional force utilisation, be similar to that of the untrained individual? An attempt to answer this question was made recently by Künstlinger, Ludwig and Stegemann (1985) who studied endurance-trained cyclists in addition to a group of healthy untrained (although recreationally active) subjects. The proportion of maximum force generating capacity utilised at 60 rpm and 100% of $\dot{V}O_2$ max was measured. The study reported that at 100% of $\dot{V}O_2$ max, values of the proportion of maximum force utilised were 74.1% (± 6.1) for the group of cyclists compared to 62.5% (± 9.4) for the untrained subjects. This result was attributed by the authors to the fact that the cyclists reached higher maximum work-loads than the untrained subjects - this was indeed the case, but it also surely suggests that the level of peripheral stress was greater in the group of cyclists, and if so, then the risk of a major limitation of peripheral origin (ie peripheral muscle fatigue) could be the case. Fatigue is defined as the inability of a muscle to maintain the required or expected force (Edwards, 1981) and is, during brief maximal contractions, peripheral in nature, that is, due to changes at or beyond the neuromuscular junction (Stephens and Taylor, 1972; Jones, 1981) or to depletion of high energy phosphates within the muscle, (Hultman, Bergstrom and McLennan-Anderson, 1967; Karlsson, Diamant and Saltin, 1971) or to lactate accumulation from anaerobic glycolysis (Karlsson, 1971; Tesch et al, 1978). Lactate accumulation causes a reduction in muscle pH which not only inhibits glycolysis (Ui, 1966) but may also affect muscle contractility directly, (Dawson, Gadian and Wilkie, 1978; Donaldson, Hermansen and Bolles, 1978).

Factors affecting force generating capacity

The limited data reported so far suggests that the measurement of the proportion of maximum force utilised during dynamic exercise could yield useful information concerning the degree of peripheral limitation experienced by the individual and the difference in magnitude of this limitation between trained and untrained individuals. It would be interesting to know, however, whether it is training 'per se' which affects proportional force utilisation at a given intensity, or, if the differences are due to inter-individual differences in factors such as muscle cross-sectional area (Maughan, Watson and Weir, 1983 a, b; Young, Stokes, Round and Edwards, 1985), or fibre type distribution (Young, 1984; Grindrod, Round and Rutherford, 1987). These factors are known to affect force generation (Tesch and Karlsson, 1978; Komi, Rusko, Vos and Vihko, 1977; Maughan, Watson and Weir, 1983 a, b; Young, Stokes, Round and Edwards, 1985), but their influence upon the proportion of maximum force utilised during sustained exercise has been the subject of no previous investigations.

Several previously mentioned studies have demonstrated the effect of contraction velocity upon maximum force generating capacity (Hill, 1922; Thorstensson, Grimby and Karlsson, 1976; Sargeant, Hoinville and Young, 1981) but it is unclear whether the proportion of maximum force utilised at a given power output is similarly affected. To date, the only report in the literature is that of Sjøgaard (1978), which has already received mention. Proportional force utilisation was measured over a range of pedal frequencies (40-100 rpm) during cycling exercise in a group of untrained subjects. Although the (mean) maximum value achieved at 100% of $\dot{V}O_2$ max did not exceed 49%, the study demonstrated a systematic reduction in the proportion of force utilised with increments in pedal frequency when data obtained at equivalent values of power output were compared. No investigation has been subsequently performed to confirm this result but it suggests the possibility of 'manipulating' the amount of force generating capacity utilised by simply altering the frequency of contraction.

Increasing contraction frequency may have an effect upon proportional force utilisation with subsequent beneficial effects (ie a reduction in peripheral stress), but the employment of this procedure may carry an energetic cost. If this is the case, there would appear to be little point in trying to alleviate one limitation if only to decrease the efficiency of the activity being performed and thus indirectly create another limitation.

The mechanical efficiency of an individual during steady-state exercise is expressed as the ratio of mechanical work accomplished to the metabolic energy expended. A synonymous term used is 'gross' efficiency. Values of gross efficiency during exercise rarely exceed 30% (Benedict and Cathcart, 1913; Seabury Adams and Ramey, 1977;

Stuart, Howley, Gladden and Cox, 1981). These values are consistent with Hill's original efficiency equation derived from measurements of the work done by the elbow flexors pulling a heavy fly-wheel (1922). However, controversy exists concerning the use of the gross efficiency calculation, since it does not isolate the 'unmeasured work' (that is, the energy required for accelerating and decelerating the limbs, stabilising the body and respiratory and cardiac work; Garry and Wishart, 1931), from the performance of the external work in question. A variety of definitions have subsequently emerged which subtract the oxygen cost of the measured work, sometimes referred o as 'base-line correction factors'. In net efficiency, the denominator is defined as the energy expended above that at rest. Work efficiency uses as the denominator the energy expended above that at zero load. Delta efficiency is defined as the average gradient of the relationship between work performed and energy expenditure between two specified limits for the work (see Gaesser and Brooks, 1975). In addition to the bewildering array of definitions exist equally confusing results of investigations of the effect of contraction frequency upon exercise efficiency. During studies of cycling exercise Gaesser and Brooks (1975) have reported a decrement in gross, net, work and delta efficiencies with increments in pedal frequency. A reduction in net efficiency at high pedal frequencies (86-88 rpm) has also been demonstrated by Pugh (1974). Several investigations have concluded that there are optimum pedal frequencies for exercise efficiency (Dickenson, 1929; Garry and Wishart, 1931; Bannister and Jackson, 1967; Seabury, Adams and Ramey, 1977; Hagberg, Mullin, Giese and Spitznagel, 1981; Coast and Welch, 1985), although these results disagree upon the absolute value of this optimum and whether it is modified by physical training. Clearly, in considering 'worthwhile strategies' for sustained dynamic exercise, in terms of speed and load which involve changes in force generating capacity, it is important to examine the effect of varying these factors upon the metabolic cost of the exercise.

Control of muscle force generating capacity: Patterns of motor unit recruitment

A discussion of muscle force generating capacity would be incomplete without reference to the mechanisms by which it is controlled. Sherrington first defined the 'motor-unit' as the functional unit of motor system output and formulated the idea of 'recruitment' to describe the gradation of total muscle force by addition and subtraction of active motor units (Liddell and Sherrington, 1925; Eccles and Sherrington, 1930). Denny-Brown (1929) showed that under some conditions such as the stretch reflex, motor units in slow, red muscles were recruited more readily than those in fast, white muscles. Denny-Brown introduced the idea of 'threshold' grades among the motor units innervating a given muscle and suggested that these were scaled according to relative intensities of excitatory and inhibitory input.

He then went on to demonstrate, in electromyographic studies of human subjects, an orderly pattern of recruitment during voluntary contractions, with the lowest threshold units showing the smallest EMG potential amplitudes (Denny-Brown, 1949). (Electromyography is a method of studying the electrical activity of a muscle. To develop tension in a muscle the motor units have to be activated. When a motor unit is activated, the movement of ions along the muscle fibre membrane results in an action potential.)

A major advance was made in 1965 when Henneman and co-workers formulated the 'size principle' of motor unit recruitment (Henneman, Somjen and Carpenter, 1965 a, b). Based upon a technique of 'labelling' the motor axons innervating gastrocnemius motor neurones and using the spike amplitudes to infer the size of the parent motor neurones, they suggested that small force; slow twitch units were innervated by small alpha motor neurones while larger faster units were innervated by correspondingly large motor neurones. Functional thresholds varied along the same continuum, starting with the lowest thresholds among the smallest motor neurones.

Quantification of the level of activity of whole muscles have most often been derived from integrated surface EMG (IEMG), a technique in which surface electrodes applied to the overlying skin record the summated potentials derived from many motor units. The investigation of muscle activity during dynamic exercise using the technique of electromyography may not only provide information concerning patterns of recruitment, but in conjunction with measurements of force generation, information concerning the magnitude and origin of peripheral muscle fatigue (Stephens and Taylor, 1972; Nilsson, Tesch and Thorstensson, 1977).

An alternative method of studying patterns of motor unit recruitment involves a technique in which the glycogen content of histochemically identifiable Type I (low threshold) and Type II (high threshold) units is estimated and the degree of depletion related to the activation of the unit. Using this technique, Gollnick, Piehl and Saltin (1974) demonstrated a preferential utilisation of slow twitch fibres during sustained submaximal cycling exercise at a constant pedal frequency. Fast twitch fibres were only activated either at supramaximal work-loads or by prolonged exercise at higher work-loads after a large number of slow twitch fibres had already been depleted of glycogen. Thus their results were in accordance with the size principle.

There are several reports in the literature, however, which indicate exceptions to this orderly pattern of motor unit recruitment. Glycogen depletion studies of human vastus lateralis muscle indicate preferential recruitment of Type IIa fibres with a lesser degree of Type IIb and only a moderate depletion in Type I fibres during repeated maximum voluntary dynamic contractions (Secher and Nygaard, 1976). Electrophysiological studies (Grimby and Hannerz, 1977) have also demonstrated preferential activation of high threshold motor units during extremely rapid voluntary shortening of the human extensor digitorum brevis muscle. The results of these studies suggest that there may be some functional significance in preferentially recruiting high threshold units, which give greater power per unit stimulus, under some conditions, such as movements which require a rapidly alternating movement of a limb in order to be effective (Spector, Gardiner, Zernicke, Roy and Edgerton, 1980).

Since changes in the proportion of force generating capacity utilised during dynamic exercise have also been reported to occur when contraction frequency is increased, it is suggested that there may be a 'link' between this phenomenon and changes in patterns of motor unit recruitment.

Establishing a method of measuring the proportion of maximum force generating capacity utilised during dynamic exercise may yield useful information concerning the level of peripheral stress experienced when the exercise is sustained. Once the proportional utilisation of maximum force generating capacity is known, then attempts may be made to offset or alleviate this component.

Varying the contraction frequency may be one such method, however, alternative methods have been employed in an attempt to offset the peripheral limitation to sustained exercise. (As suggested previously, the major limiting factor to sustained dynamic exercise may be a balance between central and peripheral factors. Therefore in such cases where the balance may be 'pushed' towards a peripheral limitation, it would be advantageous to employ methods to alleviate this.) One such method has been oral supplementation of the substance L-carnitine. Carnitine is a quaternary amine which plays a central role in lipid catabolism and energy production. Fritz (1955, 1963) identified carnitine as part of the shuttle mechanism whereby long chain fatty acids are converted to acyl carnitine derivatives and transported across the mitochondrial membrane. Animal studies have demonstrated that the utilisation of fat as a fuel exerts a sparing effect upon stores of muscle glycogen (Rennie, Winder and Holloszy, 1976). The facilitation of fat oxidation by carnitine supplementation could therefore be beneficial towards endurance performance by increasing the aerobic energy flux, sparing muscle glycogen and thereby increasing both endurance capacity and aerobic power.

A recent study by Marconi, Sassi, Cardinelli and Ceretelli (1985) claims to have demonstrated a 6% increase in the aerobic power of a group of athletes after 2 weeks of oral supplementation of carnitine (4g per day) although Cooper, Jones, Edwards, Montanari and Trevisani (1986) failed to demonstrate an improvement in the performance times of experienced marathon runners.

Aims of the Thesis

The aim of this Thesis was to measure the proportion of maximum force generating capacity (or relative force generation) utilised during normal dynamic exercise. Differences between untrained and trained subjects were investigated.

In Chapter 3 the effect of contraction frequency upon relative force generation was investigated and the implications, both in terms of offsetting peripheral stress and changes in the mechanical efficiency (Chapter 4) were discussed.

These studies were followed by electromyographic investigations (Chapters 5 and 6), conducted in order to explain the mechanism underlying the relationship between relative force generation and contraction velocity.

Finally, the effect of oral supplementation of L-carnitine was studied (Chapter 7) in an attempt to offset the peripheral limitation to sustained dynamic exercise by an alternative mechanism.

CHAPTER 2

FORCE GENERATION OF HUMAN MUSCLE

DURING SUBMAXIMAL AND MAXIMAL CYCLING EXERCISE

INTRODUCTION

There are several reports in the literature concerning the measurement of force generation during either prolonged submaximum (Hoes, Binkhorst, Smeekes-Kuyl and Vissers, 1968; Bigland-Ritchie and Woods, 1976; Sargeant and Davies, 1977) or brief maximum (Sargeant, Hoinville and Young, 1981; Dolan, 1985) cycling exercise. However, few studies have been performed in which both submaximum and maximum forces have been measured and therefore data concerning the proportion of maximum force utilised (or relative force generation) during cycling exercise is limited. Sjøgaard (1978) measured the relative leg force generation of six untrained male subjects (age range 20-34 years) during cycling exercise at two values of power output requiring 70% and 100% of maximum oxygen uptake ($\dot{V}O_2$ max) respectively, over a range of pedal frequencies from 40-100 revolutions per minute (rpm). Sjøgaard reported a systematic linear increase in relative force generation with increasing exercise intensity (expressed as % of $\dot{V}O_2$ max). At 100% of $\dot{V}O_2$ max, however, relative force generation did not exceed 49%; in other words, a large reserve of force-generating capacity was still available, ever when the subject was exerting maximum aerobic power.

A similar study by Künstlinger, Ludwig and Stegemann (1985), relating relative force generation to work-load (Watts) at a pedal frequency of 60 rpm reported a mean value of 67.5 ± 8% (SD) at maximum levels of exercise in a group of eighteen male subjects which included ten endurance-trained athletes. In this study, however, the mean peak leg forces recorded during the progressive exercise test were expressed as a proportion of the maximum isometric contractile force (MVC) rather than the maximum dynamic force generated at 60 rpm.

The purpose of the study described in this chapter was to measure the leg forces generated during a continuous progressive exercise test, in a large group of subjects (n = 33), and also to determine whether relative force generation could be influenced by the differing physiological and biochemical characteristics of the subjects' muscles. With this in mind, groups of athletes as well as healthy untrained individuals, were studied.

SUBJECTS

Thirty three subjects volunteered to participate in this study. The group included twenty healthy untrained subjects: thirteen males and seven females (age range 18-39 years) and thirteen athletes: ten males and three females (age range 17-43 years). Physical characteristics of the untrained and trained subjects are given in Tables 1 and 2 respectively.

The untrained subjects included colleagues and students within the Polytechnic of North London and the Department of Medicine, University College Faculty of Clinical Sciences. The trained subjects were all members of local athletic and cycling clubs.

Informed consent was obtained from all subjects prior to testing.

METHODS

Measurement of Maximum Force Generating Capacity under Constant Velocity Conditions

Maximum leg forces were measured isokinetically during a twenty second effort performed on a modified cycle ergometer (Fig 1) (Sargeant, Hoinville and Young, 1981). The ergometer was modified by the addition of a 3 hp electric motor driving the cranks through a variable speed gearbox enabling the appropriate pedal frequency to

SUBJECT	SEX	AGE (YRS)	HT (M)	BODY WT (Kg)	ULV (litres) (Muscle + Bone) R Leg	L leg	LBM%
MA	M	25	1.72	78.9	3.94	4.17	91.1
AE	M	38	1.64	71.8	3.38	3.53	85.2
SL	M	29	1.79	66.2	3.26	3.29	87.7
JP	M	36	1.74	89.4	3.55	3.49	72.6
PS	M	23	1.72	64.7	3.24	3.34	91.8
JH	M	25	1.84	74.2	4.89	4.63	89.8
DM	M	30	1.76	74.5	4.11	4.32	81.1
RA	M	31	1.70	65.2	4.50	4.74	89.1
NM	M	25	1.71	71.1	3.03	3.19	83.3
TW	M	18	1.91	70.8	4.09	3.90	89.2
AF	M	32	1.68	70.3	2.43	2.92	79.8
TH	M	29	1.75	72.8	3.99	3.97	87.3
AS	M	40	1.78	68.7	4.82	4.69	87.7
OB	F	24	1.68	63.0	3.19	3.16	73.0
ED	F	31	1.62	50.5	2.55	2.49	79.1
SW	F	21	1.77	84.3	3.86	3.74	70.5
SJ	F	39	1.66	51.4	1.83	1.84	73.4
NV	F	27	1.59	55.9	2.91	2.81	70.5
CG	F	24	1.66	56.0	2.35	2.37	76.0
OR	F	23	1.62	65.1	2.74	2.66	72.1

TABLE 1: PHYSICAL CHARACTERISTICS OF THE UNTRAINED SUBJECTS (n = 20)

ULV: Upper Leg Volume (Litres)

% LBM: Percentage Lean Body Mass

SUBJECT	ATHLETIC DISCIPLINE	SEX	AGE (YRS)	HT (M)	BODY WT (Kg)	ULV (litres) (Muscle + Bone) R leg	ULV (litres) (Muscle + Bone) L leg	LBM%
MS	CYCLING	M	25	1.73	72.1	4.73	4.58	88.8
NA	CYCLING	M	17	1.79	70.6	3.83	3.84	88.2
AF	CYCLING	M	36	1.68	66.0	3.66	3.44	89.9
AM	CYCLING	M	43	1.88	74.3	3.56	3.76	87.7
PS	CYCLING	M	24	1.79	73.0	4.12	4.12	90.4
IR	TRI-ATHLON	M	18	1.78	77.8	3.70	3.65	88.0
NS	MARATHON RUNNING	M	32	1.81	69.9	3.62	3.58	91.2
SP	MARATHON RUNNING	M	30	1.81	68.2	4.13	3.88	88.3
MG	WEIGHT LIFTING	M	21	1.78	100.8	6.36	5.99	86.4
GW	WEIGHT LIFTING	M	22	1.74	71.9	4.85	5.00	84.6
LM	HIGH JUMP	F	18	1.84	66.4	3.25	4.07	81.2
JH	DISCUS	F	22	1.86	83.0	2.96	3.15	72.6
ML	SHOT PUT	F	22	1.67	67.7	2.93	2.97	76.2

TABLE 2: PHYSICAL CHARACTERISTICS OF THE TRAINED SUBJECTS (n = 13)

ULV: Upper Leg Volume (Litres)

% LBM: Percentage Lean Body Mass

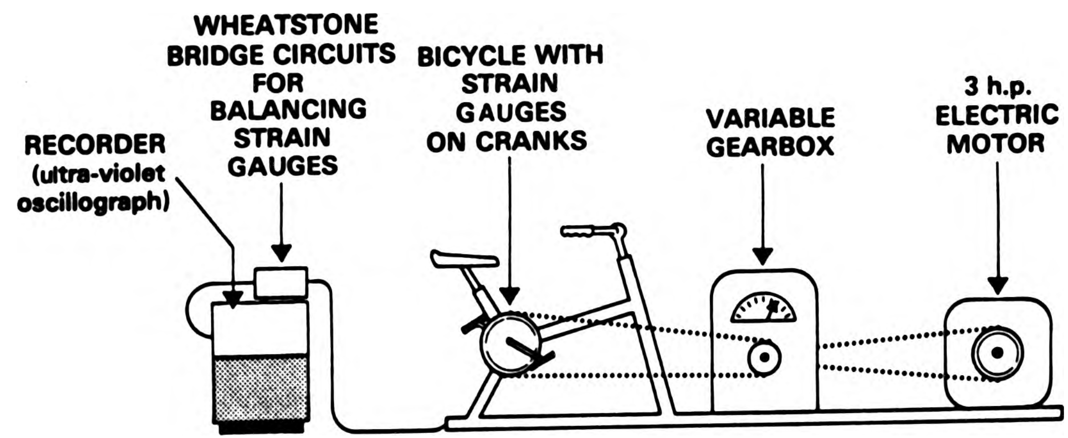


Fig. 1 : Diagrammatic representation of the isokinetic cycle ergometer used to measure maximum peak forces.

be set. The leg forces exerted on the pedals were continuously monitored by silicon strain gauges bonded to the cranks of the ergometer. The output from the strain gauges was relayed to brass slip rings which were mounted on discs attached inside each crank. The discs were in contact with metal pick-ups which relayed the output from each crank via separate Wheatstone Bridge circuits to an uv oscillograph recorder (EMI SE 9150). In this way force was recorded continuously and separately for each leg.

Crank position was indicated on the force recording by a photoelectric transistor and lamp which were aligned and mounted on either side of the left slip ring disc. The disc was indented at 15° intervals so that when the cranks were moving, corresponding markers were produced on the force record, through a separate channel. The Top Dead Centre of the left-hand crank was indicated by a triple marker.

Prior to and immediately after each test, both left and right-hand ergometer cranks were calibrated separately at a position corresponding to 90° from top dead centre by exerting a known force upon them.

After the first calibration, the subject was seated comfortably for normal cycling upon the ergometer, allowing some slight knee flexion at the bottom dead centre of each crank position. The saddle height was recorded and used for subsequent tests. The subjects' shoes were attached to the pedals with the ball of the foot over the pedal spindle.

After switching on the motor at its slowest speed, the variable gearbox was adjusted to give the appropriate pedal frequency. The subjects were then allowed between five and fifteen seconds to accustom themselves to the pedal frequency; during this time they were instructed to make no muscular effort but to merely allow their legs to be taken around by the motor. After this time, the subject was asked to make a maximum effort for twenty seconds in an attempt to speed up the motor. The characteristics of the motor were such that pedal frequency remained almost unchanged ($<4\%$) during the course of the twenty second test (Sargeant et al 1981, Dolan 1985).

Throughout the test, peak force for each leg, which was exerted at 90° from Top Dead Centre, was determined separately. The mean of the three highest consecutive values of peak force during the twenty second test was calculated for each leg individually. The calculated mean of the right and left leg values was taken to be the Maximum Peak Force (PF max).

Measurement of submaximum and maximum oxygen uptake and leg forces during a progressive exercise test

In order to measure oxygen uptake and the leg forces exerted in response to standardised submaximum and maximum work-loads, the subject was seated on the same ergometer as described for the determination of PF max. The chain of the ergometer, however, was connected to drive a conventional friction-braked ('Monark') ergometer flywheel, (Greig, Sargeant and Rutherford, 1985). This system enabled mean peak force, oxygen uptake and external power output to be measured simultaneously. (Fig 2.)

A continuous progressive exercise test was conducted at a pedal frequency of 70 rpm. This pedal frequency was maintained with the aid of a metronome and frequent checking of the rpm by the investigator via a stopwatch. The work-load was increased incrementally every five minutes from unloaded pedall ing. Work-loads were chosed to span the subjects' capacity up to and including maximum.

A semi-continuous open circuit technique was used to record

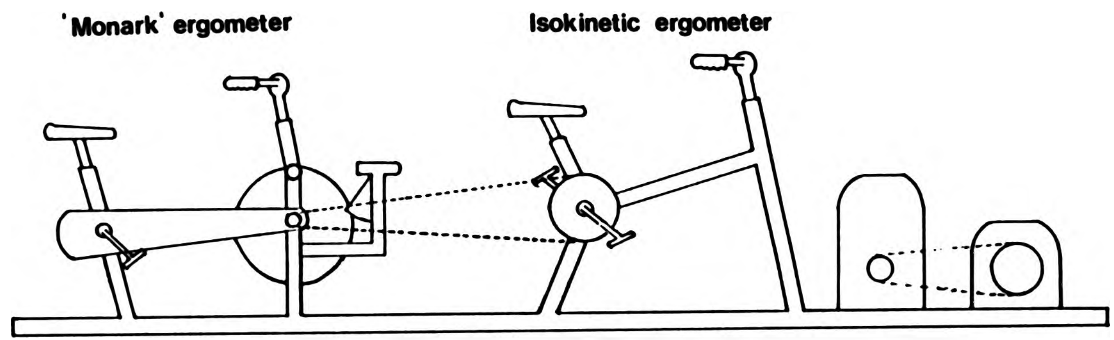


Fig. 2 : Diagrammatic representation of the Isokinetic and "Monark" ergometers connected in series for determination of average peak forces.

inspired volume (Parkinson Cowan dry gas meter), mixed expired CO_2 (PK Morgan infra-red analyser 901-Mk 2) and mixed expired O_2 (Sybron Taylor paramagnetic oxygen analyser, 570A, connected to a Dalton DC voltmeter 1045). The CO_2 analyser was calibrated prior to testing with atmospheric air and a mixture containing approximately 4% CO_2, 17% O_2 and 79% N_2. This gas mixture had previously been checked by Haldane gas analysis. The O_2 analyser was calibrated with atmospheric air and 100% N_2.

To record the electrocardiograph, the skin was cleaned thoroughly using an abrasive paste (Omni Prep, Weaver and Co, USA). Light-weight disposable electrodes (Palmer Bioscience) were attached to the skin on the mid-axillary line V5 position on the left (exploring electrode) and right (earth electrode) sides and below the right collar bone (reference electrode), ten to fifteen minutes before the progressive test. The subject was then connected to a telequipment oscilloscope (S51B) which displayed the ecg. The output from the oscilloscope was relayed to a channel on the uv oscillograph recorder. In addition, cardiac frequency was summed over every thirty seconds and displayed on a meter.

Using this system, inspired volume ($\dot{V}I$), fractional mixed expired oxygen (FeO_2), fractional mixed expired carbon dioxide ($FeCO_2$) and cardiac frequency (fc) were recorded every thirty seconds over the final two minutes of each increment in work-load along with the ecg as previously described by Sargeant, Crawley and Davies (1979).

The peak force generated during a sample of fifteen revolutions was measured for each leg and during each increment in work-load and a mean value was calculated. The mean values obtained for each leg were further averaged to obtain a value of mean peak leg force corresponding to each increment in work-load.

Measurement of % Type II fibre area from needle biopsy samples

Twenty five of the subjects volunteered to have a needle biopsy which was performed within the Department of Medicine, University College Faculty of Clinical Sciences, after obtaining approval by the Committee for the Ethics of Human Procedures, University College Hospital.

A needle biopsy technique (Bergström, 1962; Edwards, Young and Wiles, 1980) was used to obtain a sample of muscle from the lateral part of the quadriceps femoris. This site was chosen since it is free of major blood vessels and nerves and it is the major extensor of the knee joint and therefore particularly suitable for studies in which structure is to be related to function.

Prior to the biopsy, blood coagulation indices were checked. A sterile technique was used to administer a local anaesthetic (2% lignocaine) into the skin and subcutaneous tissues and a 6-7 mm incision was made with a pointed blade to allow the needle into the muscle. Immediately after the biopsy, the sample obtained was mounted on a cork disc and the fibres were orientated under a dissecting microscope, supported by a mounting medium, and then rapidly frozen in isopentane cooled to its freezing point with liquid nitrogen. The samples were stored at - 169°C until analysis. Serial transverse sections (4 μm) were cut with a microtome at - 25°C and stained for the enzyme myosin ATP-ase after pre-incubation at ph 9.4 to identify Type I (pale staining and low activity) and Type II (dark staining and high activity) muscle fibres.

Measurement of fibre areas and percentage composition of Type I and Type II fibres was made using a semi-automatic system described by Jones, King and Round (1980). A total of at least eighty fibres of each type were measured by two investigators. Where there was a difference > 10% between the two, a third person repeated the measurement. Estimates of fibre frequency did not vary by >7% between the two investigators. The coefficient of variation, made from paired unilateral quadriceps samples in thirty subjects, has been found to be 17% for fibre frequency and 8% for fibre diameter. (Wiles, Young, Jones and Edwards, 1979.)

Measurement of Upper Leg (Muscle plus Bone) Volume

An anthropometric technique (Jones and Pearson, 1969) in which the volume of the upper leg is partitioned into segments which are similar to truncated cones, was used to calculate upper leg muscle plus bone volume. (Fig 3.)

With the subject standing erect and the feet slightly apart, the height above the floor and the circumference were taken at four sites on each leg. The sites were; the gluteal furrow, one third of the subischial height up from the tibial-femoral joint space, the minimum circumference above the knee and the maximum circumference around the knee joint space.

Skin-fold thicknesses were measured with Harpenden calipers at two sites on each leg, the anterior and the posterior thigh in the mid-line at the level of one-third subischial height. Since the calipers pick up a double layer of skin-fold tissue under pressure, the reading was converted to a true single measurement using an appropriate regression equation (based on a comparison between

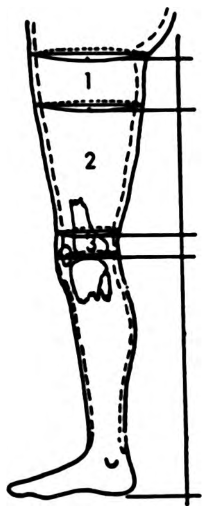


FIGURE 3: Diagram of the leg showing the sites at which anthropometric measurements were made for determination of upper leg volume.
(After Jones and Pearson, 1969)

X-Ray fat, caliper fat and the linear relationship between them) to each sex and to the fat site. (Jones, 1970.)

The formula to calculate the volume of a truncated cone was applied to each segment of the upper leg in turn, and the results were summated to give a value for upper leg volume. To calculate muscle plus bone volume, the corrected fat caliper readings for each thigh were summed and subtracted from it's diameter. The inner cone volumes were calculated as described.

Measurement of Lean Body Mass

The calculation of lean body mass was made according to the method described by Durnin and Rahaman (1967). Skinfold thicknesses were taken, using Harpenden calipers, at four sites on the left side of the body. The sites selected were: Biceps and Triceps, over the mid-point of each muscle belly; Subscapular, just below the tip of the inferior angle of the scapular at an angle of approximately 45° to the vertical; Suprailiac, just above the iliac crest in the mid-axillary line. The log. of the sum of the four skinfold thicknesses was inserted into the appropriate regression equation (based upon the linear relationship between body density and skinfold thickness) to give a value of body density. The regression equations are given below:

Men: $y = 1.1610 - 0.0632\, x$

Women: $y = 1.1581 - 0.0720\, x$

Calculation of percentage body fat from body density measurements was based upon the equation given by Siri (1956) and shown below:

$$\text{Fat (\%)} = [(4.95/\text{Density}) - 4.50] \times 100$$

Lean body mass was then calculated by subtracting the product of body weight (kg) and percentage body fat from body weight.

PROTOCOL

The subject arrived at the Laboratory in a post-absorptive state, was informed of the procedures involved, and written consent was obtained.

Physical anthropometry was performed for determination of upper leg (muscle plus bone) volume and lean body mass. The subject's height and body weight were also measured.

The subject then performed the twenty second isokinetic test at 70 rpm for determination of PF max. After a rest period, during which the ecg electrodes were attached and the ergometer chain altered to drive the conventional 'Monark' ergometer, a continuous progressive exercise test was performed, also at 70 rpm.

When the trained cyclists were tested, the ergometer saddle was changed to a racing saddle to ensure optimal performance. The cyclists also wore their cycling shorts and shoes which were equipped with metal rims on the soles to insert in front of rims on the pedal spindles.

During the progressive test, throughout which mean peak forces were recorded, the subjects were instructed to maintain a constant pedal frequency of 70 rpm; several of them experienced some difficulty in maintaining this frequency. Any data, therefore, which was collected when the pedal frequency was outside the range ± 5 rpm of the required 70 rpm, was excluded from further analysis.

Muscle biopsies were performed at a time convenient to the subject and to the medical staff of the Department of Medicine, University College London, but were always within one month of the other measurements.

STATISTICS

Conventional statistical methods were employed to calculate means ($\bar{x}$), standard deviations (SD), standard error of the means (SE), and linear correlation coefficients (r). Determination of linear regression was performed using the method of least squares. Intra-individual differences and differences between mean values were tested for significance using Student's t-tests for paired and unpaired (two-sample) data. The level of significance was denoted with "p" values. The coefficient of variation was defined as $SD/\bar{x} \times 100$.

RESULTS

Analysis was performed on the data obtained from 32 subjects since one of the trained subjects (PS) was unable to maintain pedal frequency within the defined criterion throughout the whole duration of the progressive test.

The mean peak leg forces exerted on the cranks of a cycle ergometer were recorded during each increment in power output throughout a continuous progressive exercise test performed at 70 rpm.

Fig 4 describes the relationship between $\dot{V}O_2$ (l/min) and mean peak force (N) recorded during the progressive test. The data was obtained from 32 subjects, with a total of 127 observations. The relationship was linear ($y = 49.05 + 104.36x$; obtained from regression analysis) with a significant correlation coefficient, ($r = 0.95$, $p < 0.005$).

The mean peak forces were expressed as a proportion (% PF max) of the maximum force generating capacity measured isokinetically at the same pedal frequency. (See Tables 3 and 4 for actual PF max data).

When % PF max was related to exercise intensity, expressed in terms of % $\dot{V}O_2$ max, the result again was a significant linear relationship between the two ($y = 3.29 + 0.47x$, $r = 0.88$, $p < 0.005$). There is a systematic increase in % PF max with increasing exercise intensity (Fig 5).

The mean data for the group corresponding to increments in power output requiring 25, 50, 75 and 100% respectively of $\dot{V}O_2$ max is illustrated in Fig 6. (These data are interpolated values derived from regression analysis.) Relative force generation increases from 15 $\pm$ 1% (SEM) at an exercise intensity requiring 25% of $\dot{V}O_2$ max, to 50 $\pm$ 2% (SEM) at 100% of $\dot{V}O_2$ max.

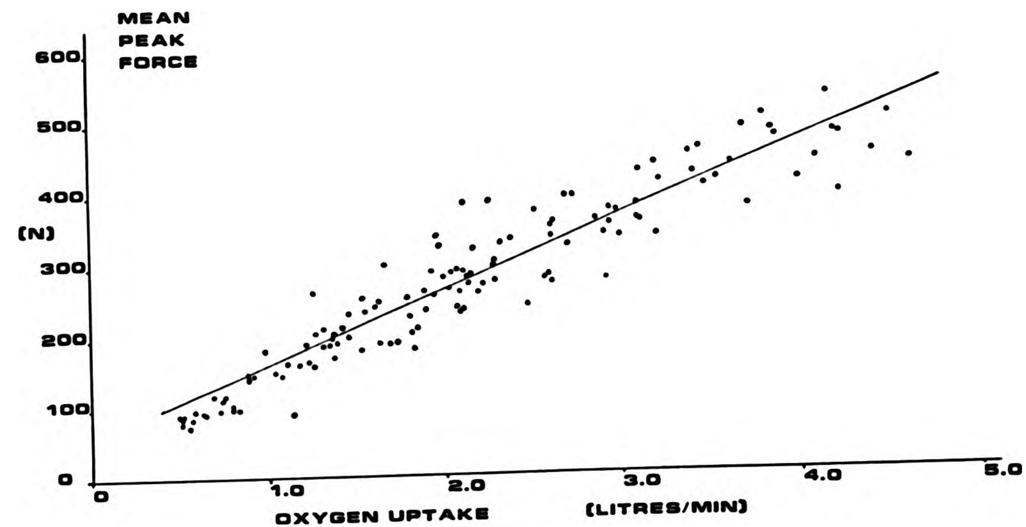


FIGURE 4

Relationship between $\dot{V}O_2$ (l/min) and mean peak force (N) recorded during a continuous progressive exercise test at 70 rpm conducted on 32 subjects

$y=49.051 + 104 \cdot 360X$; $r = 0.945$; $p<0 \cdot 005$

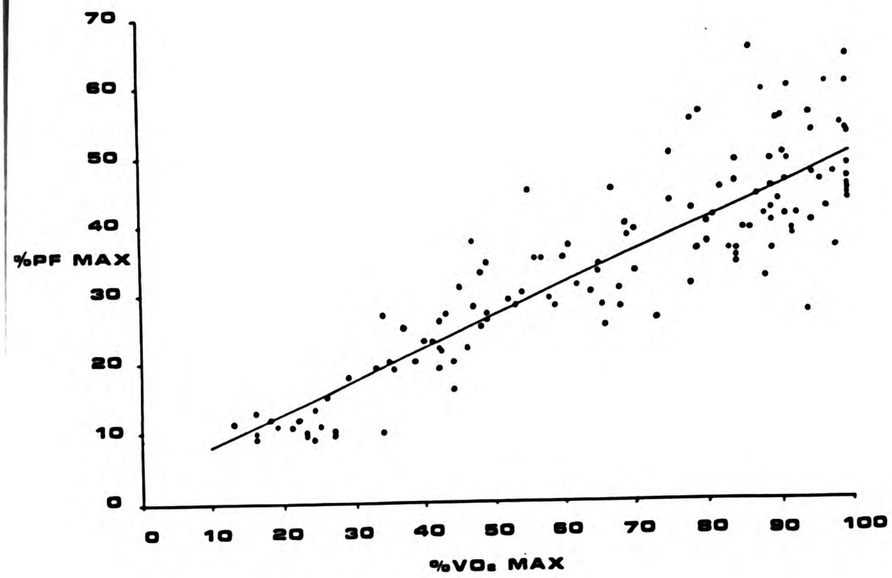


FIGURE 5

Relationship between exercise intensity (% $\dot{V}O_2$ max)

and relative force generation (% PF max)

during a progressive exercise test conducted at 70 rpm

on 32 subjects

y = 3·290 + 0·468 x; r=0.879;p<0.005

SUBJECT	% TYPE II FIBRE AREA	PF max (70 rpm) [N/1ULV]	$\dot{V}O_2$ max [ml/min/1ULV]	mean rpm
MA	70	198	392	71
AE	52	210	305	67
SL	53	256	510	72
JP	50	234	493	71
PS	57	255	383	71
JH	61	189	441	68
DM	-	187	391	69
RA	40	176	386	71
NM	78	291	519	68
TW	-	191	444	67
AF	-	336	442	71
TH	55	212	451	69
AS	52	198	336	71
OB	50	152	310	71
ED	42	221	425	68
SW	58	207	342	71
SJ	39	176	540	69
NV	45	210	456	68
CG	43	221	419	71
DR	60	243	393	69

TABLE 3: UNTRAINED SUBJECTS (n = 20)

MAXIMUM PEAK FORCE AT 70 RPM, MAXIMUM AEROBIC POWER,

% TYPE II FIBRE AREA, AND MEAN PEDAL FREQUENCY

DURING THE PROGRESSIVE EXERCISE TEST

SUBJECT	% TYPE II FIBRE AREA	PF max (70 rpm) [N/1ULV]	$\dot{V}O_2$ max ml/min/1ULV	mean rpm
MS	51	245	435	68
NA	-	218	587	73
AF	-	222	549	67
AM	-	237	583	72
IR	61	268	557	70
NS	10	209	597	66
SP	17	199	581	74
MG	57	245	300	70
GW	78	214	353	70
LM	71	244	480	67
JH	-	316	511	70
ML	65	325	402	69

TABLE 4: TRAINED SUBJECTS (n = 12)

MAXIMUM PEAK FORCE AT 70 RPM, MAXIMUM AEROBIC POWER,

% TYPE II FIBRE AREA AND MEAN PEDAL FREQUENCY

DURING THE PROGRESSIVE EXERCISE TEST

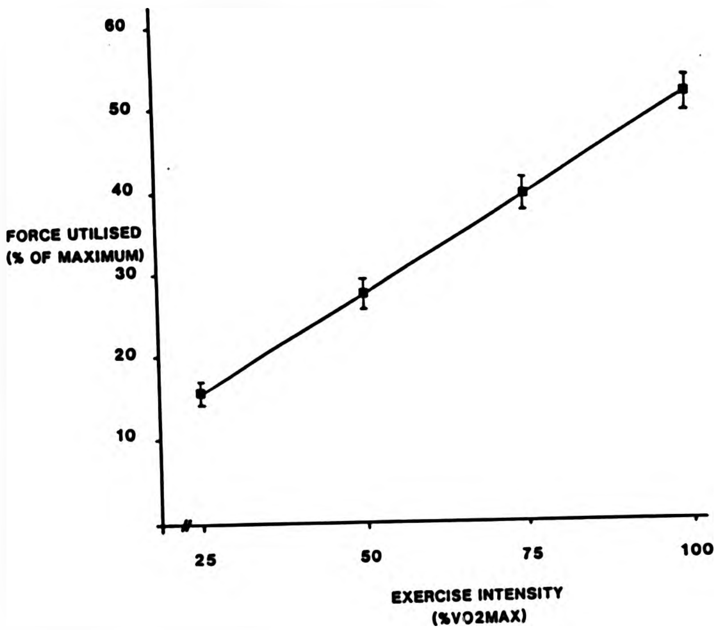


FIGURE 6

Relationship between exercise intensity (% $\dot{V}O_2$ max)

and relative force generation

mean data ± ISEM are shown

Although an obvious linear relationship exists between % PF max and % $\dot{V}O_2$ max, large differences in the individual response, in terms of relative force generation, at any given exercise intensity were observed. The intersubject variation apparent at one exercise intensity requiring 75% of $\dot{V}O_2$ max is demonstrated in the form of a histogram (Fig 7).

