The influence of training on the maximum oxygen uptake and endurance capacity of male and female subjects

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THE INFLUENCE OF TRAINING ON THE MAXIMUM OXYGEN UPTAKE AND ENDURANCE CAPACITY OF MALE AND FEMALE SUBJECTS

by

Philippa K. Bland

'A Master's Thesis'

submitted in fulfilment of the requirements for the award of Master of Philosophy of the Loughborough University of Technology

July, 1982

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ABSTRACT

Many consider that maximum oxygen uptake ($\dot{V}O_2$ max) provides a valid measure of fitness in general and endurance capacity in particular. However, in recent years evidence has accumulated suggesting that $\dot{V}O_2$ max values provide only limited information regarding endurance capacity. This study set out to investigate the influence of training on the maximum oxygen uptake and endurance capacity of male and female subjects.

The investigation consisted of three studies. The first described the relationship between $\dot{V}O_2$ max and running ability. Although the correlation between $\dot{V}O_2$ max and 2 mile run time was high ($r = -0.90$), individuals within the group with the same $\dot{V}O_2$ max performed very differently.

The second study examined the influence of short term training on $\dot{V}O_2$ max and endurance capacity. The increase in $\dot{V}O_2$ max was small (7%) when contrasted with the large improvement in endurance capacity (478%).

The above two studies both indicated that $\dot{V}O_2$ max alone does not determine endurance capacity. The third study therefore set out to examine which factors influence changes in $\dot{V}O_2$ max and endurance capacity after a period of endurance training. By adopting a single-leg exercise model (Davies and Sargeant, 1975), this study not only re-examined the relationship between $\dot{V}O_2$ max and endurance capacity but also attempted to separate local and central adaptations to training. This model was adopted because of the suggestion that increases in endurance capacity are the result of changes in the skeletal muscle (local) (Gollnick et al., 1973). Again, the increases in $\dot{V}O_2$ max were small when compared with the improvements in endurance capacity. Improvements in the trained leg (TL) were attributed to central and local adaptations to training and in the untrained leg (UTL) to central cardiovascular changes. The large increase in the endurance capacity of the TL (523%) was 404% greater than that seen in the UTL, thus supporting the view that increases in endurance capacity are largely the result of changes
in the skeletal muscle rather than improvements in the central cardiovascular system.

The findings of this study clearly demonstrate that $\dot{V}O_2$ max is a poor predictor of endurance capacity. It provides no information regarding an individual's ability to endure exercise, i.e. the ability to sustain a given submaximal work load, both before and after training. It is suggested that the fitness of an individual may be reflected not by their $\dot{V}O_2$ max value but rather by the largest fraction of that value which he or she can utilize during prolonged periods of exercise.
ACKNOWLEDGEMENTS

The author thanks all her colleagues for their constant guidance, assistance and encouragement, and wishes particularly to express her gratitude to Dr. C. Williams for his help and advice throughout the course of this study.

Finally, my sincere thanks go to all the subjects who gave up a considerable amount of their time to participate in this investigation.
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LIST OF ABBREVIATIONS

UNIT ABBREVIATIONS, PREFIXES, PHYSICAL CONSTANTS

m  metre
kg  kilogram
ml  millilitre
dl  decilitre
L   litre
mM molar concentration
sec second
min minute
hr  hour
kp  kilopond
W   watt
kJ  kilojoule

LIST OF SYMBOLS

V  gas volume
\dot{V}  gas volume per unit time (usually L.min\(^{-1}\))
\dot{V}O_{2}^{\text{max}}  maximum oxygen uptake
RER  respiratory exchange ratio (volume CO\(_2\) : volume O\(_2\)\(^{-1}\))
I  inspired gas
E  expired gas
P  gas pressure
B  barometric pressure
STPD  0°C, 760 nm Hg, dry
Q  cardiac output
\dot{Q}  cardiac output per unit time (usually L.min\(^{-1}\))
\dot{Q}^{\text{max}}  maximum cardiac output
SV  stroke volume
HR  heart rate (usually b.min\(^{-1}\))
Hb  haemoglobin concentration (g.dl\(^{-1}\))
LA  lactate concentration (mM)
a  arterial
v  venous
O_2  oxygen
CO_2  carbon-dioxide
PRE perceived rate of exertion (Borg 1973)

DIMENSIONS

wt  weight
ht  height

STATISTICAL NOTATIONS

x  arithmetic mean
S.D.  standard deviation
n  number of observations
r  correlation coefficient (Spearman rank or product-moment)
range  smallest and largest observations
p (P)  probability
*  denotes a (probably) significant difference; 0.05 > p > 0.01
**  denotes a significant difference; 0.01 > p > 0.001
***  denotes a (highly) significant difference; p < 0.001
NS  no significant difference
V  coefficient of variation

OTHERS

TL  trained leg
UTL  untrained leg
RL  right leg
LL  left leg

EXAMPLES

m.sec\(^{-1}\)  metres covered per second
\(\dot{V}_{O_2}\)  volume of oxygen.min\(^{-1}\) (oxygen uptake. min\(^{-1}\))
a-\(\bar{V}O_2\) diff arterio-venous oxygen difference (difference in oxygen content between arterial and mixed venous blood)

\(Bp\) barometric pressure

\(\dot{V}E\) volume of expired air (usually L min\(^{-1}\))

\(\dot{V}CO_2\) volume of carbon-dioxide min\(^{-1}\)

\(\dot{V}E.\bar{V}O_2\) ventilatory equivalent (ratio between pulmonary ventilation and oxygen uptake).
Part of the work presented in this thesis has been published in the following journals:


CHAPTER 1

INTRODUCTION

The ability of an individual to perform and sustain physical work is both determined and limited by a number of physiological parameters which can be altered by training.

It has been well documented that repeated exposure to a particular work task leads to both an increased ability to sustain the work and an improvement in the efficiency of the work performed. Repeated exposure to exercise resulting in a variety of adaptations that interact and lead to an increased performance capacity may be classified as training. To achieve a training effect "it is necessary to expose the organism to an overload, that is to a stress which is greater than the one regularly encountered during everyday life." (Åstrand and Rodahl, 1977, p.393).

Adaptations resulting in improved performance are particularly important to those individuals participating in competitive sport. For example

"In the runner this amounts to running a greater distance at the same pace, or covering the same distance more quickly, or covering the same distance at the same rate with less fatigue"

(Knehr et. al., 1942).

The adaptations resulting from training will depend upon the nature of the activity being performed. The adaptations resulting from a sprint training programme will be very different to those found after endurance training.

In studying both endurance athletes and the responses to an endurance training programme, researchers have concentrated predominantly on changes in maximum oxygen uptake (\(\dot{V}O_2\) max). Maximum oxygen uptake may be
defined as "the highest oxygen uptake the individual can attain during physical work while breathing air at sea level". (Åstrand and Rodahl, 1977, p.318).

Many researchers have focused their attention on changes in this parameter after a programme of endurance training because they equate \( \dot{V}O_2 \) max with physical fitness and more specifically with endurance capacity. For example, Astrand (1956) stated that

"The individual's capacity for oxygen intake should be decisive in determining his ability to sustain heavy prolonged work."

Shepherd and coworkers stated in the Bulletin of the World Health Organization that

"The directly measured maximum oxygen intake is now widely accepted as one unequivocable reference standard of cardio-respiratory fitness".

(Shepherd et. al., 1968).

Similarly, Di Prampero and Cerretti (1969) stated that

"Maximum oxygen uptake (\( \dot{V}O_2 \) max) is one of the most significant functional characteristics of the individual and an index of his capacity for performing work".

Wilmore (1968) summed up the general thoughts concerning the importance of \( \dot{V}O_2 \) max by stating that

"Maximal oxygen uptake has become widely accepted as the primary physiological variable which best defines the efficiency or capacity of the cardiovascular system. This variable is now regarded as synonymous with the term cardio-respiratory fitness and has been designated by some investigators as the most significant criterion of physical fitness".

A high \( \dot{V}O_2 \) max is undoubtedly a pre-requisite for success in endurance events because it enables a high rate of aerobic energy production necessary to sustain prolonged high intensity submaximal exercise. However, an individual's \( \dot{V}O_2 \) max is dependent upon natural endowment and although training can increase \( \dot{V}O_2 \) max, this parameter can only be improved within genetically determined limits. Although an individual may have reached the ceiling of his aerobic capacity through endurance training, continued training has been found to result
in improved performance. It is surprising therefore that many investigators have simply reported the responses to an endurance training programme without applying these findings to changes in performance. Nevertheless, the above suggests that changes in VO$_2$ max alone cannot explain changes in performance (endurance capacity).

This study therefore set out to examine more closely the association between VO$_2$ max and endurance capacity by examining the influence of training on the relationship between these two parameters. In addition, by including performance tests designed to assess endurance capacity, the experimental findings could be related to changes in endurance capacity.

Although the physiological responses, together with their biochemical basis, to endurance exercise have been well researched, the actual nature of the training response has received relatively little attention particularly in relation to prolonged submaximal exercise.

For several years, exercise physiologists have concentrated on cardiovascular (central) adaptations to endurance exercise. However, it has become increasingly evident that such exercise leads to major (local) adaptive changes in the skeletal muscle. This investigation therefore also attempted to describe more fully the contribution of central and local adaptations to improvements in endurance capacity.

Finally, the study also set out to investigate whether VO$_2$ max is "the most significant criterion of physical fitness" (Wilmore, 1968) and whether it is decisive in determining the endurance capacity of an individual i.e. the ability of an individual to sustain high intensity submaximal exercise.

Three studies were included to investigate the above and each included a performance test designed to measure endurance capacity:

1. A cross-sectional study to examine the relationship between VO$_2$ max and endurance capacity in a heterogeneous group of individuals. In this study endurance capacity was assessed
by the inclusion of a 2 mile time trial. This was included as an introductory study.

2. A longitudinal study to investigate the effects of a 5 week endurance training programme on the relationship between VO2 max and endurance capacity in a homogeneous group of individuals. Endurance capacity was determined by measuring the ability of each individual to sustain a given submaximal work load.

3. A one-legged training study to examine the effects of endurance training on the relationship between VO2 max and endurance capacity during exercise with the trained and untrained legs. The one-legged exercise model was adopted in an attempt to separate the central and peripheral responses to training. The endurance capacity of the two legs was determined by measuring the ability of each leg to sustain a given submaximal work load.
CHAPTER 2

REVIEW OF LITERATURE

2.1

ORGANIZATION OF THE LITERATURE REVIEW

1. Maximum oxygen uptake ($\dot{V}O_{2\text{max}}$) and distance running ability
   (a) Maximum oxygen uptake and running performance.
   (b) Running economy.

2. The influence of endurance training on the cardiovascular system and skeletal muscle
   (a) The influence of endurance training on maximum oxygen uptake.
   (b) The influence of endurance training on heart rate during submaximal exercise.
   (c) The influence of endurance training on lactate concentration during submaximal exercise.
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   (e) The influence of endurance training on the respiratory exchange ratio during submaximal exercise.
   (f) The influence of endurance training on skeletal muscle.

3. The influence of endurance training on endurance capacity.

4. The influence of endurance training a limited muscle mass on the responses taking place during exercise with trained and untrained muscle masses
   (a) Arm versus leg training studies.
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MAXIMUM OXYGEN UPTAKE (\(\dot{V}O_2\) max) AND DISTANCE RUNNING ABILITY

2.2.1 Maximum oxygen uptake and running performance

In the past many investigators have measured \(\dot{V}O_2\) max and the effect of training on \(\dot{V}O_2\) max equating this measure with physical fitness and more specifically with endurance capacity. These earlier studies failed to include a field test which would have provided information regarding the relationship between \(\dot{V}O_2\) max and athletic performance. It is only more recently that investigators have begun to relate laboratory measurements to performance during sporting activities by including field tests in their investigations. The endurance athlete has undoubtedly provided the greatest amount of physiological data in this area and the literature includes countless studies that have identified high aerobic capacities for athletes participating in activities such as cross-country skiing, rowing, and middle and long distance running.

The importance of \(\dot{V}O_2\) max and distance running has been studied by relating the former to the time taken to run distances varying from 1 to 2 miles up to marathon and ultra marathon distances. Initial studies in this area concentrated on \(\dot{V}O_2\) max and running time only but as more and more evidence has shown that factors other than \(\dot{V}O_2\) max influence distance running ability, submaximal measurements have received increasing attention.

A large number of the early studies investigating the relationship between selected physiological variables and distance running performance were carried out by Costill. In 1967 he examined the relationship between a battery of 16 test items and the mean time taken to run 4.7 miles over a cross-country course. The relationship between factors such as body fat, haemoglobin, resting heart rate (HR) and \(\dot{V}O_2\) max and running distance were investigated. The most conclusive finding
from this study was the direct relationship between \( \dot{V}O_2 \) \( \text{max} \) and running performance. Costill (1967) also found that the faster runners appeared to have less body fat, a higher blood haematocrit, greater maximal breathing capacity per body surface area and a lower resting heart rate.

Costill and Fox (1969) studied 6 nationally ranked marathon runners. Each runner was exposed to both maximal and submaximal tests. After these initial measurements each subject ran 10km on a level treadmill at a running speed comparable to that required to equal his best marathon performance. These tests were carried out 1 month prior to the Boston Marathon during which each subject's running pace, time and mean speed were recorded. In addition, blood lactate (LA) levels were determined 5 minutes after the race. The aerobic nature of both the 10km treadmill and the Boston Marathon runs were substantiated by the low LA values obtained 5 minutes after the exercise. Following the 10km and marathon runs the mean LA values were 1.6mM and 2.1mM respectively. During the 10km run the subjects utilized on average 74.2% of their \( \dot{V}O_2 \) \( \text{max} \). From each runner's best marathon time in the preceding 12 months, it was estimated that highly trained marathon runners utilize approximately 75% of their \( \dot{V}O_2 \) \( \text{max} \) during a marathon race. The authors concluded that these marathon runners could sustain this work intensity with very little LA accumulation. In addition, using the runners' \( \dot{V}O_2 \) \( \text{max} \), the relative energy expenditures during races varying in distance from 5 to 84km were estimated. The authors found an inverse relationship between % \( \dot{V}O_2 \) \( \text{max} \) utilized during the race, and the selected distance. Over 5km, for example, these runners utilized approximately 88% of their \( \dot{V}O_2 \) \( \text{max} \).

In the investigation reported above relatively low LA levels were found in marathon runners after a marathon race. Costill (1970) therefore set out to investigate further, blood LA levels during prolonged running at varied intensities and durations. Over all competitive distances the post-exercise blood LA values were related to the % \( \dot{V}O_2 \) \( \text{max} \) utilized during the run and an inverse curvilinear relationship between the length of the race and blood LA concentration was found. The runners being studied were highly trained and blood LA only began to rise noticeably when the oxygen requirement of the run was approximately
70% of the subjects $\dot{V}O_2$ max. When compared with data from untrained individuals, Costill concluded that in such individuals LA may begin to accumulate at lower relative work loads. Three of the runners in his study participated in a 10km treadmill run during which running speeds exceeding 85% (range 85 to 98%) $\dot{V}O_2$ max were tolerated. Towards the end of the run heart rate values exceed 180 b.min$^{-1}$ but despite the high work intensity the LA levels were relatively low (2.9 mM). From these findings Costill suggested that training not only increases $\dot{V}O_2$ max but also appears to allow the athlete to utilize a high percentage of his $\dot{V}O_2$ max with only a small accumulation of LA.

Costill and coworkers also studied the metabolic responses during submaximal and maximal exercise of a world champion marathon runner comparing the observations with data from 6 runners studied in an earlier investigation (Costill et al., 1971). When compared to other world class distance runners, this athlete was found to have a $\dot{V}O_2$ max below average (69.7 ml.kg$^{-1}$.min$^{-1}$). This suggests that factors other than $\dot{V}O_2$ max are also important during distance running and is supported by the absence of a relationship between $\dot{V}O_2$ max and marathon running performance ($r=0.08$) in the 27 athletes that the authors had examined over the previous 3 years. In addition, oxygen cost at submaximal running speeds did not separate this athlete from others since his oxygen costs at these loads were highly similar to less successful athletes. From an earlier study by Costill and Fox (1969) it was reported that top class marathon runners utilize approximately 75% $\dot{V}O_2$ max during marathon races, however there appears to be considerable individual variation. The athlete in this study was able to comfortably sustain 86% of his $\dot{V}O_2$ max, which corresponded to a running speed of 5.5m.sec$^{-1}$ (328m.min$^{-1}$), for 30 minutes with only a low accumulation of LA (2.4 mM). The success of this athlete was therefore attributed to his ability to utilize a large fraction of a high $\dot{V}O_2$ max. However, the study did not explain why individuals vary in their ability to utilize a large fraction of their $\dot{V}O_2$ max for varying lengths of time.
Costill, Thomason and Roberts (1973), from field and laboratory measurements performed on 16 male trained runners, provided a possible answer to the above question. The authors investigated the relationship between performance during a 10 mile road race and selected laboratory measurements. Maximum oxygen uptake and running time were highly correlated ($r = -0.91$). In addition, the correlation coefficients between % max HR and % max $\dot{V}O_2$ at 4.5m.sec$^{-1}$ (268m.min$^{-1}$) and the 10 mile running time were both highly significant.

From the estimated oxygen consumption during the race, the runners were found to be utilizing approximately 86% $\dot{V}O_2$ max (about 91% $\dot{V}O_2$ max when corrected for air resistance).

A high correlation was also found between blood LA at 4.5m.sec$^{-1}$ (268m.min$^{-1}$) and race time. This is not surprising since blood LA levels depend largely, although not entirely, upon the relative work load. In addition to this, at a running speed demanding 85% $\dot{V}O_2$ max, the faster runners were found to accumulate less LA. From these results it would appear that LA production influences the ability to tolerate a large $\dot{V}O_2$ max.

Briggs (1977) provided further evidence supporting the importance of the ability of an athlete to tax a large percentage of his $\dot{V}O_2$ max during distance running. He investigated the relationship between $\dot{V}O_2$ max, a 2 mile time trial, and the ability to sustain 95% $\dot{V}O_2$ max during treadmill running. The subjects were highly trained possessing a mean $\dot{V}O_2$ max of 71.9 ± 2.9 ml.kg$^{-1}$.min$^{-1}$. The correlations between running time and $\dot{V}O_2$ max ($r = -0.38$) and between running time and a treadmill run at 95% $\dot{V}O_2$ max ($r = -0.56, p < 0.05$) were obtained. The weak correlation between $\dot{V}O_2$ max and running time, in individuals of a similar ability with respect to $\dot{V}O_2$ max, supports the findings of Costill and coworkers who found no relationship between $\dot{V}O_2$ max and running ability in 27 marathon runners (Costill et. al., 1971). The advantage of the study by Briggs is that a running test over a common distance (2 miles) was included in the experiment, however, only a 2 mile time trial was included and the runners were not therefore tested over longer distances.
In addition, the 2 mile race is short and may include some anaerobic energy contribution, particularly in the early and latter stages.

Lawson and Golding (1978), however, found a significant relationship between VO$_2$ max and 2 mile run time ($r=-0.86$) indicating that this event is primarily aerobic in nature. In addition, a significant relationship was also found between the percentage of slow twitch fibres and 2 mile run time. Further, none of the indicators of anaerobic energy included in their study correlated with the 2 mile run time suggesting that the inability to supply energy anaerobically will not limit performance over this distance. However, 2 subjects in the study ran the distance at an oxygen cost in excess of 100% VO$_2$ max.

Davies (1980) in a study on 11 to 13 year old boys also found a significant relationship between running ability and VO$_2$ max ($r=-0.75$). However, the failure to include a field test over a common distance was a weakness in this investigation.

Farrell and coworkers carried out laboratory and field measurements on 18 male distance runners of varying ability. Performance data from competitive running over distances varying from 3.2km to the marathon distance were obtained. The percentage of slow twitch fibres, VO$_2$ max, running economy at 4.8m.sec$^{-1}$ (286m.min$^{-1}$) and the oxygen uptake (VO$_2$) and treadmill velocity at the "onset of plasma lactate accumulation" (OPLA) were all determined. All the above measured parameters were significantly related to performance at all running distances. From a multiple regression analysis the treadmill speed corresponding to OPLA was most closely correlated to running performance. The authors found that the slowest and fastest marathon runners ran the distance at a pace which was very similar to the treadmill speed corresponding to OPLA. They concluded that irrespective of ability all individuals selected a running pace that "just avoids the exponential rise in plasma lactate" (Farrell et. al., 1979).

The runners in this study who were the fastest over the shortest distances were also fastest over the longer distances which suggests that
the 2 mile time trial may provide useful information regarding the ability of the athlete to run longer distances. Although the authors stressed the importance of OPLA, they stated that running performance ultimately depends upon the interaction of several factors.

La Fontaine, Londeree and Ames (1981) investigated the relationship between maximal steady state (MSS) and selected running distances. MSS was defined as the treadmill speed that corresponded to a plasma lactate (LA) of 2.2mM. The authors selected this LA level because it corresponded to LA measurements made after races of varying distances. MSS was found to correlate highly with the running pace selected by athletes over distances ranging from 402.3m to 20km. These findings support the work of Costill, Thomason and Roberts (1973) and Farrell and coworkers who both stressed the importance of the relative work load at which blood LA begins to rise, and distance running performance. (Farrell et. al., 1979).

Berg and Bell (1980) found a significant relationship over the shorter distance of 1 mile and \( \dot{V}O_2 \) max (\( r = -0.74 \)). They stressed however, that running ability is dependent upon numerous factors over this distance including anaerobic capacity, age, \( \dot{V}O_2 \) max, % body fat and lower extremity length as a percentage of height. They stressed the combined importance of these factors stating that \( \dot{V}O_2 \) max is not the only determinant of success.

Some training studies have used running performance over a given distance to measure changes in endurance capacity in response to a training programme. These studies have also shown that factors other than \( \dot{V}O_2 \) max influence running ability. Daniels, Yarborough and Foster (1978), for example, found that in a group of highly trained runners who were subjected to an 8 week training programme which involved exercising at a greater intensity and volume than that to which they were accustomed, 2 mile run time increased but \( \dot{V}O_2 \) max remained unchanged.
2.2.2

Running economy

Although several authors have found that running economy, i.e. the oxygen cost at a given submaximal speed, varies considerably between runners, very few have related this to performance during running over a common distance.

Conley and Krahenbuhl (1980) determined the relationship between running economy and running performance in highly trained athletes. A weak relationship was found between \( \dot{V}O_2 \) max and run time \((r=0.12)\), but the relationship between steady-state \( \dot{V}O_2 \) at the treadmill running speeds of 4.0, 4.5 and 4.9m.sec\(^{-1}\) (241, 268, 295m.min\(^{-1}\)) were all highly correlated to the 10km run time \((p < 0.01)\). From these findings the authors concluded that in a homogeneous group of individuals with respect to \( \dot{V}O_2 \) max, running economy will account for a large variation in performance.

Mayhew, Piper and Etheridge (1979), quoting work from their unpublished research (1974), stated that \( \dot{V}O_2 \) at submaximal work loads and performance time were not closely related. However, the authors simply reported this finding and failed to explain the experimental procedures from which it was derived.

The findings of Mayhew, Piper and Etheridge (1979) are in agreement with those of Costill, Thomason and Roberts (1973) who found that at each submaximal running speed although the marathon runners in their study utilized less oxygen than the other athletes, the intra-individual variations at each running speed suggested that these differences were "random" and "non-significant". However, they did not specifically determine the relationship between the 10 mile run time and the \( \dot{V}O_2 \) at a given submaximal running speed.

Conley, Krahenbuhl and Burkett (1981) however, provided further evidence supporting the importance of running economy. They found
considerable improvement in this parameter in a 31 year old male after 18 weeks' interval and endurance training. They stated that over long distances (10,000km +) running economy may contribute significantly to the outcome of the race. The major criticism of their study is that the subject may simply have become more accustomed to treadmill running reducing the oxygen consumption at selected speeds. The authors provided no information regarding familiarization with both treadmill running and the experimental protocol necessary for the collection of expired air.

Mayhew (1977) studied the oxygen cost of trained runners at several submaximal speeds but failed to include a performance test. Nine subjects ran at speeds ranging from 2.2 to 4.9m.sec\(^{-1}\) (134 to 295m.min\(^{-1}\)). He found the \(\dot{V}O_2\)/speed relationship to be linear over the complete aerobic range. From other investigations together with the data from his study, he found the spread of \(\dot{V}O_2\) values around the means at various running speeds to be approximately the same, however, between studies there was considerable variation. This may be the result of varying training states or the degree of laboratory familiarization. In addition, Mayhew found that those individuals with the highest \(\dot{V}O_2\) max had the lowest oxygen uptakes during running at selected submaximal speeds (r=0.70). Daniels (1974) and coworkers also found this relationship (Daniels et. al., 1977).

In the above investigations, only males have been studied. The fact that males can run faster than females has been recognised ever since performance times have been recorded. If submaximal \(\dot{V}O_2\) values do not vary between the 2 sexes, this difference in running ability must be largely a function of the lower \(\dot{V}O_2\) max values measured in females. For this reason the majority of studies comparing males and females have measured submaximal \(\dot{V}O_2\) at various speeds.

Daniels and coworkers studied the aerobic responses of male and female distance runners to both maximal and submaximal exercise. The males and females were tested at 4 submaximal speeds: 3.4, 3.6, 4.0 and 4.5m.sec\(^{-1}\) (202, 215, 241 and 268 m.min\(^{-1}\)). The males had a significantly
higher $\dot{V}O_2$ max value but $\dot{V}O_2$ at the submaximal work loads did not differ between the 2 sexes, despite the tendency towards higher $\dot{V}O_2$ values in the female group (Daniels et. al., 1977). Daniels and coworkers also compared the regression curves relating $\dot{V}O_2$ and running speed for different speed ranges and found that different ranges produced different regression lines. The regression curve for the slow speeds was much flatter than that for the fast speeds. This may be the result of the difficulty the subjects had in running slowly. Vertical movement at slower speeds may result in greater energy expenditure. Daniels and coworkers reported that a comfortable running speed was reached at 3.3m/sec$^{-1}$ (200 m.min$^{-1}$).

Kollias and coworkers compared the responses of males and females to graded treadmill exercise. The female runners were all highly trained possessing a mean $\dot{V}O_2$ max value of 3.24 ± 0.17 L.min$^{-1}$ or 58.40 ± 4.86 ml.kg$^{-1}$.min$^{-1}$ (Kollias et. al., 1978). This value is very similar to the average value of 61 ml.kg$^{-1}$.min$^{-1}$ reported by Astrand and Rodahl (1977, p.409) for a group of female Swedish national runners competing over distances varying from 800 to 1500m. At running speeds ranging from 2.7 to 4.5m.sec$^{-1}$ (162 to 270 m.min$^{-1}$), no differences were found between the oxygen cost of running for the male and female runners.

Mayhew, Piper and Etheridge (1979) studied the oxygen cost of running in trained and untrained males and females. All subjects were habituated to treadmill running prior to testing. Each subject ran at 4 submaximal speeds (2.3, 2.5, 2.8 and 3.0 m.sec$^{-1}$, i.e. 135, 150, 165 and 180 m.min$^{-1}$), and although the trained individuals showed a tendency towards more economical running, the oxygen cost relative to body weight was independent of sex or degree of training.

Many of the above predictions are based on the ability to equate treadmill data with data collected in the field. McMiken and Daniels (1976) demonstrated that at treadmill speeds up to 4.3 m.sec$^{-1}$ (260 m.min$^{-1}$) there was no difference in the oxygen cost of treadmill and track running. The above studies also raise the question of the applicability of steady-state measurements made during a short treadmill run to prolonged field running.
Summary

Significant relationships have been found between: \( \dot{V}O_2 \) max; percentage of slow twitch fibres; the fraction of \( \dot{V}O_2 \) max that can be utilized; the relative work load at which lactate begins to accumulate; running economy, and distance running performance. These factors have there been associated with success.

Although conflicting findings have been reported, the weight of the available evidence suggests that there is no significant difference between the oxygen cost of running in male and female athletes.

2.3

THE INFLUENCE OF ENDURANCE TRAINING ON THE CARDIOVASCULAR SYSTEM AND SKELETAL MUSCLE

This review will concentrate on those parameters determined in this study because of the vast size of the topic.

2.3.1

The influence of endurance training on maximum oxygen uptake (\( \dot{V}O_2 \) max)

Numerous investigations have found improvements in \( \dot{V}O_2 \) max in response to an endurance training programme reporting changes that vary from 0% to 93% (Pollock, 1973).

Robinson and Harmon (1941) and Knehr, Dill and Neufeld (1942) were the first to demonstrate an increase in \( \dot{V}O_2 \) max after training sedentary individuals. Robinson and Harmon (1941) reported a 14% increase in \( \dot{V}O_2 \) max in a group of 9 males after 7 months of training, whereas Knehr and coworkers (1942) found a 7% increase in a group of 14 males after 6 months of training. The difference may possibly be explained by different training intensities. Robinson and Harmon stated
that the training was "hard" but Knehr and coworkers failed to mention
the intensity of effort involved (Knehr et. al., 1942).

Increases in $\dot{V}O_2$ max are dependent upon the initial level of fitness
and age of the subjects, and the intensity, frequency and duration of
each training session (Astrand and Rodahl, 1977, p. 426).

The classic "bed rest" study by Saltin and coworkers clearly
demonstrated the influence of initial fitness levels on changes in $\dot{V}O_2$
max. Five males were exposed to an intensive 50 day training programme
following 20 days' bed rest. Two of the subjects had engaged in physical
activity on a regular basis prior to the study while the others had
previously been sedentary. After training the sedentary subjects showed
an increased $\dot{V}O_2$ max of 33% while the previously active subjects only
showed a 4% increase. The improvement in $\dot{V}O_2$ max was even greater when
the "after bed rest" values were used, since bed rest decreased $\dot{V}O_2$ max
by 27%. The active and sedentary individuals now demonstrated increases
in $\dot{V}O_2$ max of 34% and 100% respectively. The authors concluded that
improvements in $\dot{V}O_2$ max in response to a training programme may be influenced
by habitual physical activity levels. Despite the definite differences
between the active and sedentary subjects it should be noted that the 2
groups consisted of only 2 and 3 males respectively (Saltin et. al., 1968).

As will be demonstrated in this review, the majority of training
studies have reported increases in $\dot{V}O_2$ max in sedentary individuals
in the region of 10 to 20%. The increase reported by Saltin and
coworkers in the 2 sedentary subjects is fairly large but there would
appear to be no reason to dispute their finding since the initial
$\dot{V}O_2$ max value of 2.52 L.min$^{-1}$ is average for young sedentary males

One of the greatest improvements found in $\dot{V}O_2$ max after training
has been reported by Hickson, Bomze and Holloszy (1977). For a group
of 8 subjects, ranging in age from 20 to 42 years who were exposed to
a 10 week training programme, the average increase in $\dot{V}O_2$ max was
found to be 44%. The subjects exercised 6 days a week, alternating
between bicycle ergometry and running, at maximal or near maximal levels. The initial fitness levels of the subjects varied considerably. Some were totally sedentary while others were highly trained.

Two of the sedentary subjects demonstrated increases in \( \dot{V}O_2 \) max of 52 and 53%. One of these subjects continued to train for a further 3 weeks which resulted in a 77% increase in \( \dot{V}O_2 \) max over his pre-training value of 1.68 L.min\(^{-1}\) (23 ml.kg\(^{-1}\).min\(^{-1}\)). This pre-training value is exceptionally low for a 40 year old sedentary male and although Hickson and coworkers stated that the "plateau" effect was used as the criterion for \( \dot{V}O_2 \) max, one must question the accuracy of this measurement. This low value of 1.68 L.min\(^{-1}\) is similar only to the value of 1.74 L.min\(^{-1}\) in previously sedentary subjects after 20 days' immobilization in bed (Saltin et. al., 1968). The \( \dot{V}O_2 \) max value of 1.68 L.min\(^{-1}\) is only 56% of the mean value found for a group of 21 sedentary males aged 40–49 years (Åstrand P-O 1952, p.75) and only 75% of the mean \( \dot{V}O_2 \) max value for a group of 9 non-active males aged 56–86 years (Åstrand I. et. al., 1959). The "levelling-off" criterion for \( \dot{V}O_2 \) max was used and Niemala and coworkers found that this was the only useful criterion for establishing \( \dot{V}O_2 \) max (Niemala et. al., 1980). However, Hickson and coworkers also reported a very low pre-training \( \dot{V}O_2 \) max value for the previously sedentary female in the group, aged 25 years. This subject's \( \dot{V}O_2 \) max value was only 50% of the value reported by Astrand (1952) for 31 females aged 20–25 years. The findings of Hickson and coworkers are unusual and difficult to explain since the subjects were not only familiar with the maximal test but this test was repeated 3 times prior to training. The highest oxygen uptake measurement from the 3 tests provided the pre-training \( \dot{V}O_2 \) max value. Hickson and coworkers failed to explain the unusually low pre-training values but they explained the large improvements in \( \dot{V}O_2 \) max in terms of the high intensity training programme to which their subjects had been exposed.

Ekblom and coworkers studied the effects of a 16 week training programme on 8 males. Training consisted of both cross-country running and interval type exercise 3 times a week. A control group was not included in the study, after which a 16.2% increase in \( \dot{V}O_2 \) max was reported. The subjects were of the college age (22.9 years) and none
had engaged in any regular endurance training prior to the study (Ekblom et al., 1968).

Williams and coworkers investigated the effects of training on \( \text{VO}_2 \) max. Thirteen male subjects participated in a training programme that consisted of prolonged daily exercise (4 hours) at "aerobic levels of work". This was followed by a short burst of exercise at the maximum level. A moderate increase of 7% was found in \( \text{VO}_2 \) max after training. The authors failed to state the intensity of effort involved but the 4 hour duration of each training session suggests that the intensity of effort was fairly low (Williams et al., 1967). To sustain the exercise over the 4 hour period the subjects may have been exercising at or below 50% \( \text{VO}_2 \) max. The findings of Davies and Knibbs (1971), who demonstrated that an intensity at or below 50% \( \text{VO}_2 \) max failed to increase \( \text{VO}_2 \) max, suggests that the 7% improvement in \( \text{VO}_2 \) max reported by Williams and coworkers was due to the short maximal bursts.

Ekblom (1969) trained 8 males on a bicycle ergometer over a 16 week period, reporting an improvement in \( \text{VO}_2 \) max of 8%. He concluded that although this improvement was small for previously untrained individuals it supported the findings of others (Knehr et al., 1942; Williams et al., 1967). It is interesting to note that the authors of these 3 studies all failed to mention the intensity of their training programmes.

Ribisl (1969) studied the effects of a 5 month training programme on the \( \text{VO}_2 \) max of middle-aged males. The group trained 3 times a week for 35 minutes, each session consisting of jogging, cross-country running and calisthenics. A 10% improvement in \( \text{VO}_2 \) max was measured, however, again the intensity of effort was not mentioned.

Karlsson, Nordesjö and Saltin (1974) reported a similar increase in \( \text{VO}_2 \) max (11%) in a group of 5 males (aged 20 years) after a 2 month training programme. Training was of the interval kind and consisted of 15 seconds' work at the maximum level followed by 15 seconds' jogging or walking.
Moffatt and coworkers, in a study on 46 male students, found increases in $\dot{V}O_2\,max$ of 12.3% and 7.6% for 2 groups of individuals who performed either interval or continuous type training respectively. The larger improvement in $\dot{V}O_2\,max$ found in the interval trained group may be explained by the greater intensity at which they had been training (Moffatt et. al., 1977).

Wilmore and coworkers, after a 20 week training programme, found increases in $\dot{V}O_2\,max$ of 14.8% and 13.3% in previously sedentary subjects participating in bicycle and jogging exercise respectively. Each group trained for 30 minutes 3 times a week. Wilmore and coworkers unlike many of the above authors included a control group in their study. Maximum oxygen uptake remained unchanged in this group (Wilmore et. al., 1980).

The studies reviewed above all demonstrated increases in $\dot{V}O_2\,max$. Daniels, Yarborough and Foster (1978), however, found no improvement in $\dot{V}O_2\,max$ after 8 weeks of training in a group of well trained runners. The unchanged $\dot{V}O_2\,max$ value was found despite exposing the subjects to a volume and intensity of exercise which was greater than that to which they were accustomed. The authors, however, did find a 9% increase in $\dot{V}O_2\,max$ in a group of active but untrained males. These findings support the view that the percentage improvement in $\dot{V}O_2\,max$ is related to habitual activity levels, and are in agreement with those of Ekblom (1969) who demonstrated that training only produces small improvements in the $\dot{V}O_2\,max$ of well-conditioned individuals. The results of the study by Ekblom (1969) do not compare favourably with the findings of Hickson, Bomze and Holloszy (1977) (described above) who found a linear increase in $\dot{V}O_2\,max$ over a 10 week training period. The 23% increase in $\dot{V}O_2\,max$, reported by Hickson and coworkers in a 42 year old male who had been engaged in regular endurance training for a number of years, is surprisingly substantial. Daniels, Yarborough and Foster query the accuracy of the $\dot{V}O_2\,max$ measurements made by Hickson and his coworkers.

The training experiments described above all employed male subjects, the explanation being that the studies investigating the responses of
females to training are much fewer in number. A few studies involving females will be included in this review to demonstrate that these studies have found similar improvements in $\dot{V}O_2$ max after training.

Cunningham and Hill (1975) studied women over 9 and 52 week periods. Training consisted of running twice weekly which was supervised only during the initial 9 week period. Maximum oxygen uptake increased by 34% after the first 9 weeks of training and by an additional 5% after 52 weeks. The 34% increase is large but the subjects were initially very sedentary with correspondingly low pre-training $\dot{V}O_2$ max values. In addition, $\dot{V}O_2$ max was predicted which may result in the underestimation of this parameter (Astrand and Rodahl, 1977, p.456).

Kearney and coworkers studied 27 sedentary college women who trained 3 times a week on a treadmill for 9 weeks. Half the group trained at a heart rate of 134 b.min$^{-1}$ and the other half at a heart rate of 155 b.min$^{-1}$. The $\dot{V}O_2$ max values increased by 13% and 19% respectively. The intensity of effort appeared influential in determining the extent of improvement in $\dot{V}O_2$ max (Kearney et al., 1976).

Pederson and Jørgenson (1978) found increases in $\dot{V}O_2$ max ranging from 9.5 to 13.8% after 7 weeks' training in 6 females aged 23 years. Training was performed twice weekly at a heart rate of 170 b.min$^{-1}$. The authors suggested that their findings demonstrated that no difference exists in the trainability of males and females. This is in agreement with the findings of Hanson and Nedde (1974) who also suggested that males and females respond to a training programme in the same way.

Smith and Stransky (1976) trained 10 sedentary females at a training intensity which demanded 73% of their maximum heart rate. Training consisted of 16 minute sessions, 3 days a week on a bicycle ergometer for 7 weeks. An increase in $\dot{V}O_2$ max of 6.5% was found, however, this rise was not significant when related to the control group. This illustrates the importance of including a control group noticeably lacking in the studies reviewed above. In this study the high pre-training $\dot{V}O_2$ max value of 42.3 ml.kg$^{-1}$.min$^{-1}$ for sedentary females may explain the modest improvement in $\dot{V}O_2$ max.
Summary

Endurance training clearly leads to an improvement in VO₂ max. The majority of studies reviewed above demonstrated increments ranging from 7 to 20%. Those studies that reported changes in VO₂ max that were very small or very large can generally be explained in terms of the initial level of fitness of the subjects. For example, Saltin and coworkers and Cunningham and Hill (1975) both demonstrated increases in VO₂ max of 34% in subjects with low initial fitness levels and low pre-training VO₂ max values (Saltin et. al., 1968). In contrast, the unchanged VO₂ max value in highly trained subjects reported by Daniels, Yarborough and Foster (1978) after 8 weeks of training can be linked to the high initial fitness levels of their subjects.

Intensity of effort appears to influence the degree of improvement in VO₂ max (Kearney et. al., 1976; Moffatt et. al., 1977) and it is unfortunate for the purposes of comparison that several authors failed to state and/or control the intensity of effort.

Finally, from the few studies included on females it would appear that the improvements in VO₂ max as a result of endurance training are similar in both sexes.

2.3.2

The influence of endurance training on heart rate (HR) during submaximal exercise

The decrease in heart rate (HR) at a standard submaximal work load constitutes one of the most striking and consistent adaptations to a training programme.

Astrand and Rodahl (1977, p.393) reported that Christensen (1931) was one of the first investigators to demonstrate a decreased HR at a given submaximal work load in response to training.
Knehr, Dill and Neufeld (1942) demonstrated a small fall in HR of 6 \( \text{b.min}^{-1} \) after 2 and 4 months of training in a group of 14 males. Submaximal HR was measured during a grade walking test. The absence of a further decrease after 2 months of training suggests that the intensity of effort was low. This latter assumption is supported by the more striking falls reported by other investigators over a similar period of time.

Flint, Drinkwater and Horvath (1974) reported a decrease in HR of 11 \( \text{b.min}^{-1} \) (8%) in a group of 7 females after a short 6 week training programme. The subjects trained by walking on a treadmill for 30 minutes, 3 times a week at 80% of their maximum HR. Submaximal HR before and after training was determined at a work load requiring 70% \( \dot{V}O_2 \) max. Their fall of 8% corresponds closely to the 9% decrease in HR reported by Kilbom and Astrand (1971) in a group of females in response training.

Smith and Stransky (1976) reported a decrease in HR during exercise at 2 standard submaximal work loads after 7 weeks of training on a bicycle ergometer. The mean HR values decreased by 12.2 and 12.0 \( \text{b.min}^{-1} \) at the 2 standard work loads of 74 and 98 watts respectively. This study was performed by 16 untrained but active females.

Hanson and Nedde (1974) also in a study on sedentary females reported a fall in HR of 23 \( \text{b.min}^{-1} \) during graded treadmill walking after a 4 month training programme. During the next 4 months of training, HR decreased by only 8 \( \text{b.min}^{-1} \). These results support the early findings of Christensen (1931), reported by Astrand and Rodahl (1977, p.393), who demonstrated that training lowered the HR at a given work load but further training at the same intensity failed to decrease HR. Thus, for further adaptation to take place the intensity of effort must be increased.

Andrew, Guzman and Becklake (1966) studied a group of non-athletes over 4 weeks and a group of athletes over 4 months. The former group trained on a bicycle ergometer and showed a decreased HR of 12.3 \( \text{b.min}^{-1} \).
at a given submaximal work load after 4 weeks of training. The latter group demonstrated a fall in HR of 22.2 b.min⁻¹ after 4 months of training. The larger decrease found in the ice-hockey group may be attributed to the longer period of training and the different nature of their training.

Ekblom and coworkers, after a 16 week training programme on a bicycle ergometer, demonstrated a fall in HR of 26 b.min⁻¹ during exercise at a given submaximal work load. The maximum and minimum decreases in HR were 40 and 19 b.min⁻¹ respectively. This study clearly shows the striking response of HR to an endurance training programme (Ekblom et al., 1968).

Wilmore and coworkers, however, studying the adaptations of 38 males to 20 week training programmes of jogging, bicycling and tennis, failed to demonstrate a significant decrease in HR after training (Wilmore et al., 1980). Although each group showed falls in HR after training ranging from 7.5 to 11.9 b.min⁻¹, the decreases were not statistically significant when compared to the control group who also showed a fall in HR of 9 b.min⁻¹. This study again illustrates the possible importance of including a control group noticeably absent in the vast majority of training studies. Wilmore and coworkers suggested that the fall in HR in the control group may be due to a change in their activity level over the 6 month period, of which no record was kept. The decrease in HR reported by Wilmore and coworkers is noticeably smaller than the decreases reported by other authors after training programmes of a similar intensity. The fall in HR is more akin to the decreases reported from training studies lasting only 6 to 7 weeks. Although appreciating the influence of extraneous factors, Wilmore and his coworkers failed to mention, and therefore presumably control, the time of the last meal, alcohol consumption and activity prior to the submaximal test. Such factors may have influenced their HR measurements.

It should be mentioned that the exposure of sedentary individuals to repeated exercise on 4 occasions may lead to a striking reduction in HR. Davies, Tuxworth and Young (1970) showed a marked decline in HR of
21 b.min\(^{-1}\) over 4 exposures to exercise at a given submaximal oxygen uptake. They demonstrated that this was due to the parallel downward displacement of the HR/\(\dot{V}O_2\) relationship and concluded that the changes were due to internal readjustments of the circulation to repeated exercise. They stated that the effects of familiarization with the task should not be ignored and that individuals should be exposed to the exercise at least 3 times before definitive measurements are made. This will also help to reduce the influence of anxiety on HR. The decreases in HR reported above may have been smaller if the investigators had followed this advice. However, this initial "readjustment" period constitutes adaptation and may be an important part of the training response.

**Summary**

Heart rate clearly decreases in response to a period of endurance training. The shorter programmes lasting 6 to 8 weeks reported falls in the region of 10 to 12 b.min\(^{-1}\) (Flint et. al., 1974; Smith and Stransky, 1976) and the longer programmes reported decreases in HR ranging from 20 to 26 b.min\(^{-1}\) (Ekblom et. al., 1968; Andrews et. al., 1966; Hanson and Nedde, 1974). The study by Wilmore provides an exception but illustrates the possible importance of including a control group, clearly absent in most training studies (Wilmore et. al., 1980). The review includes studies on both males and females suggesting that both sexes show similar falls in HR in response to endurance training.

The actual mechanisms causing this typical bradycardia in response to training is unknown. Arguments are provided in the literature for both the central and peripheral effects of training on HR. Ekblom (1969) suggested that the following factors contributed to this decrease during submaximal efforts:

a) increased stroke volume.

b) increased extraction of oxygen by the trained muscles which may result in a reduced blood flow at a given submaximal oxygen uptake.
c) decreased peripheral resistance.

d) an increased mechanical efficiency.

2.3.3

The influence of endurance training on lactate (LA) concentration during submaximal exercise

Reduced blood lactate concentrations at a given and or relative submaximal work load is a common finding after training. Most of the evidence is based on indirect measurements (that is, from blood LA measurements), however, Gollnick and Hermansen (1973) stated that these measurements do provide valuable information regarding the changes taking place in the muscle and the whole body and that blood LA levels provide a guide of the extent to which anaerobic processes are involved.

Robinson and Harmon (1941) studied the effects of 6 months of training on submaximal LA levels. These fell significantly during a standard submaximal running test.

Ekblom and coworkers exposed 8 males to 16 weeks of training after which the blood LA levels were significantly lower at a given submaximal work load (Ekblom et. al., 1968). Two subjects continued intensive training for 51 months (Ekblom, 1969). After this extended period the blood LA levels decreased further and lower concentrations were found at both an absolute and relative submaximal oxygen uptake. This suggests that a short period of training may lower the LA level at a given oxygen uptake but a longer period may be required to lower it at a relative oxygen uptake.

Ekblom (1969) studied 7 sedentary subjects before and after 22 weeks of training. Before and after training these subjects exercised on a bicycle ergometer for 1 hour at 75% \( \dot{V}O_2 \) max. In this study he demonstrated that training effects the changes occurring in LA levels during prolonged exercise. Prior to training LA rose during
the first 5 minutes of exercise and thereafter remained unchanged. After training blood LA also increased during the first 5 minutes of exercise but after this initial elevation, the LA level progressively decreased over the exercise period. The subjects reported that the post-training test was less uncomfortable. This subjective assessment may be linked to the lower LA levels. This study illustrates that training not only lowers LA at a given work load but also changes its response during prolonged exercise.

Karlsson, Nordesjö and Saltin (1974) studied 5 males at 65% \( \dot{V}O_2 \) max before and after a 2 month training study. The main aim of the investigation was to examine the effects of such a programme on glycogen utilization which was reduced during exercise at 65% \( \dot{V}O_2 \) max after training. Part of this reduction explains the decreased lactate concentration found after training. Their findings after training were similar to those of Ekblom (1969), that is, after the initial increase in LA, this level progressively decreased during the remaining period of exercise. Although blood LA decreased in all individuals during the 90 minute exercise test, the LA levels only approached resting values in the trained subjects. This again illustrates that in trained individuals LA decreased to a greater extent during prolonged work than in untrained individuals. The authors concluded that the decreased glycogen utilization and LA production demonstrated that the training programme had enhanced free fatty acid (FFA) oxidation.

Saltin and Karlsson (1971) studied the LA levels after 12 and 28 weeks of training. Muscle LA decreased significantly at a given submaximal work load after the first period of training and continued to fall during the second period. After 28 weeks LA was lower at both absolute and relative work loads. These findings support those of Ekblom (1969). Saltin and Karlsson attributed the decreased LA production to the activation of more type I (SO) fibres. They also found a good relationship between the oxygen deficit and LA levels and suggested that after training there is a faster acceleration of the central circulatory system to transport oxygen to the working muscles.
Hickson and coworkers studied the time course of the adaptive responses during a 9 week training period. After the initial 4 weeks of training the training work load was increased. Blood LA fell significantly during the first 2 weeks of training, after which no further decreases were found until the training work load was increased. At the new work load the blood LA level fell during the first 3 weeks but did not decrease in the final 2 weeks. The falls reported in HR followed a similar adaptive pattern (Hickson et. al., 1981). These findings demonstrate that adaptation to a training programme may be rapid and emphasize the necessity for increasing the intensity of the exercise as the training programme progresses, if further changes are desired.

Other authors have investigated the effects of training on the level of oxygen uptake at which blood LA levels begin to rise rapidly. Williams and coworkers studied the effects of training on the onset of "excess lactate" which is more commonly referred to as the anaerobic threshold. They found that at a given oxygen uptake ($\dot{V}O_2$), LA was higher in the untrained or control group and that the appearance of "excess lactate" in the blood occurred at a lower $\dot{V}O_2$ in this group (Williams et. al., 1967). The authors also found that the percentage increase after training in the level at which "excess lactate" occurred was greater than the percentage improvement in $\dot{V}O_2$ max. From previous work by the authors comparing trained and untrained individuals, "excess lactate" occurred at 40-50% and 60-69% $\dot{V}O_2$ max in untrained and trained individuals respectively. They concluded that the oxygen supply to the muscles is equal to the oxygen uptake up to a higher level in trained individuals than in untrained individuals. However, their findings may also demonstrate that these individuals are able to utilize fats up to a higher % $\dot{V}O_2$ max. Gollnick and Hermansen (1973) stated that lower lactates at a given relative work load demonstrate that training results in changes not only in oxygen transport but also in the muscles themselves.

Davis and coworkers reported similar findings when they studied the effects of 9 weeks of endurance training on anaerobic threshold
alterations. They found that the anaerobic threshold expressed in relation to absolute and relative oxygen uptake increased significantly after training (Davis et. al., 1979). This study disagrees with the above findings of Ekblom (1969) and Karlsson, Nordesjö and Saltin (1974) who stated that a long period of training was necessary to reduce LA levels at relative work loads. The trained subjects in the study by Davis and coworkers could exercise at higher relative work loads before the rapid accumulation of LA and utilization of glycogen. Davis suggested several mechanisms for the delayed onset of lactic acidosis:

1. an improved distribution of blood flow to the trained muscles.
2. an increased oxidative capacity.
3. an alteration in the muscle fibre recruitment pattern resulting in an increased activation of the type I (SO) oxidative muscle fibres.
(Support can be found in the literature for all these mechanisms).

The delayed onset of blood LA accumulation during incremental exercise supports one of the most consistent and possibly most important metabolic adaptations to endurance exercise, that is, a shift from carbohydrate to fat metabolism. Several investigators have reported a fall in the respiratory exchange ratio (RER) at a given submaximal work load after training (section 2.3.5) but some of these falls may only be apparent decreases. It is possible that in some of the studies reviewed in section 2.3.5, the subject may have been exercising above the anaerobic threshold before training but below it after training. Davis and coworkers measured the RER values below the anaerobic threshold before and after training and found that these values fell after training. They concluded that the lower LA levels and RER values definitely demonstrated a shift towards fat metabolism. (Davis et. al., 1979). Increasing evidence has shown that it is the oxidative capacity of the muscle that determines the work load at which blood LA begins to accumulate. (The effect of training on the oxidative capacity of the muscle will be reviewed below).
The level of the anaerobic threshold is of critical importance in determining the potential for prolonged endurance type exercise. Lactate production indicates glycogen utilization, and low glycogen levels limit this type of exercise. High levels of LA may also interfere with fat metabolism since it has been demonstrated that LA may interfere with free fatty acid (FFA) mobilization (Issekutz et. al., 1975). A fall in FFA mobilization may also suppress plasma glycerol levels which are important for maintaining blood glucose levels. This will accelerate the depletion of blood glucose levels and liver glycogen. Low levels of LA and increased fat utilization on the other hand inhibit glycolysis and reduce the rate of glycogen utilization. The oxidation of fats therefore has been described as having a "glycogen sparing" effect.

The decreased production of LA after training has several important implications as described above. Costill, Thomason and Roberts (1973) demonstrated that the most successful runners in a 10 mile road race were those that produced less LA at a given relative work load while running on a treadmill.

Summary

These results clearly demonstrate the profound influence that decreased lactate levels have on performance during prolonged high intensity submaximal work. Training has been found to decrease LA levels at both absolute and relative work loads. The level at which the anaerobic threshold occurs is increased by training and is higher in trained individuals than in untrained individuals at both absolute and relative work loads. Most authors consider that this fall in LA after training reflects a shift from carbohydrate to fat metabolism.
2.3.4

The influence of endurance training on oxygen uptake \((\dot{V}O_2)\) at a given submaximal work load

Although contradictory evidence regarding the effect of training on oxygen uptake \((\dot{V}O_2)\) at a given submaximal work load exists, it has generally been accepted that this parameter remains unchanged after training (Girandola and Katch, 1976; Davis et. al., 1979; Smith and Stransky, 1976). Where a decreased \(\dot{V}O_2\) has been found this has been considered to be the result of an improved mechanical efficiency to perform the work (Ekblom et. al., 1968; Kilbom and Åstrand, 1971).

Wilmore and coworkers, although demonstrating a substantial decrease in \(\dot{V}O_2\) after a 20 week training programme, reported that this was not significant when compared to the lower value also found in the control group (Wilmore et. al., 1980).

Flint, Drinkwater and Horvath (1974) suggested that the effects of training on the oxygen cost of submaximal exercise are likely to be evident before steady-state levels of oxygen uptake are achieved. They therefore studied the responses at a given submaximal work load during both the non-steady state and steady-state conditions. Nearly all other investigators have measured \(\dot{V}O_2\) and other parameters during the steady-state condition. After a 6 week training programme \(\dot{V}O_2\) was significantly higher in the non-steady state phase of the exercise but was unchanged from the pre-training value once steady-state had been reached. This indicated that before steady-state was reached the work was performed with a smaller contribution from anaerobic energy sources after training. Flint, Drinkwater and Horvath suggested that conflicts in the literature concerning the influence of training on \(\dot{V}O_2\) during submaximal work might be eliminated by ensuring that the subjects are sufficiently habituated to the task prior to any definitive pre-training measurements.

Davies, Tuxworth and Young (1970) provided evidence which fails to support the above hypothesis. In their study on the effects of
repeated exposure to exercise at a given submaximal work load, $\dot{V}O_2$
at that load remained unchanged throughout the investigation period. Their findings suggested that an improvement in mechanical efficiency occurred but this was only small and not statistically significant from day 1 to day 16.

A large number of these studies have used the bicycle ergometer. Astrand and Rodahl (1977, p.347) stated that the mechanical efficiency on an ergometer may vary ± 6%. Thus at a load of 150 watts the $\dot{V}O_2$ may vary from 1.9 to 2.3 L.min\(^{-1}\). Such a variation at a given work load is not unusual. Therefore subjects with a low mechanical efficiency prior to training may demonstrate improvements but those with a high mechanical efficiency before training may not. This initial level of mechanical efficiency may help to explain the conflicts in the literature. However, Astrand and Rodahl (1977, p.436) stated that activities such as running, walking and cycling are uncomplicated and training will only produce very small improvements in mechanical efficiency. Therefore only small changes in the oxygen cost of exercise after training can be expected.

**Summary**

Oxygen uptake either remains unchanged or decreases at a given submaximal work load after training. A fall in $\dot{V}O_2$ after training has been explained in relation to an improved mechanical efficiency. However, further explanation would appear necessary from the conflicts reported in the literature. The response to exercise with trained and untrained muscle groups may provide additional insight into the presence or absence of changes in the oxygen cost of exercise after training. These studies will be reviewed below.
The influence of endurance training on the respiratory exchange ratio (RER) during submaximal exercise

The relative contribution of carbohydrate and fat to energy metabolism is usually assessed by determining the nonprotein respiratory quotient (Astrand and Rodahl, 1977, p.487). The respiratory exchange ratio (RER) is the ratio $\frac{CO_2}{O_2}$ volume produced /02 volume utilized. Endurance training increases the individual's ability for fat utilization and several investigators have assessed this increased contribution by the non-invasive determination of the RER value.

Girandola and Katch (1976) studied 33 males before and after a 9 week training programme. Training consisted of running and calisthenics twice weekly. A control group was also included in the study. One week prior to and after training the subjects exercised for 10 minutes at 177 watts during which metabolic measurements were made. The RER values decreased by 6% and 1.2% in the trained and control groups respectively. The fall in the RER value from 0.93 to 0.87 found in the trained group was determined during the last 3 minutes of the 10 minute exercise bout. The major criticism of this study is the lack of dietary control prior to testing. No attempt was made to control the time or content of the last meal. Such standardization is critical when assessment of the relative contribution of fats and carbohydrates is required. In addition the experimental and control groups may by chance have been on different diets. A high carbohydrate diet will produce considerably higher RER values during exercise than a low carbohydrate diet (Astrand and Rodahl, 1977, p.488). However, it must be assumed that both groups were on similar mixed diets since the authors do not state otherwise. Despite the lack of standardization the magnitude of the fall in the RER values was considerably greater in the trained group than in the control group and is consistent with the increased ability to oxidize fats after endurance training.
These findings are in agreement with those of Hanson and Nedde (1974). After a period of 4 months of training the RER value fell from 0.90 to 0.80 and after an additional 4 months' training this parameter decreased further to 0.78. These authors also failed to control the diet and activity levels of their subjects prior to testing.

Davis and coworkers studied the effects of endurance training on middle-aged men. Training consisted of bicycle ergometry for 45 minutes, 4 times a week for 9 weeks (Davis et. al., 1979). The RER value in the experimental group fell significantly from 0.91 to 0.85 during exercise at a given submaximal work load. The RER values remained unchanged in the control group during the 5 minute submaximal test. Davis and coworkers controlled the time of testing but imposed no dietary restrictions. This is surprising since the main aim of this study was to determine the anaerobic threshold before and after training. Nevertheless, this study demonstrated a decrease in the RER value in the experimental but not the control group. The lower RER value in the trained group is consistent with the increased capacity to oxidize fats in response to endurance exercise.

Smith and Stransky (1976) studied 16 females of which 10 formed the experimental group and 6 the control group. Seven weeks of training failed to lower the RER value in the experimental group whilst exercising for 6 minutes at 2 standard submaximal work loads. Smith and Stransky in their discussion comment only on the significant adaptations after training. This is unusual since the presence and absence of changes both warrant discussion. Pre-test activity levels and food intake were again not controlled and may explain the unchanged RER values after training.

Wilmore and coworkers reported that the RER values at a work load of 49 watts were significantly lower for the bicycle and jogging trained groups when compared to the tennis trained and control groups (Wilmore et. al., 1980). However, no significant decreases were found in this parameter at the higher submaximal work load of 98 watts after 20 weeks of training. At this higher load the RER value fell
from 0.90 to 0.81 in the bicycle trained group and although this fall was considerable and comparable to those reported above, it was not significant when related to the control group. This group demonstrated a fall in the RER value from 0.95 to 0.91. In this study the control group showed similar responses to the experimental group on all parameters measured. If, as Wilmore and his coworkers argue, this is the result of increased activity levels the inclusion of such a group would appear to cloud the findings in the experimental group. In addition to an alteration in their activity levels, the control group may have altered their diet over the 6 month period extending from winter to summer. Also, the experiment was started at the beginning of the academic year, exposure to a different life style in all groups was therefore presumably unavoidable.

Flint, Drinkwater and Horvath (1974), in a 6 week training programme on 7 females, determined the RER values before and after training during a 30 minute exercise test at a given submaximal work load. The RER values were significantly lower after training only in the 3rd and 4th minutes of the exercise test. Although the RER values were also lower after training during the remaining 30 minutes of exercise, the falls did not reach the level of statistical significance. This may explain some of the conflicts reported above because different authors have measured the RER value at different times. Smith and Stransky (1976), for example, measured the RER value in the 6th minute of exercise. In the study by Flint and coworkers, the RER values were not significantly lower after training in the 6th minute of the submaximal exercise test but were significantly lower in the 3rd and 4th minutes of exercise. They commented that training may effect the approach to steady-state rather than the steady-state condition itself. Again, no dietary restraints were placed on the subjects.

Summary

The review includes studies on males and females and demonstrates that endurance training reduces the RER value at a given submaximal work load in both sexes.
Conflicts may exist as a result of the time at which the measurement was made, lack of dietary and other controls and the inclusion of control groups whose activity levels may be similar to those of the experimental group.

It is extremely surprising that not one of the studies above included any form of dietary control. Diet undoubtedly effects the relative contribution of carbohydrates and fats during submaximal work.

2.3.6

The influence of endurance training on skeletal muscle

Until recently it was believed that improved performance as a result of endurance training was due to an increased supply of blood and oxygen to the exercising muscles as a consequence of cardiovascular adaptation. However, over the past few years evidence has accumulated demonstrating major adaptations in the skeletal muscle that lead to an increase in the capacity for aerobic metabolism.

One of the most consistent findings is that regularly performed exercise results in an increase in the respiratory capacity of the muscle due to an increase in the enzymes involved in the oxidation of carbohydrates, fat and ketones, and the enzymes of the citric acid cycle, enzymes of the respiratory chain, and the enzymes involved in oxidative phosphorylation. Underlying the increase in the respiratory capacity is an increment in the size and number of muscle mitochondria and a change in the mitochondrial composition.

Holloszy and Booth (1976), in their extensive studies on rats, demonstrated many of the above changes which have also been found in humans after a period of endurance training. They demonstrated that the capacity of the muscle to oxidize both fats and carbohydrates was approximately doubled after 3 to 4 months of treadmill running. The mitochondria obtained from the trained rats demonstrated that the increase in oxidative capacity was accompanied by an increase in the
capacity to regenerate ATP via oxidative phosphorylation. The authors found that the enhanced respiratory capacity was due to an increase in the enzymes in the citric acid cycle, the mitochondrial respiratory chain and the enzymes involved in the breakdown of long chain fatty acids. Gollnick and King (1969) demonstrated that the mitochondria increase both in size and number in parallel with the mitochondrial enzyme content.

Muscle is extremely adaptable and changes rapidly in response to endurance training. This is supported by the work of Baldwin, Campbell and Cooke (1977) who showed, in their training study on rats, that the oxidative potential of the muscles had increased after only 2 to 3 weeks of training. However, with the exception of hexokinase, most glycolytic enzymes did not change noticeably in response to the endurance training programme.

Holloszy and Booth (1976), in their study on rats, demonstrated that the training programme led to the increased oxidation of free fatty acids.

Other changes reported in rat skeletal muscle in response to training include an increased myoglobin content (Lawie, 1953; Pattengale and Holloszy, 1967) which generally parallels the respiratory capacity of the muscles, and an increased capillary density. Salmons and Henriksson (1981) in their review reported, however, that increased capillarization was not found by all authors and was not considered by Müller (1976) to be necessary for mitochondrial adaptation. Finally, Holloszy and Booth (1976) found that their training programme was not associated with muscle hypertrophy. This result suggests an enhancement of the diffusion conditions which may contribute to an increase in muscle endurance.

The above findings apply to rodents, however similar responses and adaptations in the skeletal muscle of humans have been demonstrated in response to an endurance training programme. Several studies have demonstrated that training leads to an increased oxidative capacity in
the trained muscles (Bylund et. al., 1977; Gollnick et. al., 1973; Henriksson and Reitman, 1976; Morgan et. al., 1971; Saltin et. al., 1976; Varnauskas et. al., 1970). As in the above animal experiments the increased activity of the oxidative enzymes has been found to be accompanied by a corresponding increase in the mitochondrial protein content. In addition, morphological evidence for a corresponding increase in the mitochondrial volume has been demonstrated (Keissling et. al., 1971; Morgan et. al., 1971).

The evidence regarding the effect of endurance training on the glycolytic capacity of muscles is conflicting. The activity of these enzymes has been found to increase (Gollnick et. al., 1973), or stay the same (Morgan et. al., 1971) in response to a training programme. These conflicting findings may be partly due to differences in the response of the slow (SO or type I) and fast (FG and FOG or type IIB and type IIA) twitch fibres which differ in their proportion in different individuals.

A more detailed description of some of the training studies mentioned above in connection with the effects of endurance exercise on skeletal muscle will be given below.

Gollnick and coworkers investigated the effect of a 5 month training programme on the oxidative, glycolytic, fibre composition, fibre area and glycogen concentration of the vastus lateralis muscle of 6 subjects. The training programme consisted of exercising on a bicycle ergometer for 1 hour, 4 days a week. The load required 75 to 90% \( \dot{V}O_2 \) max. Training increased \( \dot{V}O_2 \) max by 13% (3.6 to 25%), and the activity of succinate dehydrogenase (SDH) and phosphofructokinase (PFK) by 95 and 117% respectively. The oxidative potential of both fibre types increased but the glycolytic capacity increased only in the fast twitch fibres. The slow twitch fibres were larger and covered a greater relative area after training but the percentages of slow and fast twitch fibres remained unchanged. The muscle glycogen content of the muscle increased over two fold after training (Gollnick et. al., 1973).
In the study by Gollnick and coworkers small increases in \( \dot{V}O_2 \) \(_{\text{max}} \) were accompanied by large changes in the oxidative capacity of the skeletal muscle. This evidence supports the findings which show that \( \dot{V}O_2 \) \(_{\text{max}} \) does not limit the ability to perform at submaximal intensities and may provide an explanation for the increased running time found by Daniels, Yarborough and Foster (1978) without an increase in \( \dot{V}O_2 \) \(_{\text{max}} \). The influence of the increased oxidative capacity on performance during submaximal exercise is shown by the findings of Gollnick and coworkers. At the beginning of the training period the subjects could only sustain 65\% \( \dot{V}O_2 \) \(_{\text{max}} \) for 1 hour, but as the training programme progressed they were able to exercise for the same period at 85 to 90\% \( \dot{V}O_2 \) \(_{\text{max}} \). The increased oxidative capacity which was accompanied by only a small rise in \( \dot{V}O_2 \) \(_{\text{max}} \) may play a significant role during submaximal exercise (Gollnick et. al., 1973).

Varnauskas and coworkers found that a 6 week endurance training programme decreased muscle blood flow at a fixed submaximal work load (Varnauskas et. al., 1970). This is in agreement with the findings of several other investigators. The training programme also produced a 44\% increase in SDH activity. The increase in the activity of this enzyme was smaller than that reported above by Gollnick and coworkers which may be explained by the shorter training period. The authors suggested that the increased SDH activity may reflect an increase in the ability of the muscle to extract oxygen from the blood. Support for this is provided by the decreased blood flow after training. The fall in lactic acid production, reported by the authors during submaximal work, may also be explained by the increased SDH activity. Increased SDH activity results in an improved capacity of the mitochondria for pyruvate oxidation.

Bylund and coworkers studied the metabolic and morphologic adaptations in skeletal muscle after 8 weeks and 6 months of endurance training. The oxidative enzyme activities increased significantly after 8 weeks of training, the fibre diameter of both the type I (slow twitch or slow oxidative, SO) and the type II (fast twitch or fast glycolytic, FG) fibres increased while the mitochondrial volume
increased mainly in the type II fibres. They concluded from their morphometric findings that the relative contribution of the type II fibres to the increased oxidative capacity of muscles after training may be of great importance (Bylund et. al., 1977). The improvement found in these fibres may be due to the high training intensity (80-90% \( \dot{V}O_2 \) max) which would probably include the recruitment of these fibres. Their findings clearly demonstrate both an increased oxidative capacity and an increased utilization of fatty acids during exercise. These changes in the muscle were accompanied by an improved running time over 4 km, a 10% fall in heart rate at 150 watts and an increase in \( \dot{V}O_2 \) max of 13 and 26% after 8 weeks and 6 months of training respectively.

The above findings of Bylund and coworkers are similar to those of Henriksson and Reitman (1976) who also found that the increased oxidative capacity of the muscles after training occurred in both the type I and type II fibres.

Saltin and coworkers demonstrated that training may increase the oxidative capacity of the fast twitch population. In their study they showed that endurance exercise may convert the type IIB (FG) fibres into type IIA fibres (fast oxidative and glycolytic, FOG) (Saltin et. al., 1977).

Conflicting results concerning the effect of training on capillarization exist in the literature. Ingjer (1979) found that after a period of 24 weeks of intensive endurance training the average number of capillaries per muscle fibre increased by 28.8%. Saltin and coworkers, however, found no evidence of changes in muscle capillary density after training in their classic 'bed rest' study (Saltin et. al., 1968). The increase reported by Ingjer was found in all fibres but was largest around the type I fibres and smallest around the type IIB fibres.

Andersen and Henriksson (1977) also found that endurance training (8 weeks' exercise on a bicycle ergometer) significantly increased
the capillary density by 20%. The capillary supply to each fibre (type I, IIA and IIb) increased equally in contrast to the findings of Ingjer (1979). However, the authors stated that an increase around one fibre will automatically result in an increase around another fibre, since the fibres are distributed in a mixed fashion around the muscle. Both studies obtained muscle biopsies from the quadriceps femoris. The main difference between the 2 studies being the type of training - running training in the study by Ingjer (1979) and bicycle ergometry in the study by Andersen and Henriksson (1977). Ingjer (1979) explains the difference by the way the capillary supply to the various muscle fibre types have been classified. He studied the capillary supply in relation to both ATP-ase activity and mitochondrial content and found a clear relationship between the latter and the capillary supply only. Andersen and Henriksson (1977) classified the capillary supply in relation to ATP-ase activity only. This might explain the different findings.

Fatigue during prolonged exercise is associated with glycogen depletion (Hermansen et. al., 1967; Costill et. al., 1973). Pre-exercise glycogen levels may influence the ability to perform prolonged work. Taylor (1975) provided evidence to support this (see section 2.4) and demonstrated that a period of endurance training increases the muscle glycogen content.

Summary

The findings from the training studies performed on animals and humans are very similar. Training increases the oxidative capacity of both the type I and type II fibres (Henriksson and Reitman 1976; Bylund et. al., 1977). Saltin and coworkers also provided evidence showing that type IIb fibres may be converted into type IIA fibres, thus increasing the oxidative capacity of the fast twitch population (Saltin et. al., 1977). Endurance training also increases the capacity of the mitochondria to oxidize fats (Gollnick et. al., 1973; Bylund et. al., 1977; Varnauskas et. al., 1970). The increased utilization of fats inhibits the activity of phosphofructokinase and therefore decreases
glycolysis producing a "glycogen sparing" effect. Since fatigue during prolonged exercise is associated with glycogen depletion (Hermansen et al., 1967) such a shift towards fat metabolism is of great importance to the endurance athlete.

Endurance training has also been found to increase the resting glycogen content of skeletal muscle (Gollnick et al., 1973; Taylor, 1975) which again may be significant during prolonged exercise.

Varnauskas and coworkers reported a decreased blood flow at a given submaximal work load. This indicates that the skeletal muscle is able to extract more oxygen from the blood after training (Varnauskas et al., 1970). In addition because cardiac output remains unchanged at a given submaximal work load after training, the blood flow to the splanchnic and renal regions and the skin may be increased after training.

Although the findings concerning capillarization have not always been consistent, the majority of studies indicate an increase in capillarization with training (Ingjer, 1979; Andersen and Henriksson, 1977). Whether this increase is greater around the type I fibres (Ingjer, 1979) or equal around all fibre types (Andersen and Henriksson, 1977) is not known.

In conclusion, the most consistent findings reported in the literature are that training increases the oxidative capacity of the exercising muscles and the ability of these muscles to utilize fats.

2.4

THE INFLUENCE OF ENDURANCE TRAINING ON ENDURANCE CAPACITY

The number of studies investigating the effect of endurance training on $\dot{V}O_2$ max far out number those that have measured changes in endurance capacity. In addition, although endurance capacity is a term often used it has been vaguely defined, resulting not only in
the use of different terms to explain this capacity, but also
different tests to measure it.

Different terms include "work output" (Knehr et. al., 1942),
"physical work capacity" (Ekblom et. al., 1968), "endurance time"
(Gleser, 1973) and "riding time" (Wilmore et. al., 1980). "Aerobic
performance", "aerobic power" and "endurance performance" are also
to be found in the literature.

The type of tests designed to assess changes in endurance capacity
after a period of training include performance during a \( \dot{V}O_2 \) max test
(i.e. the length of the test or the work load required to elicit \( \dot{V}O_2 
\) max), performance at maximal or near maximal levels (i.e. the ability
to sustain this load), running tests, the most common being the time
taken to run 2 miles or the distance covered in 12 minutes, and finally
the ability to sustain a given submaximal work load. Very few
investigations have included this last test as a measure of aerobic
endurance capacity.

The various tests designed to measure so-called endurance
capacity (table 2.1) together with some of the terms may be usefully
summarized as follows:-

1. test : \( \dot{V}O_2 \) max
terms : "work output" (Knehr et. al., 1942), "physical work
capacity" (Ekblom et. al., 1968), "riding time"
(Wilmore et. al., 1980).

2. test : performance at maximal or near maximal levels
term : "aerobic power" (Hickson et. al., 1977)

3. test : running performance
terms : "endurance performance" (Moffatt et. al., 1977),
"aerobic performance" (Ribis1, 1969)

4. test : submaximal exercise at a given work load to exhaustion
terms : "endurance time" (Gleser, 1973) and endurance
capacity in the present investigation.

The studies will be reviewed in the order they are summarized above.
TABLE 2.1

Increases in \( \dot{V}O_2 \) max and 'endurance' capacity in selected training studies

<table>
<thead>
<tr>
<th>STUDY</th>
<th>LENGTH OF TRNG.</th>
<th>n</th>
<th>% CHANGE ( \dot{V}O_2 ) MAX</th>
<th>% CHANGE ENDURANCE CAPACITY</th>
<th>TEST USED TO ASSESS &quot;ENDURANCE CAPACITY&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Karpovich &amp; Pestrecov 1941</td>
<td>12 wk</td>
<td>12</td>
<td>not measured</td>
<td>+1355</td>
<td>Time to exhaustion at given absolute sub-maximal WL</td>
</tr>
<tr>
<td>Knehr et al. 1942</td>
<td>6 mth</td>
<td>14</td>
<td>+7</td>
<td>+60</td>
<td>Work output during ( \dot{V}O_2 ) max test</td>
</tr>
<tr>
<td>Ekblom et al. 1968</td>
<td>16 wk</td>
<td>10</td>
<td>+17</td>
<td>+50</td>
<td>Work output during ( \dot{V}O_2 ) max test</td>
</tr>
<tr>
<td>Saltin et al. 1968</td>
<td>7 mth</td>
<td>5</td>
<td>+21</td>
<td>not significant</td>
<td>Time to exhaustion at 80% ( \dot{V}O_2 ) max</td>
</tr>
<tr>
<td>Ribisl 1969+</td>
<td>5 mth</td>
<td>15</td>
<td>+14</td>
<td>+17</td>
<td>Two mile run time</td>
</tr>
<tr>
<td>Karlsson et al. 1972</td>
<td>7 mth</td>
<td>14</td>
<td>+24</td>
<td>+17</td>
<td>Work load required to elicit ( \dot{V}O_2 ) max</td>
</tr>
<tr>
<td>Gleser &amp; Vogel 1973</td>
<td>4 wk</td>
<td>8</td>
<td>+12</td>
<td>+258</td>
<td>Time to exhaustion at given absolute sub-maximal WL</td>
</tr>
<tr>
<td>Cunningham &amp; Hill 1975 +</td>
<td>9 wk</td>
<td>17</td>
<td>+34</td>
<td>+12</td>
<td>Distance covered during 12 min. run</td>
</tr>
<tr>
<td>Taylor 1975</td>
<td>20 wk</td>
<td>13</td>
<td>+22</td>
<td>+20</td>
<td>Time to exhaustion at 60-70% ( \dot{V}O_2 ) max</td>
</tr>
<tr>
<td>Moffat et al. 1977</td>
<td>10 wk</td>
<td>46</td>
<td>+12 (IT)</td>
<td>+12 (IT)</td>
<td>Distance covered during 12 min. run</td>
</tr>
<tr>
<td>Hickson et al. 1977</td>
<td>10 wk</td>
<td>8</td>
<td>+44</td>
<td>+203</td>
<td>Time to exhaustion at maximal WL</td>
</tr>
<tr>
<td>Daniels et al. 1978+</td>
<td>8 wk</td>
<td>27</td>
<td>0 (TR)</td>
<td>+5 (TR)</td>
<td>Two mile run time</td>
</tr>
<tr>
<td>Davis et al. 1979</td>
<td>9 wk</td>
<td>9</td>
<td>+10 (UT)</td>
<td>+25</td>
<td>Work load required to elicit ( \dot{V}O_2 ) max</td>
</tr>
<tr>
<td>Wilmore et al. 1980</td>
<td>20 wk</td>
<td>9</td>
<td>+15</td>
<td>+12</td>
<td>Duration of ( \dot{V}O_2 ) max test</td>
</tr>
</tbody>
</table>

KEY
WL = work load
IT = interval training
CT = continuous training
TR = highly trained subjects
UT = untrained but active subjects
o = treadmill
+ = running tests outside the laboratory
F = females

Unless otherwise stated all subjects have used male subjects and the bicycle ergometer.
One of the first investigations to report an increased work output during a \( \dot{V}O_2 \) max test after a period of training was performed by Knehr, Dill and Neufeld (1942). The work output for 14 sedentary males increased by 60% after 6 months of training.

Ekblom and coworkers studied the effects of a 16 week training programme, consisting of both cross-country and interval running 3 times a week, on 10 sedentary males. The total work output during the \( \dot{V}O_2 \) max test, which was performed on a bicycle ergometer, increased by 50% in response to training. The authors stated that this demonstrated an increased capacity for work (Ekblom et. al., 1968).

Davis and coworkers studied the effects of 9 weeks of endurance training on a group of middle-aged men. An increase in the work rate of 28% was required to elicit \( \dot{V}O_2 \) max after training (Davis et. al., 1979). This study, unlike many, included a control group who demonstrated no change in this parameter.

Wilmore and coworkers found that after a period of 20 weeks of endurance training on a bicycle ergometer, the duration of the \( \dot{V}O_2 \) max test also performed on an ergometer, had increased by 11.6% (Wilmore et. al., 1980).

It is questionable whether the increases in either the work time or the work output during a \( \dot{V}O_2 \) max test reflect increases in aerobic endurance capacity as defined in the present investigation. The \( \dot{V}O_2 \) max test is short in duration and may only provide evidence of the ability of an individual to perform work at the maximum level. This ability may not correlate with the ability to sustain prolonged submaximal exercise.

Hickson, Bomze and Holloszy (1977) studied the effects of 10 weeks of endurance training on 8 subjects aged between 20 and 42 years. Training consisted of very high intensity work on a bicycle ergometer, 3 times a week and running on 3 alternate days. Endurance capacity was measured on the bicycle ergometer at a work load that resulted in
exhaustion after 2 to 5 minutes of exercise in the pre-training test. Training increased endurance time at this maximal load from 3.3 to 10 minutes (203%). The relationship between the improved endurance time and the increased VO₂ max (44%) after training was highly significant (p < 0.001, r = 0.97). Both parameters were measured weekly showing a linear increase over the whole 10 week period.

Geijsel (1980) also used a maximal load to measure endurance capacity in speed skaters. He selected a work load which in untrained subjects resulted in exhaustion within 60 seconds. The subjects trained 3 times a week on a bicycle ergometer for 5 months. Training increased endurance time at this maximal load from 462 to 540 seconds (17%). The use of highly trained subjects compared to the use of sedentary individuals by Hickson and his coworkers may explain the much smaller improvement found by Geijsel. However, Geijsel failed to mention the intensity and frequency of the training sessions, both of which may have been inadequate to increase endurance time significantly.

The studies by Hickson, Bomze and Holloszy (1977) and Geijsel (1980) were again both concerned with measuring exercise of a short duration at the maximum level. Therefore, they may only provide information concerning the ability of the subject to sustain very high intensity exercise for a short period of time.

The above investigations all used the bicycle ergometer to measure endurance capacity before and after training. Several authors, however, have used a running performance test outside the laboratory to measure endurance capacity. The most common of these tests being the 2 mile run or the distance covered in 12 minutes.

Ribisl (1969) studied the effects of 5 months of endurance training on middle-aged men. Training involved cross-country and interval running and calisthenics 3 times a week. The 2 mile run time increased from 17.1 to 14.7 minutes (17%) and this was accompanied by a 10% increase in VO₂ max. The authors concluded, therefore, that the improved
performance could be attributed to the greater $\dot{V}O_2$ max.

Moffatt and coworkers also used a running test to assess the effects of 2 different training programmes on endurance performance. The running test employed was the distance covered in 12 minutes. The subjects participated in either interval or continuous running twice weekly over a 10 week period. The training intensity was greater for the interval trained group. Maximum oxygen uptake and endurance both increased by 12% in the interval trained group and by 8% and 9% respectively in the continuous trained group. The authors concluded that the increased distance covered during the run was the result of the increased $\dot{V}O_2$ max values and that the distance covered in 12 minutes provided an accurate predictor of aerobic capacity (Moffatt et. al., 1977).

Daniels, Yarborough and Foster (1978), however, demonstrated that after a period of 8 weeks of training, running performance as determined by the 2 mile run may improve in the absence of an increased $\dot{V}O_2$ max. The lack of improvement in $\dot{V}O_2$ max may be explained by the use of highly trained subjects.

In both the bicycle ergometer and running tests reviewed above, the investigators have all essentially measured the ability of individuals to sustain very high intensity exercise (maximal or near maximal) over a short period of time. During such activity anaerobic energy may contribute significantly to the overall energy expended. Anaerobic energy contribution may particularly influence 2 mile running time because the individuals can run at a self-selected pace. Lawson and Golding (1979), for example, demonstrated the influence of anaerobic energy contributions during the 2 mile run by noting that 2 subjects ran the 2 mile distance in excess of 100% $\dot{V}O_2$ max. This weakens the statement by Moffatt et. al., (1977) that the 2 mile run is an accurate predictor of aerobic capacity. The 2 mile run may be performed at near maximal levels and therefore is similar in nature to the bicycle ergometer tests of Hickson, Bomze and Holloszy (1977) and Geijsel (1980).
None of the tests adopted by the above authors appear to provide a satisfactory measure of aerobic endurance capacity because they all involve some anaerobic energy contribution. Astrand and Rodahl (1977, p.30) supported this by suggesting that during a 12 minute exercise bout anaerobic energy contribution may amount to 15%. Evidence that this component may be important in activity of a short duration is provided by Moffatt and coworkers. In their study those individuals that trained at a high exercise intensity (i.e. essentially anaerobically) demonstrated the greatest improvement over 2 miles (Moffatt et. al., 1977).