Although the mean value of relative force generation at this exercise intensity is 39%, the range of values extends from 24% to 56%. The values of 24% and 56% correspond to data obtained from a weightlifter and a marathon runner respectively. In fact, the data obtained from the 'power' athletes were below the mean value for the group, whereas that obtained from the endurance-trained cyclists and runners was above the mean value (Table 5). this does not mean that the untrained subjects were confined to the mid-range; Table 5 shows that values of relative force generation obtained from the untrained subjects were represented at the extremes of the range as well as the mid-range.

The relationship between maximum dynamic strength (PF max at 70 rpm) and relative force generation at an exercise intensity requiring 75% of $\dot{V}O_2$ max is illustrated in Fig 8. The relationship was significant ($y = 52.81 - 0.02x$, $r = -0.49$, $p < 0.005$) but with high intersubject variability, which was not reduced when maximum peak forces were standardised for upper leg muscle (plus bone) volume ($y = 54.65 - 0.07x$, $r = -0.44$, $p < 0.005$).

The relationship between relative force generation (at 75% $\dot{V}O_2$ max) and % Type II fibre area was highly significant ($y = 53.72 - 0.03x$, $r = -0.67$, $p < 0.005$) although not without variability (Fig 9). Subjects with a high % Type II fibre area exerted a relatively lower proportion of maximum force generating

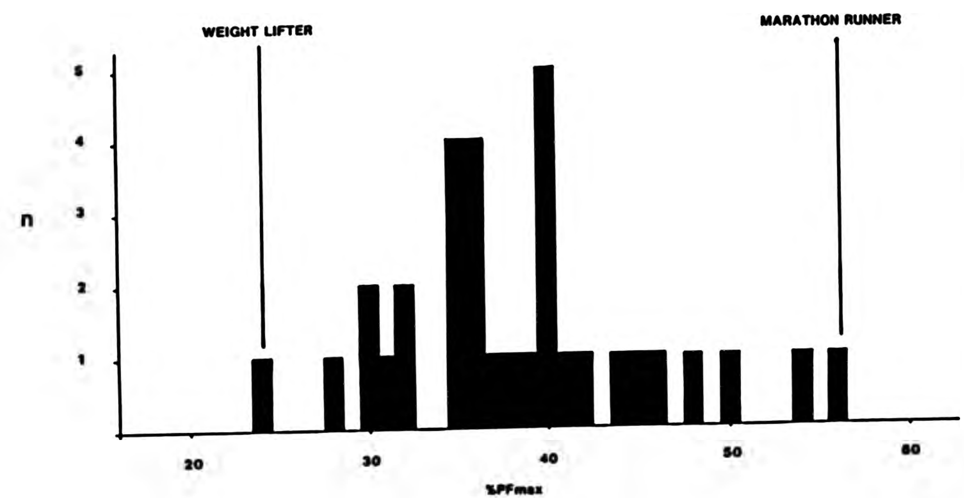


FIGURE 7

Histogram showing relative force generation of 32 subjects at a power output requiring 75% of $\dot{V}O_2$ max and at a pedal frequency of 70 rpm

SUBJECT	STATE OF TRAINING	EXERCISE INTENSITY (% $\dot{V}O_2$ max) 25	50	75	100	MEAN RPM
		% PFmax.				
MA	UNTRAINED SUBJECTS	14	23	32	42	71
AE		16	28	40	51	67
SL		14	27	40	54	72
JP		27	33	39	45	71
PS		9	19	30	41	71
DM		14	25	36	47	69
RA		15	27	40	52	71
NM		14	25	35	45	68
TW		18	31	44	57	67
AF		19	34	50	65	67
TH		13	28	42	56	69
AS		12	22	32	43	71
OB		16	26	36	46	71
ED		17	27	38	48	68
SW		17	26	35	45	71
SJ		33	43	54	64	69
NV		21	29	37	45	68
CG		17	27	36	46	71
OR		15	25	35	45	69
JH		15	28	41	53	68
MS	ENDURANCE-TRAINED ATHLETES	13	29	45	61	68
NA		2	21	40	59	73
AF		7	19	28	37	71
AM		19	33	48	62	72
IR		15	25	36	47	70
NS		23	39	56	72	66
SP		24	35	46	56	74
MC	POWER-TRAINED ATHLETES	11	17	24	30	70
GW		11	21	31	42	70
LM		15	28	40	52	67
JH		10	23	35	48	70
ML		5	18	30	42	69
$\bar{x}$ (± 1SEM)		15 (1)	27 (1)	39 (1)	50 (2)	70 (0.3)

TABLE 5

Individual values of relative force generation (% PF max) corresponding to 25, 50, 75 and 100% of $\dot{V}O_2$max respectively. Data obtained from thirty two subjects at a mean pedal frequency of 70 rpm are shown

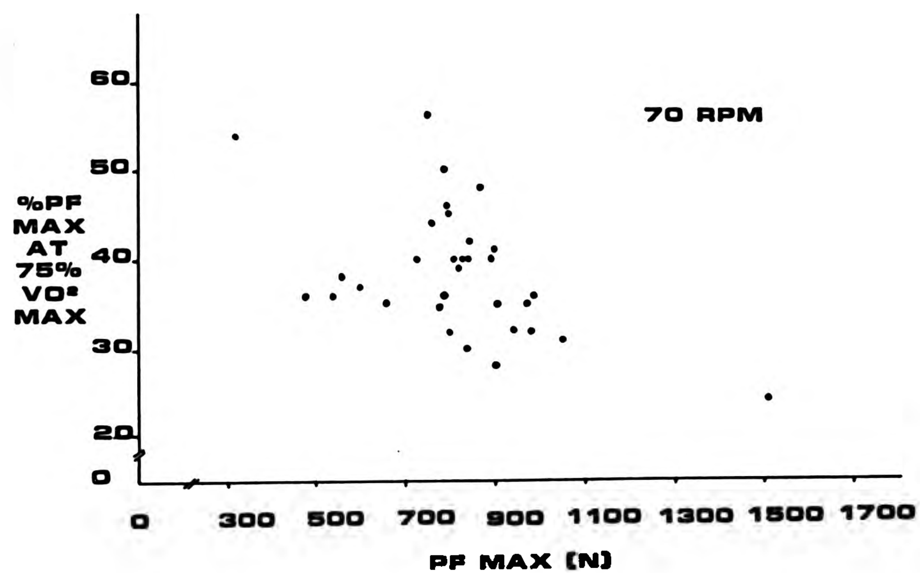


FIGURE 8

Relationship between maximum peak force at 70 rpm and relative force generation at a power output requiring 75% of $\dot{V}O_2$ max

$y = 52.81 - 0.18x$; $r = -0.493$; $p<0.005$

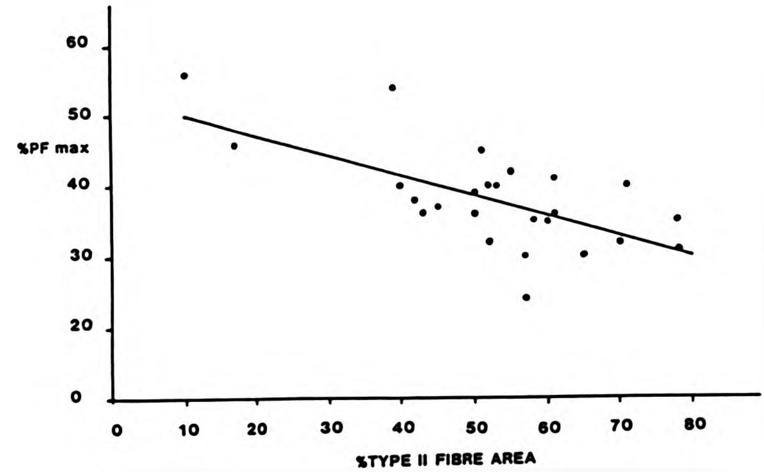


FIGURE 9

Relationship between % Type II fibre area and relative force generation at a power output requiring 75% of $\dot{V}O_2$ max

$y = 53.719 - 0.299x$; $r = -0.666$; $p<0.005$

capacity than those with a low % Type II fibre area. Conversely, subjects with a high aerobic power ($\dot{V}O_2$ max) generated a high proportion of maximum force generating capacity at any given work-load. This is illustrated in Fig 10 which relates relative force generation (at 75% $\dot{V}O_2$ max) to maximum oxygen uptake (standardised for upper leg muscle (plus bone) volume). The relationship is also highly significant ($y = 13.99 + 0.05x$, $r = 0.67$, $p < 0.005$).

To summarise the results obtained from the present study; the mean peak forces exerted on the cranks of a cycle ergometer were measured over each increment in power output during a progressive exercise test performed at 70 rpm. Mean peak force increased linearly with increasing values of oxygen uptake. When the mean peak forces were expressed as a proportion of maximum force generating capacity (at the same pedal frequency) and related to exercise intensity (% $\dot{V}O_2$ max), the result was again linear, with relative force generation increasing from 15% at 25% of $\dot{V}O_2$ max to 50% at 100% of $\dot{V}O_2$ max. A large intersubject variation in relative force generation at any given exercise intensity was observed which was apparent in the untrained as well as the trained subjects.

Relative force generation was shown to be significantly related to maximum aerobic power, and significantly inversely related to maximum dynamic strength and % Type II fibre area.

DISCUSSION

Relative Force Generation during dynamic exercise

The mean peak forces exerted on the cranks of a cycle ergometer were measured during a continuous progressive exercise test performed at 70 rpm, up to and including $\dot{V}O_2$ max. The data obtained from thirty two subjects were analysed. The linear relationship obtained

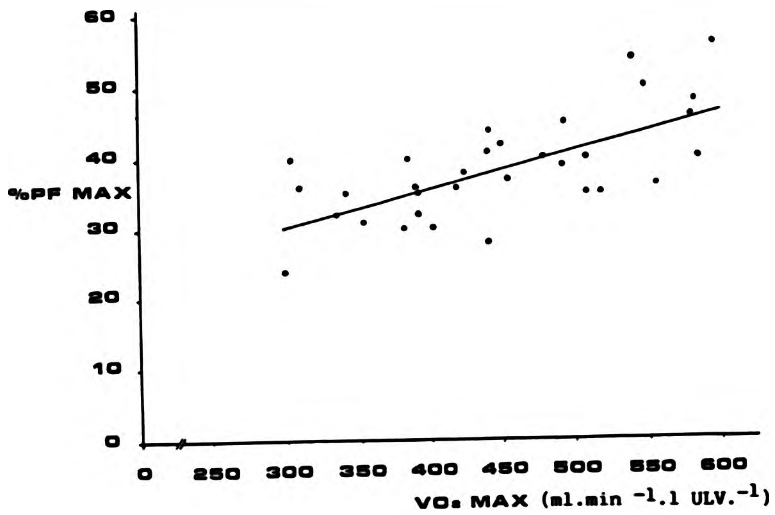


FIGURE 10

Relationship between maximum aerobic power

and relative force generation at a power

output requiring 75% of $\dot{V}O_2$ max

$y = 13.99 + 0.05\,x$; $r = 0.667$; $p < 0.005$

FIGURE 11: Section from a biopsy sample obtained from the Vastus Lateralis muscle of subject GW (Weightlifter). The section has been stained for the enzyme myosin ATP-ase after pre-incubation at pH 9.4 to identify Type I (pale staining and low activity) and Type II (dark staining and high activity) muscle fibres

between mean peak force generation and oxygen uptake is in agreement with previous studies on animal (Wilson and Stainsby, 1978) and human muscle (Bigland-Ritchie and Woods, 1976; Sargeant and Davies, 1977). A linear relationship between mean peak force and external power output has also been reported during dynamic exercise, (Hoes, Binkhorst, Smeekes-Kuyl and Vissers, 1968; Künstlinger, Ludwig and Stegemann, 1985).

The modified cycle ergometer described by Sargeant et al (1981) was used to measure maximum peak forces under isokinetic conditions (70 rpm). The leg forces subsequently measured during the progressive test were expressed as a proportion of maximum force generating capacity (under the same conditions of crank velocity) and were related to exercise intensity expressed as percentage of $\dot{V}O_2$ max. Relative force generation was shown to increase with increasing exercise intensity, as demonstrated by Sjøgaard (1978). (The data obtained by Sjøgaard also appears in a report by Löllgen, Graham and Sjøgaard, 1980.)

The most interesting result of the present study was the large intersubject variation in relative force generation at any given exercise intensity. A power output requiring 75% of $\dot{V}O_2$ max, for example, required a range of 24 to 56% of the maximum dynamic force. The values of 24% and 56% were obtained from a weightlifter and a marathon runner respectively. In fact, relative force generation was above the mean value at all exercise intensities studied for the endurance-trained athletes and below the mean value for the 'power' athletes. This illustrates how qualitative differences within human skeletal muscle, which are more pronounced in a trained athlete, determine the proportion of maximum force required during sustained dynamic exercise and this may be expected to have profound effects upon the level of peripheral stress experienced by the subject.

Relative Force Generation; relationship to muscle strength and aerobic power

The relationship between relative force generation and maximum dynamic strength (PF max at 70 rpm) was investigated in the present study and shown to be significant (as was the relationship when maximum dynamic strength was standardised for upper leg muscle (plus bone) volume). The results clearly demonstrate, however, that there were certain individuals of similar maximum dynamic strength (per litre of muscle mass) who showed differences in relative force generation at given values of power output during the progressive test. This variation was presumably due to differences in aerobic potential between the subjects, ie. those subjects of a similar PF max (per litre ULV) but a greater % PF max, (at a given value of power output), also demonstrated a greater aerobic potential ($\dot{V}O_2$ max ml l ULV^{-1} min^{-1}) (see Tables 3, 4 and 5). A further illustration of the influence of aerobic potential upon % PF max is given in Figure 10. These data suggest that those subjects whose muscles have a high aerobic potential must exert a greater proportion of their maximum force generating capacity in order to maintain a given value of power output.

Similar results were demonstrated by Künstlinger et al (1985) in which mean peak forces generated during a continuous progressive exercise test conducted at 60 rpm were measured in a group of endurance-trained cyclists and a reference group. Their data showed that at 100% of $\dot{V}O_2$ max, values of relative force generation (expressed in terms of % MVC) were significantly higher in the group of cyclists, although both groups were of similar maximum isometric strength. Curiously, there were no differences in the $\dot{V}O_2$ max between groups, but this data was not standardised for muscle size, a procedure which may have revealed differences in aerobic potential responsible for the differences in relative force generation.

A major factor influencing both aerobic potential and dynamic strength (per unit muscle size) is the fibre type distribution, which is discussed below.

Relationship between Relative Force Generation and % Type II Fibre Area

Skeletal muscle fibres differ consierably in various properties. Links between the contractile properties of a muscle and its metabolic and morphological characteristics, in terms of the distribution of fibre types have been firmly established (see reviews by Close, 1972; Burke and Edgerton, 1975; Saltin and Gollnick, 1983). Although fibre type distribution within human skeletal muscle is rather homogenous, there are large inter-individual variations in the proportions of Type I (slow twitch) and Type II (fast twitch) fibres within any given muscle. This variation and the associated differences in enzyme activities and capillarisation are reflected in various measures of physical performance, such as endurance and muscle strength, (Thorstensson, 1976; Thorstensson, Grimby and Karlsson, 1976; Coyle, Costill and Lesmes, 1979). Thorstensson (1976) demonstrated for the first time in human skeletal muscle the functional significance of Type II muscle fibres by showing a correlation between muscle performance (maximum contraction speed and the ability to produce force at high velocities) and Type II fibre distribution and area. A high percentage area of Type II fibres would seem favourable in power type athletic events where success depends upon maximising force generation, and several studies have shown that power athletes do tend towards a predominance of Type II muscle fibres. (Edström and Ekblom, 1972; Gollnick, Armstrong, Saubert, Piehl and Saltin, 1972; Costill, Daniels, Evans, Fink and Krahenbuhl, 1976; Thorstensson, Larsson, Tesch and Karlsson, 1977.) See also Fig 11.

A significant inverse correlation between % Type II fibre area and relative force generation was demonstrated in the present study. The power athletes with a high % Type II fibre area generated a lower proportion of their maximum force generating capacity than the endurance-trained cyclists and runners, at any given value of power output. This is not to say that the untrained subjects were confined to the mid-range regarding % Type II fibre area; several of them demonstrated a high % Type II fibre area (Table 3) and concomitant with this was the generation of a lower proportion of maximum force for a given exercise intensity. This implies that it was not the 'state of training' per se which influenced relative force generation but the % Type II fibre area, thus supporting the suggestion by Tesch, Wright, Vogel, Daniels, Sharp and Sjödin (1985) 'that peak force relative to MVC is modified by the CSA occupied by Type II (fast twitch) fibres'.

Evidence from recent studies relating (isometric) force per unit of muscle cross-sectional area (Force/CSA) and % Type II fibre area suggests that these fibres may be intrinsically 'stronger' than Type I fibres. A Retrospective study by Young (1984) suggests that Type II muscle fibres may be twice as strong as Type I fibres and this has been confirmed in a more recent study (Grindrod, Round and Rutherford, 1987).

Therefore, with the knowledge of the metabolic and morphologic characteristics of Type II muscle fibres, plus the possibility that they may be intrinsically stronger than Type I fibres, it is suggested that those individuals with a high % Type II fibre area, whether trained or untrained, may be able to maintain a given power output utilising a lower proportion of maximum force generating capacity.

The relationship observed in this study between % Type II fibre area and relative force generation was also subject to individual variation, that is, certain of the subjects with a similar % Type II fibre area generated different proportions of maximum dynamic force, at a given power output. This may be due to the large coefficient of variation (17%) associated with the determination of fibre frequency of distribution from biopsy samples, and also to the fact that force generation may be influenced by factors other than % Type II fibre area, such as the angle of pennation of the fibres or differences in the lever system through which the muscle transmits force (Lindahl and Movin, 1967; Alexander and Vernon, 1975).

The Functional Significance of Relative Force Generation

Previous studies have lent support to the view that the limiting factor to sustained high intensity dynamic exercise, where relatively large muscle groups are employed, such as cycling, is the ability of the cardiovascular system to transport oxygen to the exercising muscle, rather than the capacity of the muscle to utilise it. (Davies and Sargeant, 1974; Bevegård and Shepherd, 1967.)

In other words, the major limitation to sustained high-intensity exercise would not appear to be due to peripheral muscle fatigue. The results of the present study support this statement; the mean value of relative force generation (% PF max) for the group of thirty two subjects was approximately half of the maximum available force-generating capacity (at 70 rpm).

If one looks however at individual data obtained from the present study, a large variation in relative force generation is observed, and it is suggested that in certain subjects, that is, those with a high aerobic power, peripheral muscle fatigue resulting from high levels of relative force generation may become a critical factor in limiting endurance capacity.

Cycling exercise involves frequent dynamic contractions. According to Asmussen (1973), this type of exercise can only be performed for long periods of time if the developed force does not exceed 10-20% of MVC. Obviously the work load in relation to the duration of the contraction period and the intervals between the periods of contraction are critical in determining the length of time the work can be endured. Therefore, in order to assess the role of relative force generation as a possible limiting factor to maximum cycling exercise, it is obvious that the response not only to different exercise intensities should be investigated, but also the response to different pedal frequencies. This subject forms the basis of the study described in the following chapter.

CONCLUSIONS

Relative force generation was measured during a progressive exercise test conducted at 70 rpm and performed by thirty two subjects. At any given value of power output a large variation in the individual response was observed. This variation was significantly related to differences in maximum dynamic strength, aerobic power, and % Type II fibre area within the group. At a power output requiring 100% of $\dot{V}O_2$ max, the mean value of relative force generation did not exceed half of the maximum force generating capacity, however, certain of the subjects did generate well over this value and it is suggested that peripheral muscle fatigue resulting from high levels of relatice force generation may be a critical factor in determining endurance capacity.

CHAPTER 3

EFFECT OF PEDAL FREQUENCY UPON RELATIVE FORCE GENERATION

INTRODUCTION

The force developed at different velocities of contractile element shortening describes a fundamental mechanical property of skeletal muscle. The larger the force exerted by a muscle, the slower the velocity of contraction and vice versa. In dynamic muscle contractions the relationship between force generation and velocity of contraction was first investigated by Fenn and Marsh (1935) and later described by Hill (1938) as a rectangular hyperbola. Hill's equation relating the two variables of speed and load was applied to human muscle by Wilkie (1950), who calculated the velocity of contraction of the elbow flexors under conditions in which the after-load was the controlled variable. These measurements however, cannot be made in movements involving large muscle groups or more than one joint. An alternative practical approach is to control the velocity of the movement and measure the external force generated, to characterise the functional force-velocity relationship for the movement. Several investigations using isokinetic techniques to study the force-velocity relationship in the human knee extensor muscles have been performed. Several of these have reported the hyperbolic relationship obtained from earlier studies (Thorstensson, Grimby and Karlsson, 1976; Sjøgaard, 1978; Coyle, Costill and Lesmes, 1979) but other studies have demonstrated a linear force-velocity relationship rather than a hyperbolic one (Sargeant, Hoinville and Young, 1981; McCartney, Heigenhauser and Jones, 1983; Dolan, 1985).

An explanation offered for this discrepancy by McCartney et al is that the classical force-velocity testing was performed on isolated animal muscle, whereas the forces generated during a knee extension movement (eg in cycling) result from the co-operative action of several muscles operating across at least two joints.

(In addition, the motor units within these muscles are recruited physiologically, as opposed to the maximum electrical stimulation of isolated muscle preparations.)

During cycling exercise, at any given submaximal work-load, force generation will decrease with increasing pedal frequency, thus appearing to reduce the level of peripheral stress. However, maximum force generating capacity (PF max) also decreases with increasing frequency of contraction. If this was to result in a constant proportion of maximum force utilised (% PF max) for a given work-load, then the benefit of high frequencies of contraction in terms of a reduction in peripheral stress would be offset.

The purpose of the present study therefore, was to investigate the relationship between % PF max at given values of power output and crank velocity, during a continuous progressive test performed on a cycle ergometer in order to assess the importance of % PF max as a possible limiting factor to maximum exercise.

METHODS

SUBJECTS

Eleven subjects, (participants of the previous study) which included five endurance-trained athletes, were investigated in the present study. Physical characteristics of the subjects are given in Table 1.

PROTOCOL

Maximum peak force was determined for each subject using the isokinetic ergometer described in the previous study. The twenty-second test was performed over a range of pedal frequencies from 40-125 rpm respectively in order to establish a force-velocity relationship for each subject.

Continuous progressive exercise tests were conducted at 40, 70 and 100 rpm respectively, using the same apparatus and protocol as previously described. The tests were conducted in pairs and on separate days; one test to determine maximum peak force was followed, after a rest period of approximately one hour by a progressive test conducted at the same pedal frequency.

Mean peak force generation and oxygen uptake were measured over the final two minutes of each increment in power output during each of the progressive tests. In addition, ratings of perceived exertion (RPE), using the scale described by Borg (1970), were obtained from the subjects during this period. Venous blood samples were also obtained from one endurance-trained subject (MS) and one untrained subject (AS) (at 40 and 100 rpm respectively) for determination of plasma lactate concentration, using a slight modification of an enzyme based fluorometric technique (Lloyd, Burin, Smythe and Alberti, 1978).

Additional data was obtained at 60 and 80 rpm respectively from a small sub-group of subjects (n = 5).

Age (yrs)		Height (m)		Body Weight (Kg)	
Mean	SD	Mean	SD	Mean	SD
29.0	6.0	173.3	6.4	68.1	5.1

Table 1: Physical characteristics of the subjects studied

RESULTS

Maximum peak forces (PF max) were determined using the previously described technique over the range of pedal frequencies 40-125 rpm. Linear regression analysis was performed on the individual data to obtain values of PF max corresponding to 40, 60, 70, 80 and 100 rpm respectively (Fig 1). The relationship in each individual was linear over the range of pedal frequencies studied. The variability betwen individual force-velocity data was reduced considerably, but not completely, when maximum peak forces were standardised for upper leg muscle (plus bone) volume (Fig 2). The relationship obtained was linear and described by the equation: $y = 274.79 - 1.05x$, $r = -0.966$. The mean value of PF max decreased from 230.2 N/l ULV at 40 rpm to 135.4 N/l ULV at 125 rpm respectively, with a mean x intercept ($\dot{V}$ max) of 262.7 rpm.

The mean peak force (N) was determined for each increment in workload during the progressive exercise test which were conducted at 40, 70 and 100 rpm respectively. (The actual mean pedal frequencies recorded during the tests were 39.9, 69.8 and 98.9 respectively, but will be referred to as 40, 70 and 100 rpm respectively, for purposes of clarity.)

The relationship between peak force and oxygen uptake was linear for each subject and at each pedal frequency studied. The data obtained from one subject (RA) are illustrated in Figure 3.

When the mean peak forces were expressed as a percentage of maximum (% PF max) and related to exercise intensity (% $\dot{V}O_2$ max) the relationship was significantly linear for each pedal frequency studied. Again, the data obtained from one subject (RA) are illustrated in Figure 4.

The following linear regression equations describe the relation-

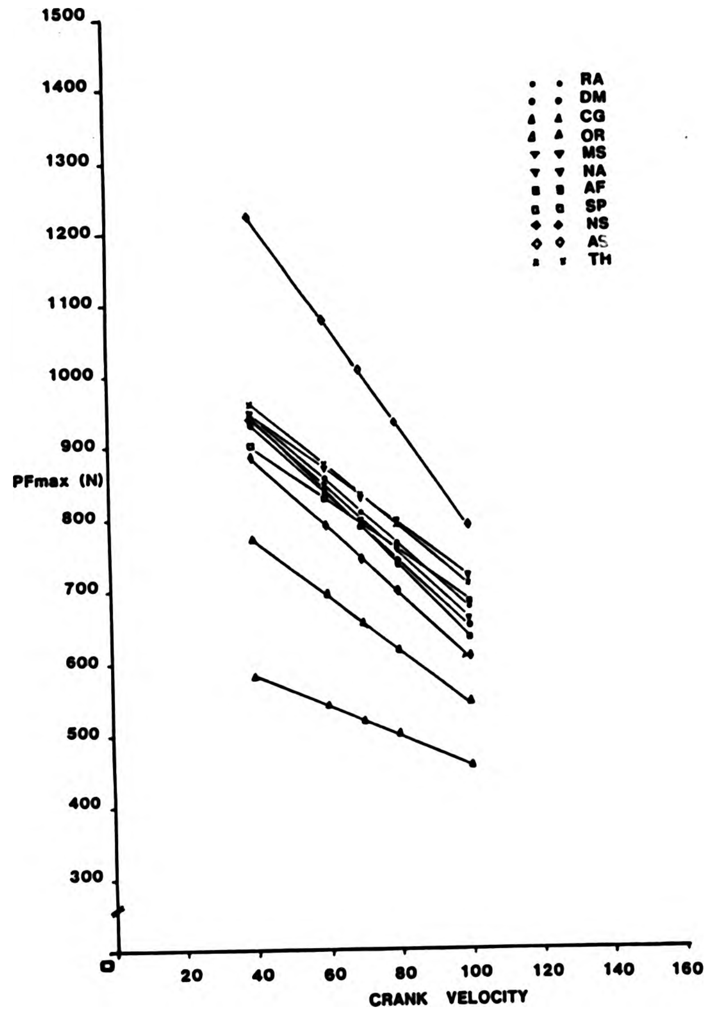


FIGURE 1

Relationship between pedal frequency (rpm) and maximum peak force (PF max) obtained from eleven subjects. Linear regression analysis was performed on the individual data to obtain values of PF max corresponding to 40, 60, 70, 80 and 100 rpm respectively

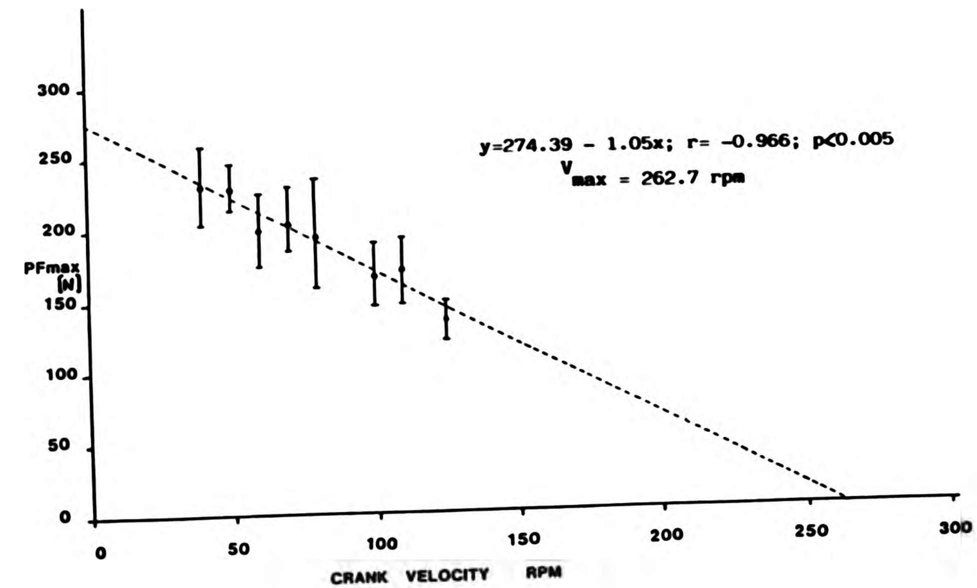


FIGURE 2

Relationship between pedal frequency (rpm) and maximum peak force standardised for upper leg muscle (plus) bone volume (PF max/1ULV). Mean data (± 1SD) obtained from eleven subjects is shown

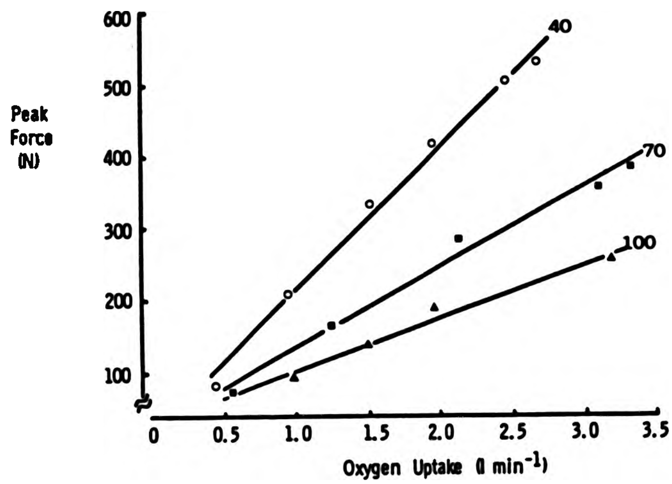


FIGURE 3

Relationship between oxygen uptake ($lmin^{-1}$) and mean peak force (N) obtained at 40, 70 and 100 rpm respectively. Individual data from subject RA are shown.

40rpm: y = 13.88 + 199.5x; r = 0.996

70rpm: y = 21.34 + 112.7x; r = 0.992

100rpm: y = 30.65 + 72.3x; r = 0.989

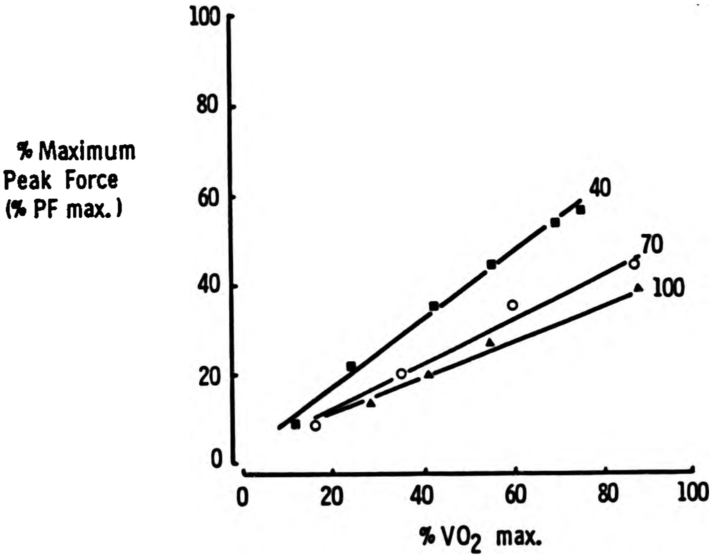


FIGURE 4

Relationship between exercise intensity (% $\dot{V}O_2$ max) and relative force generation (% PF max) obtained at 40, 70 and 100 rpm respectively. Individual data from subject RA are shown.

40rpm: $y = 2.625 + 0.737x$; $r = 0.994$

70rpm: $y = 2.627 + 0.496x$; $r = 0.992$

100rpm: $y = 4.534 + 0.381x$; $r = 0.989$

ship obtained at each pedal frequency for the group as a whole:

	mean rpm
$y = 4.485 + 0.674x$; $r = 0.855$; $p < 0.005$	39.9
$y = 1.865 + 0.522x$; $r = 0.915$; $p < 0.005$	69.8
$y = 2.226 + 0.454x$; $r = 0.832$; $p < 0.005$	98.9

where y = % PF max and x = % $\dot{V}O_2$ max.

The relationship between relative force generation and exercise intensity illustrated above was characterised by a decrease in slope as pedal frequency increased from 40 rpm to 100 rpm. In other words, at any given exercise intensity, there was a systematic decrease in relative force generation when fast pedal frequencies were compared to slow.

Since the regression analysis performed on the relationship between % $\dot{V}O_2$ max and % PF max obtained from the whole group cannot indicate individual variation at any particular exercise intensity, analysis was also performed on the individual data to determine values of % PF max corresponding to 25%, 50%, 75% and 100% of $\dot{V}O_2$ max respectively (see Tables 2-4). The mean values at these exercise intensities (± ISEM) are illustrated in Fig 5.

Mean values of relative force generation were significantly lower ($p < 0.05$) at work-loads requiring 50%, 75% and 100% of $\dot{V}O_2$ max when data obtained at 40 rpm and 70 rpm were compared (using t-tests) and at work-loads requiring 75% and 100% of $\dot{V}O_2$ max when data obtained at 70 rpm and 100 rpm were compared.

Fig 6 describes the relationship between relative force generation and pedal frequency at two values of power output requiring 75% and 100% of $\dot{V}O_2$ max respectively. At each power output there was a systematic and significant reduction in relative force generation as pedal frequency increased from 40-100 rpm.