A better measure of aerobic endurance capacity may be provided by the ability of an individual to sustain a given submaximal work load, which is the definition adopted to assess improvements in endurance capacity in the 2 training studies included in the present investigation. However, very few studies have measured performance time at a given submaximal work load before and after training which is surprising when the significance of this ability for success in many sporting activities is considered.

One of these studies was performed as early as 1941 by Karpovich and Pestrecov. They subjected 12 prisoners aged 18-50 years to a training programme lasting 6 to 12 weeks. The subjects trained daily at their own prescribed work loads. Explanation of the determination of the various training work loads for each subject was not provided. The men trained 5 days a week and exercised for as long as possible during each session. Training increased riding time on the bicycle ergometer at a given submaximal work load by 1355% (range 75 to 4420%). The maximum riding time reported by the authors for 1 subject was 6 hours and 12 minutes. The mean improvement might well have been greater because prior to the training study the men had been exposed to 5 weeks' preliminary work on the ergometers.

In addition prior to this, the men had participated in building up exercises for the legs and back 5 days a week for 1 month.
Considering these large improvements it is surprising that only a few authors have subsequently included a similar pre- and post-training performance test.

Saltin and coworkers included a measure of exercise time at 80% \( \dot{V}O_2 \) \(_{\text{max}} \) in their classic bed rest study. Work time at this intensity was measured before bed rest, after bed rest and after training. At each stage work time to exhaustion was approximately the same, the mean times being 31.2, 27.2 and 29 minutes respectively (Saltin et al., 1968). These findings do not compare favourably with those reported above. This may be explained by the recalculation of the 80% work load after bed rest and after training. Exercise at the same absolute work load on each occasion may have produced very different results.

Gleser and Vogel (1973), like Karpovich and Pestrecov (1941), measured endurance time on a bicycle ergometer at the same absolute work load before and after training. The work load corresponded to 75% of the subjects pre-training \( \dot{V}O_2 \) \(_{\text{max}} \) value. Training consisted of exercising at increasing intensities during the 16 week programme on a bicycle ergometer twice weekly and playing basketball for 3 hours on 2 alternate days. At the pre-training 75% \( \dot{V}O_2 \) \(_{\text{max}} \) work load the subjects demonstrated an improvement in endurance time of 258% after training. The authors found that this improvement was greater than that which could be accounted for by the 12% increase in \( \dot{V}O_2 \) \(_{\text{max}} \). They suggested that the training programme had lowered the rate of anaerobic metabolism.

Taylor (1975), in his study on the effects of endurance training on muscle glycogen content, included a measure of work time to fatigue at approximately 63% \( \dot{V}O_2 \) \(_{\text{max}} \). The 20 week running endurance training programme significantly increased work time to fatigue on a bicycle ergometer (20%). Although Taylor failed to mention if the absolute work load was the same in the pre- and post-training tests, it is possible that the relatively small improvement in endurance time is a consequence of the recalculation of the work load after training. Another possible explanation for the modest improvement in endurance
time may lie in the specificity of training. The subjects in Taylor's study trained by running but the endurance test was performed on a bicycle ergometer. A much larger improvement in endurance capacity may have been found if the subjects had performed a running endurance test.

Taylor noted that the increased work time was directly related to the increased muscle glycogen content and to the increased VO\textsubscript{2} max (22%). It is possible, therefore, that resting muscle glycogen levels may determine the ability to perform prolonged work since fatigue during such exercise is associated with glycogen depletion (Hermansen et. al., 1967).

Although Gollnick and coworkers did not include a measure of endurance time before and after training, they reported that prior to training the subjects were unable to sustain 75% VO\textsubscript{2} max for an hour. However, once training had begun the subjects were soon able to sustain this load for an hour, and by the end of the 5 month period all subjects were able to sustain 85-90% VO\textsubscript{2} max for the full hour (Gollnick et. al., 1973). Although the work load was not held constant the initial improvement in endurance time at 75% VO\textsubscript{2} max indicates again that training increases the ability to sustain a given submaximal work load.

The studies by Karpovich and Pestrecov (1941) and Gleser and Vogel (1973) appear to be the only investigations that have included a measure of endurance time at a given submaximal work load before and after training. Both investigations found large improvements in endurance capacity that could not be explained solely by changes in VO\textsubscript{2} max.

It should be mentioned that the exposure of individuals to a given submaximal work load increases their endurance time at this load (Gleser and Vogel, 1971). The average endurance time in the study by Gleser and Vogel increased significantly with each weekly exposure over the first 5 weeks, after which no further significant increases were reported. Endurance time increased by 50% after the
first exposure to the exercise and by 100% after the fifth exposure. Over the 5 week period $\dot{V}O_2$ max also increased by 8%, however no relationship existed between $\dot{V}O_2$ max and endurance time. The authors suggested that repeated testing may lead to a more conservative use of muscle glycogen. They concluded that the effect of repetitions should not be ignored and suggested that a stable level should be reached before certain variables are measured. However, this stable level may simply reflect adaptation to a given work load and constitute training. The levelling off after 5 weeks in endurance time in the study by Gleser and Vogel (1971) suggests that adaptation to the particular work load had occurred and in order to achieve further improvement the training intensity must be increased.

**Summary**

No standard method for the measurement of endurance capacity exists making comparisons between training studies difficult. In addition only a limited number of studies have reported changes in endurance capacity after training. The majority of these studies appear to have concentrated on improvements in endurance at or near the maximal level. These studies may provide inadequate measures of aerobic endurance because of the anaerobic energy contribution involved during such exercise. To the best of the author's knowledge only 2 studies have measured endurance time during prolonged submaximal work at the same absolute work load before and after training. These studies have shown that endurance training can substantially increase the ability of an individual to sustain a given pre-training work load.
2.5

THE INFLUENCE OF ENDURANCE TRAINING A LIMITED MUSCLE MASS ON THE RESPIRATIONS TAKING PLACE DURING EXERCISE WITH TRAINED AND UNTRAINED MUSCLE MASSES

Several investigators have studied the responses to exercise of trained and untrained limbs in an attempt to determine the extent to which central and peripheral factors participate in the adaptations to training. To investigate this problem some authors have used a model where they have trained the legs or the arms and tested the arms and legs separately, while others have trained one leg testing the trained and untrained legs both separately and together. The cardiovascular and metabolic adaptations to training described above for large muscle groups are similar for small muscle groups.

2.5.1

Arm versus leg training studies

As early as 1943, Müller exposed 1 male to a two-legged endurance training programme on a bicycle ergometer over a 10 week period. After training heart rate (HR) dropped significantly from 129 to 95 b.min\(^{-1}\) at a given oxygen uptake. After a 3 week detraining period the HR at this \(\dot{V}_O_2\) had returned to 129 b.min\(^{-1}\) despite strenuous arm training in the week prior to this test. During the period of arm training HR fell from 140 to 116 b.min\(^{-1}\) at a given \(\dot{V}_O_2\). Müller stated that the fall in HR after training the arms did not carry over to exercise performed with the legs. He concluded that the fall in HR depended upon peripheral changes in the trained muscles and not on a central training effect on the heart. It is surprising however, that these early findings by Müller did not give rise until recently to further investigations regarding central and peripheral factors.

Clausen, Trap-Jensen and Lassen (1970) compared the HR responses to arm and leg exercise before and after training of the arms and legs.
Training of the arms caused a significant fall in HR during arm exercise only. Training of the legs resulted in a fall in HR during leg exercise and a small reduction during arm exercise. The authors stated that the training effect on HR is secondary to primary changes in skeletal muscle and that the importance of direct improvements on the heart after a short period of training may have been overestimated. However, they added that training probably influenced the myocardial function since leg training lowered the HR slightly during arm exercise.

Clausen and coworkers using the same model, trained 10 males for 5 weeks on a bicycle ergometer (5 trained the arms and 5 the legs) at a HR of 170 b.min\(^{-1}\). During arm exercise after arm training \(\dot{V}O_2\), \(\dot{V}E\) and RER decreased while the arterial pH increased. No carry over to the legs was reported. During leg exercise after leg training \(\dot{V}O_2\), \(\dot{V}E\) and RER decreased as did blood lactate. Arterial and venous pH both increased. Again no carry over to the untrained muscles was found. The authors concluded the training effect was mainly local (Clausen et. al., 1971).

Clausen and coworkers also studied the central and peripheral circulatory changes after training of the arms or legs. Arm training resulted in a significant fall in HR during exercise with the arms only, whereas leg training resulted in an almost equal reduction in HR during exercise with both the trained and untrained muscle groups. During exercise with the trained muscles the vasoconstriction of the resting muscles was reduced and the oxygen extraction from the exercising muscles increased. Both cardiac output (Q) and aortic blood pressures were unchanged except during heavy arm exercise after leg training. During this exercise Q increased by 11% with a proportional decrease in the a-\(\dot{V}O_2\) difference. Stroke volume increased after training during exercise with both the trained and untrained muscles. The largest increase occurred during heavy submaximal work with the untrained arms. The above findings provide evidence for central adaptation unlike the studies reported above and the authors concluded that

"alterations in the trained muscles and central circulatory changes both contribute to the effects of physical training on circulation"

(Clausen et. al., 1973).
From the results concerning heart rate the size of the muscle mass being trained appears to be important in determining whether the myocardial function is improved. If the muscle mass is large enough the capacity of the heart is increased and this is reflected in improvements found during exercise with untrained muscles. In the study by Clausen and coworkers the training of the larger muscle mass (legs) caused a fall in HR with the smaller untrained muscle mass (arms). In 2 earlier studies (Müller, 1943; Clausen et. al., 1970) leg training did not reduce HR during exercise with the untrained arms. This may be explained by lower training intensities and the use of fewer subjects.

The findings of the study by Clausen and coworkers also suggested that different physiological mechanisms were responsible for the fall in HR during exercise with the trained and untrained muscles. During exercise with the untrained arms the fall in HR was the result of a parallel downward displacement of the HR/VO$_2$ relationship but during exercise with the trained muscles the fall was related to a decreased blood flow to the splanchnic and renal regions. The fall in HR was greatest during arm exercise after arm training.

Clausen and coworkers concluded that smaller muscle masses appear to have a greater potentiality for local improvement and that central circulatory changes occur in proportion to the muscle mass employed in training (Clausen et. al., 1973). The main criticism of this study is that different size muscle groups were trained to study transfer effects from trained to untrained muscle groups. Cardiovascular responses to exercise with small and large muscle masses are different (Appendix 1.E) and these differences may result in erroneous conclusions. For example, it is possible that local and central adaptations may be greater after training during exercise with the arms. A better model for the assessment of the relative importance of local and central factors would be provided by comparing trained and untrained muscle groups that are similar both in size and state of training.
Training increases the oxidative capacity of the muscle. No metabolic measurements providing evidence for this were made in the above study but in a subsequent investigation by the same authors (Klausen et. al., 1974) blood lactate (LA) measurements were made during both arm and leg exercise after training of the arms or legs. The number of subjects in each group, the training and the training period were the same as above. After the 5 week training programme blood LA concentration fell significantly at a given submaximal work load during exercise only with the trained muscles. This is in agreement with an earlier study by these authors (Clausen et. al., 1971). The fall in LA during exercise with the trained muscles was associated with a decreased HR, the fall in this parameter being explained by a decrease in the relative work load. Oxygen uptake and RER both fell during exercise with the trained arms only. This confirms their earlier findings (Clausen et. al., 1971). Heart rate again fell during exercise with the trained arms and legs and the untrained arms, the greatest fall occurring during exercise with the trained arms. These falls in HR support their previous findings (Clausen et. al., 1973).

The fall in blood LA concentration during exercise with the trained muscles only, as reported by Klausen and coworkers, would appear to be the result of a local phenomenon indicating an increased oxidative capacity in the trained muscles (Klausen et. al., 1971). The authors stated that the reduced anaerobic energy contribution was not the consequence of an increased blood flow to the working muscles at a given oxygen uptake because in a previous study (Clausen et. al., 1973), they had found a decreased blood flow under such circumstances. Klausen and his coworkers also stated that the decreased anaerobic energy contribution could not be explained by an increased capillarization because Hermansen and Wachtlova had found no difference in the capillarization of the muscles of trained and untrained individuals. However, as reported in section 2.3.6, both Ingjer (1979) and Andersen and Henriksson (1977) demonstrated an increase in the number of capillaries per fibre after a period of endurance training. The falls in blood LA and the RER values were
accompanied by falls in $\dot{V}O_2$ during exercise with the trained muscles. The authors suggested that this was due to:

1. an improved mechanical efficiency.
2. a decrease in the work of the heart and respiratory muscles supported by the lower HR and VE values after training.
3. a decreased rate of the removal of lactate.

The above authors using the same model in a subsequent study (Rasmussen et al., 1975) included measures of pulmonary ventilation, blood gases and blood pH. After 5 weeks of training $\dot{VE}.\dot{V}O_2^{-1}$ decreased significantly during exercise with the trained muscles only. The fall in $\dot{VE}.\dot{V}O_2^{-1}$ was associated with decreases in HR and arterial LA levels. This finding suggests that local changes in the muscle are responsible for lowering $\dot{VE}.\dot{V}O_2^{-1}$ and is supported by the lower $\dot{VE}$ value found during arm and leg exercise after training with the arms and legs respectively (Clausen et al., 1971). During exercise with the trained muscles pH generally increased. From this study and the earlier studies by these authors, it would appear that training causes adaptations in the skeletal muscle which lowers LA levels, $\dot{VE}$, HR, $\dot{VE}.\dot{V}O_2^{-1}$ and sympathetic vasoconstriction and increases the $a-\dot{V}O_2$ difference and blood pH during exercise at a given submaximal oxygen uptake. A fall in HR has also been reported during exercise with the arms after leg training and where other transfer effects have been found, these have also occurred during exercise with the untrained arms. The different size muscle groups may, however, cloud the above findings.

Ridge, Pyke and Roberts (1976) trained 10 males on either a kayak or bicycle ergometer for 1 month. The former involves arm work and the latter leg work. Training consisted of 30 minute sessions at 85-90% HR max, 4 days a week. At a given submaximal work load after training, the kayak group demonstrated significant decreases in $\dot{V}O_2$, $\dot{VE}$, HR and blood LA levels during kayak ergometry. Maximum oxygen uptake also increased for this group during kayak exercise. The subjects who had trained on a bicycle ergometer, however, did not exhibit any of the above adaptations during kayak exercise. The improvements observed during arm exercise after arm training are similar to those reported above (Clausen et al., 1973; Klausen et al., 1974). However, unlike these studies Ridge and coworkers did not find
a lower HR during exercise with the arms after leg training, i.e. the bicycle ergometer trained group did not demonstrate a lower HR during kayak exercise. This difference might be attributed to the different types of arm exercise or to the different lengths of the submaximal work tests. Ridge, Pyke and Roberts (1976) used a 6 minute submaximal test whereas Clausen and coworkers in all their studies used a 15 minute submaximal test during which HR was measured. It is possible that a steady-state condition was not achieved during the shorter test by Ridge and coworkers. This study suggests that the increase in $\dot{V}O_2\text{max}$ and the decreases in $\dot{V}O_2$, HR, $\dot{V}E$ and blood LA concentration are the result of peripheral adaptations in the muscles being trained.

McKenzie, Fox and Cohen (1978) also adopted the arm versus leg training model to assess the specificity of cardiovascular and metabolic adaptations to interval training. After arm training $\dot{V}O_2$, HR and blood LA levels decreased significantly during arm exercise at a given submaximal work load. During leg cycling only $\dot{V}O_2$ decreased. After leg training $\dot{V}O_2$, HR and LA fell significantly during leg exercise and HR and LA were lower during arm work. The $\dot{V}O_2$ values also decreased during exercise with the untrained arms but this fall was not significant. The fall in HR during exercise with the untrained arms is in agreement with the findings of others (Clausen et. al., 1973; Klausen et. al., 1974), suggesting that the training of a larger muscle mass (legs) results in a greater central and smaller local effect, the opposite being the case for the smaller muscle mass (arms). Because the training adaptations were more pronounced in the trained limb irrespective of whether this was the leg or the arm, the data were combined and analyzed in relation to trained and untrained limbs. This produced significant falls in $\dot{V}O_2$, HR and LA during exercise with both the trained and untrained limbs. The magnitude of these falls were greatest during exercise with the trained limbs. In general the specificity of the adaptations during exercise with the trained and untrained limbs pointed to local changes in the muscle. The changes during exercise with the untrained muscles, however, also suggested that central adaptations had occurred. The falls in HR and LA during exercise with the trained limbs were greater than that expected by a
fall in $\dot{V}O_2$. McKenzie, Fox and Cohen (1978) suggested, therefore, that LA and HR were controlled by a common mechanism and $\dot{V}O_2$ by a separate mechanism. During exercise with the untrained limbs, however, the falls in HR and LA were proportional to the fall in $\dot{V}O_2$ suggesting that all may be controlled by a common mechanism. The falls in $\dot{V}O_2$ and LA during exercise with the untrained limbs do not confirm the work reviewed above. The differences may be due to the higher intensity interval-type training programme or to the different way in which the data had been analyzed. The authors concluded that a central learning effect was responsible for the changes during exercise with the untrained limbs whereas physiological and biochemical changes within the skeletal muscle were responsible for the changes during exercise with the trained limbs.

Stamford and coworkers in their arm and leg training study reported increases in $\dot{V}O_2$ max and decreases in submaximal HR which were confined to the trained muscles. The subjects trained either their arms or legs, 3 days a week for 10 weeks. Since the adaptations were not seen during exercise with the untrained muscles, this investigation supports the importance of local factors for the effects derived from training (Stamford et. al., 1978a). Such peripheral adaptations may take place after only a short period of time whereas a longer period of training may be required for the elicitation of central adaptations. The fall in HR during exercise with the trained legs only is in conflict with the findings of some investigators (Clausen et. al., 1973; Klausen et. al., 1974; McKenzie et. al., 1978) but is in agreement with the findings of others (Ridge et. al., 1976). Stamford and coworkers explain their findings by stating that the central effect is lost during exercise with an unfamiliar task involving untrained muscles owing to overriding peripheral factors. The different type of leg exercise used in their study (that is bench stepping) may explain the absence of transfer effects to the untrained arm. All the above studies, with the exception of that by McKenzie, Fox and Cohen (1978) used the bicycle ergometer to train the legs.
Magel and coworkers studied the responses to arm training. To determine if there was any carry over to the legs, the subjects also performed a treadmill $\dot{V}O_2$ max test. Arm training increased arm $\dot{V}O_2$ max but the $\dot{V}O_2$ max determined during treadmill running did not change (Magel et. al., 1978). This again points to the importance of local factors. The lack of transfer may be due to the small muscle mass involved during arm work. This would agree with the suggestion by Clausen and coworkers that the smaller the muscle mass the greater the local and the smaller the general effect (Clausen et. al., 1973).

Lewis and coworkers also studied the arms and legs during exercise after training of the arms or legs. The subjects trained at 75-80% $\dot{V}O_2$ max, 4 days a week for 11 weeks. Maximum oxygen uptake increased and submaximal HR decreased during exercise with both the trained and untrained muscles. The perceived rate of exertion (PRE), however, only dropped significantly during exercise with the trained muscles at a given submaximal work load. The authors suggested that this transfer to the untrained muscles may be the result of low initial capacities for arm and leg work which might provide a greater potential for transfer (Lewis et. al., 1980). This transfer of bradycardia to the untrained limbs contradicts the findings of some investigators (Clausen et. al., 1970; Ridge et. al., 1976 and Stamford et. al., 1978) but is in agreement with the findings of others (Clausen et. al., 1973; Klausen et. al., 1974; McKenzie et. al., 1978). During submaximal work $\dot{V}O_2$, $\dot{V}E$ and $\dot{V}E.\dot{V}O_2^{-1}$ were all lower during exercise with the trained arms whereas the falls during leg exercise after leg training in these parameters were not significant. This again suggests that a smaller muscle mass may have greater potential for local adaptation. Maximum oxygen uptake increased significantly during exercise with the trained arms and legs and also with the untrained arms. The increase in $\dot{V}O_2$ max during exercise with the untrained legs was not significant possibly due to the small numbers studied (5 per group). This study by Lewis and coworkers provides evidence suggesting that there is a larger transfer effect from the trained legs to the untrained arms than vice versa.
Although LA levels were not measured the authors suggested that the lower PRE value found only during exercise with the trained limbs may be the result of a decreased LA concentration because previous investigations had shown a fall in LA during exercise with the trained limbs only (Klaussen et. al., 1974; Ridge et. al., 1976). They also stated that the PRE value was not linked to HR since this parameter also decreased during exercise with the untrained limbs. Although the fall in the PRE value would appear to be the result of local factors the authors did not rule out the possibility of a reduced central command (Lewis et. al., 1980).

**Summary of the arm versus leg training studies**

The above review illustrates that the cardiovascular and metabolic adaptations found after training a small muscle mass are the same as those found after training a large muscle mass. The investigation of the transfer of these adaptations to untrained limbs has given rise to conflicting evidence.

During exercise with the trained limbs the most consistently reported findings are a fall in HR and LA at a given submaximal work load (Müller, 1943; Clausen et al., 1970; Clausen et. al., 1971; Klaussen et. al., 1974; Ridge et. al., 1976; McKenzie et al., 1978; Stamford et. al., 1978; Lewis et. al., 1980). In addition, falls in \( \dot{V}O_2 \), \( \dot{V}E \) and \( \dot{V}E.\dot{V}O_2^{-1} \) during exercise with the trained limbs have also been reported (Clausen et. al., 1970, Clausen et. al., 1971; Rasmussen et. al., 1975; Ridge et. al., 1976; McKenzie et al., 1978; Lewis et. al., 1980). These decreases have been mainly confined to the arms only after arm training (Clausen et. al., 1970; Lewis et. al., 1980). Falls in the RER value during exercise with the trained limbs have also been reported (Clausen et. al., 1970; Klaussen et. al., 1974).

The above illustrates that the training adaptations are mainly confined to exercise with the trained limbs although some authors demonstrated a carry over effect to the untrained limbs. This was particularly the case for heart rate. A fall in HR during exercise
with the untrained arms was reported by (Clausen et. al., 1973; McKenzie et. al., 1978; Klausen et. al., 1974; Lewis et. al., 1980). Lewis and coworkers also found a significant fall in HR during exercise with the untrained legs but the magnitude of the decrease was much smaller than that found whilst exercising with the untrained arms. All studies showed a fall in LA only during exercise with the trained limbs, with the exception of McKenzie, Fox and Cohen (1978) who found a lower LA during exercise with the untrained arms.

Maximum oxygen uptake where measured, increased mainly during exercise with the trained limbs only (Ridge et. al., 1976; Stamford et. al., 1978a). However, an increase was also found during exercise with the untrained arms (Lewis et. al., 1980).

The above review clearly demonstrates the importance of local adaptations in response to training and the influence that this may have on the central circulation. Where transfer effects have been reported they have always occurred during exercise with the arms after leg training suggesting that improvements in the central system are dependent upon the size of the muscle mass being trained. For example, the increased \( \dot{V}O_2 \text{ max} \) (Lewis et. al., 1980) and the decreased LA (McKenzie et. al., 1978) reported during exercise with the untrained arms after leg training. The above findings appear to demonstrate that central adaptations to training are partly determined by whether the muscles performing the work are trained. However, it should not be overlooked that the above transfer effects have been assessed in muscle groups that differ in size and initial level of training, and show different cardiovascular adjustments during exercise. This may lead to confusing results and is a major criticism of these studies. Some authors were aware of the weakness of the arm versus leg training model. Clausen and coworkers, for example, stated that

"it is possible that peripheral and central circulatory adaptations show greater manifestation during arm exercise than during leg exercise"

(Clausen et. al., 1973).
The greater local adaptation found during exercise with the arms and the transfer effects from the trained legs to the untrained arms may be explained by the above statement.

The conflicts between the presence or absence of transfer effects is difficult to explain. Lewis and coworkers suggested that the initial level of fitness of the subjects together with the intensity, frequency and duration of each training session may be important (Lewis et. al., 1980). Stamford and coworkers suggested that the following may influence the results:

1. intensity of training.
2. relative degree of muscle mass involved.
3. overlap of involved musculature between modes of training.
4. pre-training task familiarity (Stamford et. al., 1978a).

However the above studies did not vary considerably in these factors.

Another criticism of the above studies is that they all employed small numbers of subjects and were conducted over very short periods of time (5 - 11 weeks). It is possible that local adaptation may occur more quickly than central adaptation, since skeletal muscle is highly adaptable. Central changes may have become more apparent if the training periods had been longer.

Finally, the above authors have simply reported the responses after training and have failed to apply their findings to changes in performance.

2.5.2

One-legged training studies

These are fewer in number than the arm versus leg training studies but provide a better model for studying the relative importance of central and peripheral adaptations to training. This is because they
allow comparisons to be made between muscle groups that are similar in size and degree of training and are generally highly comparable in the pre-trained state.

Gleser (1973) studied the effects of 4 weeks of one-legged training on the responses during exercise with the trained and untrained legs. The 6 subjects exercised one leg twice weekly at 75% one-legged \( \dot{V}_\text{O}_2 \) max until exhaustion was reached. After training, the trained leg demonstrated an increased \( \dot{V}_\text{O}_2 \) max and \( \dot{Q} \) max. These parameters remained unchanged during exercise with the untrained leg and during two-legged exercise. Gleser concluded that training must be a peripheral phenomenon since adaptations outside the leg would also produce an increased \( \dot{V}_\text{O}_2 \) max during exercise with the untrained leg. The peripheral resistance to blood flow decreased only during exercise with the trained leg which indicated an increased ability of the muscle vasculature to dilate or an increase in the maximal cross-sectional area of the muscle vasculature. Gleser stated that although training produces other adaptations in the skeletal muscle, peripheral vasodilation is limited and is responsible for the "plateau" observed in oxygen uptake. However, the method by which Gleser obtained the "plateau" in oxygen uptake during one-legged exercise must be questioned. His pairing method relied entirely on the equal sharing of the work load by 2 subjects, and he stated that even after practice these individuals were only "fair" at sharing the work load. Secondly, the largest improvements in \( \dot{V}_\text{O}_2 \) max were found in those individuals who had initially high values prior to training. This contradicts the findings from previous two-legged work.

Davies and Sargeant (1975) also studied the effects of one-legged training on one- and two-legged exercise at the maximum level. Seven subjects trained each leg separately for 30 minutes, 3 times a week at 80% one-legged \( \dot{V}_\text{O}_2 \) max, for 5 to 6 weeks. Before and after training no significant differences were found between the right and left legs. The \( \dot{V}_\text{O}_2 \) max and \( \dot{V}_\text{E} \) max values increased significantly during exercise with either after training. One-legged \( \dot{V}_\text{O}_2 \) max increased on average by 14%, which is in agreement with the improvements
reported by Gleser (1973). Unlike Gleser's findings, the greatest
increases were shown by those subjects with the lowest initial one­
legged VO₂ max values. The improvement in each leg was not reflected
during two-legged exercise during which only a 4.7% increase in VO₂
max was reported. Davies and Sargeant stated that the training
effect appears to be specific to the leg being exercised. The small
increase in VO₂ max during two-legged exercise supports the view
that VO₂ max is limited by the ability of the cardiovascular system
to transport oxygen to the working muscles and not by oxygen
utilization. They concluded that the effect of training at the
maximum level on a small muscle mass (one leg) is mainly peripheral
in nature but that maximum two-legged exercise is limited by the ability
of the cardiovascular system to transport oxygen to the muscles. The
inclusion of submaximal tests in this study and in Gleser's (1973) study
would have provided useful additional information concerning the
training response.

Saltin and coworkers studied the effects of a 4 week one-legged
training programme on 13 males. The subjects were split into 3 groups.
They exercised one leg with either sprint or endurance training and
the other leg oppositely or not at all. Oxygen uptake, HR and blood
LA levels were measured during one- and two-legged exercise at both
maximal and submaximal levels. Succinate dehydrogenase (SDH)
activity and myofibrillar ATP-ase activity were determined from
muscle biopsies. Eight of the subjects also performed a two-legged
1 hour test at 75% VO₂ max during which blood flow, the a–VO₂
difference, blood glucose, blood lactate, muscle glycogen and muscle
lactate were determined (Saltin et. al., 1976).

During one-legged exercise VO₂ max increased only during exercise
with the trained leg and at a given submaximal work load HR and blood
LA decreased only during exercise with the trained leg. The untrained
leg showed a small (6%) increase in VO₂ max and a very small reduction
in submaximal HR (2 - 6 b.min⁻¹). Endurance training produced the
most marked fall in LA during submaximal exercise, whereas sprint
training resulted in a significant increase in the blood LA level.
maximal work. Training did not alter the percentage of the type I or type II fibres but the relative fibre area was changed by training. Endurance training resulted in an increase in the relative fibre area of the type I fibres and sprint training increased the fibre area of both the type I and II fibres. SDH activity remained the same in the non-trained leg but increased by 19% and 33% in the sprint and endurance trained legs respectively.

During two-legged exercise \( \dot{V}O_2 \) max increased by 9% and submaximal HR decreased significantly in all 3 groups. During the 1 hour test at 75% \( \dot{V}O_2 \) max, leg blood flow was similar to the trained and untrained legs, the a-\( \dot{V}O_2 \) difference, however, was higher over the trained leg. The trained leg showed a slightly higher \( \dot{V}O_2 \) than the untrained leg which may have been the result of an uneven pedal force between the legs. The RER measurements were lower only during exercise with the sprint trained leg after training. The endurance and untrained legs showed no fall in the RER values after training. The LA level was significantly lower only during exercise with the trained leg. Consistent with the fall in LA was the smaller utilization of glycogen by the trained leg which was not compensated by a larger uptake of glucose from the blood.

The increase in \( \dot{V}O_2 \) max and decrease in submaximal HR, blood LA levels and glycogen utilization together with an increased a-\( \dot{V}O_2 \) difference, fibre ratio area and oxidative capacity of the trained muscles are well established adaptations to physical training. By training one leg and exposing the subjects to both one- and two-legged exercise insight was provided into the relationship between central and local factors. As can be seen from the above findings of Saltin and coworkers, little transfer occurred from the trained leg to the untrained leg illustrating the importance of peripheral factors. The \( \dot{V}O_2 \) max value did increase slightly during exercise with the untrained leg and during two-legged exercise suggesting that the training of one leg did result in some central adaptation which was transferred to the untrained leg. This supports the work of Clausen and coworkers (1973) who found a small increase in \( \dot{V}O_2 \) max during exercise with the arms after leg training. Saltin and coworkers concluded that the
training programme had produced

"a very specific pattern for adaptation which is partly local in nature. Of special interest is the finding that this local adaptation of the skeletal muscle appears essential for being able to elicit the more general adaptations of the central circulation also taking place with training. This focuses attention on peripheral factors as being at least essential for cardiovascular performance during exercise as any central factors."

(Saltin et. al., 1976).

The increased SDH activity, fall in LA levels and rate of glycogen utilization all point to increased fatty acid oxidation despite the absence of lower RER values after training. Such adaptations appear to be more important during prolonged submaximal work than during short maximal efforts. The absence of lower RER values may be due to no dietary control prior to the 1 hour test. It is surprising that the authors did not control activity levels or food intake prior to this test.

Henriksson (1977) studied the effects of one-legged training on 6 males. The inactive leg acted as the control and the training period lasted 8 weeks. This study concentrated on the effects of training on the oxidative capacity of the skeletal muscle. Henriksson, like Saltin and coworkers, found no differences between the right and left legs prior to training. After the training of one leg, the metabolic responses to two-legged submaximal exercise were investigated.

The SDH activity increased significantly in the trained leg only (27%) but the fibre ratio area and fibre type remained unchanged. During one-legged exercise at a given submaximal work load $\dot{V}O_2$, VE and blood LA concentration decreased, $\dot{V}E.\dot{V}O_2^{-1}$ remained unchanged and although HR fell, the decrease was not significant during exercise with the trained leg. Heart rate remained unchanged during submaximal exercise with the untrained leg. The $\dot{V}O_2$ max value increased significantly by 11% only during exercise with the trained leg.

During two-legged exercise $\dot{V}O_2$ max showed a small but non-significant increase (8%). The lack of significance may be due to
the small numbers studied but this finding compares favourably with that of Gleser (1973). During submaximal exercise, $\dot{V}O_2$ decreased but $VE$, HR and blood LA levels remained unchanged. During the post-training two-legged 1 hour test at $67\% \dot{V}O_2$ max blood flow to the trained leg was higher. This disagrees with the findings of Saltin and coworkers who found a reduced blood flow (Clausen et. al., 1973) to the trained muscles. However, this may be explained by the higher absolute work load at which the trained leg was exercising. This higher load meant that each leg was exercising at the same relative work load. The $a-\dot{V}O_2$ difference was 3% higher during exercise with the trained leg. The RER values were significantly lower during exercise with the trained leg and from these values it was calculated that 29% and 16% of the caloric expenditure in the trained and untrained legs respectively was derived from the oxidation of fat. Lactate release from the untrained leg was higher and after 50 minutes of exercise LA was taken up by the trained leg. No significant differences were found in glycogen depletion. Glycogen depletion occurred predominantly in the type I fibres, however the untrained leg showed a higher glycogen depletion in the type II fibres than the trained leg. Despite the higher work load, the similar glycogen utilization in the two legs and the lower RER and LA values during exercise with the trained leg support the findings of others who compared the responses to the same relative work load of trained and untrained individuals during exercise with a large muscle mass (Hermansen et. al., 1967; Saltin and Karlsson, 1971). This study clearly indicated greater fat utilization after training during exercise with the trained leg. This difference occurred even though the legs were exercising at different absolute work loads. If the absolute work load had been the same the differences would have been greater.

Saltin and coworkers did not find a definite relationship between the increased oxidative capacity of the muscle and fat metabolism during submaximal exercise (Saltin et. al., 1976). Henriksson (1977) in his study, however, concluded that the increased oxidative capacity which was paralleled by lower RER values and a lower release of LA showed that the shift towards fat metabolism is determined by the increased
oxidative capacity. The longer study performed by Henriksson (1977) compared with Saltin and coworkers may explain the lower RER values reported only by Henriksson after training.

Morgan and coworkers used the one-legged model to investigate adaptation to endurance training. Ten men exercised one leg, 2 hours daily for 1 month. This model allowed comparisons to be made between trained and untrained muscles from the same subject reducing the large differences in muscle metabolism between subjects. In the trained leg only the mitochondrial size, oxidative capacity and the capacity for glycogen and fat synthesis increased (Morgan et al., 1971). Such findings are consistent with those reported in section 2.3.6.

**Summary**

Unlike the arm versus leg training studies where several authors reported some transfer to the untrained arms, the training adaptations were generally confined to the trained limb. This may be explained by the training of a smaller muscle mass, that is, one leg which is similar in size to the arms. These findings support the suggestion of Clausen and coworkers that central adaptation is related to the size of the muscle mass being trained (Clausen et al., 1973). The adaptations to training after one-legged exercise are the same as those reported in sections 2.3.1 to 2.3.6. For example, an increased \( \dot{V}O_2 \) max and decreased HR and blood LA levels at submaximal work loads. The above studies have reported falls in HR, LA, RER, \( \dot{V}E \) and \( \dot{V}O_2 \) during submaximal exercise with the trained leg. \( \dot{V}E.\dot{V}O_2^{-1} \) remained essentially unchanged. Henriksson (1977) and Saltin and coworkers produced conflicting findings concerning blood flow but both were during two-legged exercise where the work load was not equally divided between the trained and untrained legs (Saltin et al., 1976). The \( \dot{V}O_2 \) max values increased only during exercise with the trained leg, although Saltin and coworkers reported a small increase during exercise with the untrained leg, and suggested that this might be the result of central adaptation. However, although every attempt had been
made in the above studies to ensure that the resting leg remained inactive, some activity could not be completely excluded which may have produced transfer effects that would not normally be found. For this reason the above studies would all have benefited from the inclusion of a separate control group rather than relying on the untrained leg for the control.

These studies, like the arm versus leg training studies, are all short in duration (4 - 8 weeks) and have only studied small numbers. As stated above it is possible that local and central factors may have different time courses for adaptation. If changes in the skeletal muscle occur more rapidly than changes in the central circulation, as has been suggested, these studies may have produced misleading results and may have overestimated the importance of local factors.

It would appear from the arm versus leg training studies and the one-legged studies that an increased oxidative capacity and fat utilization play a more important role during submaximal exercise than during maximal exercise. Henriksson (1977) demonstrated a clear link between an increased oxidative capacity and the shift towards fat metabolism after training and Saltin and coworkers provided findings supporting this, despite failing to control food intake and activity levels prior to the prolonged submaximal test (Saltin et. al., 1976).

This model has definite advantages over the arm versus leg training model because muscle masses that are strictly comparable in the pre-training state are being studied. These studies like the arm versus leg investigations have simply reported the responses to training and have failed to apply the findings to changes in performance. This is also a major criticism of the training studies that have reported the adaptations to training of a large muscle mass.

Central adaptation to training may be partly determined by whether the muscles performing the exercise are also trained (Clausen et al., 1973; Gleser, 1973; Klausen et. al., 1974; Davies and Sargeant, 1975; Saltin et. al., 1976). In any case local adaptation appears to play an important role in leading to central circulatory changes. There
seems no doubt that local and central factors are closely linked. The suggestion by Davies and Sargeant (1975) that the smaller the muscle mass the greater the potential for local improvement, and the suggestion by Clausen and coworkers that the larger the muscle mass trained the greater the occurrence of central adaptation appears to hold true when the arm versus leg and one-legged results are considered.

Very few one-legged studies have looked at transfer effects to untrained muscles during submaximal exercise. Gleser (1973) and Davies and Sargeant (1975), for example, concentrated on changes at the maximum level.

This review indicates that further investigation is required to determine the proportional contribution of central and local factors to training, by studying trained and untrained muscle groups that are strictly comparable in the pre-trained state, i.e. there is a need for more one-legged studies. There is also a need for training studies of a longer duration.
CHAPTER 3

METHOD

3.1

SUMMARY OF EXPERIMENTAL WORK

The investigation consisted of 3 major studies:
1. The relationship between $V_{O_2}$ max and running performance
2. The influence of training on $V_{O_2}$ max and endurance capacity
3. The influence of training one leg on $V_{O_2}$ max and endurance capacity.

Several methodological investigations were also included and may be summarized as follows:-

1. A comparison of the continuous and discontinuous loading oxygen uptake tests for the determination of $V_{O_2}$ max and a given submaximal work load, that will demand a known percentage of an individual's $V_{O_2}$ max (two-legged exercise). This study is reported in appendix 1.A.

2. A 4 minute continuous loading oxygen uptake test and a discontinuous oxygen uptake test for the determination of one-legged $V_{O_2}$ max and a given submaximal work load that will demand a known percentage of an individual's one-legged $V_{O_2}$ max. This study is reported in appendix 1.B.

3. Test-retest reliability during one-legged ergometry. One male repeated a discontinuous loading test on 4 occasions. This study is reported in appendix 1.C.

4. Reproducibility of the blood lactate concentrations during one- and two-legged ergometry. One male subject performed both continuous and discontinuous loading tests, during which blood samples were taken for the determination of
lactate concentrations at each work load. This study is reported in appendix 1.D.

In addition, two subsidiary studies were carried out to provide insight into the nature of one-legged exercise:

1. A study of the respiratory and metabolic responses taking place during prolonged submaximal one-legged exercise. This investigation included exercise of both 1 and 2 hour durations. During the 2 hour exercise experiment, the subjects exercised continuously but changed the exercising leg after 1 hour. This study is reported in appendix 1.E.

2. A study of the physiological responses to one- and two-legged exercise on a bicycle ergometer. This study is reported in appendix 1.F.

The above studies (excluding the 3 major investigations) were included as pilot studies permitting a full examination of the experimental methods, identification of areas of weakness and a thorough investigation of the experimental procedures by the experimenter. Full examination of the experimental procedures during one-legged exercise was particularly important as was insight into the nature of one-legged exercise particularly during prolonged submaximal work.

The 3 major studies (reported in Chapters 4, 5 and 6) included both male and female subjects of the college age group. The methodological and subsidiary investigations were performed on male subjects only.

All studies, with the exception of the running study, were performed inside the laboratory on a bicycle ergometer. The running study, which investigated the relationship between VO₂ max and running performance, included submaximal and maximal running on a treadmill and a 2 mile field test.

The experimental procedures for each investigation will be
described in the relevant subsequent chapters relating to those investigations.

There are, however, a number of factors related to the experimental procedures that are common to each of the above studies. These include:

1. The equipment.
2. Calibration of the equipment.
3. Gas analysis.
5. Laboratory conditions and instructions given to the subjects.
6. Order of measurements taken.
7. Subjective rating scale.
8. Determination of $V_{O_2} \text{max}$.
9. Determination of a given submaximal work load.
10. A 10 minute exercise test at a given submaximal load to assess the accuracy of the load calculations and the ability of the subject to reproduce a given load on the bicycle ergometer.
11. Endurance test.
12. Training methods.

3.2

EQUIPMENT

(a) Treadmill

A motor driven treadmill (Quinton) with a speed range from 0.7 to 6.7 m.sec$^{-1}$ (4.2 to 402.0 m.min$^{-1}$) and an elevation range (grade %) from 0 to 40% was used in this study to investigate the relationship between maximum oxygen uptake ($V_{O_2} \text{max}$) and running performance.