SUBJECT	EXERCISE INTENSITY (% $\dot{V}O_2$ max)				MEAN RPM
	25	50	75	100	
NA	25	48	71	94	38
MS	13	39	65	90	39
SP	23	41	59	76	39
NS	30	61	91	121	38
RA	21	39	58	76	40
DM	18	33	49	64	41
AS	14	25	36	46	40
TH	19	42	64	87	40
OR	12	26	39	52	44
$\bar{x}$	19.4	39.3	59.1	78.0	39.9
(± ISEM)	(2.0)	(3.7)	(5.6)	(7.7)	(0.3)

TABLE 2

Individual values of relative force generation (plus mean ± ISEM) corresponding to values of power output requiring 25, 50, 75 and 100% of $\dot{V}O_2$ max respectively at a mean pedal frequency of 40 rpm Data obtained from nine subjects are shown

The data obtained from subjects AF and CG respectively, were excluded from this analysis since they failed to meet the established criterion (that is, ± 5 rpm of the desired frequency) regarding maintenance of pedal frequency

SUBJECT	EXERCISE INTENSITY (% $\dot{V}O_2$ max)				MEAN RPM
	25	50	75	100	
NA	2	21	40	59	73
MS	13	29	45	61	68
AF	19	34	50	65	67
SP	24	35	46	56	74
NS	23	39	56	72	66
RA	15	27	40	52	71
DM	14	25	36	47	69
AS	12	22	32	43	71
TH	13	28	42	56	69
OR	15	25	35	45	69
CG	17	27	36	46	71
$\bar{x}$	15.2	28.4	41.6	54.7	69.8
(± ISEM)	(1.8)	(1.7)	(2.2)	(2.8)	(0.7)

TABLE 3

Individual values of relative force generation (plus mean ± ISEM) corresponding to values of power output requiring 25, 50, 75 and 100% of $\dot{V}O_2$ max respectively as a mean pedal frequency of 70 rpm Data obtained from eleven subjects are shown

SUBJECT	EXERCISE INTENSITY (% $\dot{V}O_2$ max)				MEAN RPM
	25	50	75	100	
NA	14	29	45	60	98
MS	20	34	47	61	97
AF	14	28	43	57	99
SP	18	33	49	65	97
RA	14	24	33	43	98
DM	11	23	34	46	102
AS	8	18	28	38	97
TH	6	21	35	50	102
DR	15	22	29	36	99
CG	9	20	31	42	100
$\bar{x}$	12.9	25.2	37.4	49.8	98.9
(± ISEM)	(1.4)	(1.7)	(2.5)	(3.3)	(0.6)

TABLE 4

Individual values of relative force generation (plus mean ± ISEM) corresponding to values of power output requiring 25, 50, 75 and 100% of $\dot{V}O_2$ max respectively at a mean pedal frequency of 99 rpm Data obtained from ten subjects are shown

The data obtained from subject NS were excluded from this analysis since they failed to meet the established criterion (that is, ± 5 rpm of the desired frequency) regarding maintenance of pedal frequency

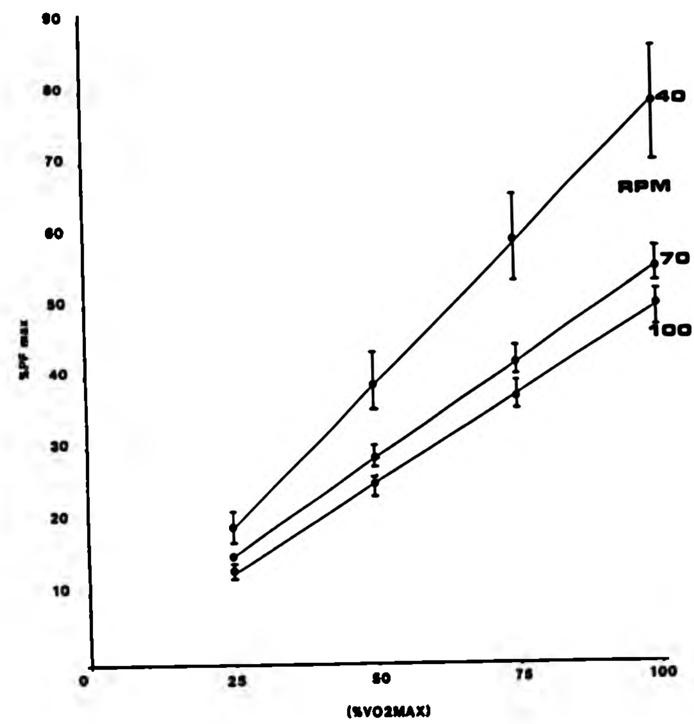


FIGURE 5

Relationship between exercise intensity (% $\dot{V}O_2$ max)

and relative force generation at pedal

frequencies of 40, 70 and 100 rpm respectively

mean data $\pm$ ISEM are shown

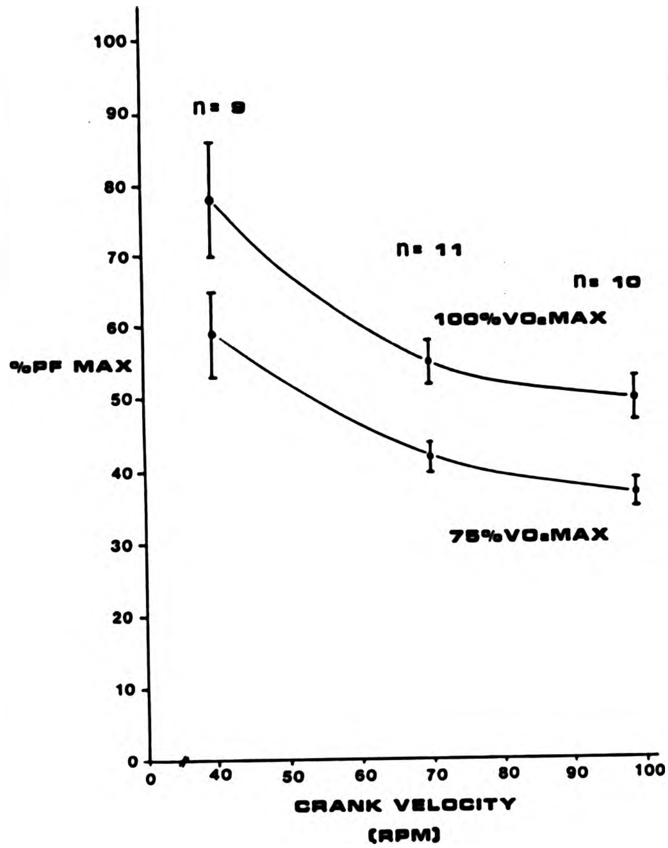


FIGURE 6

Relationship between pedal frequency (rpm) and relative force generation (% PF max) at two values of power output requiring 75% and 100% of $\dot{V}O_2$ max respectively mean data (± 1SEM) obtained from eleven subjects are shown

The data obtained at each exercise intensity appeared to describe a hyperbolic relationship. This was confirmed when the additional data obtained from the smaller sub-group of five subjects were analysed (Table 5). Figure 7 illustrates the relationship between relative force generation and pedal frequency obtained from this sub-group at a power output requiring 75% of $\dot{V}O_2$ max. Again, a systematic decrease in relative force generation was observed with increasing pedal frequency, which achieved statistical significance when data obtained at 40 rpm and 70 rpm were compared (as in the larger group of subjects), but not when data obtained at 70 rpm and 100 rpm were compared.

The mean values of % PF max at any given pedal frequency were observed to be lower, when compared with the data obtained from the larger group of subjects. This was probably due to the fact that the latter group included five endurance-trained athletes; since they possess a greater aerobic potential per litre of muscle they would be required to exert a greater proportion of their maximum force generating capacity in order to maintain a given relative work output.

Figure 8 compares data obtained from the present study with that obtained by Sjøgaard (1978). At a power output requiring 70% of $\dot{V}O_2$ max, the relationship between relative force generation and pedal frequency, in each study, was hyperbolic. Values obtained from the present study, however, were significantly greater ($p < 0.05$) at each pedal frequency. This was particularly apparent when the slow pedal frequencies (40 rpm) were compared.

Regression analysis was peformed upon the linear relationship obtained between exercise intensity (% $\dot{V}O_2$ max) and rating of perceived exertion (RPE), using the Borg RPE scale (6 - 20), at

MEAN RPM	EXERCISE INTENSITY (% $\dot{V}O_2$ max)			
	25	50	75	100
41.0 (1.1)	16.0 (2.1)	34.3 (3.1)	52.8 (5.6)	70.5 (8.1)
60.4 (0.6)	16.7 (1.4)	29.1 (1.9)	41.4 (2.9)	53.7 (4.0)
69.6 (0.6)	14.8 (0.7)	26.6 (0.8)	38.4 (1.9)	50.2 (3.0)
79.0 (1.0)	16.0 (1.6)	27.0 (2.1)	38.0 (2.9)	49.0 (3.6)
99.2 (0.9)	13.8 (1.9)	24.6 (2.4)	34.8 (3.2)	45.6 (4.2)

TABLE 5

Relationship between pedal frequency (rpm) and relative force generation (% PF max) at values of power output requiring 25, 50, 75 and 100% of $\dot{V}O_2$ max respectively Mean data ($\pm$ ISEM) obtained from a sub-group of five subjects over the range of pedal frequencies 40-100 rpm are shown

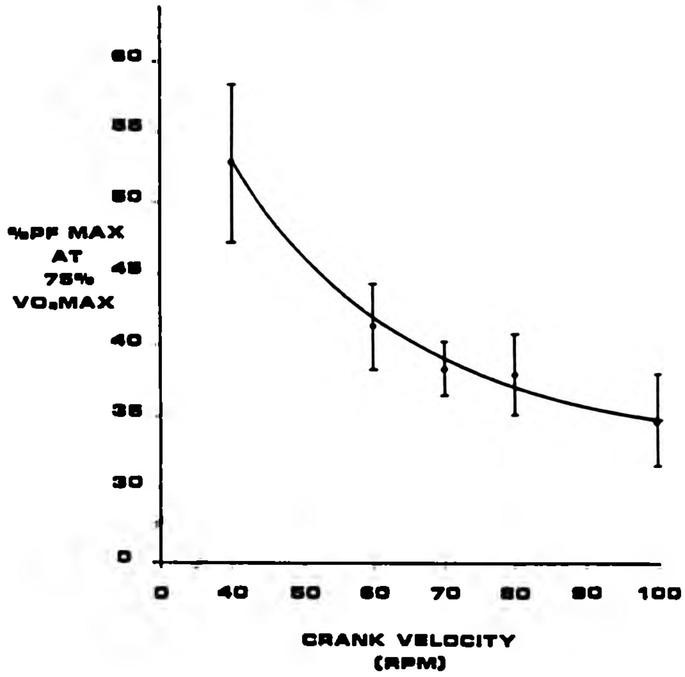


FIGURE 7

Relationship between pedal frequency (rpm) and relative force generation (% PF max) at a value of power output requiring 75% of $\dot{V}O_2$ max Mean data ($\pm$ ISEM) obtained from a sub-group of five subjects over the range of pedal frequencies 40-100 rpm are shown

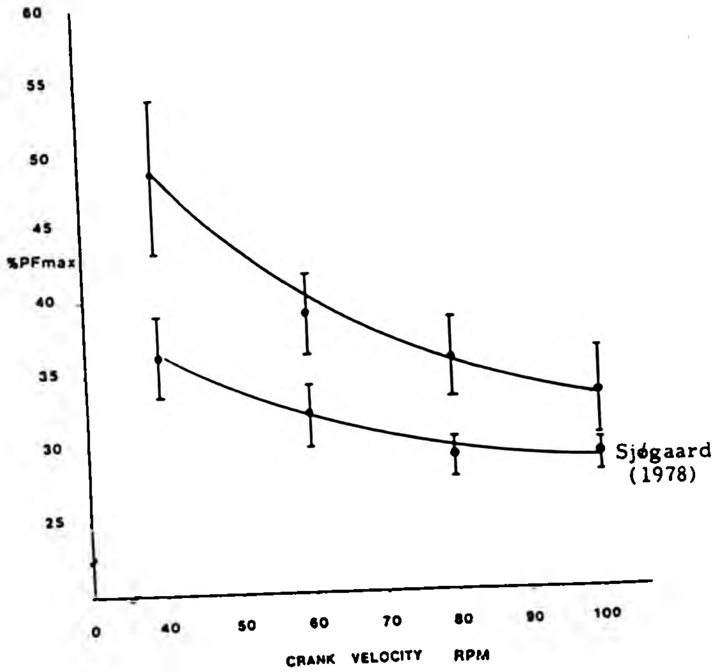


FIGURE 8

Relationship between pedal frequency (rpm) and relative force generation (% PF max) at a value of power output requiring 70% of $\dot{V}O_2$ max Mean data ($\pm$ ISEM) obtained from five subjects are shown Data (mean $\pm$ ISEM) obtained by Sjøgaard from six untrained subjects are also shown each pedal frequency. The following equations were derived:

		mean rpm
$y = 4.071 + 0.190x$	$r = 0.962$	39.9
$y = 4.045 + 0.153x$	$r = 0.919$	69.8
$y = 4.072 + 0.143x$	$r = 0.914$	98.9

where x = exercise intensity (% $\dot{V}O_2$ max)

and y = rating of perceived exertion (RPE)

The slope of the % $\dot{V}O_2$ max/RPE relationship demonstrated a progressive decline with increasing pedal frequency (Fig 9). The slope was significantly greater ($p < 0.05$) at 40 rpm than at 70 and 100 rpm respectively, although the difference in the slope between 70 rpm and 100 rpm, did not achieve statistical significance.

This data would indicate that at equivalent values of exercise intensity, the subjective rating of perceived exertion is lower at higher values of pedal frequency.

Plasma lactate concentration was measured in two subjects (one endurance-trained cyclist (MS) and one untrained (AS)) during the progressive tests performed at 40 and 100 rpm respectively. The data obtained are illustrated in Figure 10 and are shown related to exercise intensity (% $\dot{V}O_2$ max). Values of plasma lactate concentration obtained during unloaded pedalling were similar in both subjects at each pedal frequency; of the order of 1 millimolar. The data illustrates that at a given submaximal exercise intensity, values of plasma lactate concentration were greater at 40 rpm than at 100 rpm. This was particularly marked in the endurance-trained subject.

To summarise, relative force generation was determined over a range of pedal frequencies from 40-100 rpm. At any given value of power output, a systematic decrease in relative force generation was observed with increasing pedal frequency, which achieved

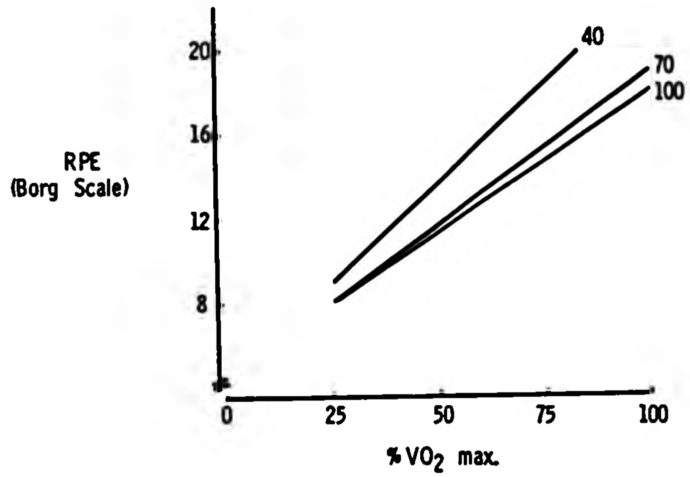


FIGURE 9

Relationship between exercise intensity (% $\dot{V}O_2$ max) and rating of perceived exertion (RPE) during continuous progressive exercise tests performed at 40 rpm (22 observations), 70 rpm (20 observations) and 100 rpm (10 observations) respectively. Interpolated values obtained from linear regression analysis are shown.

40rpm: $y = 4.071 + 0.190x$; $r = 0.962$

70rpm: $y = 4.045 + 0.153x$; $r = 0.919$

100rpm: $y = 4.072 + 0.143x$; $r = 0.914$

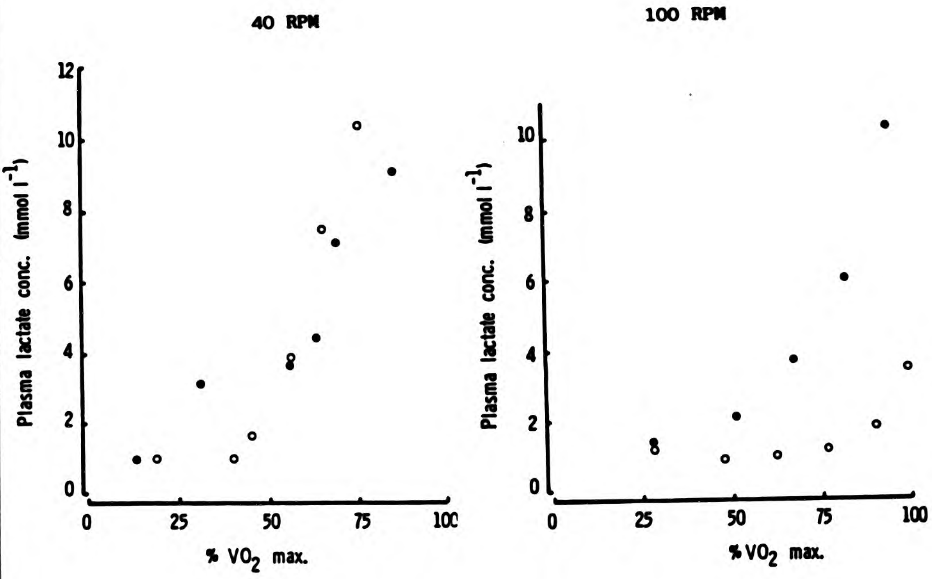


FIGURE 10

Relationship between exercise intensity (% $\dot{V}O_2$ max) and plasma lactate concentration (mmol l^{-1}) in two subjects, one trained (MS) and one untrained (AS) at 40 rpm and 100 rpm respectively

untrained subject : ●

trained subject : ○

significance at high values of power output. The relationship between relative force generation and pedal frequency appeared to be hyperbolic and this was confirmed when the additional data obtained from a sub-group of subjects was analysed.

DISCUSSION

Maximum peak forces were determined over a range of pedal frequencies using an isokinetic cycle ergometer. A force-velocity relationship was calculated for each of the eleven subjects participating in the study. In each subject there was a marked linearity of the relationship between maximum peak force and velocity. The decrease of muscle force with increasing velocity of contraction is well documented, but in classic in vitro studies has been described as hyperbolic rather than linear in nature. In these studies the force-velocity relationship was derived using animal muscle, free of the joint, during which force was measured in direct line with the actual tension developed within the muscle. The maximum peak forces measured in the present study were the resultant of a relatively complex situation in which the forces exerted upon the cranks during cycling result from the co-operative action of several muscles operating across more than one joint.

It is of interest however, that Thorstensson, Grimby and Karlsson (1976) in studies of knee extension using a Cybex dynamometer also demonstrated a linear force-velocity relationship if the value for maximum isometric tension was excluded. In vivo studies of this type measure peak torque (angular force) but this may not always reflect actual muscular tension, for the following reason:

In vivo, a muscle will register its peak torque when its joint angle has an optimal mechanical advantage (Thorstensson et al, 1976). Also, it takes a finite amount of time for individual fibres to develop peak tension. Thus the decline in peak torque could be a reflection of the muscle's inability to develop its maximum tension before it passes the optimal joint angle. Increasing the velocity of contraction would position the joint angle at a progressively disadvantageous mechanical advantage when the muscle develops its peak tension, resulting in the previously noted pattern of decline in peak torque with increasing velocity.

In the present study it is conceivable that a curvilinear effect may have been demonstrated at faster or slower pedal frequencies. The minimum pedal frequency at which maximum peak force was measured was 40 rpm and the maximum was 125 rpm. However, even in the subjects in whom data was collected over a wide range of pedal frequencies, there was no suggestion of a curvilinear relationship. In addition, studies performed by Sargeant et al (1981) and Dolan (1985) have also demonstrated a linear force velocity relationship during cycle ergometry in which a wide range of pedal frequencies were studied (22 rpm-171 rpm and 23 rpm-180 rpm respectively).

A considerable inter-subject variation was observed in the slope of the force-velocity relationship and its x and y intercepts. This variation was reduced when measurements of maximum peak force were standardised for upper leg muscle (plus bone) volume, determined between the knee and the gluteal fold. The mean data (Fig 2) is described by the equation $y = 274.79 - 1.05x$. At zero force the mean intercept on the x axis was 262.7 rpm.

Applying the standardising procedure did not reduce the inter-subject variability to within the coefficient of variation of the measurement (ie 6%: Dolan, 1985), indicating that the differences in maximum peak force generation were not accounted for solely by the volume of active muscle. It is known, however, that force generation is the resultant of several factors other than muscle volume, such as % Type II fibre area, the angle of pennation of the muscle fibres, and the lever system through which the muscle exerts force (cf Discussion; Chapter 2). An additional factor is that the group studied included both trained and untrained subjects of widely differing physical characteristics and fibre type distribution and area. This lack of homogeneity within the group would therefore also contribute to the overall inter-subject variability observed within the force-velocity relationship.

The relationship between relative force generation and exercise intensity (% $\dot{V}O_2$ max) was determined during progressive exercise tests over the range of pedal frequencies 40-100 rpm respectively. The relationship was linear for each pedal frequency studied but the slope was observed to decrease as pedal frequency increased. At all values of power output studied, there was a systematic decrease in relative force generation with increasing pedal frequency. This decrease achieved statistical significance at higher values of power output. In agreement with the results of the previous study by Sjøgaard (1978), the relationship between relative force generation and pedal frequency at a given value of power output, appeared to be hyperbolic. However, the actual values of relative force generation obtained from the present study were greater, particularly at the slower pedal frequencies (40-60 rpm). Although the data which was compared with that of Sjøgaard was obtained from a similar group (n = 5) of predominantly untrained subjects, the group nevertheless, included one endurance-trained cyclist whose results would tend to elevate the mean values obtained (see Discussion; Chapter 2). Perhaps of greater importance however is that in Sjøgaard's study, power outputs requiring 70 and 100% of $\dot{V}O_2$ max measured at 60 rpm were determined, and these values of power output were performed over the range of pedal frequencies described. This does not take into account the relationships between external power output, pedal frequency and mechanical efficiency. Previous studies have reported that the optimum pedal frequency for mechanical efficiency is within the range of 50-70 rpm, (Benedict and Cathcart, 1913; Dickinson, 1929; Garry and Wishart, 1931; Wilkie, 1960; Bannister and Jackson, 1967; Pugh, 1974; Gaesser and Brooks, 1975; Seabury, Adams and Ramey, 1977). This implies that at any pedal frequency outside of this range, a greater energy supply is required to maintain an equivalent power output. Conversely, a given value of energy supply may maintain different values of power output (and therefore force generation), depending upon the pedal frequency. This (ie the fact that the same relative work-loads may not have been compared) may explain the discrepancy between the results of the present study and those obtained by Sjøgaard.

The question arises as to why % PF max at a given value of power output decreases with increasing pedal frequency. Citterio and Agostoni (1984) suggest that at high contraction velocities the pattern of motor unit recruitment may alter in favour of a relatively small number of fast twitch units which would still be capable of maintaining the required power output, (since they give greater power per unit stimulus than slow twitch units). Their study, in which moving average electromyography (MA) of the quadriceps muscle bellies was recorded during cycling at different pedalling rates and work-loads, showed that the MA did not increase or increased less when an increment in power output was achieved by increasing the pedal frequency rather than the load. They attributed this phenomenon to a 'derecruitment' of slow twitch units and the recruitment of a smaller number of fast twitch units.

Selective recruitment of fast twitch units can occur. Although previous electrophysiological and histochemical studies have demonstrated an orderly recruitment of motor units in a progression from slow twitch to fast twitch units (Milner-Brown, Stein and Yemm, 1973; Stephens and Usherwood, 1977; Gollnick, Piehl and Saltin, 1974), there are nevertheless some reports indicating exceptions to this rule (Grimby and Hannerz, 1973; Secher and Nygaard, 1976; Stephens, Garnett and Buller, 1978).

If preferential recruitment of fast twitch units does occur at high pedal frequencies, could it occur in such a way so as to result in a lower level of % PF max, while maintaining power output? Studies of patterns of motor unit recruitment, particularly during fast dynamic contractions are subject to difficulties; in experimental technique and interpretation of the results; nevertheless an attempt was made (using quadriceps surface electromyography) to determine a relationship between the decrement in relative force generation with increasing pedal frequency and patterns of motor unit recruitment. This study is described in a later Chapter of this Thesis.

The functional significance of a reduction in relative force generation with increasing pedal frequency becomes apparent when one considerts that competitive endurance cyclists prefer pedal frequencies which are well above the apparent optimum for mechanical efficiency. Competitive cycling is unique among human powered sports in that the athlete can attain the same velocity despite markedly different rates of limb movements by varying the gear ratio. Road-racing cyclists could theoretically vary their pedalling rate to either extreme and attain the same speed; however, they routinely engage high pedal frequencies, from 80 - 110 rpm in competitive events (Hagberg, Mullin, Bahrke and Limburg, 1979; Konopka, 1981). This is in marked contrast to the recreational/

untrained cyclist who adopts much lower pedal frequencies, 50-70 rpm, which is, according to previous studies (see Pg. 90) the optimum range for mechanical efficiency. It is therefore suggested that the competitive cyclist adopts a 'strategy' through the course of training whereby a high pedal frequency is maintained in order to decrease the proportion of maximum force generating capacity utilised, particularly at higher power outputs, and thus the onset of peripheral muscle fatigue is delayed.

Not only would this strategy have a direct effect of delaying the onset of peripheral fatigue and thus prolonging exercise, but an indirect effect, as evidenced by the data obtained regarding the rating of perceived exertion (RPE) at high pedal frequencies and equivalent values of power output. Previous studies have shown that the feeling of strain in the exercising muscle may be an important peripheral factor in the rating of perceived exertion (Ekblom and Goldbarg, 1971; Pandolf and Noble, 1973; Löllgen, Ulmer and Nieding, 1977; Löllgen, Graham and Sjøgaard, 1980). Slower pedal frequencies when compared to faster frequencies at equivalent values of power output require a larger proportion of relative force generating capacity which may be associated with an elevated perception of exertion resulting from the greater relative force applied to the ergometer cranks. Although Edwards, Melcher, Hesser, Wigertz and Ekelund (1972) suggest that mechanical factors and forces acting upon the legs during exercise (ie peripheral factors) make a relatively unimportant contribution to perceived exertion, this suggestion is not confirmed by the results of the present study. In agreement with Pandolf and Noble (1973) and Löllgen, Ulmer and Nieding (1977), the results of the present study demonstrated lower RPE values at high pedal frequencies and equivalent power outputs, a result which would indicate an important relationship between relative force generation, perceived exertion and pedal frequency.

In addition, higher values of plasma lactate concentration (at equivalent values of work-load) were observed at slow pedal frequencies, in the two subjects studied. This was probably due to a more sustained contraction and increased muscle ischaemia at the slow pedal frequency.

These data indicate that high pedal frequencies are advantageous in that they require a lower proportion of maximum force-generating capacity which may result in a slower rate of lactate accumulation in plasma, (and presumably muscle, although this was not measured in the present study), with a concomitant reduction in the perception of exertion. If the proportion of force-generating capacity necessary to sustain a given power output contributes to the perception of effort it is perhaps not surprising that high pedal frequencies are preferred, particularly by the trained cyclist.

To summarise, the utilisation of high pedal frequencies require a lower level of relative force generation (at a given value of power output) and this is likely to result in a reduction in peripheral stress. This 'strategy' however, may carry an energetic cost since several previous studies have reported an optimum range of pedal frequencies for mechanical efficiency of 50-70 rpm (see Pg 16). Of interest are recent reports in the literature which suggest that competitive cyclists are actually optimally efficient over their preferred range of pedal frequencies (80-110 rpm) (Hagberg, Mullin, Giese and Spitznagel, 1981: Coast and Welch, 1985). There would therefore appear to be conflicting data concerning the relationship between pedal frequency and mechanical efficiency, particularly in the trained racing cyclist. In order to clarify this and to confirm the suggestion that a lower relative force generation may be preferred to an optimum mechanical efficiency, the relationship between pedal frquency and mechanical efficiency was further investigated and is described in the following Chapter of this Thesis.

CHAPTER 4

THE EFFECT OF PEDAL FREQUENCY UPON THE EFFICIENCY OF CYCLING EXERCISE

INTRODUCTION

The mechanical efficiency of an individual during steady-state exercise is expressed as the ratio of mechanical work accomplished to the metabolic energy expended. A synonymous term used is 'gross' efficiency. Calculations of efficiency during steady-state exercise are based on open-circuit indirect calorimetry and the assumption that the energy requirements are met by respiration. In exercising humans, however, energy is also expended to perform some other unmeasured work, which is necessary for the performance of the external work of interest. In exercise this includes the energy required for accelerating and decelerating the limbs, stabilising the body, and respiratory and cardiac work (Garry and Wishart, 1931). It also includes the energy required for the transportation of ions against electrochemical gradients and the synthesis and mobilisation of substrates (Stainsby, Gladden, Barclay and Wilson, 1980). Several methods of calculation of efficiency have been used in an attempt to isolate the unmeasured work from the performance of external work in order to obtain a value of efficiency which is representative of the 'muscle' efficiency. (Muscle efficiency is the product of the respective efficiencies of oxidative phosphorylation and excitation-contraction coupling and has been calculated, using thermodynamic considerations, to be approximately 29%; Whipp and Wasserman, 1969.)

Three definitions which subtract the oxygen cost of the unmeasured work, sometimes referred to as base-line correction factors, have been suggested by Gaesser and Brooks (1975), (Fig 1). In net efficiency, the denominator is defined as the energy expended above that at rest. Work (or apparent) efficiency uses as the denominator the energy expended above that at zero load. Delta efficiency is defined as the average gradient of the relationship between work performed and energy expenditure between two specified limits for the work done (Fig 2).

The variety of definitions of efficiency are equalled by the confusing range of values for the various measures, since it is obvious that the selection of the base-line correction factor will change estimates of energy expenditure and therefore efficiency. Stainsby et al contend that the idea of a constant physiological base-line is invalid. For base-line subtractions to be valid, the energy use represented by these base-lines must be unchanged when the work-load changes or the exercise conditions are altered. This would not appear to be the case, since many processes which do not contribute directly to the energy expended by the muscles in the performance of external work may increase or be attenuated by changes in work-load. For example, gastro-intestinal processes may be attenuated with increases in work-load (Hill, 1965). Mean body temperature increases during exercise which in turn increases the rate of metabolism by the Q10 effect (Hagberg, Mullin and Nagle, 1978). As the intensity of exercise increases, the energy use for ventilation of the lungs must also increase (Otis, 1964; Hesser, 1977). Therefore, the validity of base-line correction must be questioned. This, of course, leaves the calculation of gross efficiency as the alternative. Values of gross efficiency during exercise rarely exceed 30% (Benedict and Cathcart, 1913; Seabury, Adams and Ramey, 1977; Stuart, Howley, Gladden and Cox, 1981). These values are not only in agreement with Hill's original efficiency equation (1922) but also lend credibility to the belief that these efficiencies are actually the efficiency of the muscles in performing positive external work (muscle efficiency ≡ 29%). According to Stainsby et al this apparent agreement has no physiological basis;

in addition, Gaesser and Brooks have reported that the gross efficiency calculation does not accurately describe the relationship between energy output and work-load.

It would appear therefore, that any calculation of efficiency does not truly reflect muscle efficiency. However, if one is aware of the limitations of the various methods of calculation and is careful in their interpretation, the calculated values of exercise efficiency are nevertheless useful and may be used safely for comparative purposes, providing the conditions of the experiments are matched as closely as possible.

Perhaps it is not surprising, in view of the use of different definitions of efficiency, the different experimental protocols and the state of training of the subjects studied, that the data relating to the effect of work-load and pedal frequency upon exercise efficiency are inconsistent. Previous studies have reported increases in gross, net and work efficiencies with increments in work-load at constant pedal frequency (Gaesser and Brooks, 1975; Seabury, Adams and Ramey, 1977). Delta efficiency however has been shown to decrease with increasing work-load (Gaesser and Brooks, 1975; Stuart, Howley, Gladden and Cox, 1981). The available data concerning the effect of pedal frequency are just as equivocal: Gaesser and Brooks have reported a decrement in gross, net, work and delta efficiencies with increasing pedal frequency (range 40 rpm - 100 rpm), however a decrease in net efficiency at high pedal frequencies (86-88 rpm) has also been demonstrated (Pugh, 1974). Several investigations have concluded that there are optimum pedal frequencies for exercise efficiency (Dickinson, 1929; Garry and Wishart, 1931; Bannister and Jackson, 1967; Seabury, Adams and Ramey, 1977; Hagberg, Mullin, Giese and Spitznagel, 1981; Coast and Welch, 1985). Their results disagree, however on the absolute value of the optimum pedal frequency, whether it changes with workload and the state of training of the subject. The majority of studies support an optimum pedal frequency within the range of 40-70 rpm but the studies by Hagberg et al and Coast and Welch using trained cyclists have determined optimum pedal frequencies of 91 rpm and 83 rpm respectively.

The purpose of the present study was to investigate the effect of pedal frequency upon the exercise efficiency of a group of subejcts which included three trained racing cyclists, in order to determine whether there is an optimum pedal frequency, which differs between untrained subjects and trained cyclists, and to determine whether the previously observed phenomenon of a reduction in relative force generation during cycling at high pedal frequencies is indeed an advantage which would not be offset by a large decrement in cycling efficiency.

$$\text{Gross efficiency} = \frac{\text{work accomplished}}{\text{energy expended}} = \frac{W}{E} \times 100$$

$$\text{Net efficiency} = \frac{\text{work accomplished}}{\text{energy expended above that at rest}} = \frac{W}{E-e} \times 100$$

$$\text{Work efficiency} = \frac{\text{work accomplished}}{\text{energy expended above that of unloaded cycling}} = \frac{W}{El-Eu} \times 100$$

$$\text{Delta efficiency} = \frac{\text{delta work accomplished}}{\text{delta energy expended}} = \frac{W}{E} \times 100$$

Where W = external work performed
- E = gross energy output, including resting metabolism
- e = resting energy output
- El = energy output, loaded cycling
- Eu = energy output, unloaded cycling
- W = increment in external work performed above previous work rate
- E = increment in energy output above that at previous work rate

From Gaesser and Brooks, 1975

FIGURE 1: DEFINITIONS OF EXERCISE DEFICIENCY

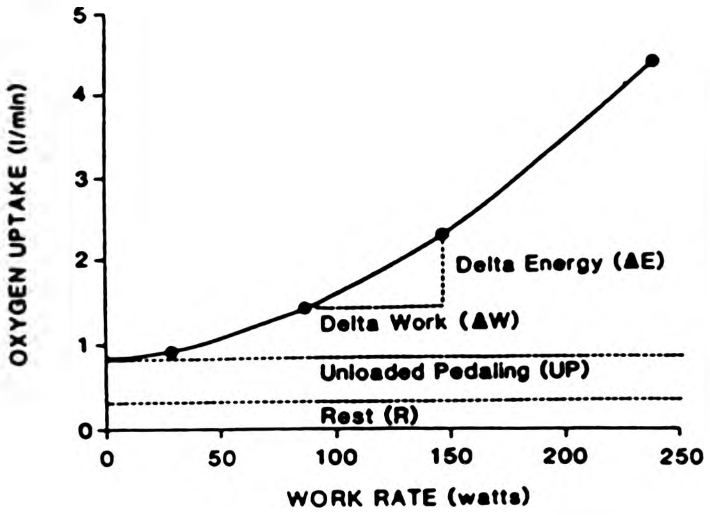


FIGURE 2

DEFINITIONS OF BASELINES FOR THE ENERGETIC COST OF CYCLING EXERCISE. R REPRESENTS THE ENERGY REQUIRED FOR PHYSIOLOGICAL MAINTENANCE AT REST. UP REPRESENTS THE ENERGY REQUIRED FOR UNLOADED PEDALLING. DELTA EFFICIENCY IS DEFINED AS THE RATIO OF DELTA WORK TO DELTA ENERGY.

From Stainsby et al, 1980

METHODS

Exercise efficiency was measured during a series of progressive exercise tests conducted at 40, 70 and 100 rpm respectively and performed by eleven subjects, which included three trained racing cyclists. The tests and the subjects themselves, were the same as those described in the previous Chapter.

Exercise efficiency was calculated using two different methods; one which incorporated a base-line correction factor (delta efficiency) and the other (gross efficiency) in which no base-line was used. (See Fig 1.)

RESULTS

The data obtained from two of the subjects at 40 rpm and one subject at 100 rpm were not included in the subsequent analysis of the results since they failed to achieve the previously described criterion regarding pedal frequency.

The relationships obtained between work performed ($\dot{W}$) and energy expenditure (E) are illustrated in Figures 3-5 and were observed to be linear for each pedal frequency studied.

The slope of the relationship demonstrated a decrement with increasing pedal frequency, from $y = 145.67 + 4.39\ x$ at 40 rpm to $y = 297.12 + 3.98\ x$ at 100 rpm respectively. (The slopes were determined by regression analysis.) The intercept of the relationship, however, increased from 40 rpm to 100 rpm, demonstrating that the energy expenditure of unloaded pedalling increased as a function of increasing pedal frequency.

Linear regression analysis was also performed on the individual data in order to obtain values of delta and gross efficiency respectively for each subject. Delta efficiency was calculated

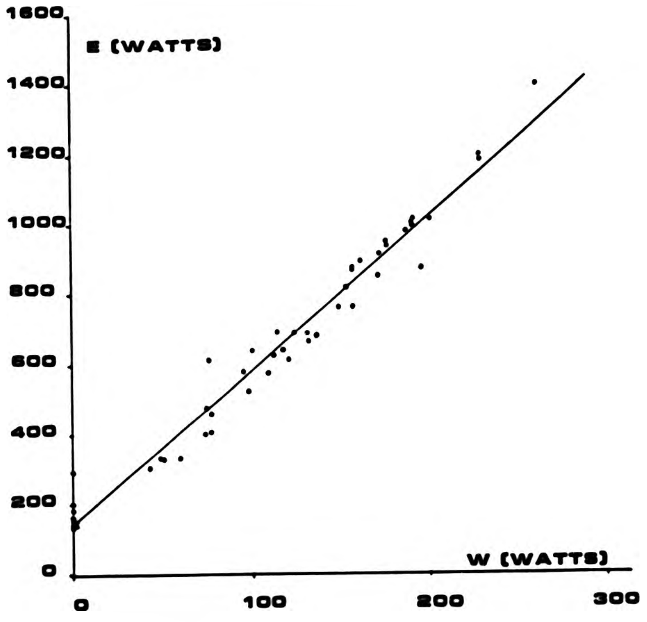


FIGURE 3

Relationship between work performed (Watts) and energy expenditure (Watts) during a progressive exercise test performed at 40 rpm

9 subjects; 49 observations

$y = 145.67 + 4.39x$; $r = 0.987$; $p<0.005$

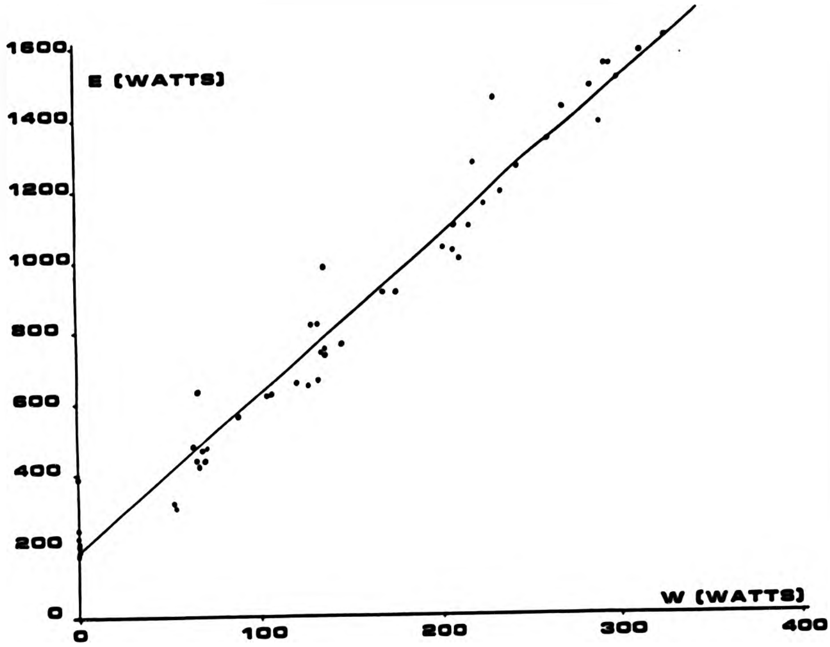


FIGURE 4

Relationship between work performed (Watts) and energy expenditure (Watts) during a progressive exercise test performed at 70 rpm

11 subjects ; 50 observations

$y = 184.0 + 4.41x$; $r = 0.985$; $p<0.005$

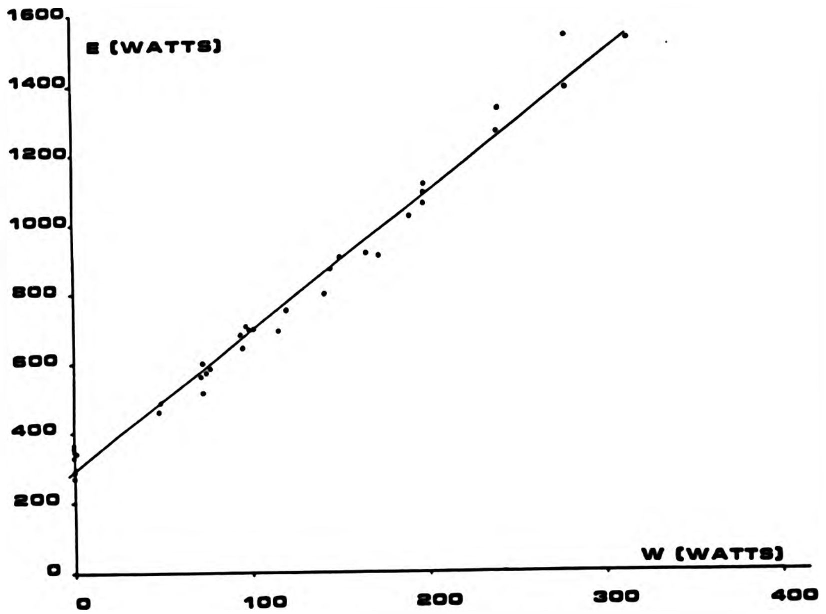


FIGURE 5

Relationship between work performed (Watts) and energy expenditure (Watts) during a progressive exercise test performed at 100 rpm

10 subjects; 35 observations

$y = 299.12 + 3.98x$; $r = 0.992$; $p<0.005$

as the reciprocal (1/b) of the slope of the equation describing the relationship between work performed and energy expenditure. Gross efficiency was calculated for values of power output requiring 50, 100 and 200 Watts respectively (interpolated data). The values obtained for delta and gross efficiency are illustrated in Tables 1 and 2 respectively.

The mean value obtained for delta efficiency was observed to increase significantly ($p < 0.05$) with increasing pedal frequency, from 23.2 ± 2.0% at 40 rpm to 25.4 ± 1.6% at 100 rpm. (However, a non-significant difference was observed when data obtained at 70 and 100 rpm were compared.) Values of gross efficiency demonstrated a significant reduction at each value of $\dot{W}$ when data obtained at 40 rpm and 100 rpm were compared. (The data obtained at 200 Watts are also illustrated in Fig 6.)

The effect of increasing power output (at constant pedal frequency) upon efficiency was again dependent upon the method of calculation. Since the relationship between work performed and energy expenditure was linear over the range of pedal frequencies studied, values obtained for delta efficiency were independent of power output. However the mean data obtained for gross efficiency demonstrated a significant ($p < 0.05$) and systematic increase with increments in power output. This pattern was apparent over the range of pedal frequencies studied (Fig 7). The data appeared to describe a hyperbolic relationship at each pedal frequency, achieving a common plateau as higher values of power output were achieved.

The mean values of delta efficiency and gross efficiency (at a value of power output of 200 Watts) obtained from the trained cyclists (subjects NA, MS and AF) were compared with the rest of the group (Table 3). Values of gross efficiency at 40 rpm and 100 rpm

SUBJECT	DELTA EFFICIENCY (%) 40 RPM	70 RPM	100 RPM
NA	26.3	26.8	25.1
MS	26.3	25.0	25.7
AF	-	22.3	25.3
SP	21.4	20.2	23.9
NS	26.3	18.8	-
RA	21.9	23.9	26.3
DM	21.6	23.6	28.6
AS	22.6	26.8	26.0
TH	24.2	24.0	26.0
OR	21.5	24.1	23.2
CG	-	24.4	23.7
$\bar{x}$	23.2	23.6	25.4
(±ISD)	2.0	2.4	1.6

TABLE 1

Values of delta efficiency (%) obtained during continuous progressive exercise tests performed by 11 subjects. Mean data (± ISD) are also shown.

GROSS EFFICIENCY (%)

SUBJECT	40 RPM			70 RPM			100 RPM		
	50w	100w	200w	50w	100w	200w	50w	100w	200w
NA	13.7	17.2	19.8	7.0	11.5	16.9	9.9	14.2	18.2
MS	10.4	14.9	19.0	9.0	13.2	17.3	10.4	14.8	18.8
AF	-	-	-	13.2	16.6	19.0	10.6	15.0	18.8
SP	14.3	17.2	17.9	16.6	18.2	19.2	9.6	13.7	17.4
NS	15.3	19.4	22.3	23.2	20.7	19.7	-	-	-
RA	14.4	17.4	19.4	13.1	16.9	19.8	10.4	14.9	19.0
DM	13.6	16.7	18.8	12.9	16.7	19.6	9.5	14.3	19.1
AS	15.7	18.5	20.3	12.2	16.7	20.4	10.4	14.9	18.9
TH	12.8	16.8	19.8	11.5	15.6	18.9	9.5	13.9	18.2
OR	13.8	16.8	18.9	13.4	17.2	20.1	10.1	14.1	17.5
CG	-	-	-	13.0	17.0	20.1	10.3	14.4	17.9
$\bar{x}$ (± 1SD)	13.8 (1.5)	17.2 (1.3)	19.6 (1.2)	13.3 (3.9)	16.5 (2.1)	19.2 (1.0)	10.1 (0.4)	14.4 (0.5)	18.4 (0.6)

TABLE 2

Values of gross efficiency (%) obtained during continuous progressive exercise tests performed at 40, 70 and 100 rpm respectively values are calculated for increments in power output corresponding to 50, 100 and 200 watts respectively Mean data (± 1SD) are also shown

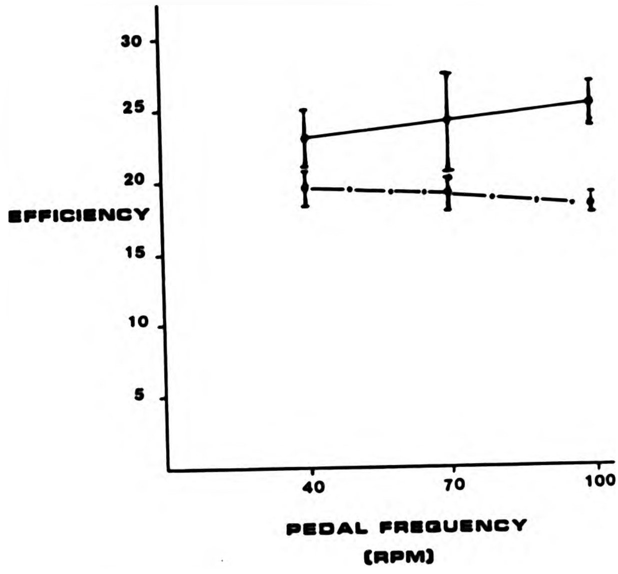


FIGURE 6

Relationship between pedal frequency (rpm) and gross (· – ·) and delta (—) efficiency values of gross efficiency corresponding to 200 watts are shown

Mean data (± ISD) are presented

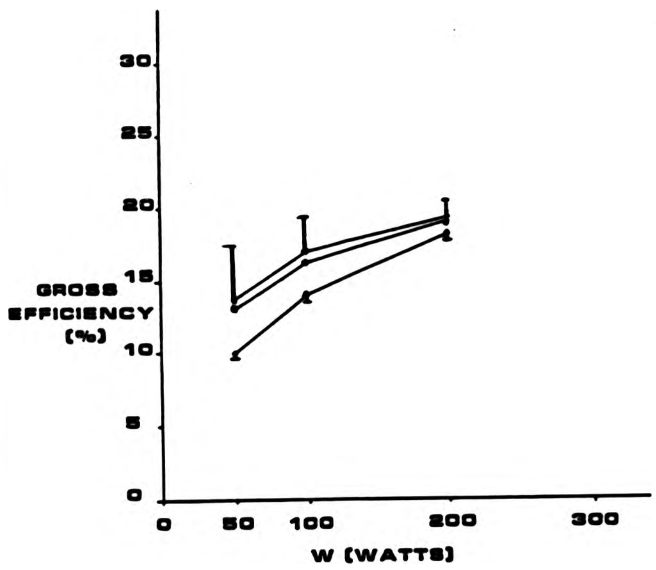


FIGURE 7

Relationship between work performed (watts) and gross efficiency (%) during continuous progressive exercise tests performed at 40, 70 and 100 rpm respectively

Mean data (± ISD) are shown

	40 RPM EFFICIENCY (%)		70 RPM EFFICIENCY (%)		100 RPM EFFICIENCY (%)	
	e	gross	e	gross	e	gross
Cyclists	24.8 (2.1)	19.4 (0.6)	24.2 (2.3)	17.7 (0.9)	25.4 (0.3)	18.6 (0.3)
Others	22.8 (1.8)	19.6 (1.4)	23.2 (2.5)	19.7 (0.5)	25.4 (1.9)	18.3 (0.7)

TABLE 3

Comparison of mean values (± ISD) of delta and gross efficiency obtained from the sub-group of trained cyclists and the rest of the group [Values of gross efficiency corresponding to a power output of 200 watts are presented] were similar in both groups at all pedal frequencies. Values of delta efficiency were identical at 100 rpm but slightly higher in the group of cyclists at 40 rpm and 70 rpm.

To summarise the results; exercise efficiency was measured during progressive exercise tests conducted over a range of pedal frequencies. Delta efficiency increased with increasing pedal frequency and was independent of power output. Comparison of gross efficiency data at 40 and 100 rpm however, demonstrated a significant decrement as pedal frequency increased. According to measurements of both delta and gross efficiency, the group of cyclists studied were no more efficient at the higher pedal frequency (100 rpm) than the rest of the group.

DISCUSSION

Exercise efficiency was calculated from data obtained from a group of eleven subjects during continuous progressive exercise tests performed at 40, 70 and 100 rpm respectively. Two different methods of calculation were used; one (delta efficiency) in which a base-line correction factor was incorporated into the calculation and the other (gross efficiency) which did not involve a correction factor.

The relationship obtained between work performed and energy expenditure was observed to be linear over the range of pedal frequencies studied. This result is in agreement with previous studies of cycling exercise (Banister and Jackson, 1967; Pugh, 1974; Suzuki, 1979) but at variance with other studies which have demonstrated a curvilinear relationship (Gaesser and Brooks, 1975; Stuart, Howley, Gladden and Cox, 1981). The data obtained by Gaesser and Brooks however does achieve linearity if the zero work (unloaded pedalling) data is discounted.

Individual regression analysis was performed on the relationship obtained between work performed and energy expenditure for each of the subjects. The mean values obtained for delta efficiency demonstrated a systematic increase from 23.2% at 40 rpm to 25.4% at 100 rpm. The range of values obtained are in good agreement with previous data concerning absolute values of delta efficiency derived from laboratory studies as well as from theoretical-thermodynamic studies (Hill, 1922; Lupton, 1923; Whip and Wasserman, 1969; Gaesser and Brooks, 1975; Suzuki, 1979; Stuart et al, 1981). The observed increase in delta efficiency with increasing pedal frequency is in agreement with some previous studies but at variance with others (using the same method of measurement). Suzuki (1979) demonstrated an increase in delta efficiency from 25.3% at 60 rpm to 28.8% at 100 rpm in one group of subjects whose quadriceps muscles contained a predominance of fast-twitch fibres but a decrease in another group of subjects whose quadriceps contained a high proportion of slow-twitch fibres. Gaesser and Brooks (1975) observed a decrease in delta efficiency (31.7% - 14.6%) from 40 rpm to 100 rpm, however their method of calculation was puzzling, since it incorporated a base-line obtained at 60 rpm which was subsequently used to calculate values of delta efficiency over the whole range of pedal frequencies studied (rather than using a base-line appropriate to the pedal frequency under study).

The data obtained from the present study resulted in an increase in delta efficiency with increasing pedal frequency. The data did not demonstrate a well-defined 'optimum' pedal frequency which has been shown in previous studies relating either efficiency or oxygen uptake to pedal frequency (cf introduction). Indeed, comparison of data obtained at 70 and 100 rpm did not reveal a significant difference in delta efficiency, indicating that although there appeared to be a 'trend' towards an increase with increasing pedal frequency, there was in fact little change over the range of pedal frequencies studied.

Due to the linearity of the relationship between work performed and energy expenditure, delta efficiency remained constant when power output was increased at constant pedal frequency. This result is at variance with previous studies in which the same method of calculation (but based upon a curvilinear work/energy relationship) was used to measure exercise efficiency (Gaesser and Brooks, 1975; Stuart et al, 1981) but in agreement with the results of Garry and Wishart (1931) and Pugh (1974) using a net efficiency calculation.

The data obtained for exercise efficiency using a method which did not incorporate a base-line correction factor demonstrated a decrease with increasing pedal frequency and an increase with increments in power output at constant pedal frequency. This result, and indeed the range of mean values of gross efficiency obained (10.1% - 21.0%) are in agreement with previous studies (Gaesser and Brooks, 1975; Seabury, Adams and Ramey, 1977; Stuart et al, 1981). It is clear, however, that concerning the effect of pedal frequency on exercise efficiency, this method of calculation did not accurately describe the relationship between work performed and energy expenditure. The slope of the relationship decreased with increasing pedal frequency (Figs 3-5), indicating that a smaller increment in energy expenditure was required to achieve a given increment in power output, but this was not reflected in the values obtained for gross efficiency. It is obvious that using a method of calculation of efficiency which does not incorporate a base-line correction factor cannot be representative of the true 'muscle efficiency' and in the opinion of

Benedict and Cathcart (1913), 'indicates little of the potentialities of the human body for severe muscular work and gives no conception of the possible efficiency of the human body as a machine'.

In the present study, it was believed that the delta efficiency data represented a more accurate description of the work/energy relationship. Since the mean values of delta efficiency at 100 rpm were the same for both the group of trained cyclists and the other members of the group, it is suggested that cycling training at high pedal frequencies does not necessarily effect an increase in efficiency at these speeds, nor may it bring about an increase in the optimum pedal frequency for exercise efficiency which has been previously suggested (Hagberg et al, 1981; Coast and Welch, 1985). The metabolic and hormonal responses of trained cyclists have been found to differ from those of untrained subjects when exercising at the same relative power output (Bloom, Johnson, Park, Rennie and Sulaiman, 1976) but their response in terms of cycling efficiency, as evidenced by the results of the present study and the previous study by Pugh (1974), would appear to be similar. Although the present study was performed in a laboratory, and involved only a small group of cyclists, the results are nevertheless in agreement with those of Pugh (1974) who studied six competition cyclists who performed both out of doors on their own bicycles and in the laboratory, using an ergometer equipped with racing frame and saddle.

The results of the present study suggest that trained racing cyclists are no more efficient at high pedal frequencies than untrained subjects. The data also indicates that cycling at a high pedal frequency of 100 rpm does not cause a major reduction in (delta) efficiency when compared with cycling at 70 rpm, in fact a small (but non-significant) increase was observed in the present study. Cycling at high pedal frequencies would appear to be advantageous in terms of both efficiency and relative force generation, as identified in the previous Chapter. Indeed one could speculate that since relative force generation is reduced at high pedal frequencies, and at equivalent values of power output, then the oxygen requirements of the exercising muscles may also be proportionately reduced, thereby bringing about a slight increase in efficiency.

CONCLUSIONS

Exercise efficiency was measured during progressive exercise tests conducted over the range of pedal frequencies 40-100 rpm. The method of calculation which appeared to best describe the relationship between work performed and energy expenditure was that which incorporated a base-line correction factor (delta efficiency). Using this method, efficiency increased with increasing pedal frequency and was independent of increments in power output (at constant pedal frequency). No apparent difference in delta efficiency was demonstrated at 100 rpm between the small group of trained cyclists and the remainder of the group. It is suggested therefore, that the advantage of cycling at high pedal frequencies in terms of a reduction in relative force generation is not offset by a reduction in exercise efficiency, indeed it may even be augmented by an increase in efficiency at these frequencies.

CHAPTER 5

THE RELATIONSHIP BETWEEN FORCE GENERATION AND SURFACE INTEGRATED EMG ACTIVITY DURING MAXIMUM DYNAMIC EXERCISE

INTRODUCTION

Electromyography (EMG) is a method of studying the electrical activity of a muscle. To develop tension in a muscle the motor units (a single motor neurone and the muscle fibres which it innervates) have to be activated. When a motor unit is activated, the movement of ions along the muscle fibre membrane results in an action potential. Quantification of the level of activity of whole muscles have most often been derived from integrated surface EMG (IEMG), a technique in which surface electrodes applied to the overlying skin record the summated potentials derived from many motor units. This technique has been used in many investigations into the relationship between the force generated by a muscle and its electrical activity as well as sites of origin and mechanisms of fatigue during both maximum isometric (Lippold, 1952; Stephens and Taylor, 1972, 1973; Bigland-Ritchie, Jones, Hosking and Edwards, 1978; Bigland-Ritchie, Jones and Woods, 1979; Bigland-Ritchie, Kukulka and Woods, 1980) and dynamic contractions (Nilsson, Tesch and Thorstensson, 1977; Komi and Viitasalo, 1976: Tesch, Komi, Jacobs, Karlsson and Viitasalo, 1983), although the latter are fewer in number, particularly those concerned with cycling exercise, (Bigland-Ritchie and Woods, 1976; Citterio and Agostoni, 1984; Viitasalo, Luhtanen, Rahkila and Rusko, 1985), the subject of the present study.

Nilsson et al, 1977, in a study of rapid maximum knee-extension movements, demonstrated a rapid decline in peak force to approximately 50% of initial values after 50 maximal contractions. No corresponding change however in the IEMG activity of Vastus Lateralis was observed. As a result of this, the IEMG/Force ratio, which illustrates changes in the relationship between electrical activity and force generation (first used by Stephens and Taylor, 1972), increased. This is in agreement with the study of Bigland-Ritchie, Jones, Hosking and Edwards (1978) of maximum (uninterrupted) isometric contractions of the quadriceps in which the surface EMG activity of Vastus Lateralis was measured. Nilsson et al suggest that since during this type of activity a large decrement in peak force generation occurs without a concomitant change in IEMG activity, the major site of fatigue must occur distal to the neuromuscular junction, that is, within the muscle itself. This suggestion however is at variance with the results of Stephens and Taylor, (1972) who in their study of maximum isometric contractions of the First Dorsus Interosseus (FDI) muscle, demonstrated a proportional decrease in both force and (smooth, rectified) EMG activity, which suggested the neuromuscular junction as the site of fatigue. Many factors however must be considered when evaluating this discrepancy, such as differences in the size and structure of the muscle under investigation, the number and type of motor units recruited in maximum isometric and dynamic contractions, and the intermittent nature of dynamic contractions.

The aim of the present study was to investigate the relationship between peak leg force, the electrical activity (surface IEMG) of Vastus Lateralis, Vastus Medialis and Rectus Femoris muscles respectively, and peripheral muscle fatigue during a maximum cycling test performed over a range of pedal frequencies, and to establish maximum values of IEMG activity of these muscles, to be used in subsequent experiments.

METHODS

Five male subjects (age range 24-40 years) were studied. The group included two endurance-trained athletes and one trained racing cyclist. The physical characteristics of the subjects are given in Table 1.

Measurement of Peak leg force

This was measured as described in Chapter 2, except that the test was performed over a 45 second period rather than over the 20 second period described previously. This was done to ensure the full characterisation of the changes in force and EMG activity as a result of the maximum test. The test was performed at four pedal frequencies, 40, 70, 100 and 125 rpm respectively (with the exception of subjects NS and SP who performed the maximum test at 40, 70 and 100 rpm respectively).

Measurement of Integrated EMG (IEMG) activity

EMG activity was recorded using surface electrodes with built-in preamplifiers (Medelec EA 1000) placed over the muscle bellies of Vastus Lateralis (VL), Vastus Medialis (VM) and Rectus Femoris (RF) of one leg (Figure 1). Before positioning the electrodes, the skin was carefully cleaned and prepared using 70% alcohol, an abrasive scouring pad and abrasive paste ('Omni', Weaver and Co, USA), in order to minimise the resistance between the electrodes and the skin. It has been previously suggested that electrode/skin resistance should not exceed 10,000 ohms (cf Lenman and Ritchie, 1983). In the present study, however, skin resistance never exceeded 5,000 ohms.

The position of each electrode was outlined using an indelible felt-tipped pen. A mapping technique using polythene sheeting was then used to record the position of each electrode in relation to the upper leg. This allowed the electrodes to be placed in exactly the same position on the leg for each of the tests.

The EMG signals were amplified, full-wave rectified and integrated over every 100 ms. The three channel integrator (response time 100 ms frequency range 0.1 Hertz-300 Hertz) was designed and constructed by the Department of Medical Physics, University College Hospital (See Appendix 2 for circuit diagrams). The leads connecting the electrodes to the integrator were taped to the leg, insulated and kept as short as possible to avoid movement artefact. Both the subject and the cycle ergometer were earthed. Surface raw and integrated EMG activity were recorded simultaneously with the leg forces applied to the ergometer cranks. A fan was directed at the subjects' legs during each of the tests, to avoid any distortion of the EMG signal due to sweating underneath the electrodes. Immediately after each test, the subject relaxed completely in order to check that the baseline EMG activity had remained unaltered.

	Age (yrs)	Height (m)	Body Weight (Kg)	% Type II fibre area
MS	25	1.73	72.1	51
SP	30	1.81	68.2	17
NS	32	1.81	69.9	10
AS	40	1.78	68.7	52
TH	29	1.75	72.8	55

TABLE 1: PHYSICAL CHARACTERISTICS OF THE FIVE MALE SUBJECTS STUDIED

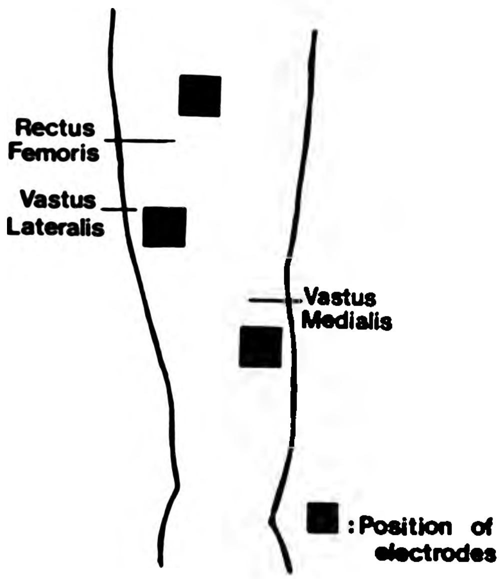


FIGURE 1

Diagram of the upper leg showing the

positioning of the surface EMG electrodes.

RESULTS

The data obtained from subject AS for the Rectus Femoris muscle at 70, 100 and 125 rpm respectively were not included in further analysis due to an unsatisfactory EMG signal resulting from sweating beneath the EMG electrode.

Over the course of each 45 second maximal effort, there was a marked loss of leg force. This decrement increased significantly with increasing pedal frequency (Table 2). The changes in IEMG activity however, were of a much smaller magnitude than the changes in leg force (Table 2). This is illustrated in Figures 2 and 3 respectively, which show a typical result obtained from the Vastus Lateralis (VL) muscle of one subject at one pedal frequency (70 rpm). Figure 2 illustrates samples of 'raw' data (raw EMG, IEMG and leg force) obtained from the first five revolutions and the final five revolutions of the 45 second test. The progressive changes in force generation and IEMG during the test are illustrated in Figure 3. It is clear that the overall decrement in force (-57%) far exceeded the overall decrement in IEMG activity (-12.9%). The mean percentage changes over the 45 second test in force and the IEMG activity of VL, VM and RF muscles at 40, 70, 100 and 125 rpm respectively, are shown in Figure 4. (For absolute IEMG and Force data, see Tables 1-4, Appendix 1.) At each pedal frequency there was a decrease in peak leg force compared to control values. This decrement achieved statistical significance ($p < 0.05$) at 70, 100 and 125 rpm respectively. In addition, the mean percentage decrement in force increased systematically and significantly ($p < 0.05$) with increasing pedal frequency.

The majority of the percentage changes in IEMG activity were non-significant (Table 2). However, significant decrements in the

PEDAL FREQUENCY: (RPM)	40				70				100				125			
		IEMG				IEMG				IEMG				IEMG		
SUBJECT	FORCE	VL	VM	RF	FORCE	VL	VM	RF	FORCE	VL	VM	RF	FORCE	VL	VM	RF
MS	- 5.0	- 6.9	- 3.0	+25.7	-18.0	-17.6	- 7.3	+12.6	-30.0	- 8.2	+ 9.1	+10.3	-34.0	- 3.2	- 5.6	-15.7
SP	- 3.0	+ 3.9	+ 0.3	+19.5	-27.0	+ 1.2	- 5.0	+27.5	-50.0	- 5.9	- 8.3	- 3.5	-	-	-	-
NS	- 6.0	-11.5	-11.9	+27.9	-23.0	-25.8	-18.6	+22.2	-47.0	-28.4	-32.2	-32.9	-	-	-	-
AS	-21.0	- 4.6	- 9.6	-26.6	-57.0	-12.9	-26.0	-	-59.0	- 6.5	- 7.0	-	-63.0	-10.9	- 3.4	-
TH	+ 2.0	+ 4.9	+17.4	+61.5	-31.0	+21.1	- 0.3	+10.6	-56.0	- 0.2	+33.0	+22.0	-57.0	- 9.9	- 7.1	+11.8
$\bar{x}$	- 7.0	- 2.8	- 1.4	+21.6	-31.0	- 6.8	-11.4	+18.2	-48.0	- 9.8	- 1.1	- 1.0	-51.0	- 8.0	-5.4	- 2.0
(± 1SD)	(9)	(7.1)	(11.6)	(31.5)	(15)	(18.4)	(10.6)	(8.0)	(11)	(10.8)	(24.1)	(23.7)	(15)	(4.2)	(1.9)	(19.5)

TABLE 2

Percentage changes in leg force and IEMG activity of Vastus Lateralis (VL), Vastus Medialis (VM) and Rectus Femoris (RF) muscles during the course of a 45 second test performed at 40 rpm, 70 rpm, 100 rpm and 125 rpm respectively.

Individual data with mean values ± 1SD are presented

[note: Subjects SP and NS did not perform the maximum test at 125 rpm. Data obtained from subject AS (RF muscle) at 70, 100 and 125 rpm respectively were excluded from further analysis due to an unsatisfactory EMG signal.]

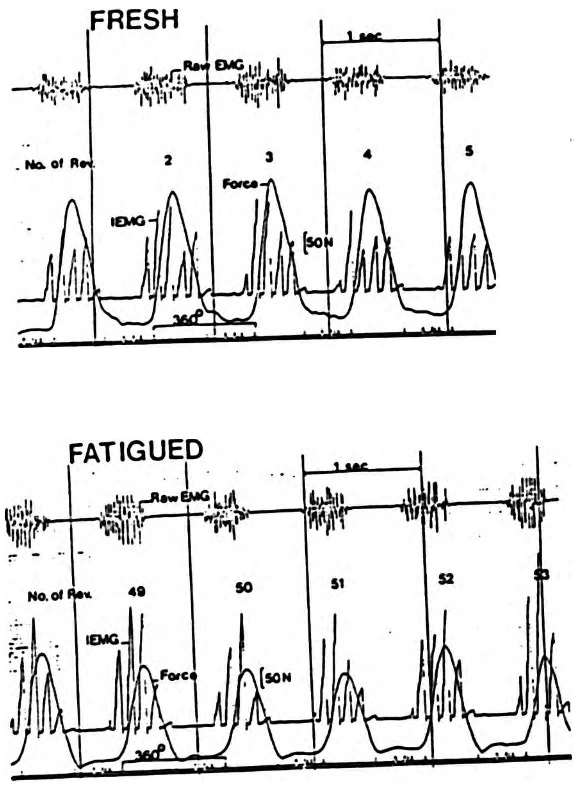


FIGURE 2

Samples of 'raw' data (raw EMG, IEMG, ie the graphical summation of the integrated signal and leg force) obtained from the Vastus Lateralis of one subject (AS) at a pedal frequency of 70 rpm. The samples were obtained from the first five revolutions ('Fresh') and the final five revolutions ('Fatigued') of the 45 second test.

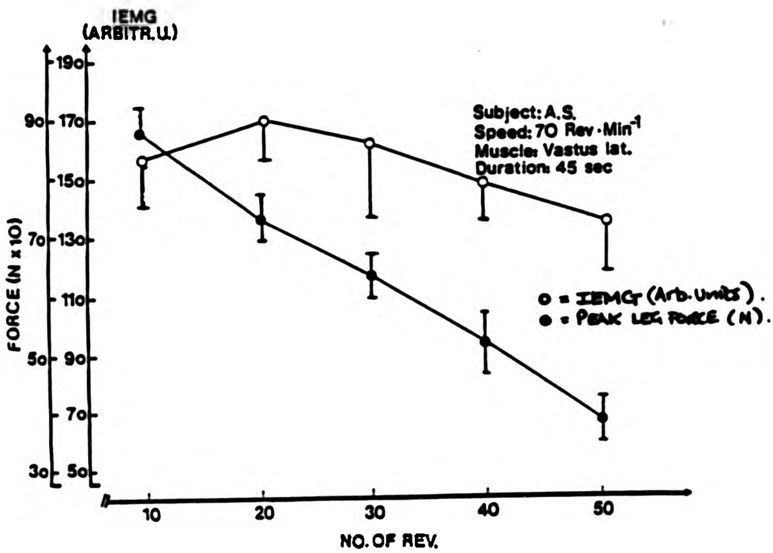


FIGURE 3

Progressive changes in force generation (N) and IEMG activity (arbitrary units) recorded from Vastus Lateralis during a 45 second test performed at 70 rpm. The data obtained from one subject (AS) is presented.

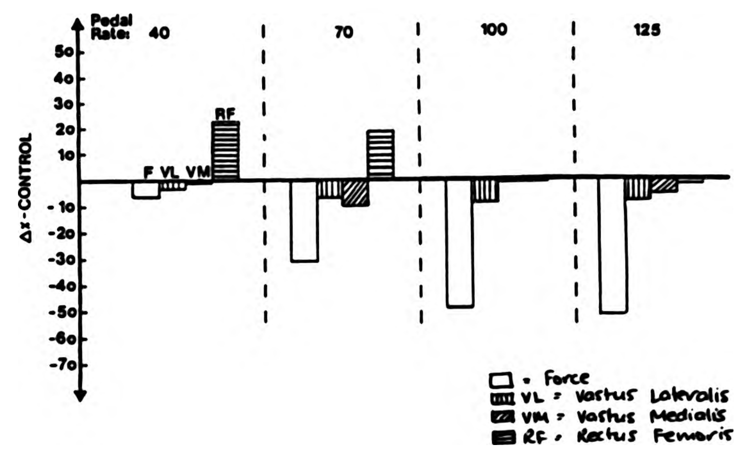


FIGURE 4

Mean percentage changes [compared to control values] in leg force and IEMG activity of VL, VM and RF muscles during the course of a 45 second test performed at 40 rpm, 70 rpm, 100 rpm and 125 rpm respectively.

IEMG activity of VL at 125 rpm, VM at 70 and 125 rpm and a significant increment in RF activity at 70 rpm compared to control values were demonstrated. The only significant systematic percentage change in IEMG activity observed with increasing pedal frequency was that of a decrement in RF activity.

The result of the large decrements in force coupled with the small decrements or increments in IEMG activity, was an increase in the IEMG/force ratio. Absolute values of the change in the IEMG/force ratio compared to control values are given in Tables 1-4, Appendix 1. The mean percentage changes (from control values) of the IEMG/force data for each muscle are illustrated in Figures 5-7 respectively. These figures clearly show the progressive increase in the IEMG/force ratio throughout the course of each 45 second test. The mean data demonstrated an increase in the IEMG/force ratio, in all muscles and in all subjects, with the exception of RF at 125 rpm, where there were slight decrements in the ratio between revolution numbers 31-40.

No significant correlation was observed between the overall percentage change in the IEMG/force ratio and percentage Type II fibre area in any of the muscles tested or at any pedal frequency studied. However, at 70 rpm and 100 rpm the ratio for VL and VM muscles of the untrained subjects (mean % Type II fibre area = 53.5%) were well above those of the trained endurance athletes (mean % Type II fibre area = 26.0%).

Although Rectus Femoris was the only muscle to demonstrate a systematic speed related change with regard to the <u>magnitude</u> of IEMG activity, other speed related changes in the pattern of IEMG activity were observed. Each muscle demonstrated a progressively earlier onset and end of the active phase with increasing pedal

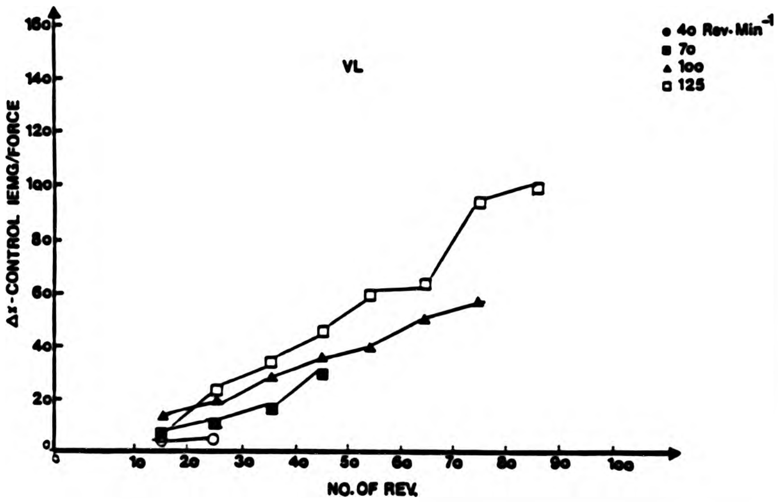


FIGURE 5

Percentage increases in the IEMG/force ratio

[compared to control values] during the course of a

45 second test performed at 40 rpm (●—●),

70 rpm (■—■), 100 rpm (▲—▲) and 125 rpm (□—□)

respectively.