(b) Bicycle Ergometer

The Monark bicycle ergometer used in this study was a modification of a construction by von Döbelin (1954). It was a mechanically braked
type, with adjustable saddle and handlebars. A free wheel Monark ergometer was used during two-legged exercise and a fixed wheel Monark ergometer during one-legged exercise. The fixed wheel ergometer was selected for use during one-legged exercise so that the passive pedal would return without assistance. The scales on both types of ergometers were calibrated in kiloponds (kp) from 0 to 7. The loads used in the present study ranged from 0.5 to 6 kp. During exercise the load was checked from an identical viewing point regularly (at least once a minute) because the warming up of the wheel and belt altered the friction.

The speedometer on the ergometer indicated the "theoretical" speed in km.hr\(^{-1}\). During two-legged exercise a marker was placed on the speedometer at 21.5 km.hr\(^{-1}\) which corresponded with the desired pedal rate. During one-legged exercise the pedal rate was faster and a marker was placed on 25 km.hr\(^{-1}\). A marker for the purpose of pedal rate control was used in the majority of experiments in this study. In some, however, a more sensitive device was used which shall be described below.

Special arrangements during one-legged exercise on a bicycle ergometer

During one-legged cycling the active foot was secured tightly with velcro at both the ankle and the toe to a metal plate that was attached to the pedal. The design of the plate incorporated a heel lock which ensured that on each occasion the foot was always in the same position. The passive pedal was removed and the inactive leg rested on a box by the side and towards the front of the bicycle ergometer. Every attempt was made to ensure that this leg remained passive, however some muscular activity in this leg could not be prevented. Other investigators have found the same problem (Ahlborg, Hagenfeldt and Wahren, 1975; Henriksson, 1977).

Upper body movement was not physically restricted but the subjects were repeatedly told to keep their trunk upright and still. To help the subjects achieve this, they were all instructed to lock their arms at the elbow whilst holding the handlebars.
(c) **Pedal rate device**

A meter (designed in our laboratory), whose needle deflection was proportional to the rate of flywheel revolutions, was placed in front of the subject. The resolution of this meter was very much greater than the speedometer on the ergometer. The scale on the meter indicated the pedal rate and was graduated from 50 to 70 pedal revolutions per minute. The subjects were instructed in all tests to maintain a constant pedal rate and were helped to do so because of the greater accuracy of this system. A constant pedal rate is particularly important when a given submaximal work load is required of the subjects, because simply by pedalling too fast or too slowly the accuracy of the load calculation may be destroyed. Unfortunately this device was not available for use throughout the study.

(d) **Revolution counter**

A mains operated device which allowed the number of flywheel revolutions per unit time to be measured was fitted to the flywheel of the bicycle ergometer. The gearing and circumference of the wheel on a Monark ergometer are such that one complete pedal revolution moves a point on the rim 6 metres. Thus if 60 pedal revolutions are achieved the distance covered will be 360 metres. The braking power (kp) multiplied by the distance travelled will provide the amount of work done in kilopondmetres (kpm).

The number of flywheel revolutions per minute were recorded during every test for the exact calculation of the work done per minute (kgm.min⁻¹). Therefore assuming a total of 222 flywheel revolutions a minute and a load of 1 kp the work done in kgm.min⁻¹ would be 360 kgm.min⁻¹.

\[
\text{kgm.min}^{-1} = \text{Number of pedal revs. per minute} \times 6 \times \text{the load setting}
\]

\[
= 360 \text{ kgm.min}^{-1}
\]
The work done per unit time, which is referred to in the text as the work lead and is synonymous with power output, is expressed in watts and not $\text{kgm.min}^{-1}$. The conversion factor to watts is as follows:

\[
1 \text{kgm.min}^{-1} = 0.1635 \text{ watts} \\
360 \text{kgm.min}^{-1} = 59 \text{ watts}
\]

(e) Heart rate monitoring

Two devices were used in this study for the monitoring of heart rate.

(i) Camtrace

Heart rate was monitored by the Camtrace (Cambridge Instruments Ltd) from 3 chest electrodes on an oscilloscope. The 3

Prior to the application of the electrodes, the skin was rubbed briskly and when necessary the area was shaved. Surgical tape was used to ensure that the electrodes remained in position during exercise. This was particularly important during maximal exercise on the treadmill.

Although monitored continuously, heart rate values were recorded every 30 or 60 seconds.

(ii) Cardiometer

The cardiometer 275 (Cardionics) heart rate device specifically designed for exercise on a bicycle ergometer was also used for heart rate monitoring. The instrument calculated the mean heart rate value from the R-R intervals and presented the results on a wide angle analogue display. It operated by means of an electrode attached to the thoracic cage approximately outside the apex of the heart. No skin preparation was required. This device also monitored heart rate continuously.
(f) **Oxygen analyser**

The Taylor Servomex oxygen analyser (type OA. 272) was used for the determination of oxygen content in expired air samples. The analyser works on the principle of the susceptibility of oxygen as a paramagnetic gas. The analyser uses a measuring cell (developed by BP) which measures the oxygen content of the gas virtually independent of the other gases present. The \( \text{O}_2 \) content is read directly off a 4" scale taut band meter. In the OA.272 analyser, the \( \text{O}_2 \) content is indicated over the ranges 0 - 5%, 0 - 25% and 0 - 100%. The desired range required throughout this study was from 16 to 21% oxygen, the 0 - 5% range was therefore adopted. Occasionally the \( \text{O}_2 \) content fell below 16%, under these circumstances the 0 - 25% range was used. The calibration of the instrument together with the gas analysis procedure are described in appendices 2.A and 2.B.

(g) **Carbon-dioxide analyser**

The Lira solid state infrared analyser (Mines Safety Appliances Ltd., model 303) was used to determine the percentage of carbon-dioxide in exhaled air. It measures the concentration of one component in a mixture and is based on the principle of infrared absorption. The Lira 303 had been calibrated by the suppliers for the measurement of \( \text{CO}_2 \) specifically on a range from 0 - 10%. The meter cannot be used without a calibration chart which converts the meter reading to a percentage of \( \text{CO}_2 \). This chart was also supplied by the manufacturers.

Calibration of the Lira together with the gas analysis procedure is described in appendices 2.A and 2.B.

(h) **Gas meter**

A Parkinson Cowan gas meter was used to measure expired air volumes. The index dial on the meter indicates 50 litres per revolution. The instrument was calibrated by passing known volumes through it from a Tissot (600 litre capacity) spirometer (Collins Ltd.). The usual
temperature and pressure corrections were made to convert the volume on the dial to a standard volume. An Edale, type 2984, thermistor was fitted to the inlet tube of the meter and connected to an Edale thermometer (model C) for the determination of the temperature of respiratory gases.

(i) Edale thermometer (Model C)

This thermometer measures the temperature in liquids, gases and solids. The temperature sensitive probe as described above was a thermistor. The instrument has a built in calibration check, is battery operated and has a scale from 0 - 50°C.

(j) Gas collection equipment

The system consisted of a Douglas Bag with a 200 litre capacity and a two way tap that was attached to the bag. Low resistance light weight (Falconia) tubing connected the Douglas Bag to a light weight low resistance respiratory valve (Jakeman and Davies, 1979), to which a rubber mouth piece was attached. The connections were tight to ensure that the whole system was as air tight as possible. The total resistance in the whole system was kept to a minimum by the use of light weight low resistance material and is in accordance with the recommendations of Astrand and Rodahl (1977, p.339). This low resistance system meant that the stress placed on the individuals was also kept to a minimum. Nose clips were used to ensure that all exhaled air passed into the Douglas Bags. Douglas Bags, with a 200 litre capacity, were used for the collection of expired air on all occasions except one when a 600 litre capacity Tissot spirometer was used.

(k) Eppendorf photometer

The Eppendorf photometer, type 1101M, with an analogue read out via a light spot galvanometer was used for the determination of blood lactate, glucose and haemoglobin concentrations. The wavelengths of the mercury (Hg) filters used in this study were 365 nm, 436 nm and
546 nm for the determination of lactate, glucose and haemoglobin concentrations respectively.

(1) **Eppendorf centrifuge**

The Eppendorf micro-centrifuge, type 5414, was used for the quick separation of precipitates. This instrument has a rotating speed of 12,000 revolutions per minute and a maximum centrifuging time of 15 minutes. The centrifuging time can be controlled by a timer and ranged from 3 to 4 minutes in this study.

(m) **Blood analysis equipment**

The Eppendorf photometer and centrifuge as described above were used for the photometric determination of lactate, glucose and haemoglobin concentrations in capillary blood samples. In addition alcohol swabs, sterilized lancets, 20 and 25 µl capillary tubes, disposable micro test tubes and automatic pipettes with disposable plastic pipette tips were also used for the collection and analysis of capillary blood samples. The volume capacity of the automatic pipettes used in this study ranged from 20 µl to 5,000 µl (Gilson).

The blood lactate and glucose assays together with the procedure used for the determination of haemoglobin concentrations are outlined in appendix 2.C. Coefficients of variation for repeated measures of lactate, glucose and haemoglobin concentrations from one sample of venous blood are included in appendix 2.D.

3.3

**CALIBRATION PROCEDURES**

Details of the calibration procedures for the gas and blood analysis equipment are included in appendix 2.A.
3.4

GAS AND BLOOD ANALYSIS

Details of these are included in appendices 2.B and 2.C.

3.5

LABORATORY CONDITIONS AND INSTRUCTIONS GIVEN TO THE SUBJECTS

Prior to each experiment the temperature, humidity, barometric pressure and atmospheric oxygen content of the laboratory were determined. The opening of windows and doors ensured that the room was adequately ventilated. The specifications of Åstrand and Rodahl (1977, p. 360) for the environmental conditions of the laboratory necessary for testing to proceed were followed. They stated that the room temperature should be between 18 and 20°C, the relative humidity between 40 and 60% and the oxygen content should not be less than 20.90%. An electric fan was available on all occasions, this was particularly important during the tests that involved prolonged work.

For practical and ethical reasons the following requirements of the subjects prior to testing could not be followed on all occasions. However, they were strictly adhered to before the prolonged submaximal endurance tests.

1. No strenuous exercise, particularly of the endurance type, was to be done in the 24 hours preceding the test. This was extended to 48 hours before the submaximal endurance tests.

2. No food, particularly a large meal, should be eaten in the hour preceding the test. This was extended to a minimum of 12 hours prior to the endurance test to ensure the subjects were in the fasted state.

3. No alcoholic beverages should be consumed in the 24 hours preceding the test.
None of the subjects in the studies smoked, so this did not pose a problem. Again, due to practical and ethical reasons, those subjects exposed to more than one test could not perform each of the tests at the same time of the day.

During the exercise tests the subjects wore shirts, shorts (athletic pants in the case of females) and trainers. Prior to each test the subjects were asked to inform the experimenter if they were suffering from any infection or injury.

3.6

ORDER OF MEASUREMENTS TAKEN

On entering the laboratory the subjects stripped down to their shorts (shirts and athletic pants in the case of the females) and were measured for height and weight. They then sat on a chair while the electrode or electrodes (depending on the heart rate device being used) were placed in position. Where blood measurements were necessary the subject's hand was immersed in warm water to cause skin vasodilation. Once the weight and height had been recorded and the blood sample taken, the subject was then ready for the ergometer or treadmill test.

3.7

SUBJECTIVE RATING SCALE

Immediately after the tests designed to elicit \( \dot{V}O_2 \) max and at specific intervals during the prolonged submaximal tests, the subjects were requested to give a rating of perceived exertion. The rating was given on a 15 point scale from 6 to 20 as devised by Borg (1973).

3.8

DETERMINATION OF MAXIMUM OXYGEN UPTAKE (\( \dot{V}O_2 \) MAX)

Two tests for the determination of \( \dot{V}O_2 \) max were administered:
1. A continuous progressive loading test.
2. A discontinuous constant load test.

3.8.1

Continuous progressive loading test

During two-legged bicycle exercise, the saddle height as described by Åstrand and Rodahl (1977, p. 335) was adjusted for each subject. The saddle height adopted was the most comfortable one for performance during heavy work, local sensations of pain may otherwise stop the test before VO2 max has been reached. The saddle height was adjusted so that the knee was only slightly bent when the pedal was in its lowest position. This height determined during the first testing session for each subject was used on all subsequent occasions.

During one-legged ergometry the saddle height was adjusted in an attempt to ensure that the angle at the knee was approximately 90° when the pedal was in its lowest position. This saddle height was adopted to restrict the contribution of the plantar flexors, to minimize postural movements and to prevent the sensation of pain at the knee joint. Again, once this height had been determined for each subject it was used on all subsequent occasions.

Once the subject was seated the nature and purpose of the test, together with a clear signalling system were described to him. Each subject received the following instructions:-

1. That the work load would be increased every 2 minutes (every 4 minutes during the one-legged tests).
2. That he must maintain a pedal rate of 60 revs. min\(^{-1}\) by keeping the speedometer marker on 21.5 km.hr\(^{-1}\) or the needle on 60 revs.min\(^{-1}\) when the special rate meter described in section 3.2 was used. During one-legged work the subjects were instructed to maintain a pedal rate of 65 revs.min\(^{-1}\) which coincided with 25 km.hr\(^{-1}\) on the speedometer and
65 revs.min$^{-1}$ on the rate meter. (This pedal frequency was selected on the basis of preliminary one-legged work in which it was found that this speed was more comfortable than the commonly adopted rate of 60 revs.min$^{-1}$ for two-legged cycling).

3. That although the end point of the test is determined by him a maximal effort is required.

4. That to ensure a minimum gas collection of 30 seconds at the end point of the test, he must indicate clearly to predict when he can only continue to exercise for one more minute, by raising 1 finger.

The mouthpiece and nose clip were then fitted and connected to an empty Douglas Bag by means of the system described in section 3.2. Before commencing the test a more than adequate number of Douglas Bags were evacuated and positioned near the experimenter.

During two-legged ergometry the work load was increased progressively every 2 minutes by 59 watts (from 59 watts) up to 235 watts for the males and up to 206 watts for the females, after which the load increases were reduced to 29 watts every 2 minutes.

During one-legged ergometry the work load was increased progressively by 29 watts (from 29 watts) up to 118 watts for the males and 88 watts for the females, after which the work load increases were reduced to 15 watts.

During treadmill running the work load was increased progressively by raising the grade of the treadmill by 2.5% (from 3.5%) every 3 minutes. Although the grade was increased every 3 minutes, the speed remained constant at 3.1 m.sec$^{-1}$ (186 m.min$^{-1}$). The instructions given to the subjects before the bicycle ergometer $\dot{V}O_2$ max test (described above) were also given to the subjects before the treadmill $\dot{V}O_2$ max test, excluding instruction number 2 concerning pedal rate.
During all types of exercise heart rate was monitored continuously by one of the methods described in section 3.2, and recorded every 30 seconds. Sixty second collections of expired air were made using the Douglas Bag technique in the last minute of each 2, 3 or 4 minute exercise period, depending upon the type of exercise. During one-legged exercise 120 second gas collections were necessary at the lower work loads because of the small volumes of exhaled air produced. (The accuracy of the measurement of expired air volumes by the gas meter are reduced if the volumes are too small).

In all three types of exercise, before the work load was increased, the subject indicated his ability to perform the next work load. The test was continued until the subject predicted that he could only sustain the exercise for another minute. If, at the end of the minute, the subject was not exhausted, he continued until subjective exhaustion was reached. During this period, where possible, a further expired air collection was made.

During the one-legged test, it was heavily stressed to the subjects that the test was designed to measure the oxygen uptake capacity of the exercising leg only. The subjects were therefore instructed not to use their upper body, arms or resting leg to help them continue exercising when they would otherwise have to stop. If upper body movement was apparent the test was discontinued and the gas collection made void. The smaller increase in the work load of 15 watts was adopted at the heavier work loads because it was found from preliminary work by the author that an increase of 29 watts terminated the test because the subject simply was not strong enough to turn the pedal. Under these circumstances one-legged \( \dot{V}O_2 \) max for that person may not have been reached. However, when the work load increased by 15 watts the subject could cope with the work load, producing a higher measured \( \dot{V}O_2 \) max.

Immediately after the test a blood sample was taken when lactate and/or glucose and/or haemoglobin measurements were required. Then the work load was reduced and the subjects pedalled or jogged to aid
recovery after bicycle ergometer and treadmill exercise respectively. The mouthpiece, nose clip and electrodes were removed, the subject got off the ergometer or treadmill and put on a tracksuit to prevent getting cold. The expired air samples were analysed as outlined in appendix 2.B.

The criteria for \( \dot{V}_O_2 \) max during both two-legged bicycle exercise and treadmill running consisted of the following:

(a) Subjective exhaustion.
(b) Respiratory exchange ratio over 1.15 (Issekutz et. al., 1962).
(c) Blood lactic acid level in excess of 8 - 9 mM (Astrand and Rodahl, 1977, p.297).
(d) The "plateau" effect (Taylor et. al., 1955).

Taylor, Buskirk and Henschel (1955) stated that the "oxygen uptake elicited by the final work load should not exceed the oxygen uptake of the previous work load by more than 3%".

This is equivalent to 0.15 (L.min\(^{-1}\)) or 2.1 (ml.kg\(^{-1}\).min\(^{-1}\)). Provided subjective exhaustion along with one or more of the other listed criteria were obtained, the measured \( \dot{V}_O_2 \) max was considered to be valid.

The criterion for \( \dot{V}_O_2 \) max during one-legged exercise was that adopted by Davies and Sargeant (1974) who found that the "plateau" effect elicited during two-legged exercise was rarely found during one-legged exercise. They stated that duplicate measurements should be made and that the difference between these measurements should not exceed 5%.

The continuous loading test described above was used not only to determine \( \dot{V}_O_2 \) max, but also to determine the relationship between oxygen uptake and work load for the calculation of a given submaximal load.
The total work time (min) and the work load (watts) that elicited the highest $\dot{V}O_2 \, L \cdot min^{-1}$ were recorded.

3.8.2

The discontinuous test

This test consisted of 4 minute exercise bouts interrupted by periods of rest. A 4 minute exercise period was selected as this was considered adequate for the elicitation of the steady-state condition (Åstrand and Rodahl, 1977, p.357). The length of the rest period was not controlled and was determined by the subject.

The discontinuous test was carried out within 3 days of the incremental test and was designed to establish and confirm the $\dot{V}O_2 \, max$ values determined during that test. (A discontinuous test was not performed on the treadmill).

A minimum of 2 work loads were included in this test, these loads being determined from the continuous loading test. The first work load, to which the subjects were exposed after a 5 minute warming up period, was the highest work load they had been able to sustain for 2 or 4 minutes (depending upon the type of exercise) during the incremental test. Provided the subjects maintained this work load for 4 minutes, the work load was increased (by 15 and 29 watts during one- and two-legged exercise respectively) after a rest period and the subjects attempted the new work load for 4 minutes. If the subject achieved this, the work load was again increased after an intervening rest period. The test was terminated when the subject failed to complete 4 minutes at a new work load. The subject was requested, as above, to indicate clearly when he could only continue to exercise for another minute.

Heart rate was monitored continuously and recorded every 30 seconds, and expired air collected for 60 seconds during the last minute at each work load. The work load that elicited the highest $\dot{V}O_2 \, max$ was recorded.
If the criteria for one- or two-legged \( \dot{V}O_2 \) max were not met this test was repeated.

3.9

**DETERMINATION OF A GIVEN SUBMAXIMAL WORK LOAD**

During two-legged exercise a given submaximal work load was calculated using a linear regression equation, an example of which is provided in appendix 2.E. This equation was used because oxygen uptake has been found to increase linearly with work load when exercising with large muscle groups (Åstrand and Rodahl, 1977, p.297). Oxygen uptake measurements at several known submaximal work loads, together with the \( \dot{V}O_2 \) max of an individual, enabled the prediction from this linear relationship of a work load which would require a known percentage of an individual's \( \dot{V}O_2 \) max.

During one-legged exercise, however, the relationship between oxygen uptake and work load is not entirely linear (Gleser, 1973; Davies and Sargeant, 1974). This prevented the use of the linear regression equation for the calculation of the work load that would elicit a known percentage of an individual's one-legged \( \dot{V}O_2 \) max. Having obtained one-legged \( \dot{V}O_2 \) max for an individual, a given submaximal work load was determined by direct extrapolation from that individual's oxygen uptake/work load relationship.

3.10

**TEN MINUTE SUBMAXIMAL TEST TO ASSESS THE ACCURACY OF THE LOAD CALCULATION**

A 10 minute exercise test at the work load calculated to elicit a known percentage of an individual's \( \dot{V}O_2 \) max was included in several of the experiments in this study. This test was designed to assess not only the accuracy of the work load calculation but also the ability of the subject to reproduce the required load on the bicycle ergometer.
During the 10 minute test heart rate was monitored continuously and recorded every 30 seconds.

Expired air was collected twice during the test. The collections were 120 seconds in duration and were made from 4 to 6 and from 8 to 10 minutes. The oxygen uptake measurement determined from the 4 to 6 minute expired air collection was used to calculate the percentage oxygen uptake at which the subject was working.

3.11

ENDURANCE TEST

This test applies to the 2 training experiments included in this study.

The test consisted of endurance exercise at a predicted work load of 75% \( \dot{V}O_2 \max \) prior to the two-legged training programme, and at 80% one-legged \( \dot{V}O_2 \max \) prior to the one-legged programme. After training the subjects repeated the test at the same absolute work load.

All subjects strictly adhered to the instructions given to them as described in section 3.5. That is, all subjects fasted for 12 hours prior to the test and did not engage in any physical activity during that time. In addition, they had not participated in any heavy endurance exercise in the 48 hours preceding the test. In this way, the metabolic state of the subjects was standardized as far as this is possible. Food intake, alcohol consumption and physical activity produce large metabolic differences and for this reason the importance of arriving in a fasted and rested state was clearly explained to all subjects.

The subjects were prepared for the test as described in section 3.6. Once seated on the ergometer the nature of the test was explained to them and they were told that:
1. they must maintain a constant pedal rate (65 and 60 revs. min⁻¹ during the one- and two-legged tests respectively). If this rate repeatedly fell by more than 2 revs. min⁻¹ the test would be terminated.

2. that gas and blood samples would be taken at various intervals during the test which meant that they would have to place the mouthpiece and nose clip in position and immerse their hand in the hot water placed beside them when requested. (This applied to the one-legged endurance test only).

The subjects started to exercise at their prescribed work loads and continued until subjective exhaustion was reached.

Two-legged endurance test

During this test heart rate was monitored continuously and recorded every 10 minutes.

One-legged endurance test

During this test oxygen uptake, heart rate, blood lactate and blood glucose measurements were made. A minimum period of 48 hours separated the testing of each leg and the exposure of each leg to the endurance test was randomized.

Heart rate was monitored continuously and recorded every minute except during the gas collections when recordings were made very 30 seconds. Flywheel revolutions were also monitored continuously and recorded every minute.

The expired air collections were made from 4 to 6, 8 to 10, 14 to 16 and 28 to 30 minutes and thereafter every 30 minutes and finally in the last 1 to 2 minutes of the exercise.
Blood samples for the determination of lactate and glucose concentrations were taken at rest and in the last minute of exercise during the pre-training endurance test. In the post-training test they were taken at rest, at the time that corresponded with the final minute of exercise in the pre-training test, at 30 minutes and thereafter every 30 minutes and finally in the last minute of exercise. The subjects were instructed to continue exercising until the final blood sample had been taken. Determinations of the perceived rate of exertion (PRE) corresponded with the blood sampling times.

Blood haemoglobin measurements were made at rest and in the final minute of exercise during the pre- and post-training tests. On each occasion a pair of blood samples were taken for the determination of lactate, glucose and haemoglobin concentrations. Duplicate lactate and glucose assays and duplicate haemoglobin readings were made on each pair of samples.

The one-legged endurance tests were all carried out between 7 and 11 a.m. for practical and ethical reasons. During the two-legged study, however, the endurance tests corresponded with the subjects' normal training times. This included training times from 1 to 2 p.m. and from 5 to 6 p.m. For this reason the subjects were not completely fasted but they did not participate in any physical activity on the day of the test and only consumed a light meal (salad) 4 to 5 hours prior to the test.

The subjects were supervised continuously to ensure that they maintained the correct pedal frequency and that during one-legged exercise they did not introduce muscular effort from other parts of the body. The work load was checked regularly (at least once a minute) and water was available to the subjects at all times, as was a towel. An electric fan was placed near the subject on all occasions.

The subjects received no information concerning the performance times of other subjects but they were allowed to know the length of time for which they had been exercising.
The exercise time and the total number of flywheel revolutions were recorded at the end of each test. A maximum time limit of 2 hours could not be avoided due to practical reasons.

The expired air and blood lactate, glucose and haemoglobin analyses were carried out as outlined in appendices 2.B and 2.C. The test was repeated at the same absolute work load after 5 weeks' training and half way through the training programme to provide information regarding the time course of the training adaptations. The mid-training endurance test was restricted to 30 minutes for practical reasons and performed on the trained leg only. During this test blood samples were taken at rest, at the time that corresponded to the final minute of exercise in the pre-training test and at 30 minutes.

3.12

TRAINING METHODS

In both training studies the subjects exercised 3 times a week over a 5 to 6 week period. The subjects trained at approximately 75% VO\text{2} max during the two-legged training study, and at approximately 80% one-legged VO\text{2} max during the one-legged training study.

Each training session was supervised by the author. The work load and pedal rate were frequently checked during each session. Heart rate and the total number of flywheel revolutions were recorded on all occasions, the former being recorded every minute. The subjects' weight, subjective "onset of sweating" and perceived rate of exertion at the end of the training session were determined weekly during both training programmes.

The subjects exercised for a maximum period of 30 minutes or until subjective exhaustion was reached if this came earlier. Once the subjects had exercised at a given work load on 3 occasions for 30 minutes (not necessarily repeatedly) the work load was increased by 15
and 29 watts during the one- and two-legged training programmes respectively.

Four free wheel Monark ergometers were used during the two-legged training study and 2 fixed wheel Monark ergometers during the one-legged training study. All pre- and post-training measurements, however, were carried out on the same free or fixed wheel ergometer depending upon the type of exercise.

3.13

DATA ANALYSIS

Statistical analysis of the data will be described in each experimental chapter. All values are presented in the text, tables and figures as means and standard deviations (SD).
CHAPTER 4

THE RELATIONSHIP BETWEEN MAXIMUM OXYGEN UPTAKE AND RUNNING PERFORMANCE

4.1

INTRODUCTION

Maximum oxygen uptake ($\dot{V}O_2$ max) has been commonly used as an indicator of fitness in general and endurance capacity in particular. The idea that the larger the $\dot{V}O_2$ max value of an individual, the greater is the endurance capacity of that individual has arisen because descriptive studies of endurance athletes have shown that they have, as a group, high $\dot{V}O_2$ max values. The aspiring endurance athlete needs to have a large capacity for oxygen transport in order to sustain a rapid rate of aerobic energy metabolism which is necessary during prolonged high speed running. The importance of a high $\dot{V}O_2$ max value for success at endurance events has been illustrated in the studies which have compared the running performances and $\dot{V}O_2$ max values of groups of individuals with a wide range of maximum oxygen uptake values (Costill et al., 1973). These studies have found high correlations between the $\dot{V}O_2$ max values and the speed of the individuals over distances of, for example 2 miles (Foster et al., 1979). Therefore it is understandable why attention has always been focused on the influence of training on $\dot{V}O_2$ max and that improvements in $\dot{V}O_2$ max have been the only criteria of success in many studies on training (Sharkey and Holleman, 1967). In the majority of these training studies little attempt has been made to dissociate the improvements in $\dot{V}O_2$ max values and the improvements in endurance capacity.

The purpose of the present study was to re-examine the relationship between $\dot{V}O_2$ max and running performance in order to explore the possibility of using a running performance test as a model for the investigation of the relationship between training induced changes in $\dot{V}O_2$ max and endurance capacity. A 2 mile time trial was chosen as the
running performance test because it is the test which has been most frequently used by other investigators (Foster et. al., 1978; Lawson and Golding, 1978). The subjects for this preliminary investigation were chosen so that they represented individuals with a wide range of \( \dot{V}O_2 \) max values and running experience.

4.2

**METHOD**

Twelve male and 19 female physical education students were subjects for this investigation. All subjects participated in regular physical activity and some engaged in serious endurance training. Prior to the start of the experiments the subjects were familiarized with all pertinent laboratory procedures. The subjects were exposed to 3 tests:

1. A grade-incremental \( \dot{V}O_2 \) max test.
2. Submaximal horizontal running at 4 speeds.
3. Two mile time trial.

1. Grade-incremental \( \dot{V}O_2 \) max test (Taylor et. al., 1955)

The subjects ran at a constant speed (3.1 m.sec\(^{-1}\) or 186 m.min\(^{-1}\)) with the grade of the treadmill being increased progressively from 3.5% by 2.5% every 3 minutes. Heart rate was monitored continuously from 3 chest electrodes on a Camtrace and displayed on an oscilloscope (Cambridge Instruments Ltd.), and recorded every 30 seconds. Expired air was collected for 60 seconds from 1 minute 45 seconds to 2 minutes 45 seconds during each 3 minute exercise period. The subjects were requested to signal clearly when they could exercise for only 1 minute longer. The final expired air collection was made immediately after this signal had been given. The expired air was analysed and oxygen uptake determined as described in appendix 2.B. The criteria for obtaining \( \dot{V}O_2 \) max included subjective exhaustion and a respiratory exchange ratio in excess of 1.15 (Issekutz et. al., 1962).
2. Submaximal running

Each subject ran for 4 minutes at no more than 4 submaximal running speeds. Three speeds were common to both sexes allowing direct comparison of the oxygen cost of running at these speeds between the male and female subjects. The 3 speeds were 2.7, 3.1 and 3.6 m.sec\(^{-1}\) (162, 186 and 216 m.min\(^{-1}\)). The speed of the treadmill was increased after each 4 minute period and so the subjects ran continuously for 16 minutes. Heart rate was monitored continuously and recorded every 30 seconds. Expired air was collected for 60 seconds during the last minute of each 4 minute exercise period. From the results of this test the speed/\(\dot{V}O_2\) regression equation for each subject was derived.

3. Two mile time trial

Running performance was determined by having each subject run 2 miles on a 400 metre cinder track. In addition to the time taken to run the 2 miles, each 400 metre lap time was recorded. The relative work loads (\(\% \dot{V}O_2\) max) at which both each 400 m and the 2 mile time trial were run, were predicted from the speed/\(\dot{V}O_2\) regression equations.

Data analysis

The t-test for uncorrelated data was employed to test for differences between the male and female subjects. Significance was accepted at the .05 level. Correlations between \(\dot{V}O_2\) max and the 2 mile run time, and between \(\dot{V}O_2\) max and running speed during the 2 mile run were both calculated. As mentioned above, the aerobic demand (\(\% \dot{V}O_2\) max) of the run and of each 400 metre lap was predicted from the speed/\(\dot{V}O_2\) regression equations. The results of those subjects who only achieved 2 speeds during the submaximal running test were excluded from these calculations. Results are presented as the means ± standard deviation (SD).
4.3

RESULTS

The mean age, height, and weight of the male and female subjects, together with the average \( \dot{V}O_2 \) max, \( \dot{V}E \) max and HR max values for the two sexes, are presented in table 4.1. The male and female \( \dot{V}O_2 \) max values were 4.78 ± 0.43 L.min\(^{-1}\) (59.81 ± 3.96 ml.kg\(^{-1}\).min\(^{-1}\)) and 2.73 ± 0.29 L.min\(^{-1}\) (47.18 ± 7.36 ml.kg\(^{-1}\).min\(^{-1}\)) respectively. The male values were significantly higher than the female values (\( p < 0.001 \)).

Although the oxygen cost of horizontal running at each submaximal speed was lower in the female group than in the male group (table 4.2, figure 4.1), the differences only reached the level of statistical significance (\( p < 0.05 \)) at the running speed of 3.1 m.sec\(^{-1}\) (186 m.min\(^{-1}\)).

During grade running at a constant speed of 3.1 m.sec\(^{-1}\) (186 m.min\(^{-1}\)), the female oxygen uptake values were again lower (table 4.2, figure 4.2) than the male values, reaching significance (\( p < 0.01 \)) at the treadmill gradients of 3.5 and 6.0%.

However, when the energy expenditure per unit body weight and time (Kcal.kg\(^{-1}\).min\(^{-1}\)) of the male and female subjects were compared, although the female values were again slightly lower, the differences did not reach significance during either submaximal speed or grade running (table 4.3, figures 4.3 and 4.4).

The running speeds corresponding to \( \dot{V}O_2 \) max, as predicted from the speed/\( \dot{V}O_2 \) regression equations for the male and female subjects were 5.2 ± 0.4 m.sec\(^{-1}\) (312 ± 24 m.min\(^{-1}\)) and 4.2 ± 0.5 m.sec\(^{-1}\) (252 ± 36 m.min\(^{-1}\)) respectively.

The 2 mile times for the male and female subjects were 11.88 ± 0.57 minutes and 15.08 ± 2.44 minutes respectively, the male time being significantly less than the female time (\( p < 0.001 \)), (table 4.4).
Consequently, the average male running speed was faster than the female running speed \((p < 0.001)\). The average running speed during the 2 mile time trial for the males was \(4.5 \pm 0.2 \text{ m.sec}^{-1}\) \((270 \pm 12 \text{ m.min}^{-1})\), and \(3.6 \pm 0.6 \text{ m.sec}^{-1}\) \((216 \pm 36 \text{ m.min}^{-1})\) for the females (table 4.4).

A high correlation was found between \(\dot{V}O_2\) max and 2 mile run time \((r = -0.90, p < 0.001)\) and also between the average running speed of the 2 mile run and \(\dot{V}O_2\) max \((r = -0.89, p < 0.001)\). These relationships are presented in figures 4.5 and 4.6.

The male and female subjects ran the 2 miles at a predicted average \(\dot{V}O_2\) of \(53.11 \pm 2.68\) and \(44.35 \pm 6.30 \text{ ml.kg}^{-1}.\text{min}^{-1}\) respectively. In the male group this corresponded to \(89.3 \pm 3.1\% \dot{V}O_2\) max and to \(89.6 \pm 4.4\% \dot{V}O_2\) max in the female group (table 4.4). Although both sexes ran the 2 mile distance at approximately \(89\% \dot{V}O_2\) max, the running speed of every individual was noticeably faster during the first and last 400 metres. The average running speed at the beginning and the end of the 2 mile time trial corresponded approximately to \(95-96\% \dot{V}O_2\) max (table 4.5), with some individuals achieving speeds in excess of \(100\% \dot{V}O_2\) max (figure 4.7).

A comparison of the oxygen cost of horizontal treadmill running in this and other studies is presented in table 4.6.

The relationship between \(\dot{V}O_2\) max and running performance in this and in other similar investigations is illustrated in table 4.7.
TABLE 4.1

Characteristics of the subjects (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>MALES</th>
<th>FEMALES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (yrs)</td>
<td>21.7 ± 2.1</td>
<td>21.1 ± 0.4</td>
</tr>
<tr>
<td>Ht. (cms)</td>
<td>181.9 ± 6.0</td>
<td>164.7 ± 5.1</td>
</tr>
<tr>
<td>Wt. (kg)</td>
<td>80.03 ± 7.36</td>
<td>58.62 ± 7.46***</td>
</tr>
<tr>
<td>( \dot{V}O_2 \text{ max (L.min}^{-1}) )</td>
<td>4.78 ± 0.43</td>
<td>2.73 ± 0.29***</td>
</tr>
<tr>
<td>( \dot{V}O_2 \text{ max (ml.kg}^{-1}.\text{min}^{-1}) )</td>
<td>59.81 ± 3.96</td>
<td>47.18 ± 7.36***</td>
</tr>
<tr>
<td>( \dot{V}E \text{ max (L.min}^{-1}) )</td>
<td>133.81 ± 15.03</td>
<td>83.22 ± 12.21***</td>
</tr>
<tr>
<td>HR max (b.min^{-1})</td>
<td>186.6 ± 6.8</td>
<td>185.2 ± 10.9</td>
</tr>
</tbody>
</table>

Level of significance between the male and female values:

*** P < 0.001
TABLE 4.2

Oxygen cost ($\dot{V}O_2\text{ml.kg}^{-1}\text{.min}^{-1}$) at submaximal speeds and during treadmill grade running at 3.1 m.sec$^{-1}$ in males and females (means ± SD)

<table>
<thead>
<tr>
<th>SPEED m.sec$^{-1}$,(m.min$^{-1}$)</th>
<th>MALES</th>
<th>FEMALES</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.2 (132)</td>
<td></td>
<td>29.00 ± 1.86 (13)</td>
</tr>
<tr>
<td>2.7 (162)</td>
<td>34.37 ± 1.50 (11)</td>
<td>33.40 ± 2.42 (17)</td>
</tr>
<tr>
<td>3.1 (186)</td>
<td>38.84 ± 1.15 (12)</td>
<td>37.34 ± 2.14* (15)</td>
</tr>
<tr>
<td>3.6 (216)</td>
<td>43.50 ± 1.05 (11)</td>
<td>42.10 ± 2.04 (11)</td>
</tr>
<tr>
<td>4.0 (240)</td>
<td>47.84 ± 1.16 (11)</td>
<td>46.31 ± 2.40 (5)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>TREADMILL GRADIENT (%)</th>
<th>MALES</th>
<th>FEMALES</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.5</td>
<td>42.91 ± 1.41 (12)</td>
<td>39.95 ± 2.45** (15)</td>
</tr>
<tr>
<td>6.0</td>
<td>49.01 ± 1.56 (12)</td>
<td>46.96 ± 1.96** (12)</td>
</tr>
<tr>
<td>8.5</td>
<td>54.63 ± 2.00 (12)</td>
<td>51.86 ± 1.53 (6)</td>
</tr>
<tr>
<td>11.0</td>
<td>59.67 ± 1.36 (8)</td>
<td></td>
</tr>
</tbody>
</table>

( ) no. of subjects

Level of significance between the male and female values:

* $P < 0.05$

** $P < 0.01$
FIG. 4.1

THE OXYGEN COST OF HORIZONTAL TREADMILL RUNNING

( ) no. of subjects
.