IEMG activity was recorded from Vastus Lateralis (VL)

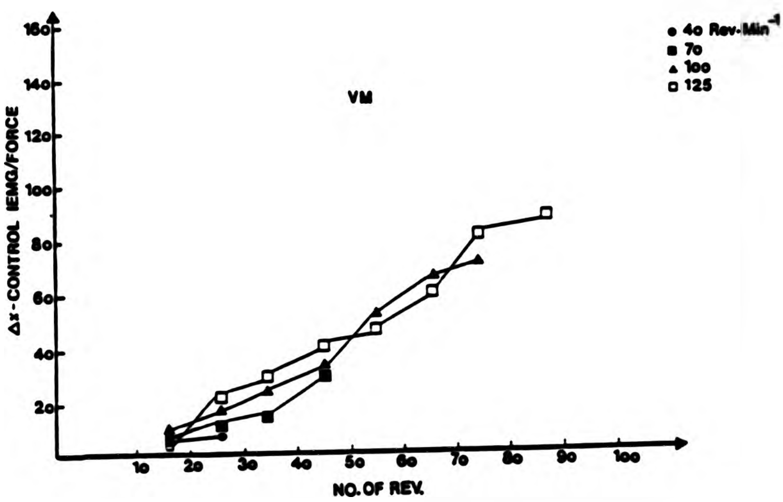


FIGURE 6

Percentage increases in the IEMG/Force ratio [compared to control values] during the course of a 45 second test performed at 40 rpm (●—●) 70 rpm (■—■), 100 rpm (▲—▲) and 125 rpm (□—□) respectively. IEMG activity was recorded from Vastus Medialis (VM)

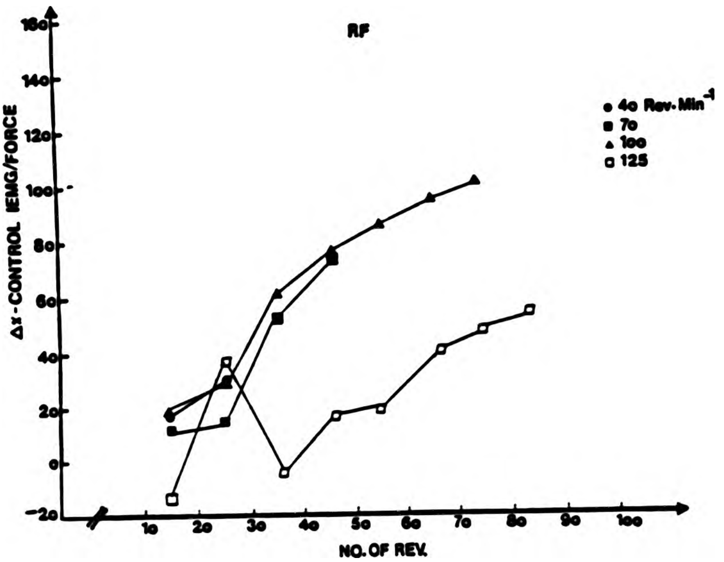


FIGURE 7

Percentage increases in the IEMG/Force ratio [compared to control values] during the course of a 45 second test performed at 40 rpm (●—●), 70 rpm (■—■), 100 rpm (▲—▲) and 125 rpm (□—□) respectively.

IEMG activity was recorded from Rectus Femoris(RF) frequency (Table 3; mean data, Figure 8). The duration of IEMG activity expressed in terms of degrees of crank revolution did not change significantly in RF when slow pedal frequencies were compared to fast, however there were significant reductions in the duration of activity of VL and VM muscles.

Another interesting observation was the fact that IEMG activity of RF at 100 and 125 rpm was very much reduced compared with the slower pedal frequencies, although the muscle continued to be activated over a large proportion of the cycle, (see Tables 3 and 4, Appendix 1, respectively).

PEDAL FREQUENCY:		40			70			100			125		
		SON	SOF	TOTAL	SON	SOF	TOTAL	SON	SOF	TOTAL	SON	SOF	TOTAL
SUBJECT													
MS	VL	- 26.1	160.0	186.1	- 34.2	133.4	167.6	- 42.6	104.4	147.0	- 54.1	103.4	157.6
	VM	- 29.5	167.2	196.7	- 34.2	138.3	172.5	- 43.8	110.1	153.9	- 54.3	100.8	155.1
	RF	-171.6	142.3	313.9	-193.3	125.3	318.6	-207.9	93.3	301.2	-202.8	103.3	306.1
SP	VL	- 40.3	178.0	218.3	- 50.9	131.2	182.7	- 55.5	108.9	164.4		-	
	VM	- 42.2	173.7	215.9	- 52.8	126.9	179.7	- 57.3	109.2	166.5			
	RF	-146.8	130.3	277.1	-160.3	118.3	278.6	-190.5	96.3	286.8			
NS	VL	- 81.5	154.5	236.0	- 93.9	121.6	215.5	- 49.9	116.2	166.1		-	
	VM	- 38.8	160.3	199.1	- 45.1	123.4	168.5	- 55.0	111.2	166.2			
	RF	-130.7	147.7	278.4	-155.5	117.2	272.7	-187.0	100.2	287.2			
AS	VL	- 32.0	158.1	190.1	- 43.4	130.8	174.2	- 65.2	105.5	170.7	- 51.2	94.3	145.5
	VM	- 31.6	161.7	193.3	- 43.7	139.6	188.3	- 59.2	109.9	169.1	- 40.9	80.2	121.1
	RF	- 63.4	95.4	158.8	- 71.9	70.2	142.1	-151.8	91.9	243.7	-	-	-
TM	VL	- 45.7	148.1	193.8	- 51.2	113.2	164.4	- 67.5	87.0	154.5	- 75.2	86.4	161.6
	VM	- 64.2	149.2	213.4	- 49.0	114.5	163.5	- 90.0	82.8	172.8	- 85.6	87.9	173.5
	RF	- 61.2	99.0	160.2	- 47.7	114.2	161.9	- 65.1	84.9	150.0	-146.8	71.2	218.0
$\bar{x}$ (± ISD)	VL	- 45.1	159.7	204.8	- 54.7	126.0	180.7	- 56.1	104.4	160.5	- 60.1	94.7	154.9
		(21.6)	(11.7)	(21.4)	(22.9)	(8.3)	(20.5)	(10.4)	(10.7)	(9.6)	(13.0)	(8.5)	(8.3)
	VM	- 37.2	166.4	203.6	- 44.9	128.5	173.5	- 61.0	103.4	163.7	- 60.2	89.6	149.9
		(6.4)	(5.5)	(10.2)	(6.9)	(10.3)	(8.0)	(17.2)	(12.0)	(7.1)	(22.0)	(10.4)	(26.5)
	RF	-114.7	129.6	237.6	-125.7	109.0	214.7	134.5	95.0	253.7	-174.8	87.2	262.0
		(50.0)	(27.7)	(72.8)	(62.5)	(22.0)	(76.6)	(68.3)	(6.5)	(61.9)	(39.5)	(22.6)	(62.2)

TABLE 3

Individual data showing onset (SON) and end (SOF) to the active phase of IEMG activity (expressed in terms of degrees of crank revolutions from Top Dead Centre) of VL, VM and RF muscles respectively, at each pedal frequency studied.

Mean data (± ISD) are also presented.

[note: Subjects SP and NS did not perform the maximum test at 125 rpm. Data obtained from subject AS (RF muscle) at 125 rpm was excluded from further analysis due to an unsatisfactory EMG signal.]

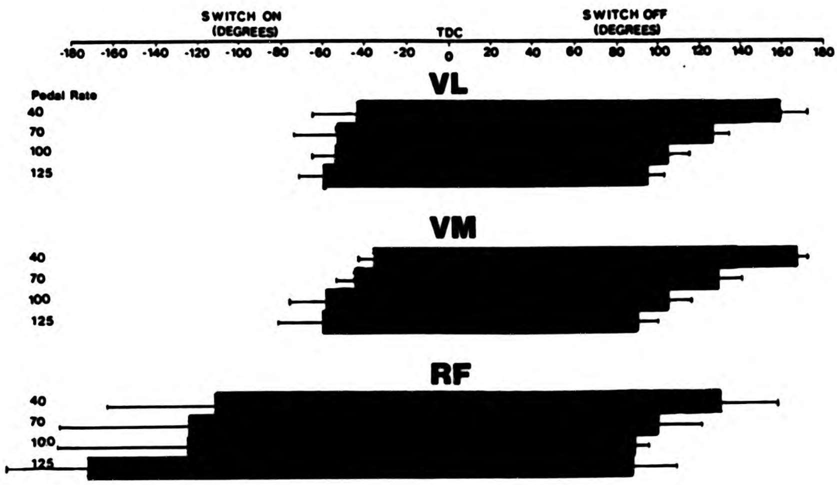


FIGURE 8

Mean data (± 1SD) showing onset (switch on) and end (switch off) to the active phase of IEMG activity [expressed in terms of degrees of crank revolution from Top Dead Centre (TDC)] of VL, VM and RF muscles respectively, at each pedal frequency studied.

DISCUSSION

Changes in Force generation and surface IEMG activity during short-term maximum exercise

Peak leg force and surface IEMG activity of vastus lateralis, vastus medialis and rectus femoris muscles respectively were measured during a 45 second maximum test, performed over a range of pedal frequencies. Over the course of the test a marked loss of force was observed at each of the pedal frequencies studied and this decrement increased systematically from 40 rpm to 125 rpm. This result is in agreement with previous studies (Sargeant, Hoinville and Young, 1981; McCartney, Heigenhauser, Sargeant and Jones, 1983; P Dolan, Personal Communication, 1985) in which a greater rate of loss of leg force with increasing pedal frequency was reported. This result may be explained by the fact that during maximal exercise of short duration, the energy for muscular contraction is derived almost exclusively from the splitting of phosphorylcreatine (PC) and glycolysis (Karlsson, 1971; Margaria, di Prampero, Aghemo, Derevenco and Mariani, 1971; Tesch, Sjödin, Thorstensson and Karlsson, 1978; Boobis, Williams and Wooton, 1983). With increasing frequency of contraction the rates of these processes will increase concomitantly, (provided that muscle power output has also increased). The result of this will be greater changes in metabolic substrates and products (such as hydrogen ions and adenine nucleotides) which in turn may exert inhibitory effects on the biochemical processes associated with muscle contraction and may therefore contribute to the greater observed rate of fatigue. Furthermore, at high frequencies of contraction, there will be less time for the removal of metabolites from the working muscle, and their intra-muscular accumulation may proceed at an accelerated rate.

The changes in the surface IEMG activity of VL, VM and RF muscles respectively over the course of the 45 second test were of a much smaller magnitude than the observed changes in force generation, and with the exception of RF, were not systematic. This resulted in an increase of the IEMG/Force ratio which was observed for each of the subjects and at each pedal frequency studied. This finding is in agreement with those reported by Nilsson, Tesch and Thorstensson, 1971, and by Bigland-Ritchie, Jones, Hosking and Edwards (1978) but in contrast to the findings of Stephens and Taylor, (1972). The latter, however, were studying maximal isometric contractions of the First Dorsal Interosseus (FDI) muscle and therefore the differences between the type of contraction and the size and structure of the muscle studied must be considered when comparing the results obtained from these studies.

Nilsson, Tesch and Thorstensson demonstrated a significant correlation between the relative increase in the IEMG/Force ratio and the percentage Type II quadriceps fibre area, indicating that the factor responsible for the decrease in force generation was localised mainly within the more glycolytic fast twitch fibres. Indeed, an increased rate of fatigue during maximum dynamic contractions has been demonstrated in subjects possessing a high % Type II fibre area of the muscle under study. (McCartney, Heigenhauser, Sargeant and Jones, 1983; Dolan, 1985.)

In the present study, no significant correlations were demonstrated between % Type II fibre area and the IEMG/Force ratio for any subject, muscle or pedal frequency, although the untrained subjects (mean % Type II fibre area = 54%) did tend towards a higher IEMG/Force ratio of the VL and VM muscles at 70 rpm and 100 rpm, than the endurance-trained athletes (mean % Type

II fibre area = 26%).

In summary therefore, the decline in maximum leg force measured over the course of the 45 second test was not matched by changes in the surface IEMG activity of the three muscles studied. This resulted in an increase in the IEMG/Force ratio which would suggest that the major site of fatigue during this type of contraction is located distal to the neuromuscular junction and is therefore peripheral rather than central in origin. In order to interpret the results in this way, it must be assumed that surface IEMG recordings are closely related to intramuscular EMG activity and provide a quantitative measure of total muscle fibre activity, and in addition, that the VL, VM and RF muscles are representative of the muscles involved in cyclical knee extension movements.

Validity of surface IEMG measurements

The validity of surface IEMG as a technique of measuring the electrical activity of the underlying muscle has been accepted by Bouisset and Maton (1973) who demonstrated a linear relationship between surface IEMG and intrmuscular IEMG activity during sub-maximum dynamic contractions of the elbow flexors. The relationship was independent of the velocity of contraction. The results of the study suggested that the activity of fibres near the surface of the muscle were representative of the activity of all the fibres involved in the activity in question and that the linearity of the relationship showed a direct ratio between the two which indicated that any value of surface IEMG activity was, via a constant, a value of intramuscular IEMG activity. In addition, Grieve and Cavanagh (1974) have demonstrated that within a given localised region of the quadriceps there was little between-site variability of surface IEMG activity, but the variability increased when the region was extended.

Although several muscles are employed during cycling exercise, the quadriceps is the largest and also shows the most vigorous activity during the downward thrust (Houtz and Fischer, 1959). Previous studies have therefore used VL as representative of the whole of the quadriceps (Bigland-Ritchie and Woods, 1976; Nilsson, Tesch and Thorstensson, 1977). Although it is accepted that the quadriceps is the major muscle group involved in cycling exercise, it is evident from the results of the present study, however, that RF differed from VM and VL with respect to changes in both magnitude and duration of IEMG activity with changes in pedal frequency. The assumption that VL alone is representative of quadriceps activity must therefore be questioned.

Changes in Duration of IEMG activity with pedal frequency

Changes in the pattern of IEMG activity with respect to duration of activity at different pedal frequencies were observed in the present study. Each muscle demonstrated a progressively earlier onset and end to the active phase with increasing pedal frequency, a phenomenon which has not been previously reported. A probable explanation for the earlier onset of IEMG activity is that at high pedal frequencies there is less time in which to develop maximum tension, therefore the muscle in question must be activated earlier in the cycle enabling maximum tension to be generated at the optimum joint angle. The earlier end to the active phase is more difficult to explain: since time to peak tension is reduced with increasing frequency of contraction, a progressively earlier onset and a reduction in total duration of activity during the cycle may perhaps be expected. Although this was evident within VL and VM muscles, it was not the case with the activity of RF, which did not demonstrate any reduction in total duration of activity even though the onset and end of activity were earlier in the cycle. Care must be taken in the interpretation of results obtained from RF since it is a two-joint muscle, acting as a hip flexor as well as a knee extensor. This may explain the differences in the results obtained from this muscle.

CHAPTER 6

THE RELATIONSHIP BETWEEN FORCE GENERATION, OXYGEN UPTAKE AND SURFACE INTEGRATED EMG ACTIVITY DURING PROLONGED CYCLING EXERCISE: EFFECT OF PEDAL FREQUENCY

INTRODUCTION

Regulation of force generation is achieved by two mechanisms, either by varying the number of active motor units (recruitment) or the motor unit firing rate (rate coding). The relative importance of recruitment versus rate coding to force generation would appear to be dependent upon the size and functional demands of the muscle under investigation: in a small muscle, such as the first dorsal interosseus (FDI), rate coding plays the major role in the generation of high levels of force, (Milner-Brown, Stein and Yemm, 1973), whereas in larger muscles such as biceps brachii and deltoid, motor unit recruitment appears to be of greater importance (Kukulka and Clamman, 1981; De Luca, Le Fever, McCue and Xenakis, 1982). It is generally accepted that during isometric contractions, the order of motor unit recruitment is dependent upon motor unit size. This phenomenon, which was first described by Henneman, Somjen and Carpenter (1965) and is known as the Size Principle, has received support from subsequent investigations, (Milner-Brown, Stein and Yemm, 1973 b; 1973 c; Monster and Chan, 1977; Stephens and Usherwood, 1977). It must be noted however, that in addition to size, motor unit contraction strength and fatigue-resistance are also important factors influencing the pattern of recruitment during graded voluntary contractions (Stephens and Usherwood, 1977; Garnett and Stephens, 1981).

It is generally accepted that slow twitch motor units are composed of small, slow conducting motorneurones and Type I muscle fibres, while fast twitch units are composed of larger, faster conducting motorneurones and Type II muscle fibres. Methods such as the glycogen depletion technique (which involves the indentification of Type I and Type II fibres) have therefore also been applied to the investigation of patterns of motor unit recruitment during isometric contractions, the results of which would also appear to support the Size Principle (Gollnick, Karlsson, Piehl and Saltin, 1974).

Few data are available regarding patterns of motor unit recruitment during dynamic movements. Using a single-fibre EMG technique, Grimby (1984) demonstrated that low-threshold motor units were mainly responsible for force generation at low levels but high threshold units were important at high levels of force generation, a relationship which is compatible with the Size Principle. The majority of investigations of patterns of motor unit recruitment during dynamic exercise, however, have utilised the glycogen depletion technique. This is a method which involves repeated sampling of muscle before, during and after exercise. The glycogen content of the fibres is usually estimated from histochemically-stained transverse sections of the samples using the periodic acid Schiff (PAS) stain which is specific for glycogen (Halkjaer-Kristensen and Ingemann-Hansen, 1979). Using this technique, Gollnick, Piehl and Saltin (1974) demonstrated a preferential utilisation of slow twitch fibres during prolonged submaximum cycling exercise at constant pedal frequency. Fast twitch fibres were only activated either at supramaximal work-loads or by prolonged exercise at lighter loads after a large number of slow twitch fibres had been depleted of glycogen. Varying the pedal frequency (and therefore relative force generation) had no effect on the pattern of fibre depletion as indicated by a decline in PAS staining intensity. Although the authors did not exclude relative force generation on the pedals as a factor contributing to the pattern of fibre depletion, they suggested that the oxygen supply to the working muscle was more important than relative tension output or contractile speed in determining patterns of glycogen depletion.

The patterns of fibre depletion observed by Gollnick et al are at variance with the study of Vøllestad (1985), who demonstrated, using an objective method of determining PAS staining intensity (Vøllestad, Vaage and Hermansen, 1984), Type I and Type II(A) fibre recruitment from the beginning of submaximal cycling exercise (75% of VO_2 max). The difference between these results may be due to the recent improvement in the technique used to estimate changes in PAS staining intensity, and the inability of Gollnick et al to histochemically identify the Type II fibre sub-groups. Unfortunately, Vøllestad et al did not investigate the effect of varying pedal frequency using their glycogen depletion technique. This subject has however been studied by Citterio and Agostini (1984), although they used the technique of surface EMG. When pedal frequency was increased at constant force the EMG signal from the quadriceps muscle bellies either remained constant or increased less than when similar increments in power output were achieved by increasing force generation at constant pedal frequency. They attributed this phenomonon to a 'derecruitment' of slow twitch motor units at high pedal frequencies, in favour of the recruitment of a smaller number of fast twitch units.

In summary, the use of different techniques to study patterns of motor unit recruitment during dynamic exercise, have given similar results in terms of a progressive recruitment of motor units in accordance with the size principle with increases in either exercise intensity or duration. Conflicting data, however has been obtained concerning patterns of recruitment when the frequency of contraction is altered.

The aim of the present study was to investigate the relationship between force generation, exercise intensity and surface IEMG activity during continuous progressive cycling exercise over a range of pedal frequencies. It was hoped that this investigation, in conjunction with the data obtained from the recent glycogen depletion study of Vøllestad (1985) would provide further information concerning regulation of force generation during dynamic exercise, a subject upon which little data presently exists.

METHODS

SUBJECTS

The same group of subjects (as described in the previous chapter), which included three endurance-trained athletes, participated in the present study. The physical characteristics of the subjects are given in Chapter 5, Table 1.

PROTOCOL

Continuous progressive exercise tests were performed by each subject at pedal frequencies of 40, 70 and 100 rpm respectively, using the same apparatus described in Chapter 2. During the final two minutes of each increment in power output, peak leg force and surface IEMG activity of VL, VM and RF muscles respectively were recorded, using the methods previously described. Oxygen uptake was also measured during this period.

Each progressive exercise test was performed (after an appropriate rest period) after the corresponding 45 second maximum test, ensuring that the EMG electrodes remained in exactly the same position for both maximum and progressive tests. A mapping technique was again used to ensure the correct repositioning of the electrodes for subsequent pairs of tests.

RESULTS

The relationship between force generation, exercise intensity and surface IEMG activity (recorded from VL, VM and RF muscles respectively) was investigated during a series of continuous progressive exercise tests performed over a range of pedal frequencies. The actual mean pedal frequencies recorded during the tests were 39 ± 1.0 (SD), 70 ± 2.5 (SD) and 98 ± 2.4 (SD) but will be referred to as 40, 70 and 100 rpm respectively for purposes of clarity.

The data obtained from subject NS at 70 rpm and at 100 rpm were not included in further analysis since they failed to achieve the defined criterion regarding maintenance of pedal frequency which has been previously described. The data obtained from subject TH at 70 rpm was only included in analysis which involved VL alone (Table 5) since the IEMG signals obtained from VM and RF at this pedal frequency were unsatisfactory (due to sweating beneath the EMG electrodes).

Relationship between Force Generation and Surface IEMG activity

Surface IEMG activity was recorded during the final two minutes of each increment in exercise intensity during the progressive tests, simultaneously with leg force. The total IEMG activity of each revolution (expressed in arbitrary units) was measured during a 10 revolution period and then averaged for each muscle individually. Values obtained for VL, VM and RF were then summed to obtain one value of IEMG activity representative of each increment in exercise intensity.

The individual data describing the relationship obtained between force generation and IEMG activity at each pedal frequency are illustrated in Figures 1-3 respectively. The relationship between force generation and IEMG activity over the range of values achieved

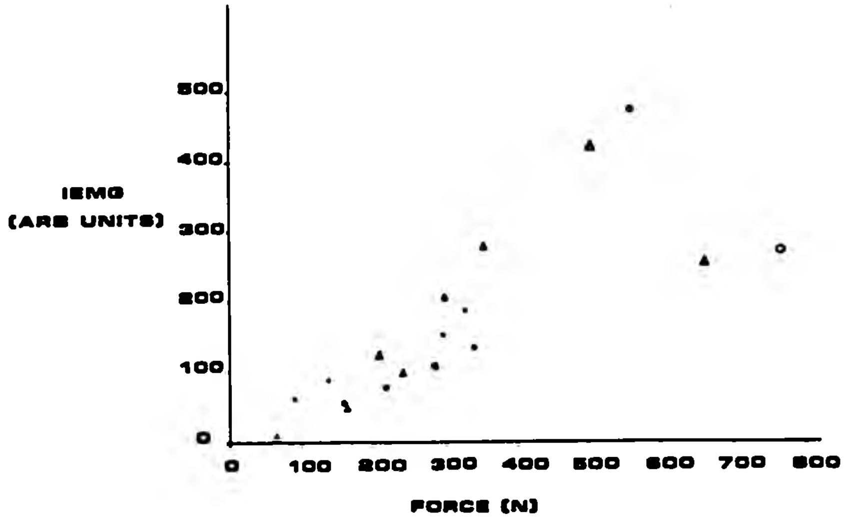


FIGURE 1

Relationship between force generation (N) and surface IEMG activity (arbitrary units) of the quadriceps obtained during a continuous progressive exercise test performed at 100 rpm.

Data obtained from 4 subjects are shown.

Values corresponding to maximal IEMG activity for each subject at this pedal frequency are also presented.

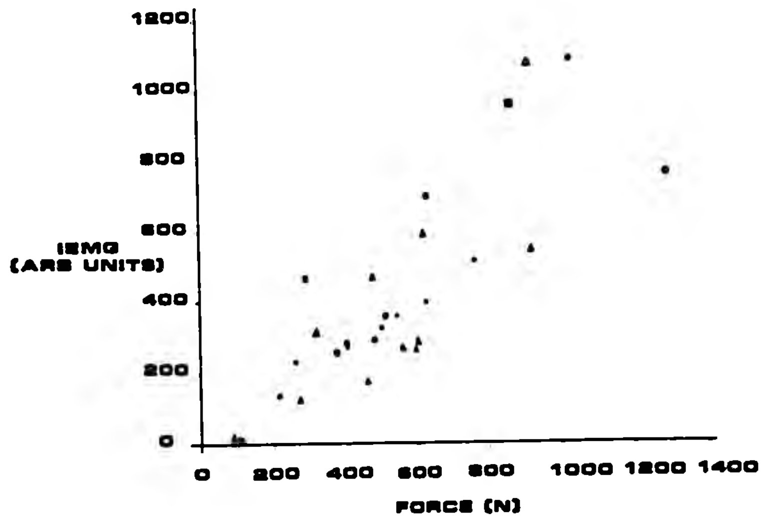


FIGURE 2

Relationship between force generation (N) and surface IEMG activity (arbitrary units) of the quadriceps obtained during a continuous progressive exercise test performed at 40 rpm.

Data obtained from 5 subjects are shown.

Values corresponding to maximal IEMG activity for each subject at this pedal frequency are also presented.

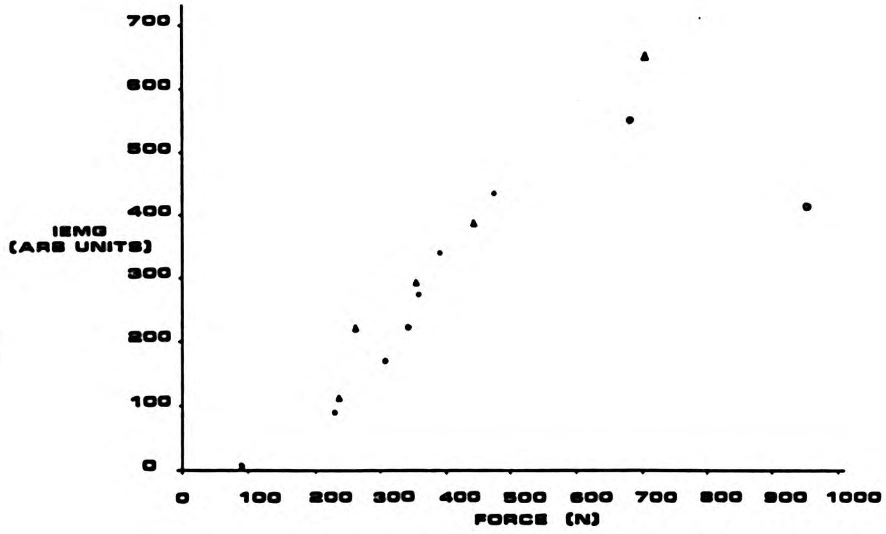


FIGURE 3

Relationship between force generation (N) and surface IEMG activity (arbitrary units) of the quadriceps obtained during a continuous progressive exercise test performed at 70 rpm.

Data obtained from 3 subjects are shown.

Values corresponding to maximal IEMG activity for each subject at this pedal frequency are also presented.

during the progressive tests appeared to be linear at each pedal frequency. Values corresponding to maximal activity of 'fresh' non-fatigued muscle, (obtained from the 45 second maximum test described in the previous Chapter), are also shown.

The IEMG/Force ratio (Table 1) increased significantly (p 0.05) with increasing exercise intensity at 40 rpm and 70 rpm. No significant increase in the ratio, however, was observed during exercise at 100 rpm.

Relationship between exercise intensity (% $\dot{V}O_2$ max) and surface IEMG activity

Exercise intensity, expressed in terms of percentage of maximum oxygen uptake (% $\dot{V}O_2$ max) was related to surface IEMG activity, also expressed as a percentage of maximum (% IEMG max). % IEMG max increased linearly with increments in % $\dot{V}O_2$ max; this relationship was significant (p 0.05) for each pedal frequency (Figures 4-6).

Individual linear regression analysis was performed upon the % $\dot{V}O_2$ max/% IEMG max data, at each pedal frequency in order to obtain values of % IEMG max corresponding to 25%, 50% 75% and 100% respectively of $\dot{V}O_2$ max. These values are illustrated in Table 2. The mean data corresponding to 25% and 100% respectively of $\dot{V}O_2$ max increased significantly from 17% to 78% at 40 rpm, 10% to 71% at 70 rpm and 8% to 54% at 100 rpm. At no time did the mean percentage activation reach maximum values, (ie 100%) during the course of the progressive tests.

Effect of Pedal Frequency upon surface IEMG activity, relative force generation and power output

Figure 7 illustrates the effect of pedal frequency upon percentage activation (% IEMG max). The mean data (± ISEM) obtained at values of exercise intensity corresponding to 75% and 100%

40 RPM

Subject	25%	50%	75%	100%
SP	0.46	0.59	0.71	0.84
NS	0.84	1.21	1.59	1.96
AS	0.34	0.54	0.74	0.94
MS	0.35	0.82	1.16	1.38
TH	0.23	0.36	0.48	0.61

70 RPM

Subject	25%	50%	75%	100%
SP	0.53	0.68	0.83	0.98
AS	0.18	0.38	0.58	0.78
MS	0.39	0.62	0.84	1.07

100 RPM

Subject	25%	50%	75%	100%
SP	0.67	0.62	0.57	0.52
AS	0.28	0.30	0.33	0.35
TH	0.09	0.22	0.34	0.47
MS	0.31	0.51	0.71	0.91

Table 1: Individual data illustrating the IEMG/Force ratio corresponding to values of exercise intensity (obtained from regression analysis) requiring 25%, 50%, 75% and 100% respectively of VO_2 max at each pedal frequency studied

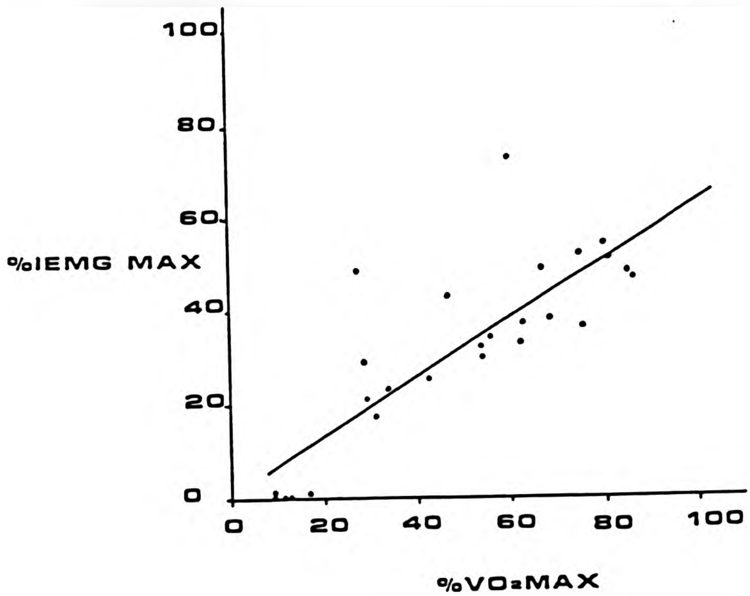


FIGURE 4

Relationship between percentage of maximum oxygen uptake (% $\dot{V}O_2$ max) and percentage of maximum IEMG activity (% IEMG max) of the quadriceps during continuous progressive cycling at 40 rpm.

Individual data from 5 subjects are shown (26 observations)

$y = 5.172 + 0.57x$; $r = 0.839$; $p < 0.005$

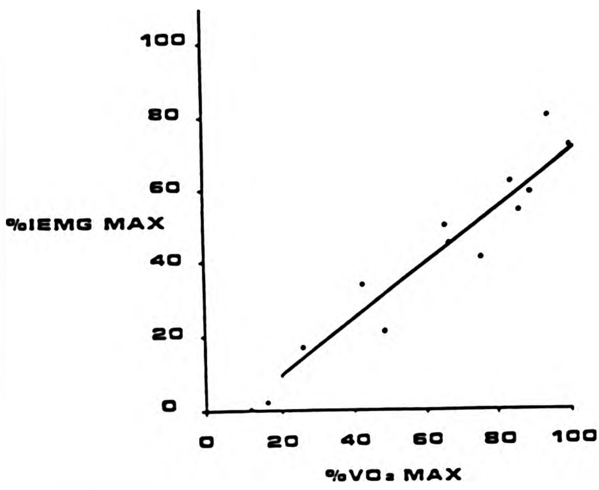


FIGURE 5

Relationship between percentage of maximum

oxygen uptake (% VO_2 max) and percentage of

maximum IEMG activity (% IEMG max) of the

quadriceps during continuous progressive cycling at 70 rpm

Individual data from 3 subjects are shown

(12 observations)

$y = 0.903 + 0.63x$; $r = 0.817$; $p<0.005$

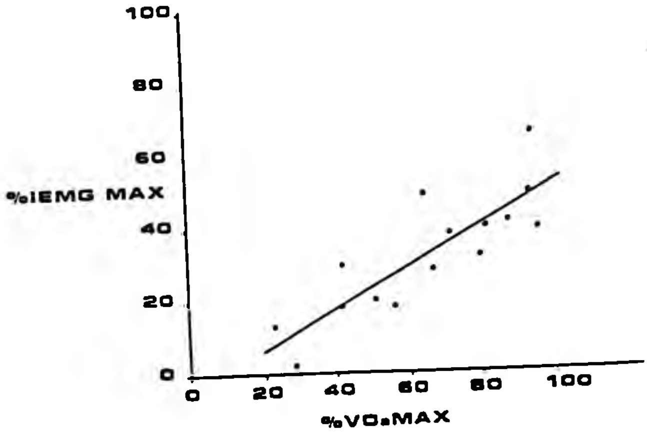


FIGURE 6

Relationship between percentage of maximum oxygen uptake (% VO_2 max) and percentage of maximum IEMG activity (% IEMG max) of the quadriceps during continuous progressive cycling at 100 rpm Individual data from 4 subjects are shown (15 observations)

$y = -8.558 + 0.80x$; $r = 0.953$; $p < 0.005$

40 RPM

	25	50	75	100 % $\dot{V}O_2$ max
SP	13.02	26.54	40.07	53.59
NS	31.07	64.35	97.62	130.90
AS	11.26	27.28	43.31	59.33
TH	10.75	30.13	49.50	68.88
MS	19.46	37.99	56.51	75.04
Mean	17.11	37.26	57.40	77.55
(± 1SEM)	(3.82)	(7.07)	(10.42)	(13.85)

70 RPM

	25	50	75	100 % $\dot{V}O_2$ max
SP	6.94	32.36	57.79	83.21
AS	6.70	24.53	42.35	60.18
MS	14.83	33.16	51.48	69.81
Mean	9.49	30.02	50.54	71.07
(± 1SEM)	(2.67)	(2.75)	(4.48)	(6.68)

100 RPM

	25	50	75	100 % $\dot{V}O_2$ max
SP	12.82	21.75	30.67	39.60
AS	0.30	17.90	35.50	53.10
TH	-0.62	17.06	34.73	52.41
MS	19.22	36.29	53.37	70.44
Mean	7.93	23.25	38.57	53.89
(± 1SEM)	(4.86)	(5.16)	(5.05)	(6.33)

TABLE 2

Individual % IEMG max data corresponding to values of power output requiring 25%, 50%, 75% and 100% respectively of $\dot{V}O_2$ max. Data obtained at 40 rpm, 70 rpm and 100 rpm are shown.

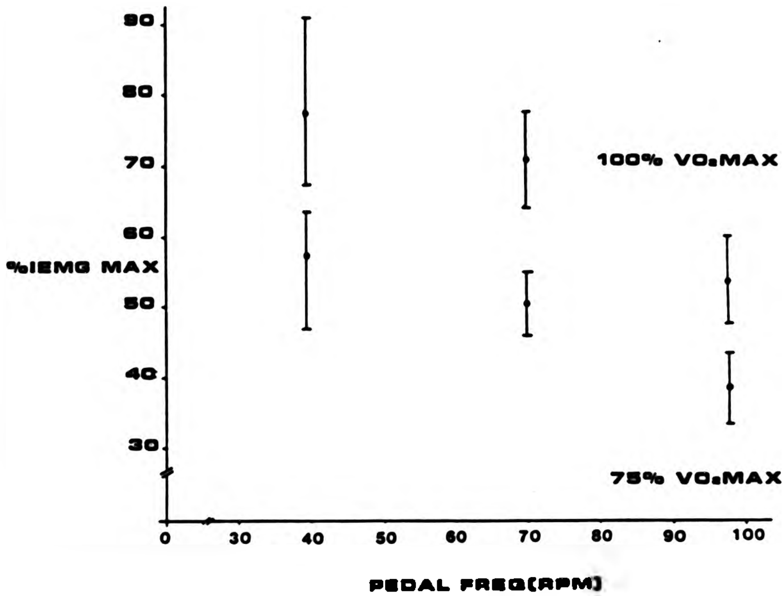


FIGURE 7

The relationship between pedal frequency (rpm) and percentage activation (% IEMG max) at two values of power output requiring 75% and 100% respectively of VO_2 max.

(Mean data ± ISEM are shown)

respectively of $\dot{V}O_2$ max are shown. (Individual data at each pedal frequency are presented in Table 2.) A significant decrement ($p < 0.05$) of % IEMG max was demonstrated when data obtained at 40 rpm and 100 rpm were compared. The differences in % IEMG max between 40 and 70 rpm respectively and between 70 and 100 rpm respectively, were of a smaller magnitude and did not achieve statistical significance. The effect of pedal frequency upon % IEMG max was similar to the previously described effect upon relative force generation (% PF max). % PF max was also calculated for each subject and at each pedal frequency during the present study. The results are illustrated in Table 3. No differences were demonstrated at each pedal frequency between the magnitude of % IEMG max and % PF max at 50, 75 and 100% respectively of $\dot{V}O_2$ max. % PF max was, however, significantly greater ($p < 0.05$) than % IEMG max at 25% of $\dot{V}O_2$ max (and at each pedal frequency).

IEMG data corresponding to values of power output requiring 75 watts and 150 watts respectively were also obtained by interpolation from regression analysis (Table 4). For each of these values of power output, a significant decrement ($p < 0.05$) of IEMG activity was demonstrated with increasing pedal frequency.

No differences in the IEMG/Force ratio were observed at each pedal frequency when data obtained at 25% and 50% of $\dot{V}O_2$ max were compared. A significant decrement ($p < 0.05$) was demonstrated, however, when higher values of exercise intensity (ie 75% and 100% of $\dot{V}O_2$ max) were compared.

Since recent glycogen depletion studies have involved muscle sampling from Vastus Lateralis, percentage activation was also calculated for this muscle alone. The data obtained is illustrated in Table 5. With only one exception, (70 rpm; 100% of $\dot{V}O_2$ max), no significant differences were observed between percentage activation of VL and that of VL, VM and RF together.

In summary, % IEMG max increased linearly with increments in exercise intensity over the range of pedal frequencies studied. A significant increase in the IEMG/Force ratio was observed as exercise intensity increased at 40 rpm and 70 rpm, but changes occurring at 100 rpm were non-significant. % IEMG max decreased with increments in pedal frequency when equivalent values of exercise intensity and power output were compared, a phenomenon similar to that previously described for relative force generation. The IEMG/Force ratio at equivalent values of exercise intensity was unchanged at low and moderate levels (25% and 50% respectively of $\dot{V}O_2$ max) but significantly lower at higher levels (75% and 100% respectively of $\dot{V}O_2$ max).

40 RPM

	25	50	75	100
SP	21.51	42.51	63.51	84.51
NS	30.38	60.56	90.73	121.00
AS	13.91	25.23	36.56	47.88
TH	20.54	42.39	64.24	86.09
MS	28.06	48.34	68.61	88.89
Mean	22.88	43.81	64.73	85.67
(± ISEM)	(2.92)	(5.70)	(8.62)	(11.59)

70 RPM

	25	50	75	100
SP	27.90	42.28	56.65	71.03
AS	13.50	22.90	32.30	41.70
MS	26.45	41.30	56.15	71.00
Mean	22.62	35.49	48.37	61.24
(± ISEM)	(4.58)	(6.30)	(8.04)	(9.77)

100 RPM

	25	50	75	100
SP	16.31	31.79	47.26	62.74
AS	6.09	19.84	33.59	47.34
TH	7.55	21.90	36.25	50.60
MS	33.91	47.26	60.61	73.96
Mean	15.97	30.20	44.43	58.66
(± ISEM)	(6.40)	(6.26)	(6.15)	(6.08)

TABLE 3

Individual % PF max data corresponding to values of power output requiring 25%, 50%, 75% and 100% respectively of $\dot{V}O_2$ max.

Data obtained at 40 rpm, 70 rpm and 100 rpm are shown

	40 RPM		70 RPM		100 RPM	
Subject	75	150	75	150	75	150
SP	167.2	296.8	82.1	191.9	87.3	120.3
NS	342.2	592.7	-	-	-	-
AS	154.9	301.9	78.9	157.6	52.7	99.9
MS	251.8	461.9	117.4	218.8	91.1	161.8
TH	125.8	228.5	-	-	43.1	82.9

Table 4: Individual data illustrating surface IEMG activity (arbitrary units) at values of power output requiring 75 watts and 150 watts respectively

40 RPM

	25	50	75	100 % $\dot{V}O_2$ max
SP	9.22	21.15	33.07	45.00
NS	3.31	22.81	42.31	61.81
AS	17.63	42.35	67.08	91.80
TH	11.72	28.17	44.62	61.07
MS	20.28	39.83	59.28	78.73
Mean	12.45	30.86	49.27	67.68
(± 1SEM)	(3.04)	(4.35)	(6.12)	(8.05)

70 RPM

	25	50	75	100 % $\dot{V}O_2$ max
SP	15.41	33.56	51.71	69.86
AS	9.56	23.36	37.16	50.96
TH	10.73	28.31	45.88	63.46
MS	3.63	18.58	33.53	48.48
Mean	9.83	25.95	42.07	58.19
(± 1SEM)	(2.43)	(3.22)	(4.13)	(5.35)

100 RPM

	25	50	75	100 % $\dot{V}O_2$ max
SP	7.72	14.95	22.17	29.40
AS	9.08	27.91	46.73	65.56
TH	1.80	17.42	33.05	48.67
MS	23.59	41.12	58.64	76.17
Mean	10.55	25.35	40.15	54.95
(± 1SEM)	(4.63)	(5.96)	(7.95)	(10.23)

TABLE 5

Individual % IEMG max data (obtained from Vastus Lateralis muscle alone) corresponding to values of power output requiring 25%, 50%, 75% and 100% of $\dot{V}O_2$ max.

Data obtained at 40 rpm, 70 rpm and 100 rpm are shown

DISCUSSION

Quadriceps surface IEMG activity, leg force, oxygen uptake and power output were measured during submaximum and maximum cycling exercise performed over a range of pedal frequencies.

The relationship between leg force and surface IEMG activity was essentially linear over the range of values attained during the course of each progressive test, a result which is in agreement with previous studies of cycling exercise, (Bigland-Ritchie and Woods, 1976; Hendriksson and Bonde-Petersen, 1974; Citterio and Agostoni, 1984).

A significant increase in the mean IEMG/Force ratio did occur over the range of values achieved during the course of the progressive tests at 40 and 70 rpm respectively, although this was not the case at 100 rpm. This was probably due to the fact that a greater utilisation of maximum force generating capacity occurs at lower pedal frequencies, which places a greater peripheral demand upon the body, with a greater likelihood of peripheral fatigue (as evidenced by an increase in the IEMG/Force ratio) particularly at higher values of exercise intensity.

Linear regression analysis was performed upon the oxygen uptake/ IEMG data, the data being expressed in each case as a percentage of maximum, further analysis giving values of % IEMG max corresponding to 25, 50, 75 and 100% respectively of $\dot{V}O_2$ max. The mean percentage activation of the subjects studied remained submaximal during the course of each progressive test; the highest mean value recorded was 78% at 100% of $\dot{V}O_2$ max and a pedal frequency of 40 rpm. However, the individual data obtained from subject NS, a marathon runner, were interesting in that when regression analysis was applied to the data obtained at 40 rpm, it appeared that values of

131% of maximum activating capacity and 121% of maximum force generating capacity were necessary in order to maintain a power output requiring 100% of $\dot{V}O_2$ max (Figure 8). The functional significance of this data is that subject NS would of course never reach $\dot{V}O_2$ max during a progressive test at this pedal frequency, since the requirement in terms of force generating capacity would be above the subject's maximum.

Although the mean values of % IEMG max remained submaximal at 100% of $\dot{V}O_2$ max, it is possible that the actual number of motor units activated within the quadriceps may have been maximal. Force modulation may be achieved in two ways, either by recruitment of motor units or by rate coding and it is therefore possible to activate a maximal number of motor units but record submaximal electrical activity, since some motor units may be firing at submaximal frequencies.

The results of the present study in conjunction with a recent glycogen depletion study, (Vøllestad, 1985) confirm the above suggestion. In a study of prolonged cycling exercise performed at 70 rpm, Vøllestad demonstrated an approximate 1:1 relationship between percentage oxygen uptake and percentage activation of Type I and Type II fibre sub-groups, determined by glycogen depletion analysis of serial samples of muscle obtained from Vastus Lateralis (VL). At levels of power output requiring 100% of $\dot{V}O_2$ max, almost all of the fibres within the muscle samples were observed to have been active. Figure 9 illustrates the relationship obtained by Vøllestad between exercise intensity and percentage activation of Type I and Type II muscle fibres, at a pedal frequency of 70 rpm. The figure shows an initial recruitment of Type I and Type II A (fast/fatigue-resistant) fibres followed by a systematic recruitment

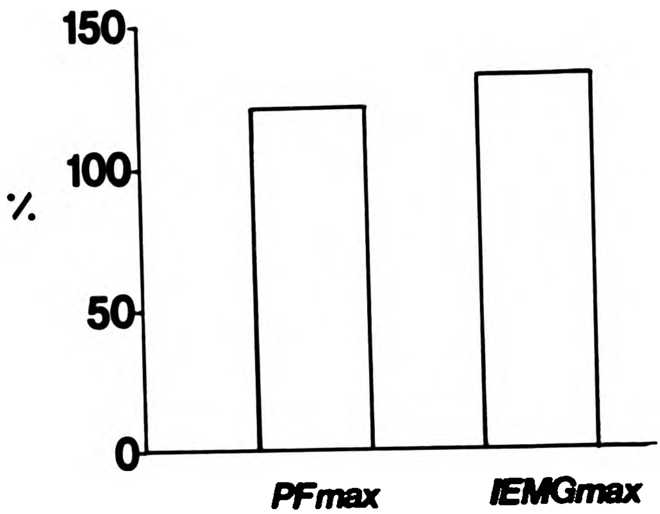


FIGURE 8

Individual data obtained from subject NS, showing values of % IEMG max and % PF max (derived from regression analysis) required to maintain 100% of $\dot{V}O_2$ max.

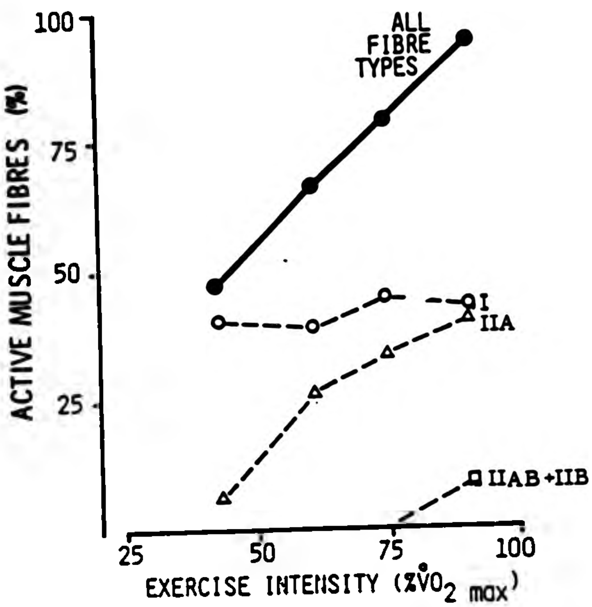


FIGURE 9

Relationship between exercise intensity (% $\dot{V}O_2$ max) and percentage activation of Type I and Type II muscle fibres during sustained cycling exercise at 70 rpm.

[From Vøllestad, 1985]

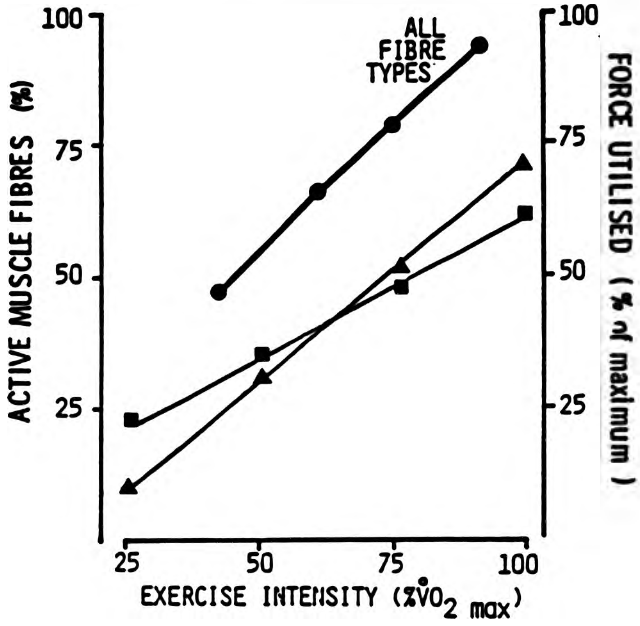


FIGURE 10

Relationship between % $\dot{V}O_2$ max and % PF max (■), % IEMG max (▲) and fibre type activation (●) during cycling exercise at 70 rpm.
[fibre type activation ●—● data is from Vøllestad, 1985]

of Type II fibre sub-groups, in order of increasing fatigue sensitivity (ie Type II A fibres followed by Type II AB and Type II B), with increments in exercise intensity. Thus the order of motor unit recruitment during prolonged dynamic exercise would appear to be in accordance with the Size Principle.

Figure 10 illustrates the same relationship as depicted in Figure 9, except that only the data for all fibre types are shown. The % IEMG max and % PF max data obtained (at 70 rpm) from the present study are also illustrated. It is clear that at 100% of $\dot{V}O_2$ max almost all of the muscle fibres within VL were activated with only 61% of maximum force generating capacity and 71% of maximum electrical activity utilised. This suggests that a certain proportion of motor units within Vastus Lateralis and indeed the quadriceps (since the IEMG activity of VL in the present study appeared to be representative of that of the quadriceps) were firing submaximally at maximum work-loads.

This result would indicate that rate coding is an important factor influencing force modulation at high levels of tension output, since at supramaximal exercise intensities, variation in firing rate would be solely responsible. This finding, which is in agreement with Vøllestad (1985), would appear to be more compatible with force modulation in small muscles rather than large muscles (Milner-Brown, Stein and Yemm, 1973 b, 1973 c; Kukulka and Clamman, 1981; De Luca, Le Fever, McCue and Xenakis, 1982). The latter studies, however, were related to isometric rather than dynamic contractions of large and small muscles. Unfortunately, it was not possible to combine IEMG and glycogen depletion data to investigate the regulation of force generation at different pedal frequencies. It is evident, however, that the relative importance of recruitment versus rate coding to force regulation may be dependent not only upon muscle size, but also upon the type and frequency of contraction. Further studies are necessary to clarify this.

As pedal frequency increased, a reduction in % IEMG max was observed which was of approximately the same order of magnitude and in parallel with % PF max. The reduction in % PF max with increasing pedal frequency would therefore appear to be the direct result of a decrease in % IEMG max. It was not possible, from the present data, to determine whether the decline in % IEMG max was due to either a reduction in motor unit firing rate, or a 'derecruitment' of motor units. Since, however, equivalent values of power output were maintained at high pedal frequencies with a concomitant reduction in IEMG activity (Table 4), a possible explanation would be a derecruitment of slow twitch motor units in favour of the recruitment of a smaller number of fast twitch units, (since they provide greater power per unit stimulus). Indirect support for this suggestion is provided by the results of Citterio and Agostoni (1984) who demonstrated that quadriceps surface IEMG activity remained constant or increased less when an increment in power output was achieved by increasing pedal frequency at constant force, than when a similar increment was achieved by increasing force at a constant pedal frequency. This phenomenon was also attributed to a derecruitment of slow twitch units with the recruitment of a smaller number of fast twitch units, that is, a selective activation of motor units according to the speed of movement.

Certain factors, however, must be taken into consideration which may conflict with this proposal, (in addition to those factors previously discussed in Chapter 5 concerning the validity of surface IEMG measurements, etc). Firstly, if a preferential recruitment of fast twitch units occurred at high pedal frequencies in order to maintain an equivalent value of power output, an increase in the IEMG/Force ratio may have been expected, since fast twitch units are more fatigue sensitive than slow twitch units. This was not demonstrated in the present study; the IEMG/Force ratio did not change significantly at low and moderate levels of exercise intensity when slow and fast pedal frequencies were compared, and indeed, a decrease was observed at higher levels. (Table 1.)

A selective activation of fast twitch motor units would also appear to be at variance with the Size Principle. However, there are reports in the literature, using both electrophysiological and histochemical techniques, indicating exceptions to the orderly recruitment of motor units (Grimby and Hannerz, 1973; Secher and Nygaard, 1976).

In conclusion, the results of the present investigation into the relationship between force generation and surface IEMG activity during prolonged cycling exercise suggest the possibility of a selective motor unit involvement at high pedal frequencies. This phenomenon may also explain the previously described reduction in % PF max when fast frequencies are compared to slow at equivalent values of power output.

CHAPTER 7

THE EFFECT OF ORAL SUPPLEMENTATION WITH L-CARNITINE UPON MAXIMUM AND SUBMAXIMUM EXERCISE CAPACITY

INTRODUCTION

The major part of this Thesis has described the investigation into the relative force generating capacity of human muscle and its importance as a possible contributing factor limiting the ability to sustain prolonged dynamic exercise. One method of offsetting this limitation which has been previously discussed is to increase, by the subject's own volition, the frequency of muscle contraction. The investigation which forms the final part of this Thesis concerns the attempt to reduce the peripheral limitation to sustained cycling exercise, not by a behavioural mechanism, but by increasing the aerobic energy flux, by oral supplementation of the substance L-Carnitine.

Carnitine (B-hydroxyγ -trimethylamino butyrate) is a quaternary amine which plays a central role in lipid catabolism and energy production. Fritz, (1955, 1963), identified carnitine as part of the shuttle mechanism whereby long chain fatty acids are converted to acyl carnitine derivatives and transported across the mitochondrial membrane. Carnitine may play a role in pyruvate oxidation by reversing the inhibition of pyruvate dehydrogenase by Acetyl CO A (Bookelman, 1978) and it may also be involved in branched chain amino acid oxidation (Van Hinsbergh, Veerkamp and Glatz, 1979).

Physical training increases the capacity of skeletal muscle to oxidise fatty acids (Havel, Carlson, Ekelund and Homoreu, 1964; Issekutz, Miller and Rodahl, 1966; Mole, Oscai and Holloszy, 1971). This requires an increased transport of fatty acids into mitochondria and changes in carnitine levels and/or the activities of its associated enzymes may be involved in the biochemical adaptation to chronic training (Froberg, Ostman and Sjøstrand, 1972). This has been reinforced by Lennon, Strathan, Shrago, Nagee, Madden, Hanson and Carter, (1983) who have shown that muscle carnitine levels are indeed greater in trained as opposed to untrained individuals.

Animal studies have demonstrated that the utilisation of fat as a fuel exerts a sparing effect upon the muscle glycogen store (Rennie, Winder and Hollszy, 1976). The facilitation of fat oxidation by carnitine supplementation could therefore be beneficial toward endurance performance. Recently, Marconi, Sassi, Cardinelli and Ceretelli, (1985) claim to have demonstrated a 6% increase in the aerobic power ($\dot{V}O_2$ max) of six athletes after oral supplementation of carnitine for two weeks (4g per day). Improvements in aerobic capacity, indicated by an increase in endurance time at a work-load requiring 80% of $\dot{V}O_2$ max have also been claimed by Eclache, Quard, Carrier, Berthillier, Marnot and Eischenberger (1979) (see Marconi et al 1985). A recent study (Cooper, Jones, Edwards, Corbucci, Montanari and Trevisani, (1986) however, has demonstrated no detectable improvement in the performance times of experienced marathon runners during a period of carnitine supplementation (4g per day).

The purpose of the present study was to investigate the effects of oral L-Carnitine supplementation upon submaximum and maximum exercise performance: Two, strictly controlled double-blind trials were performed.

METHODS

SUBJECTS

Three male and six female subjects, all healthy but untrained, participated in the first trial (Table 1). Their ages ranged from 26-31 years (mean 27 years). In the second trial there were four male and six female subjects, (Table 2), ages ranging from 24-37 years (mean 28 years). The subjects gave written consent and all procedures were approved by the Committee for the Ethics of Human Investigation, University College Hospital.

PROTOCOL

Each trial was a double-blind cross-over. In the first trial, the placebo or L-Carnitine was taken for fourteen days and after completing an exercise test the subjects immediately changed to the other substance (Figure 1). In addition, two endurance-trained athletes were studied under single-blind conditions; the investigators knowing the substance being taken. (For their physical characteristics see Table 5.) In the second trial the substances were taken for twenty eight days and there was a two week break before starting the other compound (Figure 1). Four of the subjects participated in both trials.

L-Carnitine was obtained from Sigma Tau (Pomezia, Italy) as a solution suitable for oral administration. Peppermint essence (1 ml L^{-1}) was added and the solution dispensed in 10 ml ampoules containing 1g of carnitine. A placebo solution was made containing 60g sucrose, 5g citric acid, 1 ml of peppermint essence and 10 mg quinine per L. This was dispensed in individual 10 ml ampoules. The subjects took two ampoules per day containing either placebo or carnitine.

SUBJECT	SEX	AGE (yrs)	BODYWEIGHT (kg)
MC	M	37	61.0
MH	M	27	70.0
NM	M	26	70.6
HC	F	23	61.4
PD	F	29	57.9
MT	F	24	64.3
JF	F	23	58.8
SG	F	31	77.6
KF	F	24	48.3
X		27.1	63.3
± ISD		± 4.6	± 8.6

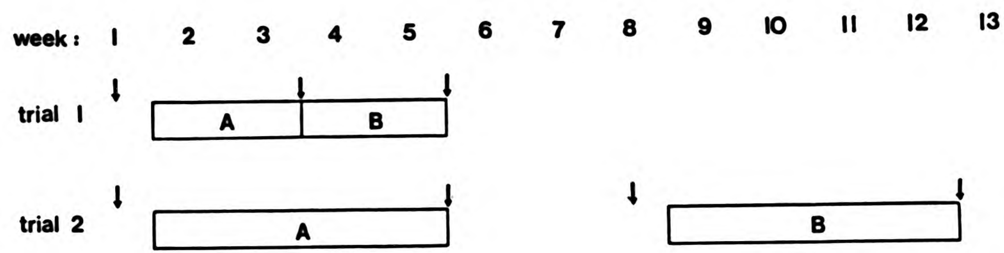
TABLE 1

Physical characteristics of the nine untrained subjects involved in Trial 1

SUBJECT	SEX	AGE (yrs)	BODYWEIGHT (kg)
MC	M	37	61.0
MH	M	27	70.0
MA	M	31	74.0
SA	M	25	67.0
PD	F	29	58.0
CG	F	25	56.0
OR	F	25	66.0
CF	F	25	45.5
MT	F	24	64.0
DN	F	36	66.0
X ± ISD		28.4 ± 4.8	62.8 ± 8.1

TABLE 2

Physical characteristics of the ten untrained subjects involved in Trial 2



↓ indicates exercise test

FIGURE 1

Experimental Protocol: Trials 1 and 2 double-blind cross-over In each trial the subjects took substance A followed by substance B. The identity of each substance was known only to one individual who was not involved in the trial

EXERCISE TESTS

The subjects were thoroughly familiarised with the experimental procedure before the control measurements were made at the start of each trial. On the days when exercise tests were performed, the subjects were asked to refrain from strenuous physical activity prior to testing and to avoid smoking, eating and drinking sweetened beverages for at least three hours beforehand. Otherwise, the subjects continued their routine activities throughout the trial period.

The exercise response in each trial was measured during a continuous progressive exercise test performed on a cycle ergometer and at 70 rpm. Oxygen uptake ($\dot{V}O_2$), carbon dioxide output ($\dot{V}CO_2$) and cardiac frequency (fc) were measured over the final two minutes of each increment in power output, as previously described in Chapter 2. In cases of doubt where the conventional criterion of a plateau of $\dot{V}O_2$ against work-load was not observed, the maximal measurement was repeated on the following day. Venous blood samples (10 ml) were obtained before and within five minutes of the cessation of exercise.

ANALYSES

Plasma L-Carnitine was assayed according to the method described by Di Donato, Cornelio, Storehi and Rimoldi (1979). Plasma B-hydroxybutyrate concentration (Trial 1) was measured using slight modifications of enzyme based fluorometric methods described by Lloyd, Burin, Smythe and Alberti (1978). Plasma lactate concentration (Trials 1 and 2) was measured by a conventional automated enzymic method, and plasma 2,3-Diphosphoglyceric acid (2,3-DPG) concentration (Trial 2) was measured using a kit supplied by the Sigma Chemical Company, Poole, England. Haemoglobin measurements (Trial 2) were made by the

Department of Haematology, University College Hospital.

RESULTS

The various procedures were well tolerated by all subjects and no untoward effects of carnitine were reported.

All of the exercise tests were performed at the same time of day and after an equal period of time following the final dose of each substance.

TRIAL 1

Maximum cardiac frequency

The mean maximal heart rate on placebo was 195 beats min^{-1} with a range of 180-207 beats min^{-1}. After two weeks of oral supplementation with carnitine, the mean maximal heart rate was 192 beats min^{-1} with a range of 178-210 beats min^{-1}. Although seven of the nine subjects demonstrated a decrease in maximal heart rate, this did not reach conventional levels of significance using a paired t test ($p < 0.1$) (Table 3).

Maximum oxygen uptake ($\dot{V}O_2$ max)

No significant changes were seen in the maximum oxygen uptake as a result of oral carnitine supplementation (Table 3).

Effect of carnitine on respiratory exchange ratio (RER)

The RER, the ratio of CO_2 produced to O_2 consumed, was determined for both carnitine and placebo runs. No significant differences were found at any time during the progressive exercise tests.

The pre- and post-exercise measurements of plasma lactate and B-hydroxybutyrate under placebo and carnitine supplemented conditions were not significantly different (Table 4).

Submaximum Cardiac Frequency

Cardiac frequency at 50% (fc 0.5) and 75% (fc 0.75) respectively of $\dot{V}O_2$ max was interpolated for each individual from linear regression of the submaximal cardiac frequency/oxygen uptake data. Figure 2

SUBJECT	$\dot{V}O_2$ MAX (ml min-1 kg-1)		fc MAX (beats min-1)		fc 0.5 (beats min-1)		fc 0.75 (beats min-1)	
	PLACEBO	L-C	PLACEBO	L-C	PLACEBO	L-C	PLACEBO	L-C
MC	43.6	43.8	190	179	107	107	148	143
MH	57.2	58.7	180	178	125	120	159	148
NM	44.0	47.3	207	210	151	140	184	173
HC	36.2	34.9	199	199	148	142	169	166
PD	45.8	47.0	191	187	132	115	166	155
MT	32.0	28.8	187	178	130	126	157	159
JF	34.4	35.1	198	193	142	144	174	171
SG	38.9	38.2	200	200	126	124	161	158
KF	40.4	40.6	199	207	138	138	170	179
X	41.4	41.6	194.6	192.3	133.2	128.4	165.3	161.3
± ISD	± 7.51	± 8.82	± 8.20	±12.49	±13.48	±13.17	±10.53	±11.91

TABLE 3

Trial 1: Effect of oral supplementation of L-Carnitine and placebo upon maximum oxygen uptake ($\dot{V}O_2$ max), maximum cardiac frequency (fc max) and submaximum cardiac frequency at values of power output requiring 50% and 75% respectively of $\dot{V}O_2$ max

Mean data ± ISD are shown

	PLACEBO		CARNITINE	
	PRE EX	POST EX	PRE EX	POST EX
TOTAL CARNITINE µmol/l	55.3	-	78.9	-
	± 7.6	-	±16.3	
LACTATE mmol/l	1.04	11.7	1.14	10.1
	± 0.66	± 2.1	± 0.28	± 2.6
β OH BUTYRATE mmol/l	0.069	0.074	0.073	0.098
	± 0.05	± 0.05	± 0.09	± 0.005

TABLE 4

Trial 1: Pre and post exercise values for plasma total carnitine, plasma lactate and β-hydroxybutyrate in untrained subjects

Mean Data ± ISD are shown

illustrates the change in the relationship between $\dot{V}O_2$ and fc with oral carnitine supplementation in one subject (PD). Following carnitine supplementation there was a significant reduction of fc 0.5 from 133 ± 13 to 128 ± 13 beats min^{-1} ($p < 0.05$). The reduction of fc 0.75 from 166 ± 11 to 161 ± 12 beats min^{-1}, however, did not reach conventional levels of significance($p < 0.02$) (Table 3).

The two endurance-trained athletes participating the single-blind study showed the same pattern of responses as the untrained subjects in Trial 1 (Table 5). There was no increase in $\dot{V}O_2$ max following carnitine supplementation, but at 50% of $\dot{V}O_2$ max there was a reduction in cardiac frequency of 16 beats min^{-1} in one subject and 3 beats min^{-1} in the other. The submaximum reduction in cardiac frequency at 75% of $\dot{V}O_2$ max however was absent in one of the subjects and only slight in the other (Table 5).

The results of Trial 1 suggested that carnitine supplementation may lead to a reduction in submaximum cardiac frequency with no change in either maximum cardiac frequency or oxygen uptake. To obtain further information and to test possible mechanisms for this, a second trial was undertaken in which the substances were taken for twice the duration, and a gap of two weeks was left between the two substances to ensure there was no cross-over effect. In addition to measurements of plasma carnitine and lactate, haemoglobin (pre-exercise) and plasma 2,3-DPG concentration (pre and post-exercise) were also measured.

TRIAL 2

Maximum Cardiac Frequency

After four weeks of oral carnitine supplementation, the mean fc max increased from 186 beats min^{-1} (range 170-210) to 187 beats min^{-1} (range 168-210), but this difference did not achieve

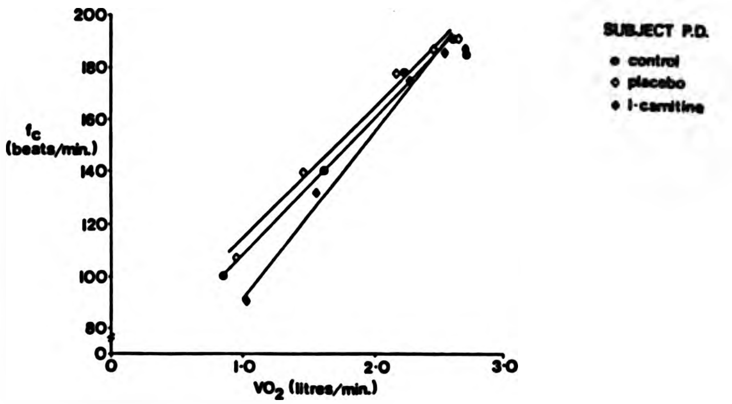


FIGURE 2

Trial 1: Effect of oral supplementation of L-Carnitine upon the relationship between oxygen uptake ($\dot{V}O_2$) and cardiac frequency (fc) in one subject (PD)

SUBJECT	SEX	AGE (yrs)	BODY WT (kg)	$\dot{V}O_2$ MAX (ml min^{-1} kg^{-1})		fc MAX (beats min^{-1})		fc 0.5		fc 0.75	
				CONTROL	L-C	CONTROL	L-C	CONTROL	L-C	CONTROL	L-C
NS	M	32	69.9	64.1	57.8	156	155	113	97	135	130
SP	M	30	68.2	68.3	67.9	192	185	127	124	157	158

TABLE 5

Physical characteristics of the endurance-trained subjects participating in the single-blind study maximal and submaximal response to exercise after L-Carnitine supplementation are also shown statistical significance (Table 6).

Submaximum cardiac frequency

Linear regression analysis was performed upon the individual submaximum cardiac frequency/oxygen uptake data to obtain values of cardiac frequency at work-loads requiring 25, 50 and 75% respectively of $\dot{V}O_2$ max. Figure 3 illustrates the mean values obtained at each exercise intensity during both carnitine and placebo supplementation. Although there was a slight decrease in the mean cardiac frequency at each exercise intensity, it was not statistically significant ($P>0.05$); the data obtained at 50% and 75% of $\dot{V}O_2$ max are given in Table 6.

Blood Biochemistry

There was no significant difference ($p>0.05$) in the plasma lactate concentration before and after exercise when placebo and carnitine supplemented conditions were compared. This was also observed for the pre-exercise plasma 2,3-DPG concentration, although the mean post-exercise value was significantly lower when under carnitine supplemented conditions. However no significant difference was observed when pre- and post-exercise values were compared for each condition. The pre-exercise haemoglobin concentration was unaltered (p 0.05) after carnitine supplementation. (Table 7.)

Four subjects (MC, MH, PD and MT) participated in both trials, but the data obtained from Trial 2 were not consistent with those of Trial 1. With only two exceptions (MC - fc 0.75; MT - fc 0.05) the change in submaximum cardiac frequency was in the opposite direction in Trial 2 compared with Trial 1.

SUBJECT	$\dot{V}O_2$ MAX (ml min-1 kg-1)		fc MAX (beats min-1)		fc 0.5 (beats min -1)		fc 0.75 (beats min-1)	
	PLACEBO	L-C	PLACEBO	L-C	PLACEBO	L-C	PLACEBO	L-C
MC	46.6	43.8	184	174	123	109	156	144
MH	60.4	-	177	178	118	129	145	157
MA	59.3	61.7	186	187	138	133	169	165
SA	60.7	61.2	210	210	150	142	182	175
PD	51.9	52.4	190	197	132	135	164	170
CG	35.0	39.1	188	195	124	132	164	163
OR	33.4	31.7	170	168	126	115	156	145
CF	32.9	33.8	200	198	152	146	176	174
MT	34.7	32.7	182	184	123	119	157	155
DN	37.2	36.2	177	174	112	109	144	140
X	45.2	43.6	186	187	130	127	161	159
(± ISD)	± 12.0	± 12.0	± 12	± 13	± 13	± 13	± 12	± 13

TABLE 6

Trial 2: Effect of oral supplementation of L-Carnitine and placebo upon maximum oxygen uptake, maximum cardiac frequency and submaximum cardiac frequency at values of power output requiring 50% and 75% respectively of $\dot{V}O_2$ max

Mean data ± ISD are shown

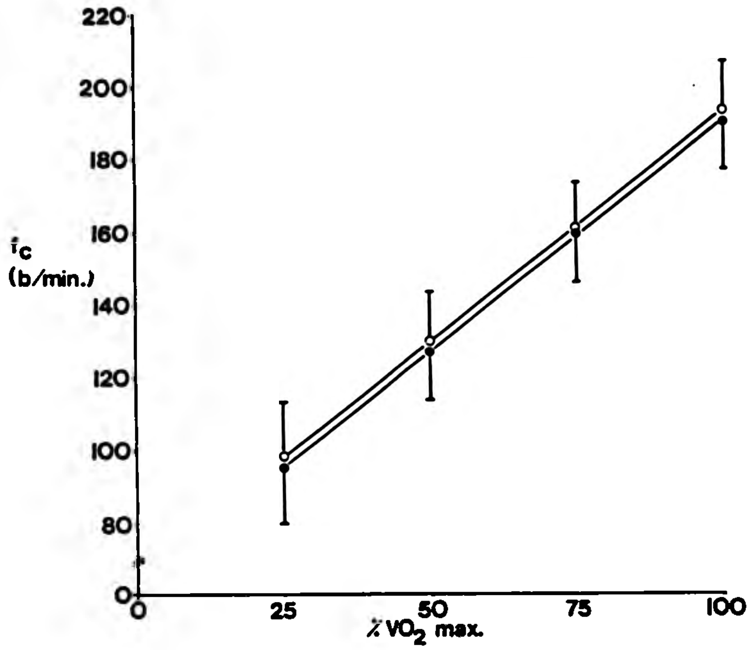


FIGURE 3

Trial 2: Effect of oral supplementation of L-Carnitine/placebo upon submaximum and maximum cardiac frequency (fc), at values of power output requiring 25, 50, 75 and 100% respectively of $\dot{V}O_2$ max

Mean data ± 1SD are shown

(Placebo supplementation O; L-Carnitine supplementation •)

	PLACEBO		CARNITINE	
	PRE EX	POST EX	PRE EX	POST EX
TOTAL CARNITINE µmol/l	41.3 ± 8.4	-	56.0 ± 8.2	-
PLASMA LACTATE mmol/l	0.86 ± 0.31	11.82 ± 4.45	0.94 ± 0.39	10.79 ± 3.03
HAEMOGLOBIN g/dl	13.7 ± 0.8	-	13.5 ± 1.3	-
2,3-DPG µmol/g haemoglobin	19.23 ± 2.97	20.64 ± 2.61	17.15 ± 1.51	16.00 ± 2.89

TABLE 7

Trial 2: Pre and post exercise values for plasma total carnitine, plasma lactate, plasma 2,3-DPG and haemoglobin concentrations in ten untrained subjects

Mean data ± ISD are shown

DISCUSSION

The effect of orally administered carnitine upon the submaximum and maximum exercise performance of a group of untrained subjects was investigated in two trials, both of which were performed under double-blind conditions and several months apart. The protocol of each trial was essentially the same, but in the second trial the same dose of carnitine was administered for a longer duration. In addition, two endurance-trained athletes were studied in parallel to Trial 1, although under single-blind conditions.

In Trial 1 there was an indication of a reduced heart-rate response at moderate levels of power output (50% of $\dot{V}O_2$ max) as a result of carnitine supplementation. It is suggested that this was not due to an habituation effect, since the subjects were carefully familiarised with the experimental procedures before the commencement of each trial to eliminate any such effects, (Davies, Tuxworth and Young, 1970) and the order in which placebo and carnitine were given were randomised.

Discounting any habituation effect, there is no obvious explanation for the observed response in terms of the known actions of L-Carnitine. The evidence obtained from the RER measurements and blood metabolites does not suggest any appreciable change in the pattern of fuel utilisation. The improvement in aerobic capacity, that is, the ability to maintain a given value of oxygen uptake under the same conditions of speed and load but with a reduction in heart-rate suggested that the action of carnitine may have been to effect changes in either stroke volume or oxygen extraction within the exercising muscle, but no direct evidence exists to support either of these points. The effect of carnitine upon the submaximum heart-rate response warranted further investigation and for this reason the second, more extensive trial was undertaken. In addition to the extension of the duration of carnitine and placebo supplemented periods, pre-exercise plasma haemoglobin and pre- and post-exercise plasma 2,3-DPG concentrations were also measured.

L-Carnitine has been used in the treatment of chronic anaemia (Trovato, Ginardi, Di Marco, Dell'aira, and Corsi, 1982) with beneficial effects, increasing the haematocrit and haemoglobin concentration. It was not known whether carnitine could cause erythrocytopaenia in otherwise healthy subjects, although such an effect could have explained the results of Trial 1.