* male and female values statistically different

[Graph showing VO₂ (ml.kg⁻¹.min⁻¹) on the y-axis and Running Speed (m.sec⁻¹) on the x-axis. The graph includes data points for males and females with different sample sizes.]
FIG. 4.2

THE OXYGEN COST OF TREADMILL GRADE RUNNING

( ) no. of subjects
- male and female values statistically different
Energy cost (Kcal.kg\(^{-1}\).min\(^{-1}\)) at submaximal speeds, and during treadmill grade running at 3.1 m.sec\(^{-1}\) in males and females (means ± SD)

<table>
<thead>
<tr>
<th>SPEED m.sec(^{-1}) (m.min(^{-1}))</th>
<th>MALES</th>
<th>FEMALES</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.2 (132)</td>
<td>0.169 ± 0.005 (11)</td>
<td>0.142 ± 0.011 (13)</td>
</tr>
<tr>
<td>2.7 (162)</td>
<td>0.167 ± 0.015 (17)</td>
<td></td>
</tr>
<tr>
<td>3.1 (186)</td>
<td>0.193 ± 0.007 (12)</td>
<td>0.187 ± 0.013 (15)</td>
</tr>
<tr>
<td>3.6 (216)</td>
<td>0.212 ± 0.011 (11)</td>
<td>0.216 ± 0.005 (11)</td>
</tr>
<tr>
<td>4.0 (240)</td>
<td>0.234 ± 0.011 (5)</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>TREADMILL GRADIENT (%)</th>
<th>MALES</th>
<th>FEMALES</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.5</td>
<td>0.213 ± 0.009 (12)</td>
<td>0.202 ± 0.012 (15)</td>
</tr>
<tr>
<td>6.0</td>
<td>0.248 ± 0.006 (12)</td>
<td>0.239 ± 0.008 (12)</td>
</tr>
<tr>
<td>8.5</td>
<td>0.280 ± 0.011 (12)</td>
<td>0.268 ± 0.007 (6)</td>
</tr>
<tr>
<td>11.0</td>
<td>0.310 ± 0.009 (8)</td>
<td></td>
</tr>
</tbody>
</table>

( ) no. of subjects
FIG. 4.3 THE ENERGY COST OF HORIZONTAL TREADMILL RUNNING

( ) no. of subjects
FIG. 4.4 THE ENERGY COST OF TREADMILL GRADE RUNNING

( ) no. of subjects

Energy Cost (Kcal. kg\(^{-1}\)min\(^{-1}\))

Treadmill Grade (%)
TABLE 4.4

Two mile run time, average running speed and average \( \% \dot{V}O_2 \text{ max} \) during the 2 mile time trial in males and females

(means ± SD)

<table>
<thead>
<tr>
<th></th>
<th>MALES</th>
<th>FEMALES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Two mile time (min)</td>
<td>11.88 ± 0.57</td>
<td>15.08 ± 2.44***</td>
</tr>
<tr>
<td>Av. running speed (m.sec(^{-1}))</td>
<td>4.5 ± 0.2</td>
<td>3.6 ± 0.6***</td>
</tr>
<tr>
<td>Av. running speed (m.min(^{-1}))</td>
<td>270.0 ± 12.0</td>
<td>216.0 ± 36.0***</td>
</tr>
<tr>
<td>Av. ( \dot{V}O_2 ) (ml.kg(^{-1}).min(^{-1}))</td>
<td>53.11 ± 2.68</td>
<td>44.35 ± 6.30***</td>
</tr>
<tr>
<td>Av. ( % \dot{V}O_2 \text{ max} )</td>
<td>89.3 ± 3.1</td>
<td>89.6 ± 4.4</td>
</tr>
</tbody>
</table>

Av. = average

Level of significance between the male and female values:

*** \( P < 0.001 \)
Fig 4.5 The relationship between $\dot{V}O_2$ max and 2 mile run time.

- Males
- Females
FIG. 4.6  THE RELATIONSHIP BETWEEN $\dot{V}O_2$ max AND AVERAGE RUNNING SPEED DURING A 2 MILE TIME TRIAL

+$ $males
- females

$V_\text{O}_2\text{ max. (ml.kg}^{-1}\text{.min}^{-1})$

Average Running Speed (m.sec$^{-1}$)
TABLE 4.5

Percentage $\dot{V}O_2$ max of each 400m during the 2 mile time trial, as predicted from the speed/$\dot{V}O_2$ regression equations, in males and females (means ± SD)

<table>
<thead>
<tr>
<th>LAP NUMBER</th>
<th>MALES</th>
<th>FEMALES</th>
<th>MALES AND FEMALES</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (400m)</td>
<td>95.7 ± 7.0</td>
<td>97.5 ± 8.3</td>
<td>96.6 ± 7.6</td>
</tr>
<tr>
<td>2 (400m)</td>
<td>87.6 ± 4.0</td>
<td>89.5 ± 4.8</td>
<td>88.6 ± 4.5</td>
</tr>
<tr>
<td>3 (400m)</td>
<td>87.7 ± 3.9</td>
<td>88.5 ± 4.7</td>
<td>88.1 ± 4.2</td>
</tr>
<tr>
<td>4 (400m)</td>
<td>87.8 ± 2.8</td>
<td>87.4 ± 4.9</td>
<td>87.6 ± 4.0</td>
</tr>
<tr>
<td>5 (400m)</td>
<td>86.8 ± 3.1</td>
<td>87.3 ± 5.3</td>
<td>87.3 ± 5.3</td>
</tr>
<tr>
<td>6 (400m)</td>
<td>86.5 ± 3.6</td>
<td>85.7 ± 4.6</td>
<td>86.1 ± 4.1</td>
</tr>
<tr>
<td>7 (400m)</td>
<td>86.9 ± 2.5</td>
<td>87.0 ± 4.7</td>
<td>87.0 ± 3.8</td>
</tr>
<tr>
<td>8 (400m)</td>
<td>95.5 ± 4.7</td>
<td>94.0 ± 5.8</td>
<td>94.8 ± 5.3</td>
</tr>
</tbody>
</table>
FIG. 4.7  PREDICTED ENERGY EXPENDITURE (% $\dot{V}O_2$ max) DURING EACH 400 METRES DURING THE 2 MILE TIME TRIAL
TABLE 4.6

Comparison of oxygen costs of horizontal treadmill running in this study
and those reported in the literature

<table>
<thead>
<tr>
<th></th>
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<tr>
<td>MALES</td>
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</tr>
<tr>
<td>2.7</td>
<td>37.2 ±2.4</td>
<td>(25.0)</td>
<td>(24.4)</td>
<td>(25.6)</td>
<td>30.1 ±2.7</td>
<td>(35.95)</td>
<td>(34.1)</td>
<td>(34.8)</td>
<td>34.4 ±1.5</td>
<td>33.4 ±2.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3.1</td>
<td>38.6 ±2.0</td>
<td>(31.8)</td>
<td>(30.5)</td>
<td>(32.7)</td>
<td>36.8 ±3.2</td>
<td>(41.10)</td>
<td>(39.3)</td>
<td>(39.7)</td>
<td>38.8 ±1.15</td>
<td>37.2 ±2.11</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3.6</td>
<td>41.6 ±2.7</td>
<td>(36.7)</td>
<td>(36.7)</td>
<td>38.7</td>
<td>41.4 ±3.4</td>
<td>(35-42)</td>
<td>(34-45)</td>
<td>(46.26)</td>
<td>(44.5)</td>
<td>(44.7)</td>
<td>43.5 ±1.05</td>
<td>42.1 ±1.95</td>
<td></td>
</tr>
<tr>
<td>4.0</td>
<td>44.6 ±3.3</td>
<td>(46.7)</td>
<td>(46.7)</td>
<td>46.6 ±3.6</td>
<td>(41-47)</td>
<td>(40-50)</td>
<td>(51.41)</td>
<td>(49.6)</td>
<td>(49.4)</td>
<td>47.8 ±1.61</td>
<td>46.3 ±2.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4.5</td>
<td>48.1 ±4.1</td>
<td>(51.7)</td>
<td>(51.7)</td>
<td>54.9</td>
<td>54.1 ±4.0</td>
<td>(47-53)</td>
<td>(46-55)</td>
<td>(56.56)</td>
<td>(54.8)</td>
<td>(54.4)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

( ) values are predicted from the regression equation developed from data in the respective studies cited.
* values taken from those cited by Mayhew, Piper and Etheridge (1979)
### TABLE 4.7

**Relationship of VO\(_2\) max to running performance in this and previous investigations**

<table>
<thead>
<tr>
<th>STUDY</th>
<th>SUBJECTS</th>
<th>(\dot{\text{VO}}_2) max RANGE (ml.kg(^{-1}).min(^{-1}))</th>
<th>TEST DISTANCE</th>
<th>PERFORMANCE RANGE (min)</th>
<th>RELATIONSHIP BETWEEN (\dot{\text{VO}}_2) max AND PERFORMANCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Costill (1967)</td>
<td>University cross-country (n=17)</td>
<td>50 - 67</td>
<td>4.7 miles</td>
<td>24.3-33.3</td>
<td>- 0.82</td>
</tr>
<tr>
<td>Costill et al., (1973)</td>
<td>trained distance runners (n=16)</td>
<td>55 - 82</td>
<td>10.0 miles</td>
<td>48.3-68.2</td>
<td>- 0.91</td>
</tr>
<tr>
<td>Briggs (1977)</td>
<td>trained distance runners (n=10)</td>
<td>67 - 76</td>
<td>2.0 miles</td>
<td>9.0-9.7</td>
<td>- 0.38</td>
</tr>
<tr>
<td>Foster et al., (1978)</td>
<td>well trained runners (n=26)</td>
<td>49 - 73</td>
<td>2.0 miles</td>
<td>9.4-14.8</td>
<td>- 0.87</td>
</tr>
<tr>
<td>Lawson and Golding (1978)</td>
<td>runners of varying ability (n=20)</td>
<td>45 - 74</td>
<td>2.0 miles</td>
<td>10.2-17.4</td>
<td>- 0.86</td>
</tr>
<tr>
<td>Farrell et al., (1979)</td>
<td>experienced runners (n=12)</td>
<td>46 - 74</td>
<td>15.0 km</td>
<td>45.9-73.6</td>
<td>- 0.89</td>
</tr>
<tr>
<td>Conley and Krahenbuhl (1980)</td>
<td>highly trained runners (n=12)</td>
<td>67 - 77</td>
<td>10.0 km</td>
<td>30.5-33.6</td>
<td>- 0.12</td>
</tr>
<tr>
<td>Present investigation (1981)</td>
<td>Physical Education students (n=31)</td>
<td>35 - 66</td>
<td>2.0 miles</td>
<td>10.9-19.0</td>
<td>- 0.90*</td>
</tr>
<tr>
<td>Present investigation (1981)</td>
<td>male P.E. students only (n=12)</td>
<td>53 - 66</td>
<td>2.0 miles</td>
<td>10.9-12.8</td>
<td>- 0.82</td>
</tr>
<tr>
<td>Present investigation (1981)</td>
<td>female P.E. students only (n=19)</td>
<td>35 - 60</td>
<td>2.0 miles</td>
<td>11.0-19.0</td>
<td>- 0.87</td>
</tr>
</tbody>
</table>

All above investigations used male subjects only. * includes both male and female students.
The male subjects had greater values for $\dot{V}O_2$ max, both in absolute terms and when expressed in ml.kg$^{-1}$.min$^{-1}$. The mean maximum oxygen uptake values for the male and female physical education (PE) students were 59.81 ± 3.96 and 47.18 ± 7.36 ml.kg$^{-1}$.min$^{-1}$ respectively. These values compare favourably with those reported by Williams (1981) for a group of PE students also at Loughborough University. He found $\dot{V}O_2$ max values of 54.3 ± 0.9 and 41.6 ± 4.8 ml.kg$^{-1}$.min$^{-1}$ in a group of male and female students respectively. As can be seen the range of values around the mean in the present study was considerably greater for the females. Their $\dot{V}O_2$ max values ranged from 35 - 60 ml.kg$^{-1}$.min$^{-1}$ compared with 53 - 66 ml.kg$^{-1}$.min$^{-1}$ in the male group (table 4.7). This can be explained by the greater variation in the activity levels and running ability of the female subjects, at least 4 of whom were engaged in regular endurance training and competitive running. Others in the group participated only in the activity sessions included in their course. Therefore, the subjects demonstrated a wide range of $\dot{V}O_2$ max values as required for the study.

The mean $\dot{V}O_2$ max values are, as expected, higher than those reported in the literature for sedentary individuals of a similar age. Atomi and Miyashita (1974) reported mean $\dot{V}O_2$ max values of 32.0 and 37.5 ml.kg$^{-1}$.min$^{-1}$ in sedentary and fairly active college women respectively. The active females participated in recreational activities only which may explain why their value is considerably lower than that found in the current study. The average value determined in this study corresponds well with the $\dot{V}O_2$ max value of 41.0 ml.kg$^{-1}$.min$^{-1}$ reported by Astrand and coworkers for 11 well trained females aged 21 years (Astrand et. al., 1964).

Ekblom and coworkers reported a mean $\dot{V}O_2$ max value of 42.0 ml.kg$^{-1}$.min$^{-1}$ for a group of sedentary males (Ekblom et. al., 1968). This value, as expected, is considerably lower than that found in the
present study and is highly comparable to the average value reported by Hazeldine (1974) in a group of sedentary Loughborough University students. Hazeldine also reported that male PE students, who engaged in regular exercise, had a $\dot{V}O_2\,_{max}$ value of $45.9 \pm 6.4 \, \text{ml.kg}^{-1}\,\text{min}^{-1}$ and those who engaged in regular training, a value of $52.4 \pm 8.1 \, \text{ml.kg}^{-1}\,\text{min}^{-1}$. These values are both lower than the average male value found in the present study ($59.8 \pm 3.96 \, \text{ml.kg}^{-1}\,\text{min}^{-1}$) and may be explained by the use of the bicycle ergometer by Hazeldine (1974) since the $\dot{V}O_2\,_{max}$ values during cycling have been reported to be 4-8% lower than those obtained during treadmill grade running (Astrand and Rodahl, 1977, p.335). In addition, the prediction of $\dot{V}O_2\,_{max}$ from submaximal work loads by Hazeldine may have led to an underestimation of this parameter. It is more useful, therefore, to compare the values from the present study with those obtained by others using a grade-incremental running test for the determination of $\dot{V}O_2\,_{max}$. Koeslag and Sloan (1976) using this method, reported a mean $\dot{V}O_2\,_{max}$ value of $58.2 \, \text{ml.kg}^{-1}\,\text{min}^{-1}$ for a group of male non-runners. This is very similar to the $\dot{V}O_2\,_{max}$ value found for the male group in this study, who were also mainly composed of non-runners.

The highest value in the female group was $60.7 \, \text{ml.kg}^{-1}\,\text{min}^{-1}$ which was obtained by a highly trained, competitive endurance runner and compares favourably with the mean $\dot{V}O_2\,_{max}$ values reported by Astrand and Rodahl (1977, p.409) for female distance runners in the national Swedish team. The highest male value of $65.8 \, \text{ml.kg}^{-1}\,\text{min}^{-1}$ was found in a top class rugby player and is similar to the highest values reported by Astrand and Rodahl (1977, p.408) in a group of national footballers.

The oxygen cost of horizontal treadmill running in the male and female groups is presented in table 4.2. Although the females were characterised by slightly lower $\dot{V}O_2$ values at the speeds studied, these differences only reached the level of statistical significance ($p < 0.05$) at the speed of $3.1 \, \text{m.sec}^{-1}$ ($186 \, \text{m.min}^{-1}$). This finding suggests that there are no sex differences in the aerobic demands of
running when the range of speeds are common to both sexes. This conclusion is consistent with the results of other studies (Daniels et al., 1977; Kollias et al., 1978; Mayhew et al., 1979). This tendency towards a lower oxygen cost of running in the female group was also evident by the significantly lower values determined during treadmill grade running at a constant speed of 3.1 m.sec$^{-1}$ (186 m.min$^{-1}$).

The lower oxygen cost of running in the female group, particularly during grade running, may be explained by the difficulty the male subjects had in running comfortably at the relatively slow speed of 3.1 m.sec$^{-1}$ (186 m.min$^{-1}$). During such running there may be a tendency to displace the body more vertically, leading possibly to a higher energy expenditure. Daniels and coworkers stated that the comfortable running speed for trained runners was 3.3 m.sec$^{-1}$ (198 m.min$^{-1}$) and above (Daniels et al., 1977). Mayhew and coworkers reported that running speeds in the 3.0-3.2 m.sec$^{-1}$ (180 to 192 m.min$^{-1}$) range are optimal for running economy (Mayhew, Piper and Etheridge, 1979). Despite the 3.1 m.sec$^{-1}$ speed adopted during the grade-incremental $\dot{V}O_2$ max test, the males clearly found this speed uncomfortably slow.

Comparisons between the oxygen cost of running for males and females is difficult. The speed ranges and running ability of the two sexes should be similar to allow comparisons to be made. However, by adopting common running speeds, the use of uncomfortably slow speeds for the male subjects is difficult to avoid.

A comparison of the oxygen costs of horizontal treadmill running in this and other studies can be seen in table 4.6. This table illustrates that the variation in oxygen consumption around the means at different speeds is similar within each study, but the variation in the oxygen cost of running at similar speeds varies slightly from study to study. This variation appears to be greatest at the slowest and fastest speeds. The use of predicted values, the degree of training of the subjects and the degree of familiarization with treadmill running may
explain some of the variation between the different studies. The values obtained in the present study are very similar to those reported by other authors. They are slightly higher (excluding the predicted values) than those shown in table 4.6, which may be explained by the use of experienced runners by the authors of the studies cited.

Despite the slightly lower oxygen cost of running in the female group, when the energy expenditure per unit body weight and time (Kcal.kg\(^{-1}\).min\(^{-1}\)) of the two sexes were compared, the differences did not reach statistical significance during either submaximal horizontal or grade running, although the female values were again slightly lower than the male values (figures 4.3 and 4.4). This finding provides further weight to the evidence in the literature which suggests that there is no difference in the energy demands of running in male and female athletes (Daniels et al., 1977). The average energy cost (Kcal.kg\(^{-1}\).min\(^{-1}\)) for the male subjects in the present study, although slightly higher, are comparable to those reported by Mayhew (1977) for 9 highly trained male runners.

As regards running performance, it appears that the greater \(\dot{V}O_2\) max value displayed by the male subjects would give them a clear advantage in endurance events. This is supported by the significantly faster 2 mile run time for the males (p < 0.001). The males and females covered the distance at the mean times of 11.88 ± 0.57 and 15.08 ± 2.44 minutes respectively. During the time trial the average predicted oxygen cost was 53.11 ± 2.68 ml.kg\(^{-1}\).min\(^{-1}\) for the male subjects and 44.35 ± 6.30 ml.kg\(^{-1}\).min\(^{-1}\) for the female subjects. When expressed as a percentage of \(\dot{V}O_2\) max this corresponded approximately to 89% \(\dot{V}O_2\) max in both sexes (table 4.4). This value was not corrected for air resistance and is therefore probably a slight underestimate of the average relative work load at which the time trial was run. The subjects were therefore probably running in excess of 90% \(\dot{V}O_2\) max.

The predictions made in this and the above studies are based on the ability to equate treadmill data with data collected in the field.
Mckmiken and Daniels (1976) demonstrated that at treadmill speeds up to 4.3 m sec\(^{-1}\) (258 m min\(^{-1}\)) there is no difference between the oxygen cost of running on the track or on the treadmill. This questions the work of Pugh (1970) on the effect of air resistance on oxygen consumption. Since the mean running speeds for the male and female subjects in this study were 4.5 ± 0.2 and 3.6 ± 0.6 m sec\(^{-1}\) respectively, the majority of the predictions made were within the speed range suggested by Mckmiken and Daniels (1976).

In addition, the predicted values for the percentage utilization of maximum oxygen uptake during the 2 mile time trial, without the correction for air resistance, are similar to the values reported by other workers. For example, 92-93% VO\(_2\)\(_{\text{max}}\) (Costill and Fox, 1969) and 82-110% VO\(_2\)\(_{\text{max}}\) (Farrell et al., 1979).

Despite an average use of approximately 89% VO\(_2\)\(_{\text{max}}\) over the 2 mile distance, all subjects in this study ran the first and last 400 metres at speeds faster than during the rest of the test distance. During the first and last minutes of the time trial the subjects utilized approximately 95-96% VO\(_2\)\(_{\text{max}}\) (table 4.5, figure 4.7) with some subjects achieving speeds in excess of 100% VO\(_2\)\(_{\text{max}}\). This shows that the 2 mile time trial is short enough to include some anaerobic contribution to energy production particularly in the early and latter stages. However, for the majority of the time trial, the work was performed submaximally and therefore aerobically. Lawson and Golding (1978) showed that this event was essentially aerobic in nature by demonstrating a high correlation between the 2 mile run time and VO\(_2\)\(_{\text{max}}\). In addition, they found that none of the indicators of anaerobic energy production included in their study correlated with the 2 mile time trial, suggesting that the ability to supply energy anaerobically did not limit performance. However, 2 subjects in their study ran the time trial in excess of 100% VO\(_2\)\(_{\text{max}}\), which indicates that over this distance some individuals may supplement their aerobic energy production with anaerobic energy production.
A high correlation (r = -0.90, p < 0.001) was found between \( \dot{V}O_2 \) max and 2 mile run time in the present study (table 4.7, figure 4.5). This relationship remained when the male and female values were analysed separately; the correlations for the two sexes being r = -0.82 (p < 0.001) and r = -0.87 (p < 0.001) respectively. Consequently the relationship between average running speed during the 2 mile run and \( \dot{V}O_2 \) max was also highly significant (figure 4.6). This relationship between \( \dot{V}O_2 \) max and running time in a group of individuals with a wide range of \( \dot{V}O_2 \) max values has been demonstrated by numerous investigators (Costill, 1967; Costill et al., 1973; Lawson and Golding, 1978; Foster et al., 1979; Farrell et al., 1979) (table 4.7).

However, when a homogeneous group of individuals with respect to \( \dot{V}O_2 \) max has been studied, the relationship between running ability and \( \dot{V}O_2 \) max disappears (Costill et al., 1971; Briggs, 1977; Conley and Krahenbuhl, 1980). Under such circumstances it is clear that factors other than \( \dot{V}O_2 \) max influence performance, since \( \dot{V}O_2 \) max alone does not discriminate between those with the fastest and slowest times over a limited range of high speeds. Despite the highly significant inverse relationship between \( \dot{V}O_2 \) max and 2 mile time in a group of individuals with a range of \( \dot{V}O_2 \) max values, the shortcomings of \( \dot{V}O_2 \) max for determining endurance capacity are evident. In the present study, for example, the female subjects 5 and 7 had similar \( \dot{V}O_2 \) max values (60.7 and 59.7 ml.kg\(^{-1}\).min\(^{-1}\) respectively), but their 2 mile run times differed considerably. Subjects 5 and 7 completed the distance in 12.58 and 10.98 minutes respectively. No. 7 achieved a faster run time by utilizing a larger fraction of her \( \dot{V}O_2 \) max (93% compared to 85% \( \dot{V}O_2 \) max by No. 5). This is an example of 2 runners very similar with respect to \( \dot{V}O_2 \) max, running experience and the type of training in which they engaged. Despite their similarities, the ability of 7 to utilize a larger fraction of her \( \dot{V}O_2 \) max probably explains the different performance times.

Another example is provided by the female subjects 10 and 1, who also had similar \( \dot{V}O_2 \) max values (40.6 and 42.9 ml.kg\(^{-1}\).min\(^{-1}\) respectively). No. 1 utilized 92% \( \dot{V}O_2 \) max during the time trial, completing
the distance in 16.20 minutes, and 10 utilized 80% \( \dot{V}O_2 \) max during the time trial, completing the distance in 19.04 minutes. Again, the faster time was achieved by the greater fractional utilization of \( \dot{V}O_2 \) max. This may be the result of the different training programmes in which these individuals were involved. The slower runner (10) was a games player and did not participate in endurance training, whereas the faster runner (1') participated in a heavy endurance training programme for swimming. Her training programme may, in part, be responsible for her ability to tax a larger fraction of her \( \dot{V}O_2 \) max. Similar examples are also evident in the results of the male group of runners and are consistent with the findings of other investigators. Costill and coworkers, for example, found no relationship between \( \dot{V}O_2 \) max and marathon running performance in a group of individuals with similar \( \dot{V}O_2 \) max values (Costill et al., 1971). They also found that the previous world record holder over the marathon distance had a \( \dot{V}O_2 \) max value that was below average for top class runners, but that he could sustain 86% of his \( \dot{V}O_2 \) max over the complete marathon distance. They concluded that, although a high \( \dot{V}O_2 \) max is of crucial importance for success in distance running, the ability to utilize a large fraction of it, is also important. The ability to sustain a high % \( \dot{V}O_2 \) max for prolonged periods appears to be largely a function of the degree of training, and provides perhaps a better index of "endurance fitness" for a particular individual than \( \dot{V}O_2 \) max alone. This is especially important when studying the influence of training on active rather than sedentary individuals, because the training induced improvements in \( \dot{V}O_2 \) max are relatively small (Astrand and Rodahl, 1977, p.318). An example of the influence of training on running performance and the \( \dot{V}O_2 \) max values of active individuals has recently been reported by Daniels, Yarborough and Foster (1978). They subjected highly trained runners to an 8 week training programme of a greater volume and intensity than that to which they were accustomed. All the subjects may, through training, have reached the ceiling of their aerobic potential because after 8 weeks their \( \dot{V}O_2 \) max remained unchanged. However, their ability to cover 2 miles in a faster time indicated that as a result of the training programme they were able to tax a larger percentage of their \( \dot{V}O_2 \) max. Such improvements point to peripheral adaptation and indicate
again that factors other than \( \dot{V}O_2 \) max influence endurance capacity. Londeree and Ames (1975) considered that \( \dot{V}O_2 \) max, as a measure of endurance capacity on its own, is inadequate, and stated that

"for a given \( \dot{V}O_2 \) max it is impossible to know whether the subject has a lot of ability and is "out of shape", if he has little ability and is in "good shape", or if he possesses an intermediate level of ability and is in "moderately good shape".

Furthermore, available evidence suggests that heredity has a greater influence than training on an individual's capacity for oxygen transport (Astrand and Rodahl, 1977, p. 319). Thus when individuals with a wide range of \( \dot{V}O_2 \) max values perform a 2 mile time trial and run at approximately similar percentages of their \( \dot{V}O_2 \) max values, as shown in the present study, then the results are largely predetermined. Therefore while the 2 mile time trial may be a useful field test for identifying those individuals in the population who have high, average or low \( \dot{V}O_2 \) max values, it is an inadequate test of endurance capacity. Training-induced improvements in \( \dot{V}O_2 \) max and endurance capacity may be better evaluated by recording how long an individual is able to exercise while utilizing a large proportion of his \( \dot{V}O_2 \) max. In this way the adaptations to training can be evaluated without giving an advantage to individuals with either high or low \( \dot{V}O_2 \) max values.

4.5

**SUMMARY**

1. A high correlation was found between 2 mile run time and \( \dot{V}O_2 \) max (\( r = -0.90 \)). Despite this \( \dot{V}O_2 \) max alone does not explain running performance. Evidence of this is provided in this study by individuals with the same \( \dot{V}O_2 \) max who completed the 2 mile distance in different times.

2. The relative work load at which the 2 mile test was run was predicted from the speed/\( \dot{V}O_2 \) regression equations. Although the average relative energy expenditure during the time trial
corresponded to 89% \( \dot{V}O_2 \) max, individual variation in the ability to tax a high percentage of \( \dot{V}O_2 \) max was found.

3. Although the 2 mile run is essentially aerobic in nature, some individuals were able to run the first and last minutes of the time trial at speeds in excess of 100% \( \dot{V}O_2 \) max.

4. The difference in male and female running time is mainly attributable to differences in \( \dot{V}O_2 \) max since at submaximal speeds, there were essentially no differences in the oxygen cost of running between the two sexes.

5. The above assumptions were made on the basis of equating treadmill data with data collected in the field. Data collected in the field automatically introduces uncontrolled variables. Although applying laboratory data to field data is unavoidable, the inclusion of a laboratory endurance test would have been preferable.

The findings of this study demonstrated that \( \dot{V}O_2 \) max is an important pre-requisite for success in high speed sustained running. Individuals with a modest \( \dot{V}O_2 \) max value would be unable to run at speeds necessary to succeed at the top competitive level however rigorous their training programme, because high speed sustained running requires a high aerobic energy production rate and therefore a high \( \dot{V}O_2 \) max.
CHAPTER 5

THE INFLUENCE OF TRAINING ON MAXIMUM OXYGEN UPTAKE
AND ENDURANCE CAPACITY

5.1

INTRODUCTION

The results reported in Chapter 4 indicate that a 2 mile performance test, while useful as a method for assessing an individual's maximum oxygen uptake as either high or low, does not readily lend itself to an accurate description of an individual's endurance capacity. Endurance capacity being defined as the ability of an individual to utilize a large proportion of his or her \( \dot{V}O_2 \) max for prolonged periods of time.

Thus the present investigation adopted a laboratory based procedure for studying the changes in \( \dot{V}O_2 \) max and endurance capacity after training. In preference to the 2 mile time trial, a submaximal test to exhaustion (at approximately 75% pre-training \( \dot{V}O_2 \) max) on a bicycle ergometer was included before and after training.

To reduce the number of uncontrolled variables, both the pre- and post-training measurements and all training sessions were carried out on a bicycle ergometer in the laboratory.

The advantages of the laboratory test over the 2 mile time trial are several:

1. it can be performed in the laboratory under highly controlled conditions.
2. the subjects could be tested at the same absolute submaximal work load before and after training, allowing the effect of training on the ability to sustain this load to be measured.
3. a submaximal work load could be selected to ensure that anaerobic energy contribution is kept to a minimum.

4. all subjects would be exercising at similar relative work loads.

The bicycle ergometer was used to provide the mode of exercise for several reasons:

1. the activity is restricted to a clearly defined muscle mass whereas in running this varies depending upon style.

2. all individuals can ride a bicycle but running is a more complex skill and therefore running experience through training may influence the changes being measured.

3. the amount of work done on a bicycle ergometer can be measured exactly.

4. the mechanical variation between individuals is smaller during cycling than during running.

The aim of the study was to examine the effects of 5 weeks' endurance training on $\dot{V}O_2$ max and endurance capacity, under highly controlled conditions.

The subjects in the study participated in badminton 3 to 4 times per week, i.e. their habitual activity levels before training were very similar. Thus the effects of the training programme on both $\dot{V}O_2$ max and endurance capacity was studied in a group of individuals with similar activity patterns.

The present study allowed a closer examination of the relationship between $\dot{V}O_2$ max and endurance capacity, i.e. the degree to which the training induced increases in $\dot{V}O_2$ max and endurance capacity can be dissociated.
5.2

METHOD

Eight subjects (6 male and 2 female) volunteered as subjects in the study. The mean age, height and weight of the subjects are presented in table 5.1. All subjects participated in regular physical activity, but none engaged in regular endurance training. The subjects did not alter their habitual physical activity levels, which consisted of playing badminton 3 to 4 times a week, during the experimental period.

Pre-training measurements

Prior to training the subjects were exposed to 3 tests:

1. Familiarization.
2. Continuous loading oxygen uptake test.
3. Endurance test.

1. Familiarization

During the first visit to the laboratory the subjects were familiarized with exercise on a bicycle ergometer and the work capacity of each subject was determined. This was achieved by the use of a continuous exercise test, during which the work load was progressively increased every 2 minutes as described in Chapter 3, section 3.8.1. The subjects continued to exercise until subjective exhaustion was reached. Heart rate was recorded every minute using the cardiometer (described in Chapter 3, section 3.2).

2. Continuous loading oxygen uptake test

The exact nature of this test is described in Chapter 3, section 3.8.1. In Chapter 3, it was stated that expired air collections, using Douglas Bags, were made in the last minute of each 2 minute exercise period. However, in this test, expired air collections were only made
TABLE 5.1

Physical characteristics of the subjects

<table>
<thead>
<tr>
<th>SUBJECT</th>
<th>AGE (yrs)</th>
<th>HEIGHT (cms)</th>
<th>WEIGHT (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>20.0</td>
<td>181.8</td>
<td>74.10</td>
</tr>
<tr>
<td>2</td>
<td>20.1</td>
<td>180.0</td>
<td>69.95</td>
</tr>
<tr>
<td>3</td>
<td>20.1</td>
<td>177.9</td>
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</tr>
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<td>4</td>
<td>23.3</td>
<td>191.2</td>
<td>83.30</td>
</tr>
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<td>5</td>
<td>20.0</td>
<td>174.0</td>
<td>69.50</td>
</tr>
<tr>
<td>6</td>
<td>24.0</td>
<td>188.1</td>
<td>72.85</td>
</tr>
<tr>
<td>7</td>
<td>21.1</td>
<td>166.9</td>
<td>59.25</td>
</tr>
<tr>
<td>8</td>
<td>18.4</td>
<td>154.5</td>
<td>55.05</td>
</tr>
</tbody>
</table>

| MEAN    | 20.6      | 176.8        | 68.04       |
| S.D.    | 1.8       | 11.8         | 8.08        |
at the higher work loads and a Tissot spirometer was used for the collection of expired air samples. In addition, the collections, of which there were a minimum of two, were made over a 30 and not a 60 second period, and the air was passed through a mixing chamber where the oxygen and carbon-dioxide contents were determined by a mass spectrometer probe. The Douglas Bag method was therefore not used. The collections were made on the basis of the results from the familiarization visit.

Prior to the test, the height and weight of the subjects were determined and the electrode placed in position. Pre- and post-exercise capillary blood samples were taken for the determination of blood lactate and blood haemoglobin concentrations. The order of the measurements taken, together with the instructions given to the subjects before the maximum test, are described in Chapter 3, sections 3.6 and 3.8.1. The blood samples were analysed for lactate and haemoglobin concentrations as described in appendix 2.C. The criteria used to indicate that \( \dot{V}O_2 \) max had been reached included:

(a) blood lactate levels in excess of 8 - 9 mM (Astrand and Rodahl, 1977, p.297).

(b) subjective exhaustion.

(c) respiratory exchange ratio in excess of 1.15 (Issekutz et. al., 1962).

3. Endurance test

The subjects exercised to exhaustion on a bicycle ergometer at approximately 75% of their pre-training \( \dot{V}O_2 \) max. The endurance test, together with the instructions given to the subjects, are described in Chapter 3, sections 3.5 and 3.11. The work load designed to elicit 75% \( \dot{V}O_2 \) max was calculated from the 100% work load, i.e. the work load corresponding to \( \dot{V}O_2 \) max. During the test heart rate was recorded every minute and the total work done (kJ) determined.
Training programme

The subjects trained 3 times a week at a work load that corresponded to 75% of their pre-training VO\textsubscript{2} max, over a 6 week period. The nature of the training programme and the measurements made are described in Chapter 3, section 3.12. At least 3 subjects trained together during any one of the training sessions which was a helpful motivational aid. The endurance test outlined above formed the first training session.

During the second week of training, a 2 minute expired air collection using the Douglas Bag technique was made from the 9th to the 11th minute of exercise. From this collection the relative work load (% VO\textsubscript{2} max) at which each subject was exercising was calculated.

Post-training

The maximum oxygen uptake and endurance tests were repeated, following the same protocol as in the pre-training tests. It is important to note that the post-training endurance test was performed at the same absolute work load as the pre-training test (i.e. at a load corresponding to 75% pre-training VO\textsubscript{2} max).

Data analysis

The t-test for correlated data was used to test for differences between the pre- and post-training measurements. Results are presented in the text and in the tables as means and standard deviations (i.e. means ± SD).

5.3

RESULTS

All subjects fulfilled the criteria adopted in this study for obtaining VO\textsubscript{2} max (table 5.2), i.e. a blood LA level in excess of 8 to 9mM and/or an RER value in excess of 1.15.
Training increased $\dot{V}O_2$ max (L.min$^{-1}$) by 6.9%, from $3.18 \pm 0.67$ to $3.39 \pm 0.69$ L.min$^{-1}$ ($p < 0.05$, table 5.3). Despite the significant increase in $\dot{V}O_2$ max, this parameter remained unchanged for some individuals. There was a similar significant increase in $\dot{V}O_2$ max when expressed in ml.kg$^{-1}$.min$^{-1}$ ($p < 0.05$) as body weight remained essentially unchanged throughout training.

With the exception of the above mentioned increases in $\dot{V}O_2$ max (L.min$^{-1}$ and ml.kg$^{-1}$.min$^{-1}$), no other significant increases were found in the measurements made in this study at the maximum level after training (table 5.3). The only exception was a decrease in the respiratory exchange ratio from $1.36 \pm 0.09$ to $1.21 \pm 0.05$ ($p < 0.001$, table 5.3).

However, several performance changes were found during the $\dot{V}O_2$ max test after training. These are illustrated in table 5.4 and the average percentage improvements may be summarized as follows:

(a) exercise time (min) increased by 29.6% ($p < 0.001$).
(b) the work load required to elicit $\dot{V}O_2$ max increased by 17.6% ($p < 0.001$).
(c) the total work (kJ) performed during the test increased by 26.3% ($p < 0.001$).
(d) $PWC_{170}$ increased by 21.7% ($p < 0.001$).

The 6 week training programme increased endurance capacity by 477.6% ($p < 0.001$), from $14.41 \pm 3.88$ to $74.05 \pm 26.27$ minutes (table 5.4). This increase was accompanied by a 478.3% increase in the total work performed (kJ) during the endurance test ($p < 0.001$).

Submaximal heart rate decreased at each work load after training during the 2 minute continuous loading test, reaching the level of statistical significance at all but the lowest work load of 59 watts (table 5.5, figure 5.1).

This trend towards lower heart rate values during submaximal exercise was also found as the training programme progressed, despite
an increase in the training work load over the 6 week period (table 5.6). The heart rate values for 5 subjects were recorded during the post-training endurance test, and when compared with the pre-training values for the same subjects, these values had decreased. The post-training heart rate values recorded between 10 and 70 minutes were all significantly lower than the pre-training value recorded at 10 minutes (table 5.7, figure 5.2).

From the expired air samples collected during the second week of training, the relative work load at which each subject was exercising was calculated. The values for the 8 subjects ranged from 57.6% to 93.6% \( \dot{V}O_2 \) max (table 5.8). The individuals therefore were training at different relative work loads.

A significant relationship was found between training intensity and the percentage increase in \( \dot{V}O_2 \) max (\( r = 0.71, p < 0.05 \)) (table 5.9), but not between training intensity and the percentage increase in endurance capacity (\( r = -0.14 \)).

There were also no relationships between pre-training \( \dot{V}O_2 \) max and the percentage change in \( \dot{V}O_2 \) max (\( r = -0.38 \)), pre-training \( \dot{V}O_2 \) max and pre-training endurance time (\( r = 0.21 \)) or between the percentage change in \( \dot{V}O_2 \) max and the percentage change in endurance capacity (\( r = 0.11 \)). A significant relationship did exist, however, between the percentage increase in the duration of the \( \dot{V}O_2 \) max and endurance tests (\( r = 0.72, p < 0.05 \)) (table 5.9).

A significant relationship also existed between pre-training endurance time and the percentage change in endurance capacity (\( r = -0.78, p < 0.05 \)) (table 5.9).