In human erythrocytes, 2,3-diphosphoglyceric acid (2,3-DPG) is bound to haemoglobin in approximately an equimolar ratio. Since haemoglobin has a preferential affinity for 2,3-DPG over oxygen, an increase in the level of this compound results in a decreased haemoglobin/oxygen affinity, (Benesch and Benesch, 1969). 2,3-DPG therefore serves as an important regulator of the oxygen supply from haemoglobin to meet tissue demands. The effects of carnitine upon 2,3-DPG have as yet not been investigated. Obviously, if carnitine were to increase 2,3-DPG concentration, this would have the effect of decreasing haemoglobin/oxygen affinity, thus shifting the oxygen dissociation curve to the right and facilitating the extraction of oxygen at the tissue level. This would be of even greater advantage during exercise, when the tissue demand for oxygen increases.

The results of Trial 2, however, appeared to be at variance with the initial observations of Trial 1. Although there was a decrease in the submaximum heart-rate response at moderate levels of power output, the shift was small and not statistically significant. The data obtained concerning plasma haemoglobin and plasma 2,3-DPG concentrations were also non-significant and cast doubt upon the earlier suggestion that carnitine may cause an increase in oxygen extraction by the working muscle either by erythrocytopaenia or by an increase in 2,3-DPG concentration.

In addition, the results of the four subjects who participated in both trials were inconsistent.

It is possible that the longer duration of oral carnitine supplementation in Trial 2 may have caused an increase in the rate of carnitine clearance from muscle, thus minimising the possible benefits of the extended duration of supplementation. Unfortunately, no data exist with which to support this suggestion.

Since it was not possible to reproduce the significant result of Trial 1, it must be concluded that there is little evidence to suggest a beneficial effect of oral carnitine supplementation upon submaximum or maximum exercise performance. An effect, if any, would appear to be small and inconsistent.

The data obtained from the present studies differ from those of Marconi et al (1985) who examined trained athletes. The subjects participating in the present studies were healthy but untrained and it is possible that this could account for the different results, although the data obtained from the two endurance-trained athletes involved in the single-blind trial were similar to those obtained from the untrained subjects in Trial 1.

The known function of carnitine is in the oxidation of fatty acids which is important during prolonged exercise. The effect of carnitine supplementation might therefore be seen during relatively prolonged exercise (ie a marathon) rather than the type of shorter-term testing utilised in the present studies. However, the previously described observations of Cooper et al (1986) on the performance times of marathon runners under carnitine supplemented conditions argue against this.

CHAPTER 8

SUMMARY AND CONCLUSIONS

The aim of this Thesis was to investigate the force generating capacity of human muscle during sustained dynamic exercise.

A large individual variation in the proportion of maximum force utilised (that is, relative force generation) at equivalent values of power output was demonstrated. At 70 rpm and at 100% of $\dot{V}O_2$ max, the mean value of relative force generating capacity in the group of subjects studied was 50%, although this was much greater in those subjects who possessed a high aerobic capacity, which was evidenced by a positive linear relationship between relative force generating capacity (% PF max) and $\dot{V}O_2$ max and a significant inverse linear relationship between % PF max and % Type II fibre area. The data also suggested that although it is generally accepted that the major factor limiting sustained dynamic exercise is central in origin (that is, the cardiac output) (Bevegard and Shepherd, 1967; Davies and Sargeant, 1974), nevertheless, certain individuals may be more likely to suffer a peripheral limitation in view of the fact that they utilise a relatively large proportion of their maximum available force generating capacity at any given value of power output.

Relative force generating capacity was then measured over a range of pedal frequencies to determine whether or not it was independent of the frequency of contraction. In agreement with previously reported data, maximum force generating capacity decreased with increasing pedal frequency. In addition, however, relative force generating capacity also demonstrated a reduction with increments in pedal frequency when equivalent values of power output were compared. (This reduction was of the order of 28% when pedal frequencies of 40 and 100 rpm were compared at 100% of $\dot{V}O_2$ max.) These data suggest that it may be of great benefit to utilise high frequencies of contraction during sustained exercise, in terms of reducing the 'risk' of peripheral fatigue as a possible limiting factor. Indeed, it is a common observation that trained racing cyclists frequently employ pedal frequencies in excess of 80 rpm during training and competition. In addition, the data also strongly suggest that progressive cycle ergometer tests designed to measure the individual's maximum aerobic power ought to be conducted at high pedal frequencies (70-100 rpm) rather than the standard 50-60 rpm in order to reduce the risk of a peripheral rather than a central limiting factor.

The employment of high pedal frequencies may be advantageous from the view of alleviating peripheral fatigue but they may be achieved at the expense of a reduction in optimal efficiency, since many previously reported studies indicate an optimal pedal frequency for cycling efficiency of 50-70 rpm. Although the previous data concerning the efficiency of dynamic exercise appear to be largely dependent upon the method of calculation, the results described in this Thesis demonstrated a trend towards an increase in cycling efficiency (delta efficiency) with increasing frequency of contraction, which is in agreement with more recent studies, and which also indicates an even greater advantage of cycling at high pedal fre quencies.

The underlying mechanism of a reduction in relative force generation with increasing frequency of contraction was investigated using the technique of surface integrated electromyography (IEMG). Maximum IEMG activity (IEMG max) was first established during an isokinetic test (which was also utilised to measure maximum peak force) conducted over a range of pedal frequencies. During the course of each test the IEMG/Force ratio increased significantly, which was due to a decrement in force generation with little change in IEMG activity.

Relative IEMG activity (% IEMG max) was investigated during a further series of progressive exercise tests conducted over a similar range of pedal frequencies. % IEMG max also demonstrated a reduction with increasing frequency of contraction (at equivalent values of power output) in parallel with % PF max so that the IEMG/Force ratio remained little changed. It is suggested that as frequency of contraction increases, a selective derecruitment of slow twitch motor units may occur in favour of the recruitment of a smaller number of fast twitch units, which give greater power per unit stimulus. Since, however, the Force/IEMG data was obtained from a small group of subjects performing over a limited number of pedal frequencies, and the data obtained are at variance with previous studies (Gollnick et al, 1974) utilising the technique of glycogen depletion, it is evident that further studies are required in order to investigate patterns of motor unit recruitment during sustained exercise of varying contractile frequency and their subsequent effect upon relative force generation.

In the final part of this Thesis, an alternative approach to reducing peripheral stress during sustained exercise was examined. The effect of oral supplementation of L-Carnitine upon maximum and submaximum exercise performance was investigated during two double-blind trials. The results of Trial 1 demonstrated a reduction in the submaximum cardiac frequency response at moderate levels of power output after carnitine supplementation. The mechanism of this action was further investigated in a second, more extensive trial. The results obtained, however, were inconsistent with those of Trial 1, in that a significant reduction in the cardiac frequency response was not demonstrated. In addition, no significant differences between pre- and post-exercise blood metabolite concentrations, which were used as indicators of a peripheral effect of carnitine, were observed. It was concluded that carnitine supplementation was of little benefit to exercise performance.

BIBLIOGRAPHY

Alexander, R. McN., Vernon, A. (1975).
The dimensions of knee and ankle muscles and the forces they exert.
J. Hum. Mov. Stud. 1 : 115-123.

Asmussen, E. (1973).
Growth in muscular strength and power. In: 'Physical Activity, Human Growth and Development ed. G.L. Rarick. Academic Press Inc. New York.

Benesch, R., Benesch, R.E. (1969).
Intracellular organic phosphates as regulators of oxygen release by haemoglobin. Nature 221 : 618-622.

Banister, E.W., Jackson, R.C. (1967).
The effect of speed and load changes on oxygen intake for equivalent power outputs during bicycle ergometry. Int. Z. angew. Physiol. einsch. Arbeitsphysiol. 24 : 284-290.

Benedict. F.G., Cathcart, E.P. (1913).
Muscular work. Carnegie Instit. Wash D.C. Publ. 187.

Bergström, J. 1962).
Muscle electrolytes in man. Scand. J. Clin. Lab. Invest. 14 Suppl. 68 : p 110.

Bevegård, S., Shepherd, J.T. (1967)
Regulation of the circulation during exercise in man. Physiol. Rev. 47 : 178-213.

Bigland-Ritchie, B., Woods, J.J. (1976).
Integrated electromyogram and oxygen uptake during positive and negative work. J. Physiol. 260 : 267-277.

Bigland-Ritchie, B., Jones, D.A., Hosking, G.P., Edwards, R.H.T. (1978).
Central and peripheral fatigue in sustained maximum voluntary contractions of human quadriceps muscle. Clin. Sci. mol. Med. 54 : 609-614.

Bigland-Ritchie, B., Jones, D.A., Woods, J.J. (1979).
Excitation frequency and muscle fatigue: electrical responses during human voluntary and stimulated contractions. Expt. Neurol. 64 : 414-427.

Bigland-Ritchie, B., Kukulka, C.G., Woods, J.J. (1980).
Surface EMG/Force relation in human muscles of different fibre composition. J. Physiol. 308 : 103P.

Bloom, S.R., Johnson, R.H., Park, D.M., Rennie, M.J., Sulaiman, W.R. (1976).
Differences in the metabolic and hormonal response to exercise between racing cyclists and untrained individuals. J. Physiol. 258 : 1-18.

Boobis, L., Williams, C., Wootton, S.A. (1983).
Human muscle metabolism during brief maximal exercise. J. Physiol. 338 : 21P-22P.

Bookelman, H. (1978).
Pyruvate oxidation in rat and human skeletal muscle. Biochem. Medicine 20 : 395-403.

Borg, G. (1970).
Perceived exertion as an indicator of somatic stress. Scand. J. Rehab. Med. (2) : 92-99.

Bousset, S., Maton, B. (1973).
Comparison between surface and intramuscular EMG during voluntary movement. In: 'New Developments in Electromyography and Clinical Neurophysiology'. ed. J.E. Desmedt. Vol. 1. pp 533-539, Karger, Basel.

Burke, R.E. Edgerton, V.R. (1975).
Motor unit properties and selective involvement in movement. In: 'Exercise and Sport Science Reviews'. New York, Academic Press. pp 31-81.

Citterio, G., Agostoni, E. (1984).
Selective activation of quadriceps muscle fibres according to bicycling rate. J. Appl. Physiol. Respirat. Environ. Exercise Physiol. 57(2) : 371-379.

Close, R.I. (1972)
Dynamic properties of mammalian skeletal muscles. Physiol. Rev. 52(1) : 129-197.

Coast, J.R., Welch, H.G. (1985).
Linear increase in optimal pedal rate with increased power output in cycle ergometry. Eur. J. Appl. Physiol. 53 : 339-342.

Cooper, M.B., Jones, D.A., Edwards, R.H.T., Corbucci, G.C., Montanari, G., Trevisani, C. (1986).
The effect of marathon running on carnitine metabolism and on some aspects of muscle mitochondrial activities and antioxidant mechanisms.
J. Sports Sci. 4 : 79-87.

Costill, D.L., Daniels, J., Evans, W., Fink, W., Krahenbuhl, G. (1976).
Skeletal muscle enzymes and fibre composition in male and female track athletes. J. Appl. Physiol. 40 : 149-154.

Coyle, E.F., Costill, D.L., Lesmes, G.R. (1979).
Leg extension power and muscle fibre composition. Med. Sci. Sports 11 : 12-15.

Davies, C.T.M., Sargeant, A.J. (1974).
Physiological responses to one- and two-leg exercise breathing air and 45% oxygen. J. Appl. Physiol. 36(2) : 142-148.

Davies, C.T.M., Sargeant, A.J. (1975).
Effects of training on the physiological responses to one- and two-leg work. J. Appl. Physiol. 38(3) : 377-381.

Davies, C.T.M., Tuxworth, W., Young, J.M. (1970).
Physiological effects of repeated exercises. Clin. Sci. 39 : 247-258.

Dawson, M.J., Gadian, D.G., Wilkie, D.R. (1978).
Muscular fatigue investigated by phosphorus nuclear magnetic resonance.
Nature (Lond.) 274 : 861-866.

De Luca, C.J., Le Fever, R.S., McCue, M.P., Xenakis, A.P. (1982).
Behaviour of human motor units in different muscles during linearly varying contractions. J. Physiol. 329 : 113-128.

Denny-Brown, D. (1949)
Interpretation of the electromyogram. Arch. Neurol. Psych. 61 : 99-128

Denny-Brown, D. (1929).
On the nature of postural reflexes. Proc. Roy. Soc. Lon. B. 104 : 252-301.

Dickinson, S. (1929).
The efficiency of bicycle-pedalling as affected by speed and load. J. Physiol. (Lond) 67 : 242-255.

Di Donato, S., Cornelio, F., Storchi, G., Rimoldi, M. (1979).
Hepatic ketogenesis and muscle carnitine deficiency. Neurology (Minneapolis) 29 : 780-786.

Dolan, P. (1985).
Maximal short-term power output from human muscle. Ph.D. Thesis. Polytechnic of North London.

Donaldson, S.K., Hermansen, L., Bolles, L. (1978).
Differential direct effects of H^+ on Ca^{++} activated force of skinned fibres from the soleus, cardiac and adductor magnus muscles of rabbits. Pflügers Arch. Eur. J. Physiol. 376 : 55-65.

Durnin, J.G.V.A., Rahaman, M.M. (1867).
The assessment of the amount of fat in the human body from measurement of skinfold thickness. Br. J. Nutr. 21 : 681-689.

Eccles, J.C., Sherrington, C.S. (1930).
Numbers and contraction values of individual motor units examined in some muscles of the limb. Proc. Roy. Soc. Lon. B. 106 : 326-357.

Edström, L., Ekblom, B. (1972).
Differences in sizes of red and white muscle fibres in vastus lateralis of musculus quadriceps femoris of normal individuals and athletes. Relation to physical performance. Scand. J. Clin. Lab. Invest. 30 : 175-181.

Edwards, R.H.T. (1981).
Human muscle function and fatigue. In: Human Muscle Fatigue: Physiological Mechanisms, pp 1-18. (Eds. R. Porter and J. Whelan). Ciba Symposium 82. Pitman Medical Press. London.

Edwards, R.H.T., Melcher, A., Hesser, C.M., Wiggertz, D., Ekelund, L. (1972).
Physiological correlates of perceived exertion in continuous and intermittent exercise with the same average power. Eur. J. Clin. Invest. 2 : 108-114.

Edwards, R.H.T., Young, A., Wiles, C. (1980).
Needle biopsy of skeletal muscle in the diagnosis of myopathy and the clinical study of muscle function and repair. New England. J. Med. 302 : 261-271.

Ekblom, B., Goldbarg, A.N. (1971).
The influence of training and other factors on the subjective rating of perceived exertion. Acta Physiol. Scand. 33 : 399-406.

Fenn, W.O., Marsh, B.S. (1935).
Muscular force at different speeds of shortening. J. Physiol. 85 : 277-297.

Fritz, I.B. (1955).
Carnitine and its role in fatty acid metabolism. Adv. Lipid Res. 1 : 285-334.

Fritz, I.B., Yue, K.I.N. (1963).
Long-chain carnitine acyltransferase and the role of acyl carnitine derivatives in the catalytic increase of fatty acid oxidation induced by carnitine. J. Lipid. Res. 4(3) : 279-287.

Froberg, S.O., Ostman, J., Sjostrand, N. (1872).
Effect of training on esterified fatty acids and carnitine in muscle and on lipolysis in adipose tissue in vitro. Acta Physiol. Scand. 86 : 166-174.

Gaesser, G.A., Brooks, G.A. (1975).
Muscular efficiency during steady-rate exercise: effects of speed and work rate. J. Appl. Physiol. 38(6) : 1132-1139.

Garnett, R., Stephens, J.A. (1981).
Changes in the recruitment threshold of motor units produced by cutaneous stimulation in man. J. Physiol. (Lond) 311 : 463-473.

Garry, R.C., 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. (Lond.) 72 : 425-437.

Gasser, H.S., Hill, A.V. (1924).
The dynamics of muscular contraction. Proc. Roy. Soc. Lon. B. 96 : 398-437.

Gollnick, P.D., Piehl, K., Saubert, IV,C.W., Armstrong, R.B., Saltin, H. (1972).
Diet, exercise and glycogen changes in human muscle fibres. J. Appl. Physiol. 33 : 421-425.

Gollnick, P.D., Piehl, K., Saltin, B. (1974).
Selective glycogen depletion pattern in human muscle fibres after exercise of varying intensity and at varying pedalling rates. J. Physiol. 241 : 45-57.

Gollnick, P.D., Karlsson, J., Piehl, K., Saltin, B. (1974).
Selective glycogen depletion in skeletal muscle fibres of man following sustained contractions. J. Physiol. 241 : 59-67.

Greig, C., Sargeant, A.J., Rutherford, O. (1985).
Proportional utilisation of maximal dynamic force during submaximal exercise in man. Clin. Physiol. 5. Suppl.4.

Grieve, D.W., Cavanagh, P.R. (1974).
The validity of quantitative statements about surface electromyograms recorded during locomotion. Scand. J. Rehab. Med. Suppl. 3 : 19-25.

Grimby, L., Hannerz, J. (1973).
Differences in recruitment order and discharge pattern of motor units in the early and late flexion reflex components in man. Acta Physiol. Scand. 90 : 555-564.

Grimby, L., Hannerz, J. (1977).
Firing rate and recruitment order of toe extensor motor units in different modes of voluntary contraction. J. Physiol. 264 : 865-879.

Grimby, L. (1984).
Firing properties of single human motor units during locomotion. J. Physiol. 346 : 195-202.

Grindrod, S., Round, J.M., Rutherford, O.M. (1987).
Type 2 fibre composition and force per cross-sectional area in the human quadriceps. J. Physiol. 390 : 154P.

Hagberg, J.M., Mullin, J.P., Nagle, F.J. (1978).
Oxygen consumption during constant-load exercise. J. Appl. Physiol. Respirat. Environ. Exercise Physiol. 45 : 381-384.

Hagberg, J.M., Mullin, J.P., Bahrke, M., Limburg, L. (1979).
Physio logical profiles and selected psychological characteristics of national class American cyclists. Int. J. Sport. Med. Phys. Fitness 19 : 341-346.

Hagberg, J.M., Mullin, J.P., Giese, M.D., Spitznagel, E. (1981). Effect of pedalling rate on submaximal responses of competitive cyclists. J. Appl. Physiol. : Respirat. Environ. Exercise Physiol. 51(2) : 447-451.

Halkjaer-Kristensen, T., Ingemann-Hansen, T. (1979). Microphotometric determination of glycogen in single fibres of human quadriceps muscle. Histochem. J. 11 : 629-638.

Havel, R.J., Carlson, L.A., Ekelund, L.G., Homoreu, A. (1964). Turnover rate and oxidation of different free fatty acids in males during exercise. J. Appl. Physiol. 19 : 613-618.

Hendriksson, J., Bonde-Petersen, F. (1974). Integrated electromyography of quadriceps femoris muscle at different exercise intensities. J. Appl. Physiol. 36 : 218-220.

Henneman, E., Somjen, G., Carpenter, D.O. (1965a). Excitability and inhibility of motor neurones of different sizes. J.Neurophysiol. 28 : 599-620.

Henneman, E., Somjen, G., Carpenter, D.O. (1965b). Functional significance of cell size in spinal motor neurones. J. Neurophysiol. 28 : 560-580.

Hesser, C.M., Linnarsson, D., Bjurstedt, H. (1977). Cardiorespiratory and metabolic responses to positive, negative and minimum load dynamic leg exercise. Respir. Physiol. 30 : 51-67.

Hill, A.V. (1922).
The maximum work and mechanical efficiency of human muscles and their most economical speed. J. Physiol. 56 : 19-41.

Hill, A.V. (1938).
The heat of shortening and the dynamic constants of muscle. Pro. Roy. Soc. Lond. B. 126 : 136-195.

Hill, A.V. (1965).
Trails and Trials in Physiology. Baltimore MD. Williams and Wilkins.

Hoes, M.J.A.J.M., Binkhorst, R.A., Smeekes-Kuyl, A.E.M.C., Vissers, A.C.A. (1968).
Measurement of forces exerted on pedal and crank during work on a bicycle ergometer at different loads. Int. Z. angew. Physiol. einschl. Arbeitsphysiol. 26 : 33-42.

Houtz, S.J., Fischer, F.J. (1959).
An analysis of muscle action and joint excursion during exercise on a stationary bicycle. J. Bone Joint Surg. 41 : 123-131.

Hultman, E., Bergström, J., McLennan-Anderson, N. (1967).
Breakdown and resynthesis of PC and ATP in connection with muscular work in man. Scand. J. Clin. Lab. Invest. 19 : 56-66.

Issekutz, B., Miller, H.I., Rodahl, K. (1966).
Lipid and carbohydrate metabolism during exercise. Fed. Proc. 25 : 1415-1420.

Jones, D.A., King, M.F., Round, J.M. (1980).
MOPPET, a rapid and accurate system for the measurement of muscle fibre cross-sectional area. J. Physiol. 305 : 5-6P.

Jones, D.A. (1981).
Muscle fatigue due to changes beyond the neuromuscular junction. in: Human Muscle Fatigue : Physiological Mechanisms. pp 178-196. (Eds. R. Porter and J. Whelan) Ciba Symposium 82. Pitman Medical Press. London.

Jones, P.R.M., Pearson, J. (1969).
Anthropometric determination of leg fat and muscle plus bone volumes in young male and female adults. J. Physiol. 204 : 63-66.

Jones, P.R.M. (1970).
An application of physiological anthropometry. Ph.D. Thesis. University of Loughborough.

Karlsson, J. (1971).
Lactate and phosphagen concentration in working muscle of man. Acta Physiol. Scand. Suppl. 358.

Karlsson, J., Diamant, B., Saltin, B. (1971).
Muscle metabolies during submaximal and maximal exercise in man. Scand. J. Clin. Lab. Invest. 26 : 385-394.

Komi, P.V., Viitasalo, J.H.T. (1976).
Signal characteristics of EMG at different levels of muscle tension. Acta. Physiol. Scand. 96 : 267-276.

Komi, P.V., Rusko, H., Vos, J., Vihko, V. (1977).
Anaerobic performance capacity in athletes. Acta Physiol. Scand. 100 : 107-114.

Konopka, P. (1981).
Ausdauer und Ausdauertrainung. Deutsches 2. Sportmed. 1 : 18-22.

Kukulka, C.G., Clamman, H.P. (1981).
Comparison of the recruitment and discharge properties of motor units in human brachial biceps and adductor pollicis during isometric contractions. Brain Res. 219 : 45-55.

Künstlinger, U., Ludwig, H.G., Stegemann, J. (1985).
Force kinetics and oxygen consumption during bicycle ergometer work in racing cyclists and reference group. Eur. J. Appl. Physiol. 54 : 58-61.

Lenman, J.A.R., Ritchie, A.E. (1983).
Clinical Electromyography. 3rd Ed. p.21. Pub. Pitman Press. Bath.

Lennon, D.F.L., Stratham, F.W., Shrago, E., Nagee, F.J., Madden, M., Hanson, P., Carter, A.L. (1983).
Effects of acute moderate intensity exercise on carnitine metabolism in males and females. J. Appl. Physiol. 55(2) : 789-795.

Liddell, E.G.T., Sherrington, C.S. (1925).
Recruitment and some other factors of reflex inhibition. Proc. Roy. Soc. Lon. B. 97 : 488-518.

Lindahl, O., Movin, A. (1967).
The mechanics of extension of the knee joint. Acta Orthop. Scand. 38 : 226-234.

Lippold, O.C.J. (1952).
The relation between integrated action potentials in a human muscle and its isometric tension. J. Physiol.(Lond.) 117 : 492-499.

Lloyd, B., Burin, J., Smythe, P., Alberti, K.G.M.M. (1978).
Enzymic fluormetric continuous-flow assays for blood glucose, lactate, pyruvate, alanine, glycerol and 3-hydroxybutyrate. Clin. Chem.24 : 1724-1729.

Löllgen, H., Ulmer, H.V., Nieding, G. (1977).
Heart-rate and perceptual response to exercise with different pedalling speed in normal subjects and patients. Eur. J. Appl. Physiol. 37 : 297-304.

Löllgen, H., Graham, T., Sjøgaard, G. (1980).
Muscle metabolites, force and perceived exertion bicycling at varying pedal rates. Med. Sci. Sports Exerc. 12(5) : 345-351.

Lupton, H. (1923).
An analysis of the effects of speed on the mechanical efficiency of human muscular movement. J. Physiol. 57 : 337-353.

Marconi, C., Sassi, G., Cardinelli, A., Ceretelli, P. (1985).
Effects of L-carnitine loading on the aerobic and anaerobic performance of endurance athletes. Eur. J. Appl. Physiol. 54 : 131-135.

Margaria, R., di Prampero, P.E., Aghemo, P., Deverenco, P., Mariani, M. (1971).
Effect of a steady-state exercise on maximal anaerobic power in man.
J. Appl. Physiol. 30(6) : 885-889.

Maughan, R.J., Watson, J.S., Weir, J. (1983a).
Strength and cross-sectional area of human skeletal muscle. J. Physiol. 338 : 37-49.

Maughan, R.J., Watson, J.S., Weir, J. (1983b).
Relationship between muscle strength and muscle cross-sectional area in male sprinters and endurance runners. Eur. J. Appl. Physiol. 50 : 309-318.

McCartney, N., Heigenhauser, G.J.F., Sargeant, A.J., Jones, N.L. (1983).
A constant-velocity cycle ergometer for the study of dynamic muscle function. J. Appl. Physiol. Respirat. Environ. Exercise Physiol. 55(1) : 212-217.

McCartney, N., Heigenhauser, J.F., Jones, N.L. (1983).
Power output and fatigue of human muscle in maximal cycling exercise.
J. Appl. Physiol. Respirat Environ. Exercise Physiol. 55(7) : 218-224.

Milner-Brown, H.S., Stein, R.B., Yemm, R. (1973b).
The orderly recruitment of human motor units during voluntary isometric contractions. J. Physiol. 230 : 359-370.

Milner-Brown, H.S., Stein, R.B., Yemm, R. (1973c).
Changes in firing rate of human motor units during linearly changing voluntary contractions. J. Physiol. 230 : 371-390.

Mole, P.A., Oscai, L.B., Holloszy, J.O. (1971).
Adaptation of muscle to exercise. Increase in levels of palmityl CoA synthetase, carnitine palmityl transferase, palmityl CoA dehydrogenase and their capacity to oxidise fatty acids. J. Clin. Invest. 50 : 2323-2330.

Monster, A.W., Chan, H. (1977).
Isometric force production by motor units of extensor digitorum communis muscle in man. J. Neurophysiol 40 : 1432-1443.

Nilsson, J., Tesch, P., Thorstensson, A. (1977).
Fatigue and EMG of repeated fast voluntary contractions in man. Acta Physiol. Scand. 101 : 194-198.

Otis, A.B. (1964).
The work of breathing. In: Handbook of Physiology Respiration. Washington D.C. : Am. Physiol. Soc. 3(1) : Ch.17 : 463-476.

Pandolf, K.B., Noble, B.J. (1973).
The effect of pedalling speed and resistance changes on perceived exertion for equivalent power outputs on the bicycle ergometer. Med. Sci. Sports : 5(2) : 132-136.

Pugh, L.G.C.E. (1974).
The relation of oxygen uptake and speed in competition cycling and comparative observations on the bicycle ergometer. J. Physiol. 241 : 795-808.

Rennie, M.J., Winder, W.W., Holloszy, J.O. (1976).
A sparing effect of increased plasma fatty acids on muscle and liver glycogen content in the exercising rat. Biochem. J. 156 : 647-655.

Saltin, B., Gollnick, P.D. (1983).
Skeletal muscle adaptability: significance for metabolism and performance. In: Handbook of Physiology, Section 10: Skeletal Muscle. Ed. S.R.Geiger. American Physiological Society. Bethesda. Maryland. U.S.A.

Sargeant, A.J., Davies, C.T.M. (1977).
Limb volume, composition and maximum aerobic power output in relation to habitual 'preference' in young male subjects. Ann. Hum. Biol. 4(1) : 49-55.

Sargeant, A.J., Crawley, M.A., Davies, C.T.M. (1979).
Physiological responses to exercise in myocardial infarction patients following residential rehabilitation. Arch. Phys. Med. Rehabil. 60 : 121-125.

Sargeant, A.J., Hoinville, E., Young, A. (1981).
Maximum leg force and power output during short-term dynamic exercise. J. Appl. Physiol. Respirat Environ. Exercise Physiol. 51(5) : 1175-1182.

Seabury, J.J., Adams, W.C., Ramey, M.R. (1977).
Influence of pedalling rate and power output on energy expenditure during bicycle ergometry. Ergonomics 20(5) : 491-498.

Secher, N., Nygaard, E. (1976).
Glycogen depletion pattern in Types I, IIA and IIB muscle fibres during maximal voluntary static and dynamic exercise. Acta Physiol. Scand. Suppl. 440 : 141.

Siri, W.E. (1956).
In: Advances in Biological and Medical Physics. (Eds. J.H. Lawrence, C.A. Tobias). Academic Press Inc.: London.

Sjøgaard, G. (1978).
Force-velocity curve for bicycle work. In: Biomechanis VI A. Ed. E. Assmussen, K. Jorgensen. University Park Press. Baltimore. U.S.A. pp 93-99.

Spector, S.A., Gardiner, P.F., Zernicke, R.F., Roy, R.R., Edgerton, V.R. (1980).
Muscle architecture and force-velocity characteristics of cat soleus and medial gastrocnemius: Implications for motor control. J. Neurophysiol. 44 : 951-960.

Stainsby, W.N., Gladden, L.B., Barclay, J.K., Wilson, B.A. (1980).
Exercise efficiency: validity of base-line subtractions. J. Appl. Physiol. Respirat. Environ. Exercise Physiol. 48(3) : 518-522.

Stephens, J.A., Taylor, A. (1972).
Fatigue of maintained voluntary muscle contraction in man. J. Physiol. 220 : 1-18.

Stephens, J.A., Taylor, A. (1973).
The relationship between integrated electrical activity and force in normal and fatiguing human voluntary muscle contractions. In: New Developments in Electromyography and Clinical Neurophysiology. Ed. J.E. Desmedt. Vol.1. pp 623-627. Karger, Basel.

Stephens, J.A., Usherwood, T.P. (1977).
The mechanical properties of human motor units with special reference to their fatiguability and recruitment threshold. Brain Res. 125 : 91-97.

Stephens, J.A., Garnett, R., Buller, N.P. (1978).
Reversal of recruitment order of single motor units produced by cutaneous stimulation during voluntary muscle contraction in man. Nature 272 : 362-364.

Stuart, M.K., Howley, E.T., Gladden, L.B., Cox, R.H. (1981).
Efficiency of trained subjects differing in maximal oxygen uptake and type training. J. Appl. Physiol. Respirat. Environ. Exercise Physiol. 50(2) : 444-449.

Suzuki, Y. (1979).
Mechanical efficiency of fast and slow twitch muscle fibres in man during cycling. J. Appl. Physiol. Respirat. Environ. Exercise Physiol. 47(2) : 263-267.

Tesch, P., Karlsson, J. (1978).
Isometric strength performance and muscle fibre type distribution in man. Acta Physiol. Scand. 103 : 47-51.

Tesch, P., Sjödin, B., Thorstensson, A., Karlsson, J. (1978).
Muscle fatigue and its relation to lactate accumulation and LDH activity in man. Acta Physiol. Scand. 103 : 413-420.

Tesch, P.A., Komi, P.V., Jacobs, I., Karlsson, J., Viitasalo, J.T. (1983).
Influence of lactate accumulation on EMG frequency spectrum during repeated concentric contractions. Acta Physiol. Scand. 119 : 61-67.

Tesch, P.A., Wright, J.A., Vogel, J.A., Daniels, W.L., Sharp, D.S., Sjödin, B. (1985).
The influence of muscle metabolic characteristics on physical performance. Eur. J. Appl. Physiol. 54 : 237-243.

Thorstensson, A. (1976).
Muscle strength, fibre types and enzyme activities in man. Acta Physiol. Scand. Suppl. 443 : 1-45.

Thorstensson, A., Grimby, G., Karlsson, J. (1976).
Force velocity relations and fibre composition in human knee extensor muscles. J. Appl. Physiol. 40 : 12-16.

Thorstensson, A., Larsson, L., Tesch, P., Karlsson, J. (1977).
Muscle strength and fibre composition in athletes and sedentary men. Med. Sci. Sports 9 : 26-30.

Trovato, G.M., Ginardi, V., Di Marco, V., Dell'Aira, A.E., Corsi, M. (1982).
Long-term L-carnitine treatment of chronic anaemia of patients with end-stage renal failure. Curr. Ther. Res. 31(6) : 1042-1048.

Ui, M. (1966).
A role of phosphofructokinase in pH-dependent regulation of glycolysis. Biochim. Biophys. Acta. 124 : 310-322.

Van Hinsbergh, V.M.W., Veerkamp, J.H., Glatz, J.F.C. (1979).
4-methyl-2-oxopentanoate oxidation by rat skeletal muscle mitochondria. Biochem. J. 182 : 353-360.

Viitasalo, J.T., Luhtanen, P., Rahkila, P., Rusko, H. (1985).
Electromyographic activity related to aerobic and anaerobic threshold in ergometer bicycling. Acta Physiol. Scand. 124 : 287-293.

Vøllestad, N.K., Vaage, O., Hermansen, L. (1984).
Muscle glycogen depletion patterns in Type I and subgroups of Type II fibres during prolonged severe exercise in man. Acta Physiol. Scand. 122 : 433-441.

Vøllestad, N.K. (1985).
Force Regulation During Exercise. Ph.D. Thesis. University of Oslo, Norway.

Whipp, B.J., Wasserman, K. (1969).
Efficiency of muscular work. J. Appl. Physiol. 26(5) : 644-648.

Wiles, C.M., Young, A., Jones, D.A., Edwards, R.H.T. (1979).
Relaxation rate of constituent muscle fibre types in human quadriceps.
Clin. Sci. 56 : 47-52.

Wilkie, D.R. (1950).
The relation between force and velocity in human muscle. J. Physiol. 110 : 249-280.

Wilkie, D.R. (1960).
Man as a source of mechanical power. Ergonomics 3 : 1-8.

Wilson, B.A., Stainsby, W.N. (1978).
Relation between oxygen uptake and developed tension in dog skeletal muscle. J. Appl. Physiol. Respirat. Environ. Exercise Physiol. 45(2) : 234-237.

Young, A. (1984).
The relative isometric strength of Type 1 and Type 2 muscle fibres in human quadriceps. Clin. Physiol. 4 : 23-32.

Young, A., Stokes, M., Round, J.M., Edwards, R.H.T. (1985).
The size and strength of the quadriceps muscles of old and young men.
Clin. Physiol. 5 : 145-154.