There was no significant difference between the pre-training haemoglobin concentration of 14.5 g.dl\(^{-1}\) and the post-training value of 14.9 g.dl\(^{-1}\). The percentage improvements in \( \dot{V}O_2 \) max and the duration of the \( \dot{V}O_2 \) max and endurance tests after training are presented in figure 5.3.
TABLE 5.2

Criteria for attaining maximum oxygen uptake

<table>
<thead>
<tr>
<th>SUBJECT</th>
<th>Δ LACTIC ACID mM</th>
<th>RESPIRATORY EXCHANGE RATIO AT VO₂ max</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PRE-TR</td>
<td>POST-TR</td>
</tr>
<tr>
<td></td>
<td>PRE-TR</td>
<td>POST-TR</td>
</tr>
<tr>
<td>1</td>
<td>11.92</td>
<td>9.24</td>
</tr>
<tr>
<td>2</td>
<td>13.14</td>
<td>12.76</td>
</tr>
<tr>
<td>3</td>
<td>12.69</td>
<td>12.63</td>
</tr>
<tr>
<td>4</td>
<td>10.34</td>
<td>13.93</td>
</tr>
<tr>
<td>5</td>
<td>11.94</td>
<td>9.68</td>
</tr>
<tr>
<td>6</td>
<td>10.78</td>
<td>11.99</td>
</tr>
<tr>
<td>7</td>
<td>8.74</td>
<td>8.80</td>
</tr>
<tr>
<td>8</td>
<td>9.62</td>
<td>8.10</td>
</tr>
<tr>
<td>MEAN</td>
<td>11.15</td>
<td>10.89</td>
</tr>
<tr>
<td>S.D.</td>
<td>1.54</td>
<td>2.18</td>
</tr>
</tbody>
</table>

Blood samples taken 4 minutes after exercise.
### TABLE 5.3

Observations during maximum work pre- and post-training (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>PRE-TRAINING</th>
<th>POST-TRAINING</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\dot{V}O_2$ (L.min$^{-1}$)</td>
<td>3.18 ± 0.67</td>
<td>3.39 ± 0.69*</td>
</tr>
<tr>
<td>$\dot{V}O_2$ (ml.kg$^{-1}$min$^{-1}$)</td>
<td>46.28 ± 4.10</td>
<td>48.87 ± 4.62*</td>
</tr>
<tr>
<td>$\dot{V}E$ (L.min$^{-1}$)</td>
<td>110.48 ± 25.94</td>
<td>104.43 ± 25.86</td>
</tr>
<tr>
<td>$\dot{V}CO_2$ (L.min$^{-1}$)</td>
<td>4.25 ± 0.83</td>
<td>4.08 ± 0.88</td>
</tr>
<tr>
<td>$\dot{V}CO_2$ (ml.kg$^{-1}$min$^{-1}$)</td>
<td>62.64 ± 5.01</td>
<td>58.63 ± 6.45</td>
</tr>
<tr>
<td>$\dot{V}E.\dot{V}O_2^{-1}$</td>
<td>35.12 ± 4.84</td>
<td>31.56 ± 4.38</td>
</tr>
<tr>
<td>RER</td>
<td>1.36 ± 0.09</td>
<td>1.21 ± 0.05***</td>
</tr>
<tr>
<td>HR (b.min$^{-1}$)</td>
<td>195.38 ± 7.71</td>
<td>190.13 ± 5.96</td>
</tr>
<tr>
<td>W</td>
<td>250.8 ± 47.4</td>
<td>294.4 ± 50.6***</td>
</tr>
<tr>
<td>Δ LA (nM)</td>
<td>11.15 ± 1.54</td>
<td>10.81 ± 2.32</td>
</tr>
</tbody>
</table>

Level of significance between pre- and post-training values:

* $P < 0.05$

*** $P < 0.001$
### TABLE 5.4

Pre- and post-training performance changes during the maximum oxygen uptake and endurance tests (means ± SD)

<table>
<thead>
<tr>
<th>TEST</th>
<th>PARAMETER</th>
<th>PRE-TRAINING</th>
<th>POST-TRAINING</th>
<th>PERCENTAGE CHANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAXIMUM OXYGEN UPTAKE TEST</td>
<td>$\dot{V}O_2$ max (L.min$^{-1}$)</td>
<td>3.18 ± 0.67</td>
<td>3.39 ± 0.69</td>
<td>6.9 ± 7.0*</td>
</tr>
<tr>
<td></td>
<td>Work time (min)</td>
<td>10.52 ± 1.74</td>
<td>13.63 ± 2.41</td>
<td>29.6 ± 10.1***</td>
</tr>
<tr>
<td></td>
<td>Total work (kJ)</td>
<td>25.05 ± 3.91</td>
<td>31.60 ± 5.60</td>
<td>26.3 ± 12.8***</td>
</tr>
<tr>
<td></td>
<td>Work load at $\dot{V}O_2$ max (watts)</td>
<td>250.8 ± 47.4</td>
<td>294.4 ± 50.6</td>
<td>17.6 ± 5.7***</td>
</tr>
<tr>
<td></td>
<td>$PWC_{170}$ (watts)</td>
<td>176.6 ± 44.8</td>
<td>213.7 ± 50.9</td>
<td>21.7 ± 13.2***</td>
</tr>
<tr>
<td>ENDURANCE TEST</td>
<td>Work time (min)</td>
<td>14.41 ± 3.88</td>
<td>74.05 ± 26.27</td>
<td>477.6 ± 347.7***</td>
</tr>
<tr>
<td></td>
<td>Total work (kJ)</td>
<td>33.00 ± 8.87</td>
<td>169.9 ± 60.20</td>
<td>478.3 ± 344.4***</td>
</tr>
</tbody>
</table>

Levels of significance between pre- and post-training values:

* $P < 0.05$

**$P < 0.001$
TABLE 5.5

Heart rate (b.min\(^{-1}\)) values pre- and post-training determined during the continuous loading oxygen uptake test (means ± SD)

<table>
<thead>
<tr>
<th>WORK LOAD (watts)</th>
<th>PRE-TRAINING</th>
<th>POST-TRAINING</th>
</tr>
</thead>
<tbody>
<tr>
<td>59</td>
<td>119.0 ± 15.0</td>
<td>113.9 ± 17.3</td>
</tr>
<tr>
<td>118</td>
<td>146.1 ± 20.6</td>
<td>134.3 ± 21.7*</td>
</tr>
<tr>
<td>177</td>
<td>170.4 ± 20.8</td>
<td>155.0 ± 22.1***</td>
</tr>
<tr>
<td>206 (7)</td>
<td>181.1 ± 17.9</td>
<td>163.4 ± 16.5***</td>
</tr>
<tr>
<td>235 (6)</td>
<td>183.7 ± 18.3</td>
<td>168.5 ± 13.2**</td>
</tr>
</tbody>
</table>

( ) number of subjects when less than whole group

Level of significance between pre- and post-training values:

* \( P < 0.05 \)

** \( P < 0.02 \)

*** \( P < 0.001 \)
FIG. 5.1 HEART RATE VALUES DETERMINED DURING THE PRE- AND POST-TRAINING CONTINUOUS LOADING EXERCISE TESTS

( ) no. of subjects when less than whole group

. pre- and post-training values statistically different
### TABLE 5.6

Heart rate ($b.min^{-1}$) values recorded weekly during a 6 week training programme (means ± SD)

<table>
<thead>
<tr>
<th>TIME (min)</th>
<th>WEEK 1</th>
<th>WEEK 2</th>
<th>WEEK 3</th>
<th>WEEK 4</th>
<th>WEEK 5</th>
<th>WEEK 6</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>169.3</td>
<td>169.5</td>
<td>158.9</td>
<td>167.3</td>
<td>169.1</td>
<td>165.5</td>
</tr>
<tr>
<td></td>
<td>± 14.5</td>
<td>± 13.3</td>
<td>± 8.9</td>
<td>± 11.1</td>
<td>± 8.6</td>
<td>± 12.1</td>
</tr>
<tr>
<td>10</td>
<td>182.0</td>
<td>176.6</td>
<td>169.9</td>
<td>175.3</td>
<td>176.5</td>
<td>173.9</td>
</tr>
<tr>
<td></td>
<td>± 16.3</td>
<td>± 14.3</td>
<td>± 10.8</td>
<td>± 10.5</td>
<td>± 7.8</td>
<td>± 9.4</td>
</tr>
<tr>
<td>15</td>
<td>180.0</td>
<td>178.8</td>
<td>173.9</td>
<td>177.4</td>
<td>182.4</td>
<td>174.8</td>
</tr>
<tr>
<td></td>
<td>± 15.1 (5)</td>
<td>± 14.0</td>
<td>± 5.8 (7)</td>
<td>± 6.8 (7)</td>
<td>± 7.8</td>
<td>± 7.3 (5)</td>
</tr>
<tr>
<td>20</td>
<td>182.6</td>
<td>173.9</td>
<td>178.0</td>
<td></td>
<td></td>
<td>178.0</td>
</tr>
<tr>
<td></td>
<td>± 13.8 (7)</td>
<td>± 8.1 (7)</td>
<td>± 4.8 (4)</td>
<td></td>
<td></td>
<td>± 9.7 (5)</td>
</tr>
<tr>
<td>25</td>
<td>183.0</td>
<td>177.6</td>
<td></td>
<td></td>
<td></td>
<td>179.3</td>
</tr>
<tr>
<td></td>
<td>± 16.0 (5)</td>
<td>± 6.8 (7)</td>
<td></td>
<td></td>
<td></td>
<td>± 10.4 (4)</td>
</tr>
<tr>
<td>30</td>
<td>190.5</td>
<td>180.8</td>
<td></td>
<td></td>
<td></td>
<td>181.0</td>
</tr>
<tr>
<td></td>
<td>± 10.5 (4)</td>
<td>± 6.7 (6)</td>
<td></td>
<td></td>
<td></td>
<td>± 9.1 (4)</td>
</tr>
</tbody>
</table>

( ) number of subjects when less than whole group

+ 1 subject exercising at higher work load
++ 2 subjects exercising at higher work load
+++ 5 subjects exercising at higher work load
TABLE 5.7

Heart rate (b.min$^{-1}$) values recorded during the pre- and post-training endurance tests (means ± SD)

<table>
<thead>
<tr>
<th>TIME (min)</th>
<th>PRE-TRAINING</th>
<th>POST-TRAINING</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>176.0 ± 8.3</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>190.6 ± 8.0</td>
<td>163.2 ± 10.9***</td>
</tr>
<tr>
<td>20</td>
<td></td>
<td>165.0 ± 12.1***</td>
</tr>
<tr>
<td>30</td>
<td></td>
<td>168.6 ± 14.0**</td>
</tr>
<tr>
<td>40</td>
<td></td>
<td>171.6 ± 15.2*</td>
</tr>
<tr>
<td>50</td>
<td></td>
<td>173.0 ± 15.1*</td>
</tr>
<tr>
<td>60 (4)</td>
<td></td>
<td>169.0 ± 10.4**</td>
</tr>
<tr>
<td>70 (3)</td>
<td></td>
<td>172.7 ± 11.6**</td>
</tr>
</tbody>
</table>

( ) number of subjects when less than whole group

Level of significance between the pre-training 10 min. value and the post-training values recorded between 10 and 70 min:

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$
FIG. 5.2

HEART RATE VALUES DETERMINED DURING THE PRE-AND POST-TRAINING ENDURANCE TESTS

( ) no. of subjects when less than whole group
TABLE 5.8

Training intensity (\(\% \dot{V}O_2 \text{ max}\)) for each subject as determined from expired air collections made in the second week of training

<table>
<thead>
<tr>
<th>SUBJECT</th>
<th>WORK LOAD (watts)</th>
<th>(\dot{V}O_2) (L.min(^{-1}))</th>
<th>(\dot{V}O_2) max (L.min(^{-1}))</th>
<th>% (\dot{V}O_2) max</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>177</td>
<td>2.42</td>
<td>3.25</td>
<td>74.5</td>
</tr>
<tr>
<td>2</td>
<td>177</td>
<td>2.39</td>
<td>3.29</td>
<td>72.6</td>
</tr>
<tr>
<td>3</td>
<td>177</td>
<td>2.44</td>
<td>2.73</td>
<td>89.4</td>
</tr>
<tr>
<td>4</td>
<td>265</td>
<td>3.29</td>
<td>4.26</td>
<td>77.2</td>
</tr>
<tr>
<td>5</td>
<td>206</td>
<td>3.05</td>
<td>3.26</td>
<td>93.6</td>
</tr>
<tr>
<td>6</td>
<td>235</td>
<td>2.23</td>
<td>3.87</td>
<td>57.6</td>
</tr>
<tr>
<td>7</td>
<td>147</td>
<td>2.06</td>
<td>2.55</td>
<td>80.8</td>
</tr>
<tr>
<td>8</td>
<td>118</td>
<td>1.48</td>
<td>2.25</td>
<td>65.8</td>
</tr>
<tr>
<td>MEAN</td>
<td>187.8</td>
<td>2.42</td>
<td>3.18</td>
<td>76.4</td>
</tr>
<tr>
<td>S.D.</td>
<td>46.9</td>
<td>0.56</td>
<td>0.67</td>
<td>11.8</td>
</tr>
</tbody>
</table>
### Table 5.9

Pre- and post-training relationships between $\dot{V}O_2\ max$, training intensity and endurance capacity

<table>
<thead>
<tr>
<th>X</th>
<th>Y</th>
<th>$r$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-training $\dot{V}O_2\ max$</td>
<td>Pre-training endurance time</td>
<td>0.21</td>
</tr>
<tr>
<td>Pre-training $\dot{V}O_2\ max$</td>
<td>Percentage change in $\dot{V}O_2\ max$</td>
<td>-0.38</td>
</tr>
<tr>
<td>Training intensity ($%\ \dot{V}O_2\ max$)</td>
<td>Percentage change in $\dot{V}O_2\ max$</td>
<td>0.71*</td>
</tr>
<tr>
<td>Training intensity ($%\ \dot{V}O_2\ max$)</td>
<td>Percentage change in endurance</td>
<td>-0.14</td>
</tr>
<tr>
<td>Percentage change in $\dot{V}O_2\ max$</td>
<td>Percentage change in endurance</td>
<td>0.11</td>
</tr>
<tr>
<td>Percentage change in duration of $\dot{V}O_2\ max$ test</td>
<td>Percentage change in duration of endurance test</td>
<td>0.72*</td>
</tr>
<tr>
<td>Pre-training endurance time</td>
<td>Percentage change in duration of endurance test</td>
<td>-0.78*</td>
</tr>
<tr>
<td>Pre-training $\dot{V}O_2\ max$ test time</td>
<td>Post-training $\dot{V}O_2\ max$ test time</td>
<td>0.94**</td>
</tr>
</tbody>
</table>

Level of significance between relationships: 

* $P < 0.05$

** $P < 0.01$
FIG. 5.3 PERCENTAGE IMPROVEMENT AFTER TRAINING IN \( \dot{\text{VO}}_2 \) \text{max} AND THE DURATION OF THE \( \dot{\text{VO}}_2 \) \text{max} AND ENDURANCE TESTS
5.4

DISCUSSION

The effects of training on $\dot{V}O_2_{\text{max}}$

The group mean maximum oxygen uptake increased by 7% (range -2% to 19%) from 3.88 to 3.39 L.min$^{-1}$ ($p < 0.05$), after 6 weeks training on a bicycle ergometer. This supports the conclusive evidence in the literature that training of the endurance type leads to an increase in $\dot{V}O_2_{\text{max}}$ in previously untrained individuals (Knehr et. al., 1942; Ekblom et. al., 1968; Saltin et. al., 1968; Gleser and Vogel, 1973; Wilmore et. al., 1980; Hickson et. al., 1981).

Although the 7% increase in $\dot{V}O_2_{\text{max}}$ found in the present study is modest, this improvement compares favourably with the findings of several other investigations which have examined the effect of training on $\dot{V}O_2_{\text{max}}$ (Knehr et. al., 1942; Ribisl, 1969; Gleser and Vogel, 1973; Moffatt et. al., 1977; Daniels et. al., 1978).

Daniels, Yarborough and Foster (1979) reported an increase of 10% in $\dot{V}O_2_{\text{max}}$ after 4 weeks' training in a group of previously untrained Physical Education students. Despite an increase in the amount of training after the first 4 weeks, there was no further increase in $\dot{V}O_2_{\text{max}}$. This may be the result of an increase in the duration and not the training intensity of each training session. When an individual is exposed to a given exercise intensity he adapts to that intensity. If further improvements are required, for example in $\dot{V}O_2_{\text{max}}$, the exercise intensity must be increased (Hickson et. al., 1981). The subjects in the study by Daniels and coworkers may have lowered and not increased their intensity of effort in order to achieve the longer duration of the training sessions.
Gleser and Vogel (1973) reported a 6% (range -2% to 12%) increase in $\dot{V}O_2$ max after 9 weeks' training in a group of 8 previously untrained but active males. Both the increase and the variation in the changes in $\dot{V}O_2$ max are very similar to those found in the present investigation, despite their use of a training programme that was of a greater intensity, frequency and duration.

Knehr, Dill and Neufeld (1942) reported an increase of 7% in $\dot{V}O_2$ max after 6 months' training. Despite the 6 month duration of their programme, the increase in $\dot{V}O_2$ max is the same as that reported in the present study after only 6 weeks. Although the authors fail to provide information concerning the intensity of their training programme, the modest increase in $\dot{V}O_2$ max suggests that the subjects were exercising at a low relative work load (% $\dot{V}O_2$ max).

Moffatt and coworkers reported an 8% increase in $\dot{V}O_2$ max in 23 Physical Education students after 10 weeks' endurance training (Moffatt et. al., 1977). This increase compares favourably with that found in the present investigation. The slightly larger improvement in $\dot{V}O_2$ max (10% compared with 7%) may be attributed to their longer training programme and the greater intensity of that programme.

The above examples include training investigations that have reported similar improvements in $\dot{V}O_2$ max to that found in the present study, despite variations in the length of the training programmes and the intensity, frequency and duration of effort within each training session.

Several other investigations, despite being very similar in length to the training programme adopted in this study, have reported much greater increases in $\dot{V}O_2$ max. Hickson, Bomze and Holloszy (1977), for example, reported a 26% increase in $\dot{V}O_2$ max after 6 weeks' training in a group of active but untrained males. This large increase in $\dot{V}O_2$ max may be attributed to the high intensity and frequency of their training programme, which involved exercising 6 days a week on a bicycle ergometer, during which the subjects completed six 5-minute
exercise bouts designed to elicit \( \dot{V}_{O_2} \text{max} \) during that period.

Cunningham and Hill (1975) also reported a large increase in \( \dot{V}_{O_2} \text{max} \) after 9 weeks' training in a group of females. The authors provided little information regarding the intensity of the exercise, but the large increase may be explained by the use of subjects who had low initial \( \dot{V}_{O_2} \text{max} \) values as a result of prior immobilization due to trauma. This explanation is supported by the findings reported in the literature which have shown that the lower the pre-training \( \dot{V}_{O_2} \text{max} \) value the greater the improvement in \( \dot{V}_{O_2} \text{max} \) after training (Pollock, 1973).

Hickson and coworkers demonstrated a much larger increase in \( \dot{V}_{O_2} \text{max} \) over a 6 week training period (19\%) than that found in this study (Hickson et. al., 1981). This again may be the result of the greater intensity and frequency of their training programme.

Pederson and Jørgensen (1978) reported a 14\% increase in \( \dot{V}_{O_2} \text{max} \) after 7 weeks' training in 6 females. Their programme was very similar to that adopted in this study, with regard to its length and the intensity and duration of each training session. Despite these similarities, their subjects showed a greater improvement in \( \dot{V}_{O_2} \text{max} \) (14\% compared to 7\%). This difference is difficult to explain but may be the result of lower initial fitness levels.

The above examples demonstrate that changes in \( \dot{V}_{O_2} \text{max} \) as a result of training vary considerably from study to study. Comparisons between studies should therefore be made with caution, and factors influencing the improvements in \( \dot{V}_{O_2} \text{max} \) should not be ignored. These include: the initial level of fitness and the age of the subjects; the intensity, frequency and duration of each training session, and the length of the programme (Åstrand and Rodahl, 1977, p.426).

Comparison between training studies regarding changes in \( \dot{V}_{O_2} \text{max} \) may be further complicated by biological variations in \( \dot{V}_{O_2} \text{max} \) (Katch, Sady and Freedman, 1982). They found that
"for any one individual \( \dot{V}O_2 \) max can be expected to range ± 5.6%, 68% of the time, and 98% of the time it can vary within a range of ± 11.2%, regardless of whether or not there is an experimental treatment effect".

(Katch, Sady and Freedman, 1982)

However, it must be remembered that these findings are from one laboratory using a small number (n=5) of subjects, and may not necessarily be referred to values determined elsewhere. In our laboratory, no such variations were found from repeated measurements on the same subjects. A large number of subjects repeated the \( \dot{V}O_2 \) max test several times, showing variations that were no greater than ± 2% (Dr. C. Williams - personal communication). Although biological variations cannot be ignored it is suggested that not too much emphasis should be placed on such variations. This suggestion is supported by several other authors (Taylor et. al., 1955; Mitchell et. al., 1958) who reported that, in repeated determinations of \( \dot{V}O_2 \) max on the same subject, the standard deviation, which includes both biological and methodological variables, is only 3 per cent.

The different changes in \( \dot{V}O_2 \) max (-2% to +19%) found in the 8 subjects in the present investigation demonstrates that variations in the changes in \( \dot{V}O_2 \) max after training not only exist between studies, but also between individuals exposed to the same training programme. This emphasizes that care must be taken when examining the effects of training on \( \dot{V}O_2 \) max and also when evaluating the effectiveness of a training programme on the basis of changes in \( \dot{V}O_2 \) max.

Gollnick and coworkers found similar variations in the changes in \( \dot{V}O_2 \) max in a group of 6 male subjects after a 5 month training programme. The average increase in \( \dot{V}O_2 \) max in their study was 13% with a range from 3.6 to 25%. The authors attributed this range to the initial fitness levels of the subjects and the type of training programme adopted (Gollnick et. al., 1973).

Several investigators have demonstrated that changes in \( \dot{V}O_2 \) max are related to the initial level of fitness, this being the pre-training \( \dot{V}O_2 \)
max value (Davies and Knibbs, 1971; Durnin et al., 1960; Saltin et al., 1968; Sharkey, 1970). Sharkey (1970) reported that the percentage increase in \( \dot{V}O_2 \) max was inversely related to the initial \( \dot{V}O_2 \) max value. However, no such relationship was found in the present study. Pre-training \( \dot{V}O_2 \) max values, therefore, cannot explain the variation in the changes in \( \dot{V}O_2 \) max after the 6 week training period. This finding also questions the use of \( \dot{V}O_2 \) max for assessing the initial fitness levels of a group of individuals.

The inter-individual variations in changes in \( \dot{V}O_2 \) max in the present study are most likely to be the result of varying training intensities, since, with the exception of age and initial fitness levels, many investigators consider training intensity to be the most important factor influencing the training response (Crewes and Roberts, 1968; Moffatt et al., 1977; Shephard et al., 1968; Hickson et al., 1977; Hickson et al., 1981). The significant relationship found in the present investigation between training intensity and the percentage change in \( \dot{V}O_2 \) max \( (r = -0.72, p < 0.05) \) provides supportive evidence for this factor. Subjects 5 and 3, who trained at 94% and 89% of their pre-training \( \dot{V}O_2 \) max respectively, demonstrated the greatest increases in \( \dot{V}O_2 \) max, with 5 showing a 19% and 3 a 15% increase. In contrast, an improvement in \( \dot{V}O_2 \) max of only 3% was found in subject 6, who trained at 58% of his pre-training \( \dot{V}O_2 \) max.

From these examples it can be seen that the individuals were training at very different relative work loads (% \( \dot{V}O_2 \) max). This was unintentional as all subjects were set to train at the same relative work load (75% pre-training \( \dot{V}O_2 \) max). However, from expired air samples collected in the second week of training, the subjects were found to be exercising at work loads ranging from 58% to 94% of their pre-training \( \dot{V}O_2 \) max value.

The variation in training intensities may be due to the use of the 2 minute continuous loading test. Two minutes may be inadequate for the oxygen transport system to adjust to a given work load so that when the work load is increased, the subject may still be adjusting to the
lower work load. This might result in the overestimation of the maximum work load from which the training work load was calculated. Thus, although the continuous loading test, may as research shows, yield valid VO\textsubscript{2} max values (Maksud and Coutts, 1971), it might be difficult to establish the work load corresponding to VO\textsubscript{2} max from this test. However, this fails to explain why some subjects were exercising above the prescribed work load while others were exercising below it.

Other factors contributing to the range of training intensities may include:

1. Variation between bicycle ergometers (all Monark).
2. Familiarization with the exercise.
3. Adaptation to the exercise.

Although the range of training intensities may be partly explained by the above mentioned factors, this study suggests that further investigation into the methodology employed for the determination of a given submaximal work load may be necessary.

The very small changes in VO\textsubscript{2} max of 2 to 4% found in 4 of the 8 subjects (one of whom showed a 2% decrease) is difficult to explain. Normally the absence of changes in VO\textsubscript{2} max can be attributed to the use of very highly trained subjects, or to a training programme that provides insufficient stimulus for adaptation to occur. The latter would be the case if the intensity, frequency and duration of each training session were inadequate. However, neither of these factors would appear to exist in this study. None of the subjects was highly trained and the training programme, which involved exercising 3 times a week at approximately 75% pre-training VO\textsubscript{2} max, fulfilled the criteria suggested by "The American College of Sports Medicine" (1973) for developing and maintaining fitness and also the training guidelines summarized by Moffatt and coworkers (Moffatt et. al., 1977). Both suggested, from a review of the literature, that the intensity of training should be above 60% VO\textsubscript{2} max, the duration of each training session should be at least 15 minutes, and that training should take place 3 - 4 times a week.
Only one subject was training below 60% $\dot{V}O_2\max$, as determined from expired air collections made in the second week of training, which may explain his small 3% increase in $\dot{V}O_2\max$. Such a change may be the result of the combined effects of biological and methodological variations (Astrand and Rodahl, 1977, p.298). However, other subjects who also showed improvements in $\dot{V}O_2\max$ of only 3 to 4%, were training at exercise intensities between 70 to 80% of their pre-training $\dot{V}O_2\max$.

The short duration of the training programme (6 weeks) may explain the very small changes in $\dot{V}O_2\max$ found in some subjects. However, examples of increases in $\dot{V}O_2\max$ after 4 weeks (Daniels et. al., 1978) and after 6 weeks (Hickson et. al., 1977, Hickson et. al., 1981) can be found in the literature. It should be mentioned that in these short studies both the training intensity and frequency were greater than that adopted in the present investigation. It is possible that, to produce increases in $\dot{V}O_2\max$ in some subjects when the training period is short, the intensity of exercise should be increased. The increase in $\dot{V}O_2\max$ in the present study of more than 15% in the 2 subjects who trained above 88% of their pre-training $\dot{V}O_2\max$ supports this statement, and is in agreement with the suggestion by The American College of Sports Medicine (1973) that a short high intensity programme is the most suitable for increasing $\dot{V}O_2\max$. This is highlighted by subject 5 who trained at 94% $\dot{V}O_2\max$ and increased his $\dot{V}O_2\max$ by 19%.

Another possible explanation for the variation in the changes in $\dot{V}O_2\max$ after training may be the result of varying rates of adaptation. Some individuals may respond to a training stimulus more rapidly than others.

Despite the variation in changes in $\dot{V}O_2\max$, all subjects demonstrated improved performances during the $\dot{V}O_2\max$ test (table 5.4). The work load required to elicit $\dot{V}O_2\max$ increased by 17.6% ($p < 0.001$) and the duration of the $\dot{V}O_2\max$ test increased by 29.6% ($p < 0.001$). The improvements in the above parameters, which occurred in some subjects in the absence of a change in $\dot{V}O_2\max$, again illustrates that a training
programme should not be evaluated solely on the basis of changes in $\dot{V}O_2$ max. Both the increases in performance time and the work load required to elicit $\dot{V}O_2$ max indicate an increased capacity for exercise on a bicycle ergometer and suggests that, when determining $\dot{V}O_2$ max, performance measurements such as these should also be made as they provide useful additional information. In fact, some investigators have used such performance changes during the $\dot{V}O_2$ max test to measure changes in "endurance capacity" after training (Ekblo\m et. al., 1968; Wilmore et. al., 1980) (table 2.1).

The increased duration of the $\dot{V}O_2$ max test (29.6%) was greater than the improvement reported by Wilmore and coworkers after a 20 week endurance training programme (Wilmore et. al., 1980). The smaller increase cannot be explained by different training programmes because the training programme adopted by Wilmore and coworkers was very similar to that used in the present investigation. The smaller improvement, despite the longer programme, may be the result of difference experimental protocols for the determination of $\dot{V}O_2$ max. In the present study the work load was increased by 59 watts (from 59 watts) every 2 minutes, whereas Wilmore and coworkers increased the work load by 25 watts (from 25 watts) every minute. Few studies have included a measure of exercise time during the $\dot{V}O_2$ max test, and comparison between those that have, is not facilitated by the variety of test protocols used for the determination of $\dot{V}O_2$ max.

The higher work load required to elicit $\dot{V}O_2$ max after training (17.6%) in the present study, is very similar to that reported by Karlsson and coworkers after a 7 month training programme (Karlsson et. al., 1972). Their increase was the same, despite their use of a training programme that was longer in duration, involved exercising at a greater intensity, and produced a much greater improvement in $\dot{V}O_2$ max (24% compared to 7% in the present study).

A possible explanation for the same improvement in the work load required to elicit $\dot{V}O_2$ max in the two studies, despite the use
of different training programmes, may lie in the specificity of training. In the study by Karlsson and coworkers, all laboratory tests were performed on the bicycle ergometer, but training consisted predominantly of running. It would appear that running training greatly increased \( \dot{V}O_2 \text{max} \), but only moderately increased the capacity of the individuals for bicycle exercise. In contrast, all laboratory tests and training in the present investigation were performed on a bicycle ergometer and, even after the short 6 week training programme, the capacity of all the individuals to exercise on a bicycle ergometer had increased, despite the absence of a change in \( \dot{V}O_2 \text{max} \) for some of the subjects. These results support the specificity of training concept, and suggest that bicycle training increases the capacity for exercise on a bicycle ergometer. This specificity of training suggests that peripheral adaptations may be important in increasing the capacity of a group of individuals to perform a given task. When comparing the results of different studies it must be mentioned again that the use of different experimental protocols for the determination of \( \dot{V}O_2 \text{max} \) may influence the findings.

Davis and coworkers reported a 28% increase in the work load required to elicit \( \dot{V}O_2 \text{max} \) after 9 weeks’ training on a bicycle ergometer (Davis et. al., 1979). Despite the use of middle-aged subjects, their increase was greater than that found in the present investigation. The use of totally sedentary subjects, the longer training programme, the greater increase in \( \dot{V}O_2 \text{max} \), and the use of a different protocol for the determination of \( \dot{V}O_2 \text{max} \) may help to explain the difference between the two studies.

Although comparison between studies is difficult, the inclusion of performance measurements during the \( \dot{V}O_2 \text{max} \) test would appear to provide useful additional information regarding the effectiveness of a training programme.
The effects of training on submaximal heart rate

All subjects showed the typical bradycardia of training at submaximal work levels both during and following the programme of endurance training. After training, the heart rate values during the 2 minute continuous loading test were lower at each submaximal work load (figure 5.1).

The heart rate values recorded during training decreased as the training programme progressed, despite increases in the intensity of the exercise. During the sixth week of training the average heart rate values were lower than those monitored during the first week, even though the training work load for all subjects had been increased (table 5.6).

This bradycardia of training was most clearly observed when the pre- and post-training heart rate values, determined for 5 subjects during the endurance tests, were compared. The post-training values between 10 and 70 minutes were all significantly lower than the pre-training value recorded at 10 minutes. The post-training 10 minute value was 27.4 b.min$^{-1}$ (14%) lower than the pre-training value measured at the same time. At 50 minutes the average heart rate value was still 18 b.min$^{-1}$ lower than the pre-training 10 minute value. The decrease at 10 minutes was greater than that reported by Flint, Drinkwater and Horvath (1974), who found a fall in heart rate of 11 b.min$^{-1}$ (8%) at a given submaximal work load after a 6 week training programme. This decrease was smaller than that reported in the present investigation, despite the use of a training programme that was not only the same length as that employed in the present study, but also very similar with respect to the intensity, frequency and duration of each training session. The smaller drop may be the result of the effects of familiarization with the exercise. The subjects were exposed to the exercise task on 4 occasions before any definitive measurements were made. During the 4 exposures heart rate may have decreased, reducing the overall drop found after 6 weeks. This influence of repeated exposure to a given task on heart rate is
supported by the rapid decrease found in this parameter during the first 2 weeks of training in the present investigation. Davies, Tuxworth and Young (1970) reported a marked decline in heart rate of 21 b.min\(^{-1}\) over 4 exposures to exercise at a given submaximal oxygen uptake. Although the above may explain the small decrease reported by Flint and coworkers, it is not easy to distinguish between learning and actual physiological adaptations. The early fall may be the beginning of the training response. However, the effects of repeated exposure to a given task before any definitive measurements are made should not be ignored when making comparisons between training studies.

Larger and more similar decreases in heart rate after training at a given submaximal work load, have been reported by numerous other investigators (Hanson and Nedde, 1974; Ekblom et al., 1968).

The fall in heart rate at a given submaximal work load found in this study is consistent with the findings reported in the literature.

**The effects of training on endurance capacity**

The most striking finding in the present 6 week training study was the large increase in endurance capacity (478%, range 150 - 1163%) \((p < 0.001)\), despite only a modest improvement in \(\dot{V}O_2\) max (7%, \(p < 0.05)\). It is clear that changes in \(\dot{V}O_2\) max do not reflect changes in endurance capacity (figure 5.3).

The absence of simple relationships between pre-training endurance time and pre-training \(\dot{V}O_2\) max \((r = 0.21)\) and between changes in \(\dot{V}O_2\) max and changes in endurance capacity after training \((r = 0.11)\), as found in the present study, indicate that \(\dot{V}O_2\) max alone is an insensitive indicator of endurance capacity.

This training study demonstrated that improvements in endurance capacity can occur in the absence of a change in \(\dot{V}O_2\) max. An example
was provided by subject 2. Training increased his endurance capacity by 1163.2% but did not alter his \( \dot{V}O_2 \text{max} \) (-2%). Another example was provided by subject 6, who improved his endurance capacity by 344.4% and his \( \dot{V}O_2 \text{max} \) by only 3.1%. Other similar examples can also be found in the results of this study, since only 4 of the 8 subjects increased their \( \dot{V}O_2 \text{max} \) by 3 to 4% after training. Such a change in \( \dot{V}O_2 \text{max} \), as mentioned above, may simply be the result of methodological and biological variations and not due to training. The average increase in \( \dot{V}O_2 \text{max} \) (7%) was, therefore, only slightly greater than the variations in \( \dot{V}O_2 \text{max} \) determination.

The large variation in the changes in endurance capacity (150 - 1163.2%) is difficult to explain. Unlike \( \dot{V}O_2 \text{max} \), no simple relationship was found between endurance capacity and training intensity. Training intensity alone does not, therefore, explain the variation in improvements in endurance capacity. This suggests that different factors may influence the changes in \( \dot{V}O_2 \text{max} \) and the changes in submaximal endurance capacity in response to a training programme.

Several authors have suggested that an inverse relationship exists between the capacity being trained, and the individual's initial ability for that capacity. Pollock (1973) reported, for example, that Müller in 1962 found an inverse relationship between the improvement in strength and the initial level of strength. The finding of a significant relationship between pre-training endurance time and the percentage increase in endurance capacity in the present study \( (r = -0.78, p < 0.05) \) provides supportive evidence for the above, and may help to explain the variation in improvements in endurance capacity. However, this is unlikely to account for any more than a little of the variation found in the improvements in this parameter between the 8 subjects after training.

It is difficult to compare the findings of this study with those in the literature because, to the best of the author's knowledge, only two other investigators have included a pre- and post-training endurance test to exhaustion at a fixed submaximal work load (table 2.1).
Karpovich and Pestrecov (1941) reported an average increase in endurance time on a bicycle ergometer of 1355% (range 75 to 4420%) after 6 to 12 weeks of training. Although the authors did not measure $\dot{V}O_2$ max, it is unlikely that the large gain in endurance time would have been accompanied by an equivalent improvement in $\dot{V}O_2$ max, since the greatest increase in $\dot{V}O_2$ max reported, is that by Saltin and coworkers (100%) in a study on bed rest and training. It would appear, therefore, that $\dot{V}O_2$ max alone cannot explain the increase in endurance time reported by Karpovich and Pestrecov (1941).

It is difficult to compare their improvement in endurance capacity with that found in this study because their average value includes measurements made after varying weeks of training.

Gleser and Vogel (1973) reported a 12% increase in $\dot{V}O_2$ max, and a 258% increase in endurance time on a bicycle ergometer whilst exercising at approximately 75% pre-training $\dot{V}O_2$ max, after 4 months' training. Despite the longer training programme, the increase in endurance capacity is less than the 478% improvement found in the present study. The specificity of training concept may explain the difference between the two studies. In this study all tests and training were performed on a bicycle ergometer at a submaximal work load, which corresponded during the majority of the training programme to the work load at which the subjects exercised during the endurance test. The subjects trained at a submaximal work load on a bicycle ergometer, and it was at this work load and during this type of activity that the improvement was found.

In the study by Gleser and Vogel however, the subjects trained twice weekly at 90% $\dot{V}O_2$ max on a bicycle ergometer, and participated in basketball for 3 hours on 2 other days. The training programme adopted by these authors was not as specific to the endurance task as that employed in the present investigation and may explain their smaller reported improvement in endurance capacity (endurance time).
In addition, the higher intensity of their training programme (90% compared to 75% \( \dot{V}O_2 \) max) meant that each training session on the bicycle ergometer would probably have been shorter in duration than that in the present study. To increase submaximal endurance capacity, it is possible that the duration of each training session may be more important than the exercise intensity.

It is evident from the present investigation and the two studies discussed above, that changes in \( \dot{V}O_2 \) max alone cannot explain the variations in the ability of an individual to sustain high intensity submaximal exercise.

The large gain in endurance capacity may be the result of adaptations in the skeletal muscle, i.e. an enhanced oxidative capacity (Collnick et. al., 1973) (Chapter 2, section 2.3.6). This would result in the improved extraction of oxygen by the exercising muscles and a higher \( \dot{V}O_2 \) max after training. However, improvements in \( \dot{V}O_2 \) max during exercise with a large muscle mass may be limited by the cardiovascular system's capacity for oxygen transport (Davies and Sargeant, 1975). Therefore, changes in the skeletal muscle leading to an increased ability to extract oxygen, may only be reflected by small or modest improvements in \( \dot{V}O_2 \) max, as is suggested by the findings in this study.

Under conditions where the cardiovascular system is not limiting, i.e. during exercise with a limited muscle mass, training induced adaptations in the skeletal muscles may be more closely reflected by changes in \( \dot{V}O_2 \) max.
5.5

SUMMARY

1. The 6 week training programme increased $\dot{V}O_2$ max by 7% and endurance capacity by 478% indicating that $\dot{V}O_2$ max alone cannot explain the large gain in endurance capacity.

2. No relationship was found between pre-training $\dot{V}O_2$ max and pre-training endurance capacity ($r = 0.21$) or between the percentage improvement in $\dot{V}O_2$ max and the percentage improvement in endurance capacity after training ($r = 0.11$), suggesting that $\dot{V}O_2$ max is an insensitive indicator of endurance capacity.

3. A significant relationship was found between training intensity and improvements in $\dot{V}O_2$ max after training ($r = 0.71$, $p < 0.05$) supporting the findings reported in the literature that a short, high intensity programme is probably the most effective for increasing $\dot{V}O_2$ max (American College of Sports Medicine, 1973; Pollock, 1973; Hickson et. al., 1978).

4. Both the work load required to elicit $\dot{V}O_2$ max and the duration of the $\dot{V}O_2$ max test increased after training indicating that such performance measurements provide the investigator with useful additional information regarding the effectiveness of a training programme.

5. A significant relationship was found between the percentage increase in the duration of the $\dot{V}O_2$ max and endurance tests ($r = 0.72$, $p < 0.05$), indicating again the usefulness of making performance measurements during the $\dot{V}O_2$ max test, particularly if the inclusion of a performance test, as in this study, is impractical.

6. Submaximal heart rate values decreased significantly after training during both the continuous loading oxygen uptake and endurance tests, supporting the typical bradycardia of training reported in the literature.
The findings of this study suggest that improvements in endurance capacity are not reflected by changes in $\dot{V}O_2$ max. Maximum oxygen uptake, therefore, should not be the sole criterion for evaluating the effectiveness of a training programme.

It is concluded that $\dot{V}O_2$ max alone does not reflect endurance capacity in a group of individuals before and after training because, as demonstrated in the present study, from the measurement of $\dot{V}O_2$ max it is impossible to know whether the individual possesses a high, average or low endurance capacity.
INTRODUCTION

The improvements in maximum oxygen uptake (\(\dot{V}O_2\) max) after training are modest when compared with the improvements in endurance capacity as shown in the study described in the previous chapter (Chapter 5). The modest improvements in \(\dot{V}O_2\) max may be attributable to the limited adaptability of the cardiovascular system to deliver oxygen to the working muscles.

When exercise is performed with a limited muscle mass, e.g. one leg, the capacity of the cardiovascular system for oxygen transport is not exceeded. Under these conditions, larger training - induced improvements in \(\dot{V}O_2\) max of individually exercised limbs occur (14%) than when the two limbs are exercised simultaneously (5%) (Davies and Sargeant, 1975). Thus it appears that the adaptive response of the skeletal muscles for oxygen extraction are greater than that of the cardiovascular system for oxygen transport.

The relative improvements in the central cardiovascular system and the peripheral skeletal muscles in response to training may be usefully explored by using a one-legged exercise model (Davies and Sargeant, 1975). Only one leg is trained while the other leg acts as the untrained control and yet both legs share a common cardiovascular system.
Improvements in the endurance capacity of the trained limb would be the result of both central and peripheral adaptations, while improvements in the endurance capacity of the untrained limb would be the result of central adaptations only.

Therefore, the aim of the present study was to re-examine the relationship between $\dot{V}O_2$ max and endurance capacity after training and to attempt to describe the proportional contribution of central and peripheral adaptations to improvements in endurance capacity.

6.2

METHOD

Eight Physical Education students (3 male and 5 female) participated as subjects in the study. The mean age, height and weight of the subjects are presented in table 6.1. All individuals participated in regular physical activity, but none engaged in endurance training. The subjects did not alter their habitual activity levels during the experimental period.

Pre-training measurements

Prior to training the subjects were exposed to 4 tests:

1. Familiarization.
2. Four minute continuous loading oxygen uptake test.
3. Discontinuous oxygen uptake test.
4. Endurance test.

1. Familiarization

During the first visit to the laboratory the subjects were familiarized with one-legged bicycle exercise. This was achieved by the use of a continuous exercise test during which the work load was progressively increased every 4 minutes as described in Chapter 3,
TABLE 6.1

Physical characteristics of the subjects

<table>
<thead>
<tr>
<th>SUBJECT</th>
<th>AGE (yrs)</th>
<th>HEIGHT (cms)</th>
<th>WEIGHT (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>20.5</td>
<td>180.3</td>
<td>82.10</td>
</tr>
<tr>
<td>2</td>
<td>20.1</td>
<td>170.2</td>
<td>54.57</td>
</tr>
<tr>
<td>3</td>
<td>22.6</td>
<td>178.8</td>
<td>71.40</td>
</tr>
<tr>
<td>4</td>
<td>20.4</td>
<td>164.4</td>
<td>59.50</td>
</tr>
<tr>
<td>5</td>
<td>34.3</td>
<td>165.0</td>
<td>64.50</td>
</tr>
<tr>
<td>6</td>
<td>20.4</td>
<td>173.2</td>
<td>67.90</td>
</tr>
<tr>
<td>7</td>
<td>21.2</td>
<td>169.5</td>
<td>60.04</td>
</tr>
<tr>
<td>8</td>
<td>20.6</td>
<td>178.8</td>
<td>73.75</td>
</tr>
</tbody>
</table>

| MEAN    | 22.5      | 172.5        | 66.83       |
| S.D.    | 4.8       | 6.3          | 8.91        |
section 3.8.1. The subjects continued to exercise until subjective exhaustion was reached. This test was performed by both the right and left legs. The special arrangements for one-legged cycling are described in Chapter 3, section 3.2.

2. Four minute continuous loading oxygen uptake test

The exact nature of this test, which was performed by both the right and left legs, is described in Chapter 3, section 3.8.1. This test was performed to determine one-legged VO₂ max and the oxygen uptake/work load relationship during one-legged exercise. From this test the training work load was estimated. The order of the measurements taken, together with the instructions given to the subjects before the VO₂ max test, are described in Chapter 3, sections 3.6 and 3.8.1. The expired air samples were analysed and oxygen uptake calculated using standard formulae for the open circuit Douglas Bag method and expressed in L.min⁻¹ or ml.kg⁻¹.min⁻¹ (appendix 2.B).

3. Discontinuous oxygen uptake test

This test was performed within 3 days of the incremental test and was designed to establish and confirm the VO₂ max values determined during that test. This test was again performed by both the right and left legs and is fully described in Chapter 3, section 3.8.2. The one-legged VO₂ max value was accepted if the two values determined during the continuous and discontinuous tests did not exceed a difference of 5% (Davies and Sargeant, 1974).

4. Endurance test

The subjects exercised to exhaustion on a bicycle ergometer at approximately 80% one-legged VO₂ max. The endurance test, together with the measurements made and the instructions given to the subjects, are described in Chapter 3, sections 3.11 and 3.5. A minimum period of 48 hours elapsed between the testing of both the right and left legs.
Data analysis

The data was subdivided into the following 5 sections:

1. Pre-training.
2. Post-training.
3. Pre- versus post-training: \( \hat{V}O_{2} \) max test.

Pre-training data

The t-test for uncorrelated data was used to test for differences between the right and left legs. Significance was accepted at the \( \cdot 05 \) level.

Post-training data

The t-test for uncorrelated data was used to test for differences between the trained and untrained legs. Significance was accepted at the \( \cdot 05 \) level.

Pre- versus post-training data

The t-test for correlated data was used to test for differences between the pre- and post-training data. Significance was accepted at the \( \cdot 05 \) level. N.B. When analysing the respiratory and heart rate values determined during the pre- and post-training endurance tests, the values determined from 8 to 10 minutes were used. The 8 to 10 minute values were selected because the subjects should be in the steady-state condition. At 4 to 6 minutes, it is unlikely that this condition would have been reached and by 14 to 16 minutes the measurements may be influenced by the changes taking place during prolonged submaximal exercise.
Pre-, mid- and post-training data

The t-test for correlated data was used to test for differences between the pre- and mid-training endurance tests and between the mid- and post-training endurance tests. Comparisons between the tests (as above) were made from the respiratory and heart rate values determined from 8 to 10 minutes of exercise. Significance was accepted at the .05 level.

Training data

A time course study was made difficult because of alterations in the training work loads at different times for different subjects during the 5 week period. This made it impractical to analyse statistically the changes in heart rate during the training programme.

Body weight, perceived rate of exertion and subjective onset of sweating were recorded weekly. A one-way analysis of variance for repeated measures was used to test for differences over the 5 week period. Significance was accepted at the .05 level.

All data are presented in the text and in the tables and figures as means and standard deviations (i.e. means ± SD).

6.3

PRELIMINARY METHODOLOGICAL INVESTIGATIONS

The 4 minute continuous loading oxygen uptake test, for the determination of both one-legged $\dot{V}O_2$ max and a given submaximal training work load, was adopted in the present study on the basis of two preliminary investigations. These studies involved:

1. a comparison of the 2 minute continuous and the 4 minute discontinuous loading oxygen uptake tests for the determination of both $\dot{V}O_2$ max and a given submaximal work load (two-legged exercise).
2. a 4 minute continuous loading oxygen uptake test and a discontinuous oxygen uptake test for the determination of one-legged $\dot{V}O_2$ max and a given submaximal work load (one-legged exercise).

The details of these studies are fully reported in the appendices (1.A and 1.B).

Summary of the findings from the above studies

1. Continuous and discontinuous loading oxygen uptake tests during two-legged ergometry

The 2 tests showed no differences at the maximum level in the following parameters: $\dot{V}O_2$, HR, VE, $VE.\dot{V}O_2^{-1}$ and RER. No significant differences were found between the 2 tests in the oxygen uptake and heart rate values determined at each submaximal work load. This suggests that the relationships between both $\dot{V}O_2$ and work load and between HR and work load were the same during the 2 tests.

During the 10 minute exercise tests (described in Chapter 3, section 3.10), at the predicted 75% work loads (calculated using linear regression equations as described in appendix 2.E) as determined from the continuous and discontinuous data, the subjects were found to be exercising at $76.6 \pm 4.8$ and $76.2 \pm 2.3\% \dot{V}O_2$ max respectively. Although both tests were highly accurate at predicting the 75% $\dot{V}O_2$ max work load, the range of values around the mean was greater when the data from the continuous loading test was used (appendix 1.A).

2. A 4 minute continuous loading oxygen uptake test and a discontinuous oxygen uptake test during one-legged ergometry

Although the above tests were performed during two- as opposed to one-legged exercise, because of the small differences found between them, it was decided to employ the faster continuous loading test.
The 2 minute continuous loading test used above was increased to a 4 minute continuous loading test on the basis of the findings during two-legged exercise, and because of the evidence that 4 to 5 minutes is required to elicit the steady-state condition (Astrand and Rodahl, 1977, p. 357). The exercise work load was increased every 4 minutes by 29 watts (from 29 watts) up to 118 watts, after which the work load increments were reduced to 15 watts. The smaller increases at the higher work loads were made on the basis of preliminary measurements carried out on 3 of the 5 male subjects in the investigation, during which it was found that an increase of 29 watts terminated the test because the subject simply was not strong enough to turn the pedal. Under these circumstances one-legged \( \dot{V}O_2 \) max for that person may not have been reached. When the work load was increased by 15 watts however, the subject could cope with the work load producing a higher measured \( \dot{V}O_2 \) max.

No significant differences were found between the measurements made at the maximum level during the continuous and discontinuous tests and no significant differences were found between the right and left legs at this level. The one-legged \( \dot{V}O_2 \) max values from the continuous and discontinuous tests were 2.59 ± 0.29 and 2.68 ± 0.39 L.min\(^{-1}\) respectively for the right leg, and 2.61 ± 0.41 and 2.74 ± 0.40 L.min\(^{-1}\) respectively for the left leg.

No differences were found between the right and left legs in the oxygen uptake or heart rate values determined at each submaximal work load. As would be expected, therefore, the calculated work loads for the elicitation of 75% one-legged \( \dot{V}O_2 \) max were the same for both legs. The calculated values were 121.1 ± 14.8 and 119.8 ± 13.7 watts for the right and left legs respectively.

From the oxygen uptake measurements made at 4 to 6 minutes during the 10 minute exercise tests (described in Chapter 3, section 3.10), the subjects were calculated to be exercising at 75.7 ± 3.0 and 72.9 ± 3.2% one-legged \( \dot{V}O_2 \) max with the right and left legs respectively. The oxygen uptake values, from which these percentages were calculated, were the same for both the right and left legs.
On the basis of the above findings, which are reported in greater detail in appendix 1.B, the 4 minute continuous loading oxygen uptake test was considered sufficient for both the determination of \( \dot{V}O_2 \) max and the estimation of a submaximal training work load during one-legged exercise.

6.4

RESULTS

PRE-TRAINING: \( \dot{V}O_2 \) MAX TEST

No differences were found between the right leg (RL) and the left leg (LL) prior to training on all measurements made during one-legged cycling at both submaximal and maximal levels (table 6.2 and figures 6.1 and 6.2). The mean \( \dot{V}O_2 \) max values for the RL and the LL were 2.21 ± 0.36 and 2.16 ± 0.28 L.min\(^{-1}\) respectively (table 6.2). Although the relationship between \( \dot{V}O_2 \) (L.min\(^{-1}\)) and work load (watts) was essentially linear, there was a tendency for \( \dot{V}O_2 \) (L.min\(^{-1}\)) to increase disproportionately with work load at the higher work loads.

The absence of any differences during exercise with the right and left legs allowed the random allocation of each leg to the trained or untrained groups. When the trained (experimental) and untrained (control) legs were compared before training, no differences were found between the two legs during exercise. The \( \dot{V}O_2 \) max values for the trained (TL) and untrained (UTL) legs were 2.16 ± 0.29 and 2.21 ± 0.34 L.min\(^{-1}\) respectively (table 6.3).

The one-legged \( \dot{V}O_2 \) max value taken in this study was the highest recorded value determined from either the continuous or the discontinuous oxygen uptake tests, provided the difference between the two values was less than 5%. The discontinuous test produced the majority of these \( \dot{V}O_2 \) max values.
The maximum heart rate values determined during the one-legged oxygen uptake tests were $176.9 \pm 9.5$ (b.min$^{-1}$) for the TL and $176.5 \pm 10.5$ (b.min$^{-1}$) for the UTL (table 6.3).

The duration of the 4 minute continuous loading oxygen uptake test was the same for the TL and the UTL. The average test time for the TL was $14.71 \pm 1.80$ minutes and $14.09 \pm 2.37$ minutes for the UTL.

**PRE-TRAINING ENDURANCE TEST**

The work load required to elicit 80% VO$_2$ max with one leg, as extrapolated from each subject's oxygen uptake/work load relationship, was the same for the RL and the LL. The mean values were $103.1 \pm 11.3$ and $102.4 \pm 9.5$ watts respectively (table 6.4).

No differences were found between the RL and the LL on all measurements made during the pre-training endurance test (table 6.4). The ability of each leg to sustain approximately 80% one-legged VO$_2$ max was the same. The average test time for the RL was $17.80 \pm 5.28$ minutes and $19.19 \pm 3.67$ minutes for the LL. The blood lactate and blood glucose levels, together with the perceived rate of exertion (PRE) determined at the end of the test were the same for the right and left legs. The blood lactate (LA mM) concentrations for the RL and the LL were $6.95 \pm 1.48$ and $7.54 \pm 2.14$ mM respectively. The oxygen uptake values (L.min$^{-1}$) determined from 4 to 6 minutes were also the same for both the RL and the LL, and did not differ from the estimated 80% VO$_2$ max value (table 6.4).

Again the absence of any differences between the RL and the LL, allowed the random allocation of each leg to the trained and untrained groups. Comparisons between the TL and the UTL prior to training during the endurance test also showed no differences (table 6.5).

The work load required to elicit 80% one-legged VO$_2$ max was the same for the TL and the UTL ($102.4 \pm 9.4$ and $103.2 \pm 11.3$ watts respectively) and the ability of each leg to sustain approximately 80% one-legged VO$_2$
max was the same. The mean test times were 17.18 ± 4.80 and 19.67 ± 3.96 minutes for the TL and UTL respectively. The blood lactate and glucose levels, together with the PRE, were the same during exercise with the TL and the UTL at the end of the endurance test. The blood LA levels at the end of the test were 6.96 ± 1.92 mM for the TL and 7.53 ± 1.77 mM for the UTL. From the expired air samples collected from 4 to 6 minutes during the endurance test, the subjects were calculated to be exercising at 83.8 ± 1.6 and 80.3 ± 5.8% one-legged \( \dot{V}O_2 \) max, with the TL and UTL respectively. The oxygen uptake values (L.min\(^{-1}\)) determined from 4 to 6 minutes were the same during exercise with the TL and the UTL (table 6.5).

**Summary**

No differences were found between the right and left legs prior to training on all measurements made at both submaximal and maximal levels. This allowed the random allocation of the right and left legs to training. No differences were also found between the trained (TL) and untrained (UTL) legs on all measurements made before training. All subjects fulfilled the criterion for \( \dot{V}O_2 \) max, that is, a difference of less than 5% between two measured values. The 4 minute continuous loading oxygen uptake test permitted the accurate calculation of the work load required to elicit 80% one-legged \( \dot{V}O_2 \) max.

**POST-TRAINING: \( \dot{V}O_2 \) MAX TEST**

No difference was found between the \( \dot{V}O_2 \) max values determined during exercise with the TL and the UTL after training. The mean values were 2.40 ± 0.35 and 2.30 ± 0.35 L.min\(^{-1}\) respectively (table 6.6). No differences were also found between the two legs in any of the parameters determined in this study at the maximum level (table 6.6).

The duration of the 4 minute continuous loading oxygen uptake test was greater during exercise with the TL than with the UTL (p < 0.05). The mean \( \dot{V}O_2 \) max test times were 20.82 ± 2.49 minutes for the TL and 17.80 ± 3.15 minutes for the UTL (table 6.6).
No differences were also found between the two legs after training during the continuous loading test at the submaximal level.

The differences found during the endurance test between the TL and UTL after training, will be reported below.

Summary

With the exception of the duration of the 4 minute continuous loading VO\(_2\) max test, no statistically significant differences were found between the TL and the UTL during exercise at the maximum level after training.

**PRE- Versus Post-Training: VO\(_2\) Max Test**

The VO\(_2\) max values increased during exercise with the TL and the UTL after training. During exercise with the TL VO\(_2\) max increased by 11.2% (from 2.16 ± 0.29 to 2.40 ± 0.35 L.min\(^{-1}\)) (p < 0.001) and by 4.4% (from 2.21 ± 0.34 to 2.30 ± 0.35 L.min\(^{-1}\)) (p < 0.05) during exercise with the UTL (table 6.7). The net percentage increase in VO\(_2\) max of the TL over the UTL was therefore 6.8% (table 6.10).

No changes were found after training during exercise with either leg in any of the other parameters determined at the maximum level. The duration of the VO\(_2\) max test increased by 43.8% during exercise with the TL (p < 0.001) and by 29.8% during exercise with the UTL (p < 0.05) (table 6.7). The net percentage improvement of the TL over the UTL was therefore 14% (table 6.10). The work load (watts) required to elicit VO\(_2\) max also increased during exercise with the TL and the UTL. However, this increase only reached the level of statistical significance during exercise with the TL (p < 0.05). The maximum work load increased by 16.8% and 7.5% during exercise with the TL and the UTL respectively (table 6.7).

During the 4 minute continuous loading oxygen uptake test, the absolute work loads (watts) at which the subjects exercised were the
same before and after training, allowing direct comparisons to be made at each of the submaximal work loads. With the exception of heart rate (HR), no differences were found during exercise with either leg after training in any of the parameters determined at each work load. During exercise with the TL and the UTL, the HR values were significantly lower at the work loads of 98 watts and above (figures 6.3 and 6.4). Pre-exercise HR decreased from 76.3 ± 6.9 to 67.4 ± 4.0 b.min⁻¹.

Summary

The $\dot{V}O_2$ max values (L.min⁻¹) increased during exercise with the TL and the UTL, as did the duration of the $\dot{V}O_2$ max test (min). In both cases the magnitude of the increase was greatest during exercise with the TL. The work load (watts) required to elicit $\dot{V}O_2$ max increased only during exercise with the TL. No other changes were found at the maximum level during exercise with either leg.

At the submaximal level $\dot{V}O_2$ (L.min⁻¹) remained unchanged after training but heart rate showed a significant fall during exercise with the TL and the UTL at the higher work loads after training.

PRE-VERSUS POST-TRAINING: ENDURANCE TEST

Endurance capacity

The 5 week training programme resulted in a 523% (from 17.21 ± 4.78 to 101.88 ± 15.57 minutes) ($p < 0.001$) improvement in the ability of the TL to sustain the original 80% one-legged $\dot{V}O_2$ max work load. The UTL also showed an improvement in endurance capacity of 118.9% (from 19.78 ± 3.98 to 43.52 ± 36.28 minutes) (table 6.7). This increase, however, was not statistically significant and the net percentage improvement of the TL over the UTL was 404% (table 6.7).

The improvements in endurance capacity were large when contrasted with the improvements in $\dot{V}O_2$ max after training. This is clearly
illustrated in figure 6.5 which shows the changes in: \( \dot{V}O_2 \) max; the duration of the \( \dot{V}O_2 \) max test and endurance capacity during exercise with the TL and the UTL after training. This figure also illustrates very clearly the larger increase in the endurance capacity of the TL \((p < 0.001)\) compared with the smaller improvement in the endurance capacity (NS) of the UTL after training.

The significant improvement in the endurance capacity of the TL remained, even when the improvement of the UTL for each individual was taken into account and subtracted from their TL improvement \((p < 0.001)\). When calculated in this way the endurance capacity of the TL increased by 239.1% \((from 17.21 \pm 4.78 to 58.36 \pm 35.02 \text{ minutes})\). The large increase in the endurance capacity of the TL leg resulted in a significant difference between the post-training endurance times of the TL and the UTL \((p < 0.001)\) \(\text{(table 6.8)}\).

**Blood lactate (LA) concentration**

Blood lactic acid concentration fell significantly during exercise with TL and the UTL after training. This comparison was made between the pre-training value determined in the last minute of the endurance test and the equivalent time in the post-training test \(\text{(table 6.7)}\). Blood LA concentration during exercise with the TL decreased by 31.1% \((from 6.96 \pm 1.92 to 4.65 \pm 1.51 \text{ mM})\) \((p < 0.001)\) and by 19.8% during exercise with the UTL \((from 7.53 \pm 1.77 to 6.04 \pm 1.63 \text{ mM})\) \((p < 0.001)\). The net percentage decrease in the blood LA concentration of the TL over the UTL was therefore 11.3% \(\text{(table 6.10)}\). During exercise with the TL and the UTL, blood LA concentration increased significantly during the first 15 minutes of exercise, after which the blood lactate concentration decreased during the remainder of the exercise period \(\text{(figures 6.6 and 6.7)}\). This was most clearly shown during exercise with the TL in the post-training endurance test \(\text{(figure 6.6)}\). During this test the decrease in blood LA concentration from the first measurement \(\text{(excluding the pre-exercise measurement)}\) to the last measurement was statistically significant \((p < 0.001)\). It is not known whether this pattern would have occurred during exercise with the UTL in the
post-training endurance test, because of the inability of this leg to sustain the work load. A small decrease in blood lactate concentration (excluding the pre-exercise measurement) did occur between the first and second blood lactate measurements (figure 6.7) but this fall did not reach the level of statistical significance. The larger fall in blood lactate concentration during exercise with the TL resulted in a significant difference between the post-training blood lactate values for the TL and the UTL (p < 0.05) (table 6.8).

**Blood glucose concentration**

Blood glucose concentration (mM) decreased only during exercise with the TL after training (p < 0.01). This comparison was made between the pre-training value determined in the last minute of the endurance test and the equivalent time in the post-training test. Blood glucose concentration decreased by 14.3% during exercise with the TL (from 4.81 ± 0.44 to 4.11 ± 0.30 mM) (table 6.7).

**Perceived rate of exertion**

The perceived rate of exertion (PRE), recorded when blood lactate and blood glucose measurements were made, decreased during exercise with the TL and the UTL leg after training (table 6.7). The PRE value fell by 37.0% (from 18.4 ± 0.7 to 11.6 ± 2.1) (p < 0.001) during exercise with the TL, and by 8.1% (from 18.8 ± 0.5 to 17.3 ± 1.6) during exercise with the UTL (p < 0.01). The net percentage fall in the PRE of the TL compared with the UTL was 28.9% (table 6.10). The larger fall in PRE during exercise with the TL compared with the UTL resulted in a significant difference in the PRE values between the two legs after training (p < 0.001). The post-training values for the TL and the UTL were 11.6 ± 2.1 and 17.3 ± 1.6 respectively (table 6.8).

**The submaximal respiratory and heart rate responses**

When analysing the respiratory and heart rate values during the pre- and post-training endurance tests, the values obtained from 8 to
10 minutes will be reported (table 6.9). The 8 to 10 minute values were selected because the subjects should be in the steady-state condition. At 4 to 6 minutes it is unlikely that this condition would have been reached and by 14 to 16 minutes the measurements may be influenced by the changes taking place during prolonged submaximal exercise. During the post-training endurance test, the following parameters were all lower during exercise with the TL but not the UTL after 5 weeks' training: \( \dot{V}O_2 \) (L.min\(^{-1}\)), \( \dot{V}E \) (L.min\(^{-1}\)), \( \dot{V}CO_2 \) (L.min\(^{-1}\)) and \( \dot{V}E \cdot \dot{V}O_2 \) (table 6.9). The RER values remained the same during exercise with the TL and the UTL and HR (b.min\(^{-1}\)) decreased during exercise with the TL and the UTL after training (table 6.9). The absolute work loads at which the subjects were exercising during the pre- and post-training endurance tests were the same, allowing the direct comparison above to be made (table 6.9).

### The oxygen cost of one-legged exercise

The oxygen cost of one-legged exercise with the TL decreased by 12.8% (from 1.93 ± 0.29 to 1.66 ± 0.17 L.min\(^{-1}\)) (p < 0.001). During exercise with the UTL the oxygen cost of one-legged exercise only decreased by 1.6%, demonstrating a greater fall for the TL of 11.2% (table 6.9). This decrease during exercise with the TL compared with the UTL resulted in a significant difference in the \( \dot{V}O_2 \) values between the two legs after training (table 6.8). The post-training values for the TL and the UTL were 1.66 ± 0.17 and 1.81 ± 0.33 (L.min\(^{-1}\)) respectively (table 6.8). This fall in the oxygen cost of one-legged exercise, together with the increased \( \dot{V}O_2 \) max values found during exercise with the TL and the UTL reported above (table 6.7), resulted in the subjects exercising at a lower relative work load after training. In the pre-training endurance tests the subjects were exercising at 89.2 ± 2.8% and 83.2 ± 5.9% one-legged \( \dot{V}O_2 \) max with the TL and the UTL respectively. After training the subjects were exercising at 69.6 ± 4.9% one-legged \( \dot{V}O_2 \) max with the TL and 78.4 ± 6.4% one-legged \( \dot{V}O_2 \) max with the UTL (table 6.9).
Ventilation (\(\dot{V}E\))

The \(\dot{V}E\) (L.min\(^{-1}\)) value during exercise with the TL decreased by 28.8% (from 62.10 ± 14.24 to 43.69 ± 8.86 L.min\(^{-1}\)) (\(p < 0.001\)). Although a fall in the ventilation also occurred during exercise with the UTL, this was of a much smaller magnitude (5.3%) and did not reach the level of statistical significance (table 6.9). The net percentage decrease in the \(\dot{V}E\) of the TL over the UTL was 23.5%.

The submaximal heart rate (HR) response

The HR values decreased during exercise with the TL and the UTL after training. During exercise with the TL, HR decreased by 10.3% (from 171.5 ± 9.0 to 154.8 ± 7.5 b.min\(^{-1}\)) (\(p < 0.001\)) and by 6.0% (from 169.8 ± 7.5 to 160.1 ± 9.8 b.min\(^{-1}\)) during exercise with the UTL (\(p < 0.001\)) (table 6.9). Although HR decreased during exercise with the TL and the UTL, the magnitude of the fall was again greater for the TL. The net percentage decrease in the HR of the TL over the UTL was 4.3% (table 6.10).

Ventilatory equivalent (\(\dot{V}E.\dot{V}O_2\)\(^{-1}\))

During exercise with the TL, the \(\dot{V}E.\dot{V}O_2\)\(^{-1}\) value decreased by 16.9% (from 31.96 ± 5.15 to 26.43 ± 3.87) (\(p < 0.05\)). A decrease of only 4.6% was found during exercise with the UTL and this fall was not statistically significant (table 6.9).

Respiratory exchange ratio (RER)

During exercise with the TL and the UTL the RER values decreased by 2.4% and 1.5% respectively (table 6.9). These decreases, however, did not reach the level of statistical significance.

A summary of the percentage improvements during exercise with the TL and the UTL in selected parameters after training, together with the net improvement of the TL over the UTL are presented in table 6.10.
The responses to training reported above during exercise with the TL and the UTL were determined from measurements made after 8 to 10 minutes of exercise. Similar changes were also found after 4 to 6 and 14 to 16 minutes of exercise. For example, if $\dot{V}E$ decreased significantly only during exercise with the TL after 8 to 10 minutes of exercise, this parameter also decreased significantly only during exercise with this leg after 4 to 6 and 14 to 16 minutes of exercise. Tables 6.11 to 6.16 and figures 6.8 to 6.12 clearly illustrate this. The above direct statistical comparisons between the pre- and post-training data could be made because the subjects exercised at the same absolute work load during both the pre- and post-training endurance tests (table 6.17).

Figures 6.8 to 6.12 show the nature of the responses taking place before and after training during prolonged one-legged submaximal exercise with the TL and the UTL in the following parameters: $\dot{V}O_2$, $\%$ one-legged $\dot{V}O_2$ max, $\dot{V}E$, HR and RER. These parameters essentially remained stable over the exercise period, particularly during exercise with the TL after training. The only exceptions being the oxygen cost of one-legged exercise, which increased significantly from 4-6 to 8-10 minutes of exercise ($p < 0.01$) (figure 6.8), and the gradual fall in the RER values over the exercise period (figure 6.12). During exercise with the TL in the post-training endurance test, the RER value determined after 90 minutes of exercise was significantly lower than the value determined after 16 minutes of exercise ($p < 0.01$) (figure 6.12). The RER values also decreased significantly in the post-training endurance test during exercise with the UTL.

**Summary**

The physiological changes found after training during exercise with the TL were accompanied by smaller changes during exercise with the UTL. In the case of $\dot{V}O_2$ max, the duration of the $\dot{V}O_2$ max test, blood lactate concentration, perceived rate of exertion and heart rate, these smaller changes reached the level of statistical significance.
The following parameters changed significantly during exercise only with the TL after training: the work load required to elicit \( \dot{V}O_2 \) max; endurance capacity; blood glucose concentration; \( \dot{V}O_2 \) (L.min\(^{-1}\)); \( \dot{V}E \) (L.min\(^{-1}\)); \( \dot{V}CO_2 \) (L.min\(^{-1}\)) and \( \dot{V}E.\dot{V}O_2 \) \(^{-1}\).

The RER values remained unchanged after training during exercise with the TL and the UTL.

PRE-, MID- AND POST-TRAINING ENDURANCE TESTS

The mid-training endurance test (time limit 30 minutes) which was performed only by the TL, was included to provide some insight into the time course of the training adaptations.

Blood lactate concentration and PRE comparisons were made between the pre-training values determined in the last minute of exercise, and the equivalent time in the mid- and post-training endurance tests. The fall in blood LA concentration was significant between both the pre- and mid-training tests \((p < 0.01)\) and between the mid- and post-training tests \((p < 0.001)\). Blood LA concentration decreased from \(6.96 \pm 1.92\) mM in the pre-training test to \(5.46 \pm 1.51\) and \(4.65 \pm 1.51\) mM in the mid- and post-training tests respectively (table 6.18, figure 6.13).

The PRE values fell from \(18.4 \pm 0.7\) in the pre-training test to \(13.4 \pm 2.3\) \((p < 0.001)\) and \(11.6 \pm 2.1\) \((p < 0.05)\) in the mid- and post-training tests respectively (table 6.18).

As above, the respiratory and heart rate values determined at 8 to 10 minutes will be reported. The oxygen cost of one-legged submaximal exercise decreased by 11.2% \((from 1.93 \pm 0.29 to 1.70 \pm 0.2 \text{ L.min}^{-1})\) \((p < 0.01)\) between the pre- and mid-training endurance tests. The decrease between the mid- and post-training tests was considerably smaller \((2.1%)\) and did not reach the level of statistical significance. The larger fall between the pre- and mid-training tests is clearly illustrated in figure 6.14.
The VE values showed a very similar adaptative response. This parameter decreased by 20.6% (from 62.10 ± 14.24 to 49.11 ± 12.55 L.min\(^{-1}\)) \((p < 0.01)\) between the pre- and mid-training tests. The decrease between the mid- and post-training tests was much smaller (9.6%) and also did not reach the level of statistical significance (table 6.18, figure 6.15).

The HR values again showed the same adaptative response over the 5 week training period. Heart rate decreased by 8.2% (from 171.5 ± 9.0 to 156.5 ± 12.0 b.min\(^{-1}\)) \((p < 0.01)\) between the pre- and mid-training tests. The fall between the mid- and post-training tests was small (1.9%) and not statistically significant (table 6.18, figure 6.16).

The \(\dot{V}E.\dot{V}O_2\) values decreased by 10.6% (from 31.96 ± 5.15 to 28.51 ± 4.97) \((p < 0.01)\) between the pre- and mid-training tests, and by only 6.8% between the mid- and post-training tests. Again the adaptation to training occurred mainly during the first half of the training of the programme (table 6.18).

The \(\dot{V}CO_2\) values did not differ significantly from test to test, but the larger decrease was again found in the first half of the training programme (table 6.18).

The RER values remained unchanged from test to test, as did the absolute work load (watts) at which the subjects were exercising. The absence of a change in the absolute work load allowed the direct comparisons above to be made between each endurance test.

**Summary**

The adaptations to training clearly occurred mainly during the first half of the training programme, i.e. during the first 2.5 weeks. This was most evident in the following three parameters: heart rate, ventilation and the oxygen cost of submaximal one-legged exercise (figures 6.14 to 6.16).
The blood LA concentration, PRE and ˙VCO₂ values continued to fall throughout the training programme, but again, the magnitude of the changes were smaller during the second half of the programme.

A summary of the percentage changes occurring between the pre- and mid- and between the mid- and post-training endurance tests are presented in table 6.19.

GENERAL SUMMARY

1. Prior to training no differences were found between the right and left legs, or between the legs allocated to the trained or untrained groups, during one-legged exercise at both submaximal and maximal levels.

2. The ˙VO₂ max values increased during exercise with the TL (p < 0.001) and with the UTL (p < 0.05).

3. The duration of the 4 minute continuous loading oxygen uptake test also increased during exercise with the TL and the UTL, with the magnitude of the increase being greater for the TL.

4. The work load required to elicit ˙VO₂ max after training increased significantly during exercise only with the TL.

5. During the ˙VO₂ max test, oxygen uptake did not change at each of the submaximal work loads after training, but heart rate decreased during exercise with the TL and the UTL at the work loads of 98 watts and above.

6. The endurance capacity of the TL increased by 523% (p < 0.001) and by 118.9% (NS) in the UTL. When the improvement in the endurance capacity of the UTL for each individual was subtracted from the improvement in the TL, the increased endurance capacity of the TL remained statistically significant (p < 0.001). Here the UTL was used strictly as a control and when calculated in this way the endurance capacity of the TL increased by 239% after training.
7. During the endurance test the following parameters decreased significantly only during exercise with the TL after training: $\dot{V}O_2$ (i.e. the oxygen cost of one-legged submaximal exercise); $\dot{V}E$, $\dot{V}CO_2$ and $\dot{V}E.\dot{V}O_2^{-1}$.

8. Blood lactate concentration, PRE and heart rate decreased significantly during exercise with the TL and the UTL during the endurance test. Despite this, the magnitude of the falls were considerably greater for the TL. This can be seen when the blood lactate and PRE values for the TL and the UTL are compared after training. Both parameters were significantly lower for the TL.

9. The RER values remained unchanged after training during exercise with the TL and the UTL.

10. When the time course of the adaptive changes were analysed, although the adaptive processes continued throughout training, the greatest changes occurred during the first half of the training programme (table 6.19).

Finally, the physiological changes found after training during exercise with the TL were accompanied by smaller changes during exercise with the UTL.
TABLE 6.2

Pre-training maximum values for the right and left legs

(means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>RIGHT LEG</th>
<th>LEFT LEG</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\dot{V}O_2$ (L.min$^{-1}$)</td>
<td>2.21 ± 0.36</td>
<td>2.16 ± 0.28</td>
</tr>
<tr>
<td>$\dot{V}E$ (L.min$^{-1}$)</td>
<td>81.41 ± 16.10</td>
<td>85.56 ± 19.21</td>
</tr>
<tr>
<td>$\dot{V}CO_2$ (L.min$^{-1}$)</td>
<td>2.48 ± 0.46</td>
<td>2.49 ± 0.34</td>
</tr>
<tr>
<td>RER</td>
<td>1.14 ± 0.05</td>
<td>1.14 ± 0.04</td>
</tr>
<tr>
<td>$\dot{V}E.\dot{V}O_2^{-1}$</td>
<td>37.23 ± 5.17</td>
<td>39.50 ± 5.54</td>
</tr>
<tr>
<td>HR (b.min$^{-1}$)</td>
<td>175.8 ± 9.30</td>
<td>177.4 ± 10.53</td>
</tr>
<tr>
<td>W</td>
<td>129.1 ± 14.0</td>
<td>129.2 ± 12.5</td>
</tr>
<tr>
<td>$\dot{V}O_2$ max test time (min)</td>
<td>14.47 ± 1.91</td>
<td>14.17 ± 2.35</td>
</tr>
</tbody>
</table>
FIG. 6.1  THE OXYGEN COST OF ONE-LEGGED CYCLING

\[ \dot{V}O_2 (L.min^{-1}) \]

Work Load (watts)
FIG. 6.2  HEART RATE VALUES FOR THE RIGHT AND LEFT LEGS DETERMINED DURING THE PRE-TRAINING CONTINUOUS LOADING EXERCISE TEST

( ) no. of subjects when less than whole group

---

HEART RATE (b.min⁻¹)

Work Load (watts)
TABLE 6.3

Pre-training maximum values for the trained (TL) and untrained (UTL) legs (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>TL</th>
<th>UTL</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1}))</td>
<td>2.16 ± 0.29</td>
<td>2.21 ± 0.34</td>
</tr>
<tr>
<td>( \dot{V}E ) (L.min(^{-1}))</td>
<td>85.56 ± 19.21</td>
<td>85.07 ± 15.60</td>
</tr>
<tr>
<td>( \dot{V}CO_2 ) (L.min(^{-1}))</td>
<td>2.44 ± 0.44</td>
<td>2.54 ± 0.35</td>
</tr>
<tr>
<td>RER</td>
<td>1.14 ± 0.04</td>
<td>1.14 ± 0.05</td>
</tr>
<tr>
<td>( \dot{V}E.\dot{V}O_2 )(^{-1})</td>
<td>37.27 ± 5.36</td>
<td>39.46 ± 5.38</td>
</tr>
<tr>
<td>HR (b.min(^{-1}))</td>
<td>176.6 ± 9.5</td>
<td>176.5 ± 10.5</td>
</tr>
<tr>
<td>W</td>
<td>128.3 ± 13.9</td>
<td>130.1 ± 12.7</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) max test time (min)</td>
<td>14.71 ± 1.80</td>
<td>14.09 ± 2.37</td>
</tr>
</tbody>
</table>
TABLE 6.4

Physiological responses and performance time determined during the pre-training endurance test for the right and left legs (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>RIGHT LEG</th>
<th>LEFT LEG</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predicted 80% one-legged $\dot{V}O_2$ max (L.min$^{-1}$)</td>
<td>1.77 ± 0.29</td>
<td>1.73 ± 0.22</td>
</tr>
<tr>
<td>$\dot{V}O_2$ (L.min$^{-1}$) at 4-6 min.</td>
<td>1.83 ± 0.26</td>
<td>1.76 ± 0.28</td>
</tr>
<tr>
<td>Predicted 80% work load (watts)</td>
<td>103.1 ± 11.3</td>
<td>102.4 ± 9.5</td>
</tr>
<tr>
<td>Work load (watts) at 4-6 min.</td>
<td>104.6 ± 12.4</td>
<td>105.7 ± 10.8</td>
</tr>
<tr>
<td>% one-legged $\dot{V}O_2$ max at 4-6 min</td>
<td>83.1 ± 3.8</td>
<td>80.0 ± 5.1</td>
</tr>
<tr>
<td>Endurance test time (min)</td>
<td>17.80 ± 5.28</td>
<td>19.19 ± 3.67</td>
</tr>
<tr>
<td>Lactic acid (mM) at end of test</td>
<td>6.95 ± 1.48</td>
<td>7.54 ± 2.14</td>
</tr>
<tr>
<td>Glucose (mM) at end of test</td>
<td>4.72 ± 0.34</td>
<td>5.03 ± 0.62</td>
</tr>
<tr>
<td>PRE at end of test</td>
<td>18.5 ± 0.5</td>
<td>18.6 ± 0.7</td>
</tr>
</tbody>
</table>

NB Predicted values are included for direct comparison with actual values.
Physiological responses and performance time determined during the pre-training endurance test, for the trained (TL) and untrained (UTL) legs (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>TL</th>
<th>UTL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predicted 80% one-legged $\dot{V}O_2$ max (L/min)</td>
<td>1.73 ± 0.25</td>
<td>1.77 ± 0.28</td>
</tr>
<tr>
<td>$\dot{V}O_2$ (L/min) at 4-6 min.</td>
<td>1.81 ± 0.24</td>
<td>1.77 ± 0.29</td>
</tr>
<tr>
<td>Predicted 80% work load (watts)</td>
<td>102.4 ± 9.4</td>
<td>103.2 ± 11.3</td>
</tr>
<tr>
<td>Work load (watts) at 4-6 min.</td>
<td>102.5 ± 9.3</td>
<td>107.5 ± 13.0</td>
</tr>
<tr>
<td>% one-legged $\dot{V}O_2$ max at 4-6 min.</td>
<td>83.8 ± 1.6</td>
<td>80.3 ± 5.8</td>
</tr>
<tr>
<td>Endurance test time (min)</td>
<td>17.18 ± 4.80</td>
<td>19.67 ± 3.96</td>
</tr>
<tr>
<td>Lactic acid (mM) at end of test</td>
<td>6.96 ± 1.92</td>
<td>7.53 ± 1.77</td>
</tr>
<tr>
<td>Glucose (mM) at end of test</td>
<td>4.81 ± 0.44</td>
<td>4.90 ± 0.55</td>
</tr>
<tr>
<td>PRE at end of test</td>
<td>18.4 ± 0.7</td>
<td>18.8 ± 0.5</td>
</tr>
</tbody>
</table>

NB Predicted values are included for direct comparison with actual values
TABLE 6.6

Post-training maximum values for the trained (TL) and untrained (UTL) legs (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>TL</th>
<th>UTL</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\dot{V}O_2$ (L.min$^{-1}$)</td>
<td>2.40 ± 0.35</td>
<td>2.30 ± 0.35</td>
</tr>
<tr>
<td>$\dot{V}E$ (L.min$^{-1}$)</td>
<td>92.55 ± 21.13</td>
<td>83.59 ± 14.17</td>
</tr>
<tr>
<td>$\dot{V}CO_2$ (L.min$^{-1}$)</td>
<td>2.78 ± 0.40</td>
<td>2.59 ± 0.35</td>
</tr>
<tr>
<td>RER</td>
<td>1.16 ± 0.03</td>
<td>1.16 ± 0.04</td>
</tr>
<tr>
<td>$\dot{V}E\cdot\dot{V}O_2^{-1}$</td>
<td>38.85 ± 5.52</td>
<td>37.81 ± 6.75</td>
</tr>
<tr>
<td>HR (b.min$^{-1}$)</td>
<td>180.9 ± 5.9</td>
<td>174.1 ± 6.3</td>
</tr>
<tr>
<td>$W$</td>
<td>149.2 ± 18.9</td>
<td>142.4 ± 15.7</td>
</tr>
<tr>
<td>$\dot{V}O_2$ max test time (min)</td>
<td>20.82 ± 2.49</td>
<td>17.80 ± 3.15*</td>
</tr>
</tbody>
</table>

Level of significance between the TL and UTL after training:

* $P < 0.05$
TABLE 6.7

\( \dot{V}O_2 \) max, endurance time and other selected parameters determined during the pre- and post-training endurance tests for the trained (TL) and untrained (UTL) legs (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>LEG</th>
<th>PRE-TR</th>
<th>POST-TR</th>
<th>Δ</th>
<th>PERCENTAGE CHANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \dot{V}O_2 ) max (L.min(^{-1}))</td>
<td>TL</td>
<td>2.16 ± 0.29</td>
<td>2.40 ± 0.35</td>
<td>0.24</td>
<td>11.2 ± 7.4***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>2.21 ± 0.34</td>
<td>2.30 ± 0.35</td>
<td>0.09</td>
<td>4.4 ± 4.6*</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) max test Time (min)</td>
<td>TL</td>
<td>14.53 ± 1.71</td>
<td>20.79 ± 2.51</td>
<td>6.26</td>
<td>43.8 ± 15.3***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>13.93 ± 2.26</td>
<td>17.78 ± 3.15</td>
<td>3.85</td>
<td>29.8 ± 27.7*</td>
</tr>
<tr>
<td>Work load (watts) at ( \dot{V}O_2 ) max</td>
<td>TL</td>
<td>128.3 ± 13.9</td>
<td>149.2 ± 18.9</td>
<td>20.9</td>
<td>16.8 ± 14.3*</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>130.1 ± 12.7</td>
<td>142.4 ± 15.7</td>
<td>9.8</td>
<td>7.5 ± 10.4</td>
</tr>
<tr>
<td>Endurance Time (min)</td>
<td>TL</td>
<td>17.21 ± 4.78</td>
<td>101.88 ± 15.57</td>
<td>84.7</td>
<td>523.0 ± 146.6***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>19.78 ± 3.98</td>
<td>43.52 ± 36.28</td>
<td>23.8</td>
<td>118.9 ± 161.4</td>
</tr>
<tr>
<td>Lactate (mM) +</td>
<td>TL</td>
<td>6.96 ± 1.92</td>
<td>4.65 ± 1.51</td>
<td>2.31</td>
<td>31.1 ± 21.0***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>7.53 ± 1.77</td>
<td>6.04 ± 1.63</td>
<td>1.63</td>
<td>19.8 ± 9.1***</td>
</tr>
<tr>
<td>Glucose (mM) +</td>
<td>TL</td>
<td>4.81 ± 0.44</td>
<td>4.11 ± 0.30</td>
<td>0.70</td>
<td>14.3 ± 11.4**</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>4.90 ± 0.55</td>
<td>4.79 ± 1.12</td>
<td>0.11</td>
<td>1.8 ± 20.8</td>
</tr>
<tr>
<td>Perceived rate of exertion +</td>
<td>TL</td>
<td>18.4 ± 0.7</td>
<td>11.6 ± 2.1</td>
<td>6.8</td>
<td>37.0 ± 9.1***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>18.8 ± 0.5</td>
<td>17.3 ± 1.6</td>
<td>1.5</td>
<td>8.1 ± 6.7**</td>
</tr>
</tbody>
</table>

+ values determined in the last minute of the pre-training test and the corresponding time in the post-training test

Level of significance between pre- and post-training values:

* \( P < 0.05 \)

** \( P < 0.01 \)

*** \( P < 0.001 \)
HEART RATE VALUES FOR THE TRAINED LEG DETERMINED DURING THE PRE- AND POST TRAINING CONTINUOUS LOADING EXERCISE TESTS

( ) no. of subjects when less than whole group
. pre- and post-training values statistically significant
FIG. 6.4 HEART RATE VALUES FOR THE UNTRAINED LEG DETERMINED DURING THE PRE- AND POST-TRAINING CONTINUOUS LOADING EXERCISE TESTS

( ) no. of subjects when less than whole group
. pre- and post-training values statistically different
FIG. 6.5 PERCENTAGE IMPROVEMENT AFTER TRAINING IN $\dot{V}O_2$ max AND THE DURATION OF THE $\dot{V}O_2$ max AND ENDURANCE TESTS FOR THE TRAINED AND UNTRAINED LEGS