APPENDIX 1

TABLE 1

40 RPM

SUBJECT	REV NO:	1-10 VL	1-10 VM	1-10 RF	11-20 VL	11-20 VM	11-20 RF	21-30 VL	21-30 VM	21-30 RF
MS	FORCE(N)	884			859			839		
	IEMG	277.8	295.4	459.5	264.1	289.6	538.6	262.0	286.4	577.8
	IEMG/FORCE	0.31	0.33	0.52	0.31	0.34	0.63	0.31	0.34	0.69
SP	FORCE(N)	965			995			937		
	IEMG	259.0	317.6	444.2	300.5	316.6	504.1	279.5	318.7	530.6
	IEMG/FORCE	0.28	0.33	0.46	0.30	0.32	0.51	0.30	0.34	0.57
NS	FORCE(N)	834			788			780		
	IEMG	361.9	316.4	242.1	333.6	296.2	268.8	320.2	278.6	309.6
	IEMG/FORCE	0.43	0.38	0.29	0.42	0.38	0.34	0.41	0.36	0.40
AS	FORCE(N)	1227			1142			972		
	IEMG	235.9	198.5	302.3	241.4	203.0	304.2	225.0	179.4	221.8
	IEMG/FORCE	0.19	0.16	0.25	0.21	0.18	0.27	0.23	0.18	0.23
TH	FORCE(N)	865			891			882		
	IEMG	136.2	193.4	188.8	145.2	220.2	252.5	142.9	227.0	305.0
	IEMG/FORCE	0.16	0.22	0.22	0.16	0.25	0.28	0.16	0.26	0.35

TABLE 2

70 RPM

SUBJECT	REV NO:	1-10 VL	1-10 VM	1-10 RF	11-20 VL	11-20 VM	11-20 RF	21-30 VL	21-30 VM	21-30 RF	31-40 VL	31-40 VM	31-40 RF	41-50 VL	41-50 VM	41-50 RF
MS	FORCE	661			624			596			582			544		
	IEMG	218.0	161.4	257.5	196.4	159.5	275.3	184.0	145.0	241.1	179.9	143.2	266.5	179.8	149.7	290.0
	IEMG/FORCE	0.33	0.24	0.39	0.31	0.26	0.44	0.29	0.24	0.39	0.31	0.25	0.46	0.33	0.28	0.53
SP	FORCE	666			660			612			548			486		
	IEMG	149.9	186.8	234.9	163.5	197.8	250.5	176.6	190.5	267.9	173.0	190.0	310.7	151.7	177.4	299.4
	IEMG/FORCE	0.23	0.28	0.35	0.25	0.30	0.38	0.29	0.31	0.44	0.32	0.35	0.57	0.31	0.37	0.62
NS	FORCE	690			647			617			581			529		
	IEMG	194.7	171.7	201.8	172.5	154.1	215.4	163.5	153.1	202.1	152.5	139.5	206.2	144.5	139.8	246.5
	IEMG/FORCE	0.28	0.25	0.29	0.27	0.24	0.33	0.26	0.25	0.33	0.26	0.24	0.35	0.27	0.26	0.47
AS	FORCE	881			734			642			524			381		
	IEMG	157.3	118.2	111.2	169.5	115.7	112.2	164.1	115.0	109.1	152.7	90.7	-	137.0	87.5	-
	IEMG/FORCE	0.18	0.13	0.14	0.23	0.16	0.16	0.26	0.18	0.16	0.29	0.17	-	0.36	0.23	-
TH	FORCE	910			861			772			698			625		
	IEMG	62.5	174.5	68.7	64.4	173.7	76.4	68.0	182.7	67.1	69.3	176.9	76.8	75.7	173.9	76.0
	IEMG/FORCE	0.07	0.19	0.08	0.07	0.20	0.09	0.09	0.24	0.09	0.10	0.25	0.11	0.12	0.28	0.12

TABLE 3

100 RPM

SUBJECT	REV NO	1-10			11-20			21-30			31-40			41-50			51-60			61-70			71-80		
		VL	VM	RF	VL	VM	RF	VL	VM	RF	VL	VM	RF	VL	VM	RF	VL	VM	RF	VL	VM	RF	VL	VM	RF
HS	FORCE	489			456			423			415			398			374			356			344		
	IEMG	131.1	115.5	184.8	127.5	122.5	194.8	117.6	114.2	185.0	137.0	116.9	183.0	118.0	111.4	190.1	114.7	107.3	191.7	110.4	116.0	180.6	120.3	126.0	203.8
	IEMG/FORCE	0.27	0.24	0.38	0.28	0.27	0.43	0.28	0.27	0.44	0.33	0.28	0.44	0.30	0.28	0.48	0.31	0.29	0.51	0.31	0.33	0.51	0.35	0.37	0.59
SP	FORCE	553			515			453			413			388			349			299			277		
	IEMG	105.3	115.3	219.6	113.5	125.8	230.3	108.3	121.0	248.2	99.3	111.1	277.1	108.1	110.9	284.0	105.6	117.2	264.6	93.5	117.4	240.3	97.2	105.7	212.0
	IEMG/FORCE	0.19	0.21	0.40	0.22	0.24	0.49	0.24	0.27	0.55	0.24	0.27	0.67	0.28	0.29	0.73	0.30	0.34	0.76	0.31	0.39	0.80	0.35	0.38	0.77
HS	FORCE	615			524			469			419			399			382			338			323		
	IEMG	116.3	132.8	186.4	105.3	122.4	184.5	102.6	111.4	170.1	94.9	105.2	164.6	90.1	99.7	154.7	90.8	103.2	153.2	98.3	100.7	144.6	83.3	90.0	125.0
	IEMG/FORCE	0.19	0.22	0.30	0.20	0.23	0.35	0.22	0.24	0.36	0.23	0.25	0.39	0.23	0.25	0.39	0.24	0.27	0.40	0.29	0.30	0.43	0.26	0.28	0.39
AS	FORCE	735			697			605			491			426			357			322			303		
	IEMG	80.0	96.0	98.1	95.2	96.5	131.8	84.2	93.8	113.7	82.3	95.8	-	82.8	84.7	-	71.7	80.2	-	70.5	77.3	-	74.8	89.3	-
	IEMG/FORCE	0.11	0.13	0.13	0.14	0.14	0.19	0.14	0.16	0.19	0.17	0.20	-	0.20	0.20	-	0.20	0.22	-	0.22	0.24	-	0.25	0.29	-
TH	FORCE	650			597			497			432			387			327			297			286		
	IEMG	62.1	57.5	121.3	66.2	62.5	124.4	57.6	62.2	124.3	65.6	66.7	132.9	62.4	77.5	143.7	56.1	85.2	140.9	62.1	81.3	135.4	62.0	76.5	148.0
	IEMG/FORCE	0.10	0.09	0.19	0.11	0.10	0.21	0.12	0.13	0.25	0.15	0.15	0.31	0.16	0.20	0.37	0.17	0.26	0.43	0.21	0.27	0.46	0.22	0.27	0.52

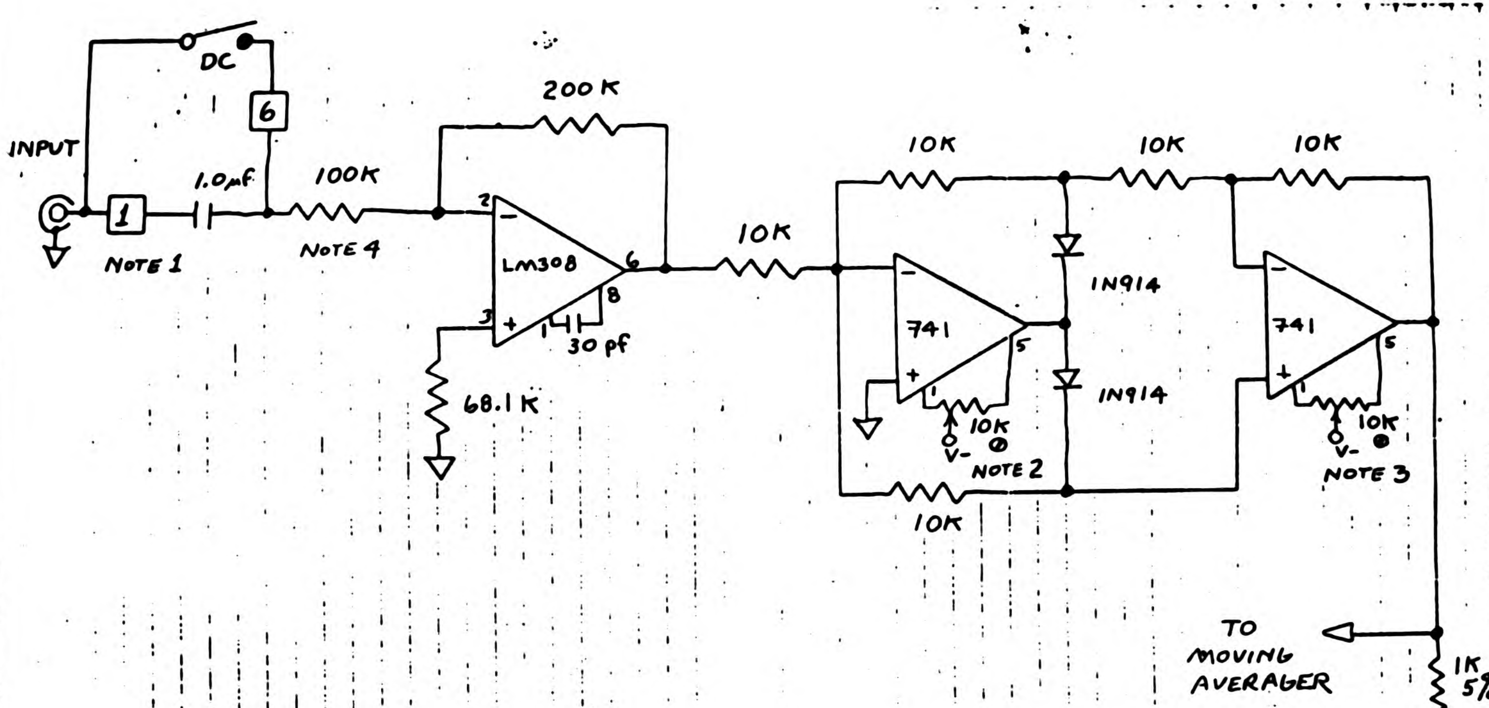
TABLE 4

125 RPM

SUBJECT	REV NO	1-10 VL	1-10 VM	1-10 RF	11-20 VL	11-20 VM	11-20 RF	21-30 VL	21-30 VM	21-30 RF	31-40 VL	31-40 VM	31-40 RF
HS	FORCE	454			416			401			382		
	IEMG	88.7	105.1	160.1	82.9	95.4	106.5	78.8	95.3	111.2	86.1	99.5	100.2
	IEMG/FORCE	0.20	0.23	0.35	0.20	0.23	0.26	0.20	0.24	0.48	0.23	0.25	0.26
AS	FORCE	431			375			308			265		
	IEMG	91.2	26.5	-	89.8	22.8	-	96.5	27.7	-	81.5	26.4	-
	IEMG/FORCE	0.21	0.06	-	0.24	0.06	-	0.31	0.09	-	0.31	0.10	-
TH	FORCE	518			430			385			337		
	IEMG	41.6	112.3	44.2	36.7	102.7	46.2	40.4	115.5	47.9	40.6	110.7	51.9
	IEMG/FORCE	0.08	0.22	0.09	0.09	0.24	0.11	0.10	0.30	0.12	0.12	0.33	0.15

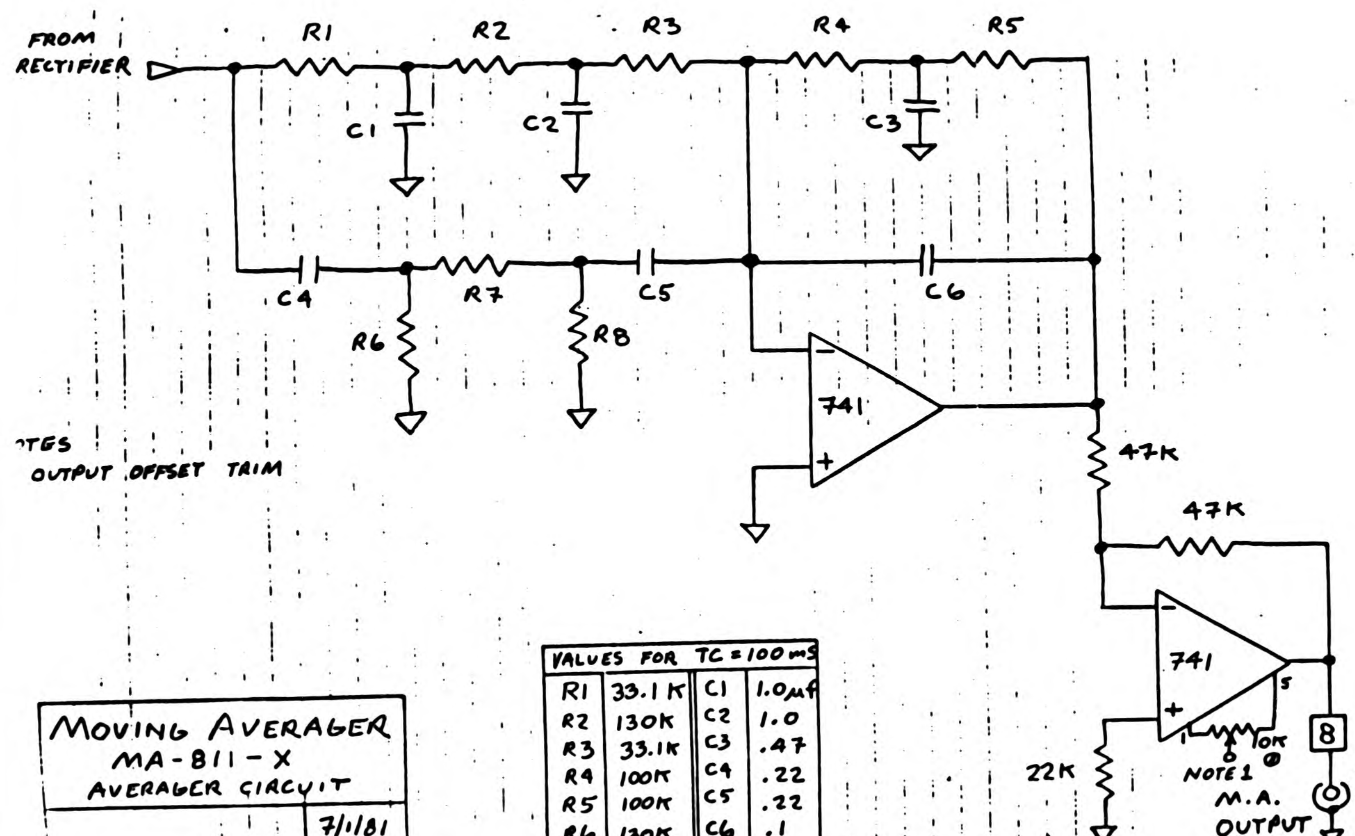
SUBJECT	REV NO	41-50 VL	41-50 VM	41-50 RF	51-60 VL	51-60 VM	51-60 RF	61-70 VL	61-70 VM	61-70 RF	71-80 VL	71-80 VM	71-80 RF	81-90 VL	81-90 VM	81-90 RF
HS	FORCE	361			341			333			317			299		
	IEMG	80.0	96.2	114.9	80.2	96.2	114.0	80.0	92.4	125.7	83.3	95.3	121.9	85.9	99.2	134.9
	IEMG/FORCE	0.22	0.27	0.32	0.24	0.28	0.33	0.24	0.28	0.38	0.26	0.30	0.38	0.29	0.33	0.45
AS	FORCE	232			207			182			161			159		
	IEMG	87.9	23.2	-	88.2	23.8	-	89.9	23.8	-	85.6	20.8	-	81.9	25.6	-
	IEMG/FORCE	0.38	0.10	-	0.43	0.11	-	0.43	0.11	-	0.53	0.13	-	0.52	0.16	-
TH	FORCE	330			301			273			231			224		
	IEMG	40.2	121.9	64.6	32.6	110.0	58.9	35.8	116.8	62.0	36.3	119.9	59.0	37.5	104.3	49.4
	IEMG/FORCE	0.12	0.37	0.20	0.11	0.37	0.20	0.13	0.43	0.23	0.16	0.52	0.26	0.17	0.47	0.22

APPENDIX 2



MOVING AVERAGER MA-811-X INPUT AMP. & RECTIFIER
7/1/81

NOTES
1. NUMBERS IN BOX REFER TO EDGE CONNECTOR №
2. RECT. SYMMETRY TRIM
3. RECT. OFFSET TRIM
4. ALL RESISTORS 1% ½W UNLESS NOTED



TES
OUTPUT OFFSET TRIM

VALUES FOR TC = 100 mS			
R1	33.1 K	C1	1.0 µf
R2	130K	C2	1.0
R3	33.1K	C3	.47
R4	100K	C4	.22
R5	100K	C5	.22
R6	130K	C6	.1
R7	510K		
R8	130K		

MOVING AVERAGER
MA-811-X
AVERAGER CIRCUIT
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APPENDIX 3

A: Reprint of : Greig, C., Rutherford, O., Sargeant, A.J. (1986). Effect of pedalling rate on the muscle force required during cycling exercise in man. J. Physiol. 377 : 109P.

[*From the Proceedings of the Physiological Society*, 25–26 *March* 1986
Journal of Physiology, 377, 109*P*, 1986]

Effect of pedalling rate on the muscle force required during cycling exercise in man

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In a previous communication we reported the muscle force and fibre recruitment patterns during dynamic exercise performed pedalling a cycle ergometer at 70 rev/min (Greig, Sargeant & Vollestad, 1986). We have now investigated the effect of different pedalling rates on the muscle force required in submaximal exercise. Ten healthy young subjects were studied performing a series of three progressive exercise tests at nominal pedalling rates of 40, 70 and 100 rev/min. During the last 2 min of each 5 min incremental work load, mean peak force ($\bar{F}_p$) and oxygen uptake ($\dot{V}_{O_2}$) were determined. At each pedalling rate there was a progressive linear increase of $\bar{F}_p$ with work load, and at any work load $\bar{F}_p$ was inversely related to the pedalling rate. Maximum leg force ($F_{p\,max}$) was also measured over the same range of pedalling rates using an isokinetic cycle ergometer (Sargeant, Hoinville & Young, 1981), and thus $\bar{F}_p$ during progressive tests could be expressed as a proportion of the maximum force available at the same velocity of contraction.

Interestingly, and despite the fact that maximum force itself decreased with increasing velocity, the results showed that the *proportion* of maximal force required at any given submaximal level of $\dot{V}_{O_2}$ also fell with increased pedalling rate. Hence at a work load corresponding to 75% of $\dot{V}_{O_2\,max}$ the proportion of the maximum force required was 54 ± 13% at 40 rev/min but only 39 ± 7% at 100 rev/min (mean ± S.D.; $P < 0.001$). This greater reserve of force-generating capacity at higher pedalling rates suggests a lower peripheral stress, and this could be an important factor in delaying the onset of fatigue during sustained activity.

However, it should be recognized that such an apparent advantage could be off-set or negated if there were any significant decrease in mechanical efficiency consequent upon the higher pedalling rates, since this would necessitate a greater energy supply for the same external power output (see, for example, Benedict & Cathcart, 1913; Hill, 1922). This aspect is the subject of further investigation.

REFERENCES

BENEDICT, F. G. & CATHCART, E. P. (1913). Muscular work. *Publs Carnegie Instn*, no. 187.
GREIG, C., SARGEANT, A. J. & VOLLESTAD, N. K. (1986). *J. Physiol.* 371, 176*P*.
HILL, A. V. (1922). *J. Physiol.* 56, 19–41.
SARGEANT, A. J., HOINVILLE, E. & YOUNG, A. (1981). *J. appl. Physiol.* 51, 1175–1182.

B: Reprint of : Greig, C., Hortobagyi, T., Sargeant, A.J. (1985). Quadriceps surface E.M.G. and fatigue during maximal dynamic exercise in man. J. Physiol. 369 : 180P.

[*From the Proceedings of the Physiological Society*, 11–13 *July* 1985
Journal of Physiology, **369**, 180*P*, 1985]

Quadriceps surface e.m.g. and fatigue during maximal dynamic exercise in man

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In the present study we have measured the surface e.m.g. and the leg forces exerted during a 45 s maximal effort on an isokinetic cycle ergometer (Sargeant, Hoinville & Young, 1981). Experiments were performed on 5 healthy male subjects at four pedalling speeds: 50, 70, 110 and 125 crank rev./min. Surface electrodes with built-in preamplifiers (Medelec EA 1000) were situated over the belly of vastus lateralis (VL), vastus medialis (VM) and rectus femoris (RF) of one leg. The signals were then rectified and integrated (i.e.m.g.) every 100 ms, and simultaneously recorded with the forces applied to the cranks. Despite the marked loss of force (~ 50%) over 45 s, the i.e.m.g. activity remained at the control level or slightly increased. Hence there was an increase in the i.e.m.g./force ratio at all speeds, in all muscles and all subjects. These findings are in agreement with those reported by Nilsson, Tesch & Thorstensson (1977) and by Bigland-Ritchie, Jones, Hosking & Edwards (1978), but in contrast to the findings of Stephens & Taylor (1972), who were, however, studying maximal isometric contractions of the first dorsal interosseus muscle.

The pattern of e.m.g. activity demonstrated some speed-related changes. Hence VL and VM showed a progressively earlier onset and end to the active phase at the higher speeds, although the duration of activity expressed in terms of degrees of crank revolution did not change significantly. i.e.m.g. of rectus femoris at 125 rev/min showed very low total activity compared with the slow speeds, although the muscle appeared to be activated over a much longer proportion of the cycle. These observations point to the need for caution in comparing dynamic strength data obtained at different movement speeds, since even in a very simple cyclical activity there appears to be marked change in the pattern of activation and possibly the proportional contribution of active muscles.

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REFERENCES

Bigland-Ritchie, B., Jones, D. A., Hosking, G. P. & Edwards, R. H. T. (1978). *Clin. Sci. mol. Med.* **54**, 609–614.
Nilsson, J. P., Tesch, A. & Thorstensson, A. (1977). *Acta physiol. scand.* **101**, 194–198.
Sargeant, A. J., Hoinville, E. & Young, A. (1981). *J. Appl. Physiol.* **55**, 1175–1182.
Stephens, J. A. & Taylor, A. (1972). *J. Physiol.* **220**, 1–18.

C: Reprint of : Greig, C., Sargeant, A.J., Vøllestad, N.K. (1985). Muscle force and fibre recruitment during dynamic exercise in man. J. Physiol. 371 : 176P.

[*From the Proceedings of the Physiological Society*, 12–14 *September* 1985
Journal of Physiology, 371, 176*P*, 1985]

Muscle force and fibre recruitment during dynamic exercise in man

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We have measured the leg forces exerted during progressive exercise tests on a conventional cycle ergometer and expressed these as a proportion of the maximum force available at the same pedal speed of 70 rev/min (see Sargeant, Hoinville & Young, 1981). In a group of thirty-one healthy subjects the mean proportion of maximal force utilized was 23 ± 5 % (S.D.) at a work load corresponding to 40 % of $\dot{V}_{O_2,max}$ increasing linearly to 51 ± 9 % at 100 % $\dot{V}_{O_2,max}$ (Fig. 1).

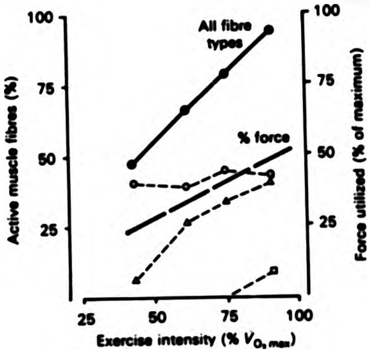

Fig. 1. Proportions of maximal force utilized (--) and of active muscle fibres (●—●) in relation to exercise intensity. Values are also given for the component fibre-type populations: type I, ○; type IIA, △; types IIAB and IIB combined, □.

Subsequently the proportion and type of the active muscle fibres in vastus lateralis were identified from glycogen-depletion measurements of needle biopsies (see Vøllestad, Vaage & Hermansen, 1984). The results indicated that at maximum oxygen uptake virtually all of the muscle fibres would have been active even though only ~ 50 % of maximal force was being generated (Fig. 1). This observation was presumably a reflection of submaximum activation of muscle fibres.

REFERENCES

Sargeant, A. J., Hoinville, E. & Young, A. (1981). *J. appl. Physiol.* 51, 1175–1182.
Vøllestad, N. K., Vaage, O. & Hermansen, L. (1984). *Acta physiol. scand.* 122, 433–441.

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The effect of oral supplementation with L-carnitine on maximum and submaximum exercise capacity. Eur. J. Appl. Physiol. 56 : 457-460.

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The effect of oral supplementation with L-carnitine on maximum and submaximum exercise capacity

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Summary. Two trials were conducted to investigate the effects of L-carnitine supplementation upon maximum and submaximum exercise capacity. Two groups of healthy, untrained subjects were studied in double-blind cross-over trials. Oral supplementation of 2 g per day L-carnitine was used for 2 weeks in the first trial and the same dose but for 4 weeks in the second trial. Maximum and submaximum exercise capacity were assessed during a continuous progressive cycle ergometer exercise test performed at 70 rpm. In trial 1, plasma concentrations of lactate and β-hydroxybutyrate were measured pre- and post-exercise. In trial 2, pre- and post-exercise plasma lactate were measured. The results of treatment with L-carnitine demonstrated no significant changes in maximum oxygen uptake ($\dot{V}_{O_{2max}}$) or in maximum heart rate. In trial 1, there was a small improvement in submaximal performance as evidenced by a decrease in the heart-rate response to a work-load requiring 50% of $\dot{V}_{O_{2max}}$. The more extensive trial 2 did not reproduce the significant result obtained in trial 1, that is, there was no significant decrease in heart rate at any given submaximal exercise intensity, under carnitine-supplemented conditions. Plasma metabolic concentrations were unchanged following L-carnitine, in both trials. It is concluded, that in contrast to other reports, carnitine supplementation may be of little benefit to exercise performance since the observed effects were small and inconsistent.

Key words: L-Carnitine — $\dot{V}_{O_{2max}}$ — Submaximum heart rate

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Introduction

Carnitine (β-hydroxy γ-trimethylamino butyrate) is a quaternary amine which plays a central role in lipid catabolism and energy production. Fritz (1955, 1963) identified carnitine as part of the shuttle mechanism whereby long chain fatty acids are converted to acyl carnitine derivatives and transported across the mitochondrial membrane. Carnitine may play a role in pyruvate oxidation by reversing inhibition of pyruvate dehydrogenase by Acetyl CoA (Bookelman et al. 1978) and it may also be involved in branched chain amino acid oxidation (Van Hinsbergh et al. 1979).

Training increases the capacity of skeletal muscle to oxidise fatty acids (Havel et al. 1964; Issekutz et al. 1966; Mole et al. 1971). This requires an increased transport of fatty acids into mitochondria and changes in carnitine levels and/or the activities of its associated enzymes may be involved in the biochemical adaptation to chronic training (Froberg et al. 1972). This has been reinforced by Lennon et al. (1983) who have shown that muscle carnitine levels are indeed greater in trained as opposed to untrained individuals.

Recently, Marconi et al. (1985) have reported a 6% increase in the maximal aerobic capacity of six athletes after oral supplementation of carnitine for 2 weeks (4 g per day). Improvements in submaximal capacity, indicated by an increase in endurance time at a work-load of 80% $\dot{V}_{O_{2max}}$, have been demonstrated by Eclache et al. (1979). We have also observed that subjects taking carnitine report feeling better able to cope with submaximal exercise. These (unpublished) observations were, however, all open trials in which both subject and investigators knew what was being taken and the possible benefits. For this reason we have now carried out two strictly controlled double-blind trials of carnitine observing the effects on both submaximal and maximal exerise capacity.

Subjects and methods

The first trial consisted of three male and six female subjects, (Table 1) all fit but untrained. Ages ranged from 26 to 31 years (mean 27 years) and body weights from 58 to 78 kg. In the second trial there were four male and six female subjects, ages ranging from 24 to 37 years (mean 28) and weights from 48 to 70 kg. The subjects gave written consent and all procedures were approved by the Committee for the Ethics of Human Investigation, University College Hospital.

Trial design. Both trials were a double blind cross-over. In the first the placebo or L-carnitine was taken for 14 days and after completing an exercise test the subjects immediately changed to the other substance. In the second trial the substances were taken for 28 days and there was a 2-week break before starting the other compound.

Table 1. Physical characteristics of the nine untrained subjects involved in trial 1

Subject	Sex	Age (years)	Body weight (kg)
MC	M	37	61.0
MH	M	27	70.0
NM	M	26	70.6
HC	F	23	61.4
PD	F	29	57.9
MT	F	24	64.3
JF	F	23	58.8
SG	F	31	77.6
KF	F	24	48.3
$\bar{X}$		27.1	63.3
±1 SD		±4.6	±8.6

L-carnitine. L-Carnitine was obtained from Sigma Tau (Pomezia, Italy) as a solution suitable for oral administration. Peppermint essence (1 ml l^{-1}) was added and the solution dispensed in 10-ml ampoules containing 1 g cartinine. A placebo solution was made containing 60 g sucrose, 5 g citric acid, 1 ml peppermint essence and 10 mg quinine in 1 l H_2O. This was dispensed in individual 10-ml ampoules. The subjects took two ampoules per day containing either placebo or carnitine.

Exercise testing. The subjects were throughly familiarised with the experimental procedure before the control measurements were made at the start of the trial. On the days when exercise tests were performed, the subjects were asked to refrain from strenuous physical activity prior to testing and to avoid smoking, eating and drinking sweetened beverages for at least 3 h beforehand. Otherwise, subjects continued their routine activities throughout the trial period.

The exercise response in each trial was measured during a progressive test performed on a cycle ergometer. Work-loads were chosen to span the subjects capacity up to and including a maximum. At submaximal levels oxygen uptake ($\dot{V}_{O_2}$), carbon dioxide output ($\dot{V}_{CO_2}$) and cardiac frequency (fc) were measured over the final 2 min of each 5-min workload, as previously described (Sargeant et al. 1979). Maximal oxygen uptake ($\dot{V}_{O_2max}$) was measured at supramaximal loads. In cases of doubt where the conventional criterion of a plateau of $\dot{V}_{O_2}$ against workload was not observed, the maximal measurements were repeated on the following day. Venous blood samples (10 ml) were obtained before and 5 min post-exercise.

Biochemical analyses. L-Cartinine and its esters were assayed according to the method described by Di Donato et al. (1979). β-Hydroxybutyrate was measured using slight modifications of enzyme-based fluorometric methods described by Lloyd et al. (1978). Lactate was measured by a conventional automated enzymic method.

Results

The various procedures were well tolerated by all subjects and no untoward effects of carnitine were reported.

Table 2. Trial 1: effect of oral supplementation of L-carnitine and placebo upon maximum oxygen uptake, maximum cardiac frequency and submaximum cardiac frequency at a value of power output requiring 50% of $\dot{V}_{O_2max}$

Subject	$\dot{V}_{O_2max}$ (ml · min^{-1} kg^{-1})		fc_{max} (beats · min^{-1})		$fc_{0.5}$ (beats · min^{-1})	
	Placebo	L–C	Placebo	L–C	Placebo	L–C
MC	43.6	43.8	190	179	107	107
MH	57.2	58.7	180	178	125	120
NM	44.0	47.3	207	210	151	140
HC	36.2	34.9	199	199	148	142
PD	45.8	47.0	191	187	132	115
MT	32.0	28.8	187	178	130	126
JF	34.4	35.1	198	193	142	144
SG	38.9	38.2	200	200	126	124
KF	40.4	40.6	199	207	138	138
$\bar{X}$	41.4	41.6	194.6	192.3	133.2	128.4
±1 SD	±7.5	±8.8	±8.2	±12.4	±13.4	±13.1

Table 3. Pre- and post-exercise values for plasma total carnitine, plasma lactate and β-hydroxybutyrate in untrained subjects. (Trial 1) Mean ±1 SD

	Placebo		Carnitine	
	Pre-ex	Post-ex	Pre-ex	Post-ex
Total carnitine ($\mu mol\ l^{-1}$)	55.3 ±7.6	—	78.9 ±16.3	—
Lactate ($mmol\ l^{-1}$)	1.04 ±0.66	11.7 ±2.1	1.14 ± 0.28	10.1 ±2.6
β-OH butyrate ($mmol\ l^{-1}$)	0.069 ±0.05	0.074 ±0.05	0.073 ± 0.09	0.098 ±0.005

Maximum cardiac frequency (fc max) and maximum oxygen uptake ($\dot{V}_{O_2max}$)

There were no significant differences ($P>0.1$) between measurements of placebo and carnitine maximal heart rates and maximum oxygen uptake in either trial (Tables 2, 4).

Effect of carnitine on respiratory exchange ratio (RER)

The RER, the ratio of CO_2 produced to O_2 consumed, was determined for both carnitine and placebo runs. No significant differences were found in either trial at any time during the progressive exercise tests.

Submaximum cardiac frequency

Cardiac frequency at 50% (fc 0.5) and 75% (fc 0.75) of $\dot{V}_{O_2max}$ was interpolated for each individual from linear regression of the submaximum cardiac frequency/oxygen uptake data. Values of cardiac frequency at 50% of $\dot{V}_{O_2max}$ were significantly reduced ($P<0.05$) after carnitine supplementation in trial 1 (Table 2) but not in trial 2 ($P<0.2$:Table 4). Cardiac frequency at 75% of $\dot{V}_{O_2max}$ showed no significant differences in either trial.

Blood biochemistry

In trial 1 the pre- and post-exercise measurements of plasma lactate and β-hydroxybutyrate concentration under plabeco and carnitine supplemented conditions were not significantly different (Table 3). In trial 2, there was not signficant difference between pre- and post-exercise values of plasma lactate concentration (Table 5).

Discussion

The effect of orally administered carnitine upon submaximum and maximum exercise perform-

Table 5. Trial 2: pre- and post-exercise values for plasma total carnitine and plasma lactate in ten untrained subjects. Mean ±1 SD

	Placebo		Carnitine	
	Pre-ex	Post-ex	Pre-ex	Post-ex
Total carnitine ($\mu mol\ l^{-1}$)	41.3 ±8.4	—	56.0 ±8.2	—
Plasma lactate ($mmol\ l^{-1}$)	0.8 ±0.3	11.8 ±4.4	0.9 ±0.3	10.7 ±3.0

Table 4. Trial 2: effect of oral supplementation of L-carnitine and placebo upon maximum oxygen uptake, maximum cardiac frequency and submaximum cardiac frequency at a value of power output requiring 50% of $\dot{V}_{O_2max}$

Subject	$\dot{V}_{O_2max}$ ($ml \cdot min^{-1}\ kg^{-1}$)		fc_{max} ($beats \cdot min^{-1}$)		$fc_{0.5}$ ($beats \cdot min^{-1}$)	
	Placebo	L–C	Placebo	L–C	Placebo	L–C
MC	46.6	43.8	184	174	123	109
MH	60.4	—	177	178	118	129
MA	59.3	61.7	186	187	138	133
SA	60.7	61.2	210	210	150	142
PD	51.9	52.4	190	197	132	135
CG	35.0	39.1	188	195	124	132
OR	33.4	31.7	170	168	126	115
CF	32.9	33.8	200	198	152	146
MT	34.7	32.7	182	184	123	119
DN	37.2	36.2	177	174	112	109
$\bar{X}$	45.2	43.6	186	187	130	127
(±1 SD)	±12.0	±12.0	±12	±13	±13	±13

ance was investigated in two trials, both of which were performed under double-blind conditions, and several months apart. The protocol of each trial was essentially the same, but in the second trial the same dose of carnitine was administered for a longer duration.

In trial 1 there was an indication of a reduced heart-rate response at moderate levels of power output (50% of $\dot{V}_{O_{2max}}$) as a result of carnitine supplementation. We do not feel that this was an habituation effect since the subjects were carefully familiarised with the experimental procedures before the commencement of the trial to eliminate any such effects (Davies et al. 1973), and the order in which placebo and carnitine were given was randomised.

The suggestion of a change in submaximum exercise heart rate with carnitine treatment warranted further investigation, and for this reason the second, more extensive trials, was undertaken. Although there was a suggestion of a decreased heart rate at submaximum load in some subjects there was no significant effect of carnitine.

Our results differ from those of Marconi et al. (1985), who examined trained athletes. Our subjects were fit but essentially untrained, and it is possible that this could account for the different results. However, we have also examined the effects of carnitine in two trained endurance runners and found no evidence of change in oxygen uptake.

The known function of carnitine is in the oxidation of fatty acids, which is important in prolonged exercise. The effect of carnitine supplementation might therefore be seen during prolonged exercise rather than the type of short-term testing used in this study. However, our observations on the performance of marathon runners argue against this (Cooper et al. 1986).

References

Bookelman H (1978) Pyruvate oxidation in rat and human skeletal muscle. Biochem Med 20:395–403

Cooper MB, Jones DA, Edwards RHT, Corbucci GC, Montanari G, Trevisani C (1986) The effect of marathon running on carnitine metabolism and on some aspects of muscle mitochondrial activities and antioxidant mechanisms. J Sport Sci 4:79–258

Davies CTM, Tuxworth W, Young JM (1970) Physiological effects of repeated exercises. Clin Sci 39:247–258

Di Donato S, Cornello F, Storchi G, Rimoldi M (1979) Hepatic ketogenisis and muscle carnitine defficiency. Neurology 29:780–786

Eclache JP, Quard S, Carrier H, Berthiller G, Marnot B, Eischenberger D (1979) Effets d'une adjonction de carnitine au régime alimentaire sur l'exercise intense et prolongé. Place de l'alimentation dans la préparation biologique à la compétition. Comptes Rendus du colloque de St-Etienne

Fritz IB (1963) Carnitine and its role in fatty acid metabolism. Adv Lipid Res 1:285–334

Fritz IB, Yue KTN (1963) Long-chain carnitine acyltransferase and the role of acyl carnitine derivatives in the catalytic increase of fatty acid oxidation induced by carnitine. J Lipid Res 4:279–287

Froberg SO, Ostman J, Sjostrand N (1972) Effect of training on esterified fatty acids and carnitine in muscle and on lipolysis in adipose tissue in vitro. Acta Physiol Scand 86:166–174

Havel RJ, Carlson LA, Ekelund LG, Homoreu A (1964) Turnover rate and oxidation of different free fatty acids in males during exercise. J Appl Physiol 19:613–618

Issekutz B, Miller HI, Rodahl K (1966) Lipid and Carbohydrate metabolism during exercise. Fed Proc 25:1415–1420

Lennon DFL, Strathan FW, Shrago E, Nagee FJ, Madden M, Hanson P, Carter AL (1983) Effects of acute moderate intensity exercise on carnitine metabolism in males and females. J Appl Physiol 55:789–795

Lloyd B, Burin J, Smythe P, Alberti KGMM (1978) Simple automated enzymic fluorometric assays for blood glucose, lactate, pyruvate, alanine, glycerol and 3-hydroxybutyrate. Clin Chem 24:1724–1729

Marconi C, Sassi G, Cardinelli A, Ceretelli P (1985) Effects of L-carnitine loading on the aerobic and anaerobic performance of endurance athletes. Eur J Appl Physiol 54:131–135

Mole PA, Oscai LB, Holloszy JO (1971) Adaptation of muscle to exercise. Increase in levels of palmityl CoA synthetase, carnitine palmityl transferase, palmityl CoA dehydrogenase and their capacity to oxidise fatty acids. J Clin Invest 50:2323–2330

Sargeant AJ, Crawley MA, Davies CTM (1979) Physiologic responses to exercise in myocardial infarction patients following residential rehabilitation. Arch Physiol Med Rehab 60:121–125

Trovato GM, Ginardi V, Di Marco V, Dell'aira AE, Corsi M (1982) Long-term L-carnitine treatment of chronic anaemia of patients with end-stage renal failure. Curr Ther Res 31:1042–1048

Van Hinsbergh VMW, Veerkamp JH, Glatz JFC (1979) 4-methyl-2-oxopentanoate oxidation by rat skeletal muscle mitochondria. Biochem J 182:353–360

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