Trained Leg

Untrained Leg

- $\dot{V}O_2$ max
- $\dot{V}O_2$ max Test Time
- Endurance Time

/// local factors
/// central factors
TABLE 6.8

Physiological responses and performance time determined during the post-training endurance test for the trained (TL) and untrained (UTL) legs (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>TL</th>
<th>UTL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Endurance test time (min)</td>
<td>101.88 ± 15.57</td>
<td>43.52 ± 36.28***</td>
</tr>
<tr>
<td>Lactic acid (mM)</td>
<td>4.65 ± 1.51</td>
<td>6.04 ± 1.63*</td>
</tr>
<tr>
<td>Perceived rate of exertion</td>
<td>11.6 ± 2.1</td>
<td>17.3 ± 1.6***</td>
</tr>
<tr>
<td>$\dot{V}O_2$ (L.min$^{-1}$)</td>
<td>1.66 ± 0.17</td>
<td>1.81 ± 0.33*</td>
</tr>
<tr>
<td>$\dot{V}E$ (L.min$^{-1}$)</td>
<td>43.69 ± 8.86</td>
<td>55.57 ± 19.34</td>
</tr>
<tr>
<td>$\dot{V}CO_2$ (L.min$^{-1}$)</td>
<td>1.69 ± 0.20</td>
<td>1.88 ± 0.37</td>
</tr>
<tr>
<td>RER</td>
<td>1.02 ± 0.06</td>
<td>1.04 ± 0.05</td>
</tr>
<tr>
<td>$\dot{V}E.\dot{V}O_2^{-1}$</td>
<td>26.43 ± 3.87</td>
<td>30.43 ± 3.04</td>
</tr>
<tr>
<td>HR (b.min$^{-1}$)</td>
<td>154.8 ± 7.5</td>
<td>160.1 ± 9.8</td>
</tr>
<tr>
<td>W</td>
<td>103.4 ± 9.9</td>
<td>104.4 ± 12.4</td>
</tr>
</tbody>
</table>

* values determined in the last minute of the pre-training test and the corresponding time in the post-training test

Level of significance between the TL and UTL after training:

* $P < 0.05$

*** $P < 0.001$
FIG. 6.6 BLOOD LACTATE CONCENTRATIONS FOR THE TRAINED LEG DETERMINED DURING THE PRE- AND POST-TRAINING ENDURANCE TESTS

( ) no. of subjects when less than whole group
. pre- and post-training values statistically different
FIG. 6.7 BLOOD LACTATE CONCENTRATIONS FOR THE UNTRAINED LEG DETERMINED DURING THE PRE- AND POST-TRAINING ENDURANCE TESTS

( ) no. of subjects

- pre- and post-training values statistically different

---

Lactic Acid (mM)

Time (min.)
Table 6.9

Respiratory and heart rate values determined during the pre- and post-training endurance tests for the trained (TL) and untrained (UTL) legs (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>LEG</th>
<th>PRE-TR</th>
<th>POST-TR</th>
<th>Δ</th>
<th>PERCENTAGE CHANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\dot{V}O_2$ (L.min$^{-1}$)</td>
<td>TL</td>
<td>1.93 ± 0.29</td>
<td>1.66 ± 0.17</td>
<td>0.27</td>
<td>12.8 ± 7.0***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>1.84 ± 0.30</td>
<td>1.81 ± 0.33</td>
<td>0.03</td>
<td>1.6 ± 8.7</td>
</tr>
<tr>
<td>% one-legged $\dot{V}O_2$ max</td>
<td>TL</td>
<td>89.2 ± 2.8</td>
<td>69.6 ± 4.9</td>
<td>19.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>83.2 ± 5.9</td>
<td>78.4 ± 6.4</td>
<td>4.8</td>
<td></td>
</tr>
<tr>
<td>$\dot{V}E$ (L.min$^{-1}$)</td>
<td>TL</td>
<td>62.10 ± 14.24</td>
<td>43.69 ± 8.86</td>
<td>18.41</td>
<td>28.8 ± 8.8***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>59.30 ± 12.25</td>
<td>55.57 ± 14.34</td>
<td>3.73</td>
<td>5.3 ± 21.5</td>
</tr>
<tr>
<td>$\dot{V}CO_2$(L.min$^{-1}$)</td>
<td>TL</td>
<td>2.01 ± 0.33</td>
<td>1.69 ± 0.20</td>
<td>0.32</td>
<td>14.6 ± 9.4***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>1.95 ± 0.35</td>
<td>1.88 ± 0.37</td>
<td>0.07</td>
<td>3.0 ± 8.2</td>
</tr>
<tr>
<td>RER</td>
<td>TL</td>
<td>1.04 ± 0.03</td>
<td>1.02 ± 0.06</td>
<td>0.02</td>
<td>2.4 ± 6.3</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>1.06 ± 0.05</td>
<td>1.04 ± 0.05</td>
<td>0.02</td>
<td>1.5 ± 3.7</td>
</tr>
<tr>
<td>$\dot{V}E.\dot{V}O_2^{-1}$</td>
<td>TL</td>
<td>31.96 ± 5.15</td>
<td>26.43 ± 3.87</td>
<td>5.53</td>
<td>16.9 ± 7.2*</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>32.38 ± 4.47</td>
<td>30.43 ± 3.04</td>
<td>1.95</td>
<td>4.6 ± 15.2</td>
</tr>
<tr>
<td>HR (b.min$^{-1}$)</td>
<td>TL</td>
<td>171.5 ± 9.0</td>
<td>154.8 ± 7.5</td>
<td>16.7</td>
<td>10.3 ± 5.4***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>169.8 ± 7.5</td>
<td>160.1 ± 9.8</td>
<td>9.7</td>
<td>6.0 ± 2.9***</td>
</tr>
<tr>
<td>W</td>
<td>TL</td>
<td>105.9 ± 9.9</td>
<td>103.4 ± 9.9</td>
<td>2.5</td>
<td>2.1 ± 9.1</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>108.9 ± 13.3</td>
<td>104.4 ± 12.4</td>
<td>4.5</td>
<td>4.0 ± 5.0</td>
</tr>
</tbody>
</table>

Level of significance between pre- and post-training values:

* $P < 0.05$
*** $P < 0.001$

N.B. All values determined after 8 to 10 minutes of exercise
TABLE 6.10

Difference in the percentage change between the trained (TL) and untrained (UTL) legs after training

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>PERCENTAGE CHANGE AFTER TRAINING</th>
<th>NET IMPROVEMENT OF TL</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TL</td>
<td>UTL</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) max (L.min(^{-1}))</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td></td>
<td>11.2%</td>
<td>4.4%</td>
</tr>
<tr>
<td>Endurance Time (min)</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td></td>
<td>523.0%</td>
<td>118.9%</td>
</tr>
<tr>
<td>Lactate (mM)</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td></td>
<td>31.1%</td>
<td>19.8%</td>
</tr>
<tr>
<td>PRE</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td></td>
<td>37.0%</td>
<td>8.1%</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1}))</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td></td>
<td>12.8%</td>
<td>1.6%</td>
</tr>
<tr>
<td>( \dot{V}E ) (L.min(^{-1}))</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td></td>
<td>28.8%</td>
<td>5.3%</td>
</tr>
<tr>
<td>RER</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.4%</td>
<td>1.5%</td>
</tr>
<tr>
<td>( \dot{V}E.\dot{V}O_2 )(^{-1})</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td></td>
<td>16.9%</td>
<td>4.6%</td>
</tr>
<tr>
<td>HR (b.min(^{-1}))</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td></td>
<td>10.3%</td>
<td>6.0%</td>
</tr>
</tbody>
</table>

+ percentage increase after training
o percentage decrease after training
TABLE 6.11

\( \dot{V}_O_2 \) (L.min\(^{-1}\)) for the trained (TL) and untrained (UTL) legs determined during the pre- and post-training endurance tests (means ± SD)

<table>
<thead>
<tr>
<th>TIME (min)</th>
<th>LEG</th>
<th>PRE-TR</th>
<th>POST-TR</th>
<th>( \Delta )</th>
<th>PERCENTAGE CHANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 - 6</td>
<td>TL</td>
<td>1.81 ± 0.24</td>
<td>1.61 ± 0.17</td>
<td>0.20</td>
<td>10.8 ± 6.1***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>1.77 ± 0.29</td>
<td>1.73 ± 0.28</td>
<td>0.04</td>
<td>2.1 ± 9.8</td>
</tr>
<tr>
<td>8 - 10</td>
<td>TL</td>
<td>1.93 ± 0.29</td>
<td>1.66 ± 0.17</td>
<td>0.27</td>
<td>12.8 ± 7.0***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>1.84 ± 0.30</td>
<td>1.81 ± 0.33</td>
<td>0.03</td>
<td>1.6 ± 8.7</td>
</tr>
<tr>
<td>14 - 16</td>
<td>TL</td>
<td>1.94 ± 0.37</td>
<td>1.65 ± 0.18</td>
<td>0.29</td>
<td>13.7 ± 8.4***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>1.85 ± 0.30</td>
<td>1.77 ± 0.31</td>
<td>0.08</td>
<td>6.3 ± 7.9</td>
</tr>
</tbody>
</table>

Level of significance between pre- and post-training values:

*** P < 0.001
FIG. 6.8 THE OXYGEN COST OF ONE-LEGGED SUBMAXIMAL EXERCISE FOR THE TRAINED AND UNTRAINED LEGS DETERMINED DURING THE PRE- AND POST-TRAINING ENDURANCE TESTS

( ) no. of subjects when less than whole group
. pre- and post-training values statistically different

Trained Leg

Untrained Leg

$\dot{V}O_2$ (L min.$^{-1}$)

Time (min.)

$a$ - $b$ - $c$ - $d$ - $e$ - $f$ - $g$ - $h$ - $i$ - $j$ - $k$ - $l$ - $m$ - $n$ - $o$ - $p$ - $q$ - $r$ - $s$ - $t$ - $u$ - $v$ - $w$ - $x$ - $y$ - $z$
### TABLE 6.12

Relative work load (% one-legged $\dot{V}O_2$ max) during exercise with the trained (TL) and untrained (UTL) legs in the pre- and post-training endurance tests (means ± SD)

<table>
<thead>
<tr>
<th>TIME (min)</th>
<th>LEG</th>
<th>PRE-TR</th>
<th>POST-TR</th>
<th>$\Delta$</th>
<th>PERCENTAGE CHANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 - 6</td>
<td>TL</td>
<td>83.8 ± 1.6</td>
<td>67.4 ± 5.6</td>
<td>16.4</td>
<td>19.5 ± 6.8</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>80.3 ± 5.8</td>
<td>75.1 ± 4.9</td>
<td>5.2</td>
<td>6.0 ± 10.5</td>
</tr>
<tr>
<td>8 - 10</td>
<td>TL</td>
<td>89.2 ± 2.8</td>
<td>69.6 ± 4.9</td>
<td>19.6</td>
<td>21.9 ± 6.6</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>83.2 ± 5.9</td>
<td>78.4 ± 6.4</td>
<td>4.8</td>
<td>5.5 ± 9.5</td>
</tr>
<tr>
<td>14 - 16</td>
<td>TL</td>
<td>89.0 ± 6.0</td>
<td>69.2 ± 4.5</td>
<td>19.8</td>
<td>22.0 ± 7.2</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>83.9 ± 5.7</td>
<td>77.0 ± 4.9</td>
<td>6.9</td>
<td>7.7 ± 9.6</td>
</tr>
</tbody>
</table>
FIG. 6.9 ESTIMATED ENERGY EXPENDITURE (% \( \text{VO}_2 \) max) FOR THE TRAINED AND UNTRAINED LEGS DETERMINED DURING THE PRE- AND POST- TRAINING ENDURANCE TESTS

( ) no. of subjects when less than whole group
TABLE 6.13

Pulmonary ventilation (VE L.min⁻¹) for the trained (TL) and untrained (UTL) legs determined during the pre- and post-training endurance legs (means ± SD)

<table>
<thead>
<tr>
<th>TIME (min)</th>
<th>LEG</th>
<th>PRE-TR</th>
<th>POST-TR</th>
<th>Δ</th>
<th>PERCENTAGE CHANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 - 6</td>
<td>TL</td>
<td>57.5 ± 14.86</td>
<td>41.98 ± 7.36</td>
<td>15.52</td>
<td>25.4 ± 10.3**</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>55.52 ± 11.78</td>
<td>52.27 ± 11.50</td>
<td>3.25</td>
<td>4.6 ± 18.9</td>
</tr>
<tr>
<td>8 - 10</td>
<td>TL</td>
<td>62.10 ± 14.24</td>
<td>43.69 ± 8.86</td>
<td>18.41</td>
<td>28.8 ± 8.8**</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>59.30 ± 12.25</td>
<td>55.57 ± 14.34</td>
<td>3.73</td>
<td>5.3 ± 21.5</td>
</tr>
<tr>
<td>14 - 16</td>
<td>TL</td>
<td>64.87 ± 14.71</td>
<td>43.78 ± 7.99</td>
<td>21.09</td>
<td>31.8 ± 11.1***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>63.08 ± 11.90</td>
<td>52.75 ± 12.68</td>
<td>10.33</td>
<td>15.5 ± 19.9</td>
</tr>
</tbody>
</table>

Levels of significance between pre- and post-training values:

** P < 0.01
*** P < 0.001
FIG. 6.10 VENTILATION VALUES FOR THE TRAINED AND UNTRAINED LEGS DETERMINED DURING THE PRE- AND POST-TRAINING ENDURANCE TESTS

(*) no. of subjects when less than whole group
. pre- and post-training values statistically different

Trained Leg

Untrained Leg
TABLE 6.14

Heart rate (b.min\(^{-1}\)) values for the trained (TL) and untrained (UTL) legs determined during the pre- and post-training endurance tests (means ± SD)

<table>
<thead>
<tr>
<th>TIME (min)</th>
<th>LEG</th>
<th>PRE-TR</th>
<th>POST-TR</th>
<th>Δ</th>
<th>PERCENTAGE CHANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 - 6</td>
<td>TL</td>
<td>164.9 ± 9.6</td>
<td>147.0 ± 10.3</td>
<td>17.9</td>
<td>11.4 ± 5.8***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>163.1 ± 8.3</td>
<td>152.3 ± 9.8</td>
<td>10.8</td>
<td>6.7 ± 2.5***</td>
</tr>
<tr>
<td>8 - 10</td>
<td>TL</td>
<td>171.5 ± 9.0</td>
<td>154.8 ± 7.5</td>
<td>16.7</td>
<td>10.3 ± 5.4***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>169.8 ± 7.5</td>
<td>160.1 ± 9.8</td>
<td>9.7</td>
<td>6.0 ± 2.9***</td>
</tr>
<tr>
<td>14 - 16</td>
<td>TL</td>
<td>175.8 ± 9.8</td>
<td>158.1 ± 7.4</td>
<td>17.7</td>
<td>9.1 ± 4.4***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>174.1 ± 7.1</td>
<td>161.7 ± 7.2</td>
<td>12.4</td>
<td>7.8 ± 3.3***</td>
</tr>
</tbody>
</table>

Level of significance between pre- and post-training values:

*** P < 0.001
FIG. 6.11 HEART RATE VALUES FOR THE TRAINED AND UNTRAINED LEGS DETERMINED DURING THE PRE-AND POST-TRAINING ENDURANCE TESTS

- ( ) no. of subjects when less than whole group
- * pre- and post-training values statistically different

**Trained Leg**

- Pre-training values are indicated by "pre-training".
- Post-training values are indicated by "post-training".

**Untrained Leg**

- Pre-training values are indicated by "pre-training".
- Post-training values are indicated by "post-training".
TABLE 6.15

Ventilatory equivalent ($\dot{V}E.\dot{V}O_2^{-1}$) for the trained (TL) and untrained (UTL) legs determined during the pre- and post-training endurance tests (means ± SD)

<table>
<thead>
<tr>
<th>TIME (min)</th>
<th>LEG</th>
<th>PRE-TR</th>
<th>POST-TR</th>
<th>Δ</th>
<th>PERCENTAGE CHANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 - 6</td>
<td>TL</td>
<td>31.69 ± 5.66</td>
<td>26.13 ± 3.63</td>
<td>5.56</td>
<td>16.8 ± 7.5***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>31.77 ± 4.48</td>
<td>30.17 ± 3.47</td>
<td>1.60</td>
<td>4.1 ± 11.3</td>
</tr>
<tr>
<td>8 - 10</td>
<td>TL</td>
<td>31.96 ± 5.15</td>
<td>26.43 ± 3.87</td>
<td>5.53</td>
<td>16.9 ± 7.2*</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>32.38 ± 4.47</td>
<td>30.43 ± 3.04</td>
<td>1.95</td>
<td>4.6 ± 15.2</td>
</tr>
<tr>
<td>14 - 16</td>
<td>TL</td>
<td>33.09 ± 3.60</td>
<td>26.49 ± 3.65</td>
<td>6.60</td>
<td>19.9 ± 7.7***</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>34.29 ± 5.43</td>
<td>29.83 ± 2.91</td>
<td>4.46</td>
<td>11.3 ± 14.7</td>
</tr>
</tbody>
</table>

Levels of significance between pre- and post-training values:

* P < 0.05
*** P < 0.001
TABLE 6.16

Respiratory exchange ratio (RER) for the trained (TL) and untrained (UTL) legs determined during the pre- and post-training endurance tests (means ± SD)

<table>
<thead>
<tr>
<th>TIME (min)</th>
<th>LEG</th>
<th>PRE-TR</th>
<th>POST-TR</th>
<th>Δ</th>
<th>PERCENTAGE CHANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 – 6</td>
<td>TL</td>
<td>1.10 ± 0.05</td>
<td>1.03 ± 0.07</td>
<td>0.07</td>
<td>6.0 ± 8.5</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>1.13 ± 0.04</td>
<td>1.09 ± 0.04</td>
<td>0.04</td>
<td>3.1 ± 3.6</td>
</tr>
<tr>
<td>8 – 10</td>
<td>TL</td>
<td>1.04 ± 0.03</td>
<td>1.02 ± 0.06</td>
<td>0.02</td>
<td>2.4 ± 6.3</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>1.06 ± 0.05</td>
<td>1.04 ± 0.05</td>
<td>0.02</td>
<td>1.5 ± 3.7</td>
</tr>
<tr>
<td>14 – 16</td>
<td>TL</td>
<td>1.02 ± 0.04</td>
<td>1.01 ± 0.05</td>
<td>0.01</td>
<td>1.0 ± 5.7</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>1.04 ± 0.03</td>
<td>1.01 ± 0.04</td>
<td>0.03</td>
<td>3.4 ± 4.7</td>
</tr>
</tbody>
</table>
FIG. 6.12 THE RESPIRATORY EXCHANGE RATIO (RER) VALUES FOR THE TRAINED AND UNTRAINED LEGS DETERMINED DURING THE PRE- AND POST-TRAINING ENDURANCE TESTS

( ) no. of subjects when less than whole group

Trained Leg

Untrained Leg
TABLE 6.17

Work load (watts) during exercise with the trained (TL) and untrained (UTL) legs determined during the pre- and post-training endurance tests (means ± SD)

<table>
<thead>
<tr>
<th>TIME (min)</th>
<th>LEG</th>
<th>PRE-TR</th>
<th>POST-TR</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 - 6</td>
<td>TL</td>
<td>102.5 ± 9.3</td>
<td>103.3 ± 7.8</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>107.8 ± 13.0</td>
<td>103.4 ± 12.6</td>
</tr>
<tr>
<td>8 - 10</td>
<td>TL</td>
<td>103.3 ± 9.9</td>
<td>103.3 ± 9.9</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>108.9 ± 13.3</td>
<td>104.4 ± 12.4</td>
</tr>
<tr>
<td>14 - 16</td>
<td>TL</td>
<td>104.1 ± 8.6</td>
<td>102.4 ± 13.9</td>
</tr>
<tr>
<td></td>
<td>UTL</td>
<td>110.0 ± 13.9</td>
<td>102.4 ± 11.2</td>
</tr>
</tbody>
</table>
### TABLE 6.18

Time course of the adaptive responses in several parameters (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>ENDURANCE TEST</th>
<th>MID-TR</th>
<th>Δ</th>
<th>PERCENTAGE CHANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1}))</td>
<td>1.93 ± 0.29</td>
<td>1.70 ± 0.21</td>
<td>0.23</td>
<td>11.2 ± 8.4**</td>
</tr>
<tr>
<td>% ( \dot{V}O_2 ) max (one-leg)</td>
<td>89.2 ± 2.8</td>
<td>79.1 ± 6.7</td>
<td>10.1</td>
<td></td>
</tr>
<tr>
<td>( \dot{V}E ) (L.min(^{-1}))</td>
<td>62.10 ± 14.24</td>
<td>49.11 ± 12.55</td>
<td>12.99</td>
<td>20.6 ± 12.8**</td>
</tr>
<tr>
<td>( \dot{V}CO_2 ) (L.min(^{-1}))</td>
<td>2.01 ± 0.33</td>
<td>1.79 ± 0.26</td>
<td>0.22</td>
<td>9.9 ± 12.8</td>
</tr>
<tr>
<td>RER</td>
<td>1.04 ± 0.03</td>
<td>1.05 ± 0.06</td>
<td>0.01</td>
<td>1.2 ± 6.9</td>
</tr>
<tr>
<td>( \dot{V}E \cdot \dot{V}O_2 )</td>
<td>31.96 ± 5.15</td>
<td>28.51 ± 4.97</td>
<td>3.45</td>
<td>10.6 ± 9.1**</td>
</tr>
<tr>
<td>HR (b.min(^{-1}))</td>
<td>171.5 ± 9.0</td>
<td>156.5 ± 12.0</td>
<td>15.0</td>
<td>8.2 ± 4.6**</td>
</tr>
<tr>
<td>W</td>
<td>105.9 ± 9.9</td>
<td>103.4 ± 8.6</td>
<td>2.5</td>
<td>1.9 ± 7.8</td>
</tr>
<tr>
<td>+ Lactate (mM)</td>
<td>6.96 ± 1.92</td>
<td>5.46 ± 1.51</td>
<td>1.50</td>
<td>19.8 ± 16.4**</td>
</tr>
<tr>
<td>PRE</td>
<td>184 ± 0.7</td>
<td>13.4 ± 2.3</td>
<td>5.0</td>
<td>26.9 ± 14.4***</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>ENDURANCE TEST</th>
<th>MID-TR</th>
<th>POST-TR</th>
<th>Δ</th>
<th>PERCENTAGE CHANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1}))</td>
<td>1.70 ± 0.21</td>
<td>1.66 ± 0.17</td>
<td>0.04</td>
<td>2.1 ± 5.9</td>
<td></td>
</tr>
<tr>
<td>% ( \dot{V}O_2 ) max (one-leg)</td>
<td>79.1 ± 6.7</td>
<td>69.6 ± 4.93</td>
<td>9.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \dot{V}E ) (L.min(^{-1}))</td>
<td>49.11 ± 12.55</td>
<td>43.69 ± 8.86</td>
<td>5.42</td>
<td>9.6 ± 8.1</td>
<td></td>
</tr>
<tr>
<td>( \dot{V}CO_2 ) (L.min(^{-1}))</td>
<td>1.79 ± 0.26</td>
<td>1.69 ± 0.20</td>
<td>0.10</td>
<td>5.2 ± 6.5</td>
<td></td>
</tr>
<tr>
<td>RER</td>
<td>1.05 ± 0.06</td>
<td>1.02 ± 0.06</td>
<td>0.03</td>
<td>4.3 ± 5.6</td>
<td></td>
</tr>
<tr>
<td>( \dot{V}E \cdot \dot{V}O_2 )</td>
<td>28.51 ± 4.97</td>
<td>26.43 ± 3.87</td>
<td>2.08</td>
<td>6.8 ± 5.9</td>
<td></td>
</tr>
<tr>
<td>HR (b.min(^{-1}))</td>
<td>156.5 ± 12.0</td>
<td>154.8 ± 7.46</td>
<td>1.7</td>
<td>1.9 ± 5.6</td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>103.4 ± 8.6</td>
<td>103.3 ± 9.9</td>
<td>0.1</td>
<td>0.1 ± 4.1</td>
<td></td>
</tr>
<tr>
<td>+ Lactate (mM)</td>
<td>5.46 ± 1.51</td>
<td>4.65 ± 1.51</td>
<td>0.81</td>
<td>15.5 ± 11.0***</td>
<td></td>
</tr>
<tr>
<td>PRE</td>
<td>13.4 ± 2.3</td>
<td>11.6 ± 2.1</td>
<td>1.8</td>
<td>17.0 ± 19.9*</td>
<td></td>
</tr>
</tbody>
</table>

+ values determined in the last minute of the pre-training test and the corresponding time in the post-training test.

Level of significance between pre-, mid- and post-training values:

* P < 0.05  
** P < 0.01  
*** P < 0.001

N.B. All values determined after 8 to 10 minutes of exercise during the endurance tests.
FIG. 6.13 BLOOD LACTATE CONCENTRATIONS FOR THE TRAINED LEG DETERMINED DURING THE PRE-, MID- AND POST-TRAINING ENDURANCE TESTS

( ) no. of subjects when less than whole group

• pre- and mid-training values statistically different
• mid- and post-training values statistically different
FIG. 6.14 THE OXYGEN COST OF ONE-LEGGED SUBMAXIMAL EXERCISE FOR THE TRAINED LEG DETERMINED DURING THE PRE-, MID- AND POST-TRAINING ENDURANCE TESTS
FIG. 6.15 VENTILATION ($\dot{V}E$) VALUES FOR THE TRAINED LEG DETERMINED DURING THE PRE-, MID- AND POST-TRAINING ENDURANCE TESTS.
FIG. 6.16 HEART RATE VALUES FOR THE TRAINED LEG DETERMINED DURING THE PRE-, MID- AND POST-TRAINING ENDURANCE TESTS
TABLE 6.19

Comparison of the percentage changes between the pre- and mid- and between the mid- and post endurance tests

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>PERCENTAGE DECREASE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MID-TR</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1}))</td>
<td>11%</td>
</tr>
<tr>
<td>( \dot{V}E ) (L.min(^{-1}))</td>
<td>21%</td>
</tr>
<tr>
<td>( \dot{V}E \cdot \dot{V}O_2 )(^{-1})</td>
<td>11%</td>
</tr>
<tr>
<td>HR (b.min(^{-1}))</td>
<td>8%</td>
</tr>
<tr>
<td>Lactate (mM)</td>
<td>20%</td>
</tr>
<tr>
<td>PRE</td>
<td>27%</td>
</tr>
</tbody>
</table>

All percentages represent decreases during submaximal exercise.
DISCUSSION

Pre-training

Prior to training no differences were found between the right and left legs during one-legged ergometry at both submaximal and maximal levels. This is in agreement with the findings of other investigators (Saltin et al., 1976; Henriksson, 1977). The mean \( \dot{V}O_2 \) max values for the right and left legs were \( 2.21 \pm 0.36 \) and \( 2.16 \pm 0.28 \) L.min\(^{-1}\) respectively. It is difficult to compare these values with those in the literature because the group studied included both male and female subjects. The mean \( \dot{V}O_2 \) max values for the 3 males were \( 2.57 \) and \( 2.43 \) L.min\(^{-1}\) for the right and left legs respectively. These values are very similar to the mean \( \dot{V}O_2 \) max value of \( 2.41 \) L.min\(^{-1}\) reported by Davies and Sargeant (1975) for 5 male subjects, and the mean \( \dot{V}O_2 \) max value of \( 2.59 \) L.min\(^{-1}\) reported by Saltin (1975) for 13 male students. Other authors, however, have reported higher values (Gleser, 1973; Henriksson, 1977).

The criteria for \( \dot{V}O_2 \) max in one-legged bicycle tests may explain some of the variation in the one-legged \( \dot{V}O_2 \) max values reported in the literature. During preliminary one-legged experiments (appendix 1.B) and in the present study, the "levelling off" criterion was not found. Other authors have also failed to elicit the "plateau" effect (Davies and Sargeant, 1975; Stamford et al., 1978b), while others have obtained the characteristic "levelling off" in \( \dot{V}O_2 \) (Gleser, 1973; Saltin et al., 1976; Henriksson, 1977). Saltin and coworkers not only failed to define the "levelling off" criterion for \( \dot{V}O_2 \) max, but they also failed to include data demonstrating this "plateau" effect during one-legged exercise. However, they stated that they achieved this "levelling off" in \( \dot{V}O_2 \) by exposing the individuals to different combinations of submaximal and maximal work loads on different days (Saltin et al., 1976). At each of the submaximal work loads, the \( \dot{V}O_2 \) measurements were higher than those reported by Davies and Sargeant (1975), who failed to elicit the "plateau" effect. Davies and Sargeant stated that this was the result of a decline in the apparent mechanical efficiency at the higher work loads thought to be the result of increased postural activity.
Saltin and coworkers may not have restricted postural movement at the lower work loads, which may explain the higher submaximal $\dot{V}O_2$ values they reported, and their ability to obtain the "plateau" effect.

Gleser (1973) demonstrated a definite "levelling off" in $\dot{V}O_2$ but only by removing postural movements. He achieved this by measuring one-legged $\dot{V}O_2$ max while the subjects were in the standing, not the sitting position. His values, however, relied completely on the cooperation of two subjects to ensure equal sharing of the work load.

The most useful criterion for $\dot{V}O_2$ max is the "plateau" effect, but because of the difficulty in achieving this, the criterion adopted by Davies and Sargeant (1975) would appear to be the most appropriate during one-legged exercise. They stated that duplicate measurements should be made and that the difference between these measurements should not exceed 5%.

This study indicated that values within ±5% could be obtained on two occasions in nearly every individual. Two subjects did show differences between 5 and 6%, which may be explained by use of two protocols, namely the continuous loading and the discontinuous tests, for the determination of one-legged $\dot{V}O_2$ max.

The variation in the $\dot{V}O_2$ max values reported in the literature and between subjects may also be due to the use of the resting leg, postural and arm muscles to varying degrees. However, the good reproducibility found in the present study suggests that the individual repeatedly uses the same muscles and does reach an "all out stage". The subjects used in the present investigation were all highly motivated Physical Education students and, therefore, the use of the trunk, arms and resting leg muscles may have been more pronounced than in less motivated subjects, despite repeatedly being told by the experimenter to minimize such movements. Nevertheless, the $\dot{V}O_2$ max values could be replicated and so the precision of the measurements were acceptable.

One factor that may influence the contribution of different muscles to varying degrees is saddle height. The saddle height adopted in the
present study was set in an attempt to ensure that the angle at the knee was approximately $90^\circ$ when the pedal was in its lowest position. This height was used to restrict the contribution of the plantar flexors and to minimize postural movements. From observations, it was clear that at a higher saddle height upper body movement played an increasing part.

The contribution of the resting leg may vary from study to study according to its position. Most authors simply state that the leg rested on a box by the side of the bicycle ergometer. However, it was found in this study that if the box was positioned here, the subject pushed against the box with each pedal revolution. To reduce this "pushing effect" which provided additional momentum, the box was placed well in front of the subject, so that the passive leg was fully extended and only the back of the heel rested on the box. Even in this position not all muscular activity in this leg was eliminated. This problem has been highlighted by Ahlborg, Hagenfeldt and Wahren (1975), who could not eliminate all activity in the passive leg, even when the leg was placed in a sling at an angle of approximately $135^\circ$ to the trunk.

The variations described above do not enhance direct comparisons between the measurements made during the different studies. However, such variations should not be over emphasized and detract from the usefulness of this model for investigating central and peripheral adaptations to training.

The relationship between $\dot{V}O_2$ and work load was not entirely linear as it is during two-legged exercise. At the higher work loads, $\dot{V}O_2$ increased disproportionately with work load. This is in agreement with the findings of Davies and Sargeant (1975). The most likely explanation for this, as they suggested, is an apparent decline in mechanical efficiency at the higher work loads associated with increased postural movement. The $\dot{V}O_2$ values obtained in this study at each submaximal work load are, again, difficult to compare with those in the literature because of the inclusion of female subjects (data on male subjects only is reported in the literature). At each submaximal work load, $\dot{V}O_2$ has been found to be higher during one- than during two-legged exercise (appendix 1.F). This decreased efficiency during one-legged work may be explained by the oxygen uptake of the non-exercising muscles (Ahlborg et al., 1975).
Pre-training endurance test

During this test no differences were found between the right and left legs. The right and left legs were able to sustain approximately 80% one-legged \( \dot{V}O_2 \) max for 17.8 and 19.2 minutes respectively.

From the expired air samples collected at 4 to 6 minutes during the endurance test, the subjects were calculated to be exercising at 83.1% one-legged \( \dot{V}O_2 \) max with the right leg and 80.0% one-legged \( \dot{V}O_2 \) max with the left leg. Although the subjects had not reached the steady-state condition, as reflected by the significant increase in the oxygen cost of the exercise from this and the subsequent measurement at 8 to 10 minutes \((p < 0.001)\), this value was used for the above calculation. The 4 to 6 minute \( \dot{V}O_2 \) value was used because it corresponds with the exercise time at each submaximal work load, from which the \( \dot{V}O_2 / \text{work load} \) relationships were established.

From the \( \dot{V}O_2 \) measurements made at 8 to 10 minutes, the subjects were calculated to be exercising at 87.5% and 85.0% one-legged \( \dot{V}O_2 \) max with the right and left legs respectively. These values probably reflect more closely the relative work loads at which the subjects were exercising during the pre-training endurance tests.

The blood lactate (LA) and blood glucose concentrations and the pre values determined in the last minute of the endurance tests, were the same during exercise with the right and left legs. The blood LA levels were 6.95 ± 1.48 and 7.54 ± 2.4 mM for the right and left legs respectively. To the best of the author's knowledge, no prolonged one-legged submaximal exercise to exhaustion has been reported in the literature, preventing a comparison of the blood LA levels at exhaustion. These concentrations, however, are very similar to the mean blood LA concentration of 7.57 mM found at the end of a 2 minute continuous loading \( \dot{V}O_2 \) max test (appendix 1.F). This blood LA value is similar to the value of 7.5 mM reported by Saltin and coworkers at the end of their \( \dot{V}O_2 \) max test (Saltin et. al., 1976).
The end point of these pre-training endurance tests was very definite. All subjects complained of intense pain in the quadricep muscles. The subjects ceased to exercise as a result of the perception of local sensations in the muscle and not as a result of the perception of general discomfort.

Since there were no differences between the right and left legs for all variables studied, the allocation of each leg to the trained and untrained groups was randomized. As shown in section 6.4, no differences were also found between the trained and untrained groups, i.e. between the trained and untrained legs before training.

**Pre- versus post-training**

**Maximum oxygen uptake (\(\dot{V}_{O_2} \text{ max}\)) and one-legged training**

The \(\dot{V}_{O_2} \text{ max}\) values increased during exercise with the trained leg (TL) by 11.2% (\(p < 0.001\)) after training (from 2.16 ± 0.29 to 2.40 ± 0.35 L.min\(^{-1}\)) and by 4.4% (\(p < 0.05\)) during exercise with the untrained leg (UTL). The net improvement in \(\dot{V}_{O_2} \text{ max}\) of the TL over that seen in the UTL was therefore 6.8%. These findings indicate that, although local factors clearly influence \(\dot{V}_{O_2} \text{ max}\), some central adaptation occurred which could be transferred to the UTL. The larger improvement in \(\dot{V}_{O_2} \text{ max}\) after training during exercise with the TL compared with the UTL, despite a common cardiovascular system, suggests that the larger increase was the result of improved oxygen extraction by the trained muscles.

The increase in \(\dot{V}_{O_2} \text{ max}\) during exercise with the TL is in agreement with the findings of Davies and Sargeant (1975). They reported an increase in one-legged \(\dot{V}_{O_2} \text{ max}\) of 14%, after a training programme very similar to that employed in the present investigation, with respect to the intensity, frequency and duration of each training session. Since both legs were trained independently in their study, the effect of training one leg only on \(\dot{V}_{O_2} \text{ max}\) during exercise with the contralateral limb was not investigated.
Gleser (1973) reported an increase in \( \dot{V}O_2 \) max of 12.8\% during exercise with the TL after 4 weeks' training in 6 males. Although \( \dot{V}O_2 \) max during exercise with the UTL (control leg) increased by 3.2\%, this improvement was not significant. However, these findings also suggest that training one leg resulted in some central changes that were transferred to the UTL.

Saltin and coworkers reported a 24\% increase in \( \dot{V}O_2 \) max during exercise with the TL (\( p < 0.001 \)) and a 6\% (\( p < 0.05 \)) increase during exercise with the UTL after 4 to 5 weeks' one-legged endurance training in a group of 3 males. This study, again, illustrates that one-legged exercise caused some central improvement, which was transferred to the UTL. The large increase in \( \dot{V}O_2 \) max of 24\% during exercise with the TL is difficult to explain. The training programme was of a short duration (4 weeks) and the intensity of effort during each training session was lower than in the present study (75\% one-legged \( \dot{V}O_2 \) max). The intensity of effort, as shown in the last chapter, would appear to be the most influential factor determining the improvement in \( \dot{V}O_2 \) max after only a short period of training involving large muscle groups. This may not necessarily, but probably does, apply to the training of a limited muscle mass. Although the large increase in \( \dot{V}O_2 \) max reported by Saltin and coworkers is difficult to explain it should be mentioned that the 24\% improvement during exercise with the TL was obtained from a very small sample size (\( n=3 \)) (Saltin et. al., 1976).

Henriksson (1977) reported increases in \( \dot{V}O_2 \) max of 11.3\% (\( p < 0.05 \)) during exercise with the TL and 3.6\% during exercise with the UTL, after 8 weeks' one-legged endurance training. These findings, despite the longer training programme, are very similar to the findings in the present investigation. If these findings are analysed in the same way as in the present study, the improvement in \( \dot{V}O_2 \) max of the TL over that seen in the UTL was 7.7\%.
The findings from the present study and the above investigations demonstrate that one-legged training causes changes at the periphery, which results in an increased \( \dot{V}O_2 \) max during exercise with the TL. However, in all these investigations some improvement in \( \dot{V}O_2 \) max was also found during exercise with the UTL, suggesting that central adaptations had taken place which could be transferred to the untrained muscles.

The maximum ventilation (\( VE \)) values remained unchanged after training during exercise with both the TL and the UTL. This does not compare favourably with the findings reported in the literature which have shown that a one-legged training programme increases \( VE \) at the maximum level during exercise with the TL (Saltin et. al., 1976; Henriksson, 1977).

Although \( \dot{V}O_2 \) max increased in the present study during exercise with both the TL and the UTL, performance improvements after training during the \( \dot{V}O_2 \) max test were mainly confined to the TL. The work load required to elicit \( \dot{V}O_2 \) max increased only during exercise with the TL \((p < 0.05)\), and although the duration of the \( \dot{V}O_2 \) max test increased during exercise with the TL \((p < 0.001)\) and the UTL \((p < 0.05)\), the magnitude of the increase was greater for the TL. This suggests that changes in performance during the \( \dot{V}O_2 \) max test are not reflected by changes in \( \dot{V}O_2 \) max.

**Summary**

The one-legged training studies reported above showed similar increases in \( \dot{V}O_2 \) max during exercise with the TL and the UTL, as found in the present investigation. All authors reported increases in \( \dot{V}O_2 \) max during exercise with the TL and the UTL with the magnitude of the increase being greater during exercise with the TL. The increases in \( \dot{V}O_2 \) max during exercise with the TL were all significant, but the improvements in this parameter during exercise with the UTL only reached the level of statistical significance in the present study and in the study by Saltin and coworkers (Saltin et. al., 1976).
findings suggest that improvements in $\dot{V}O_2\max$ occur as a result of marked local adaptations, combined with some central adaptation which can be transferred to the UTL during exercise.

In the arm versus leg training studies where $\dot{V}O_2\max$ was measured, improvements were generally confined to the trained limbs (Ridge et al., 1976; Stamford et al., 1978a). Where increases were reported in the untrained limbs, the transfer nearly always occurred from the trained legs to the untrained arms (Clausen et al., 1973), suggesting that the size of the muscle mass being trained may influence the extent of the central adaptations taking place.

Possible factors contributing to the increased $\dot{V}O_2\max$ after training during exercise with the trained and untrained limbs

Maximum oxygen uptake ($\dot{V}O_2\max$) depends upon the ability of the muscle to extract available oxygen from the blood, and the ability of the cardiovascular system to deliver sufficient oxygen to the exercising muscles.

As stated above, $\dot{V}O_2\max$ increased by 11.2% and 4.4% during exercise with the TL and the UTL respectively. It may be possible to attribute 4.4% of the increase in $\dot{V}O_2\max$ to central adaptations, such as improved myocardial function and 6.8% of the improvement to adaptations in the periphery. The larger increase in $\dot{V}O_2\max$ during exercise with the TL, despite the same cardiovascular system, suggests that the larger increase was the result of either an improved oxygen extraction, or an increased ability of the muscle to accept an increased blood flow.

Factors contributing to an increased $\dot{V}O_2\max$ during exercise with the untrained leg (UTL)

Although the 4.4% increase in $\dot{V}O_2\max$ after training during exercise with the UTL probably reflects improvements in the central circulation, it should be mentioned that the criterion for $\dot{V}O_2\max$ adopted in this study was the presence of duplicate measurements with
a difference between them that was no greater than 5%. Although some subjects showed larger improvements in $\dot{V}O_2$ max than 5%, e.g. 11.2% by subject 4, the average 4.4% increase in $\dot{V}O_2$ max during exercise with the UTL is below the possible day to day variation in one-legged $\dot{V}O_2$ max. Nevertheless, since 7 of the 8 subjects demonstrated an increased $\dot{V}O_2$ max value during exercise with this leg after training, the possible influence of a one-legged training programme on the central cardiovascular system cannot be ignored.

Such factors may include improved myocardial function, resulting in an increased maximum cardiac output ($\dot{Q}$ max) to the exercising leg. It is unlikely that the arterio-venous oxygen difference (a-$\dot{V}O_2$ diff) over the UTL increased, which suggests that part of the increase in $\dot{V}O_2$ max during exercise with this leg was due to an enhanced oxygen supply and not to an increased oxygen extraction. Evidence supporting this suggestion is provided by Clausen and coworkers, who reported an increased $\dot{V}O_2$ max during exercise with the untrained arms after leg training (Clausen et. al., 1973). The measured a-$\dot{V}O_2$ difference over the untrained arms was unaltered by leg training. These authors demonstrated that training results in central circulatory changes that allow an increased cardiac output ($\dot{Q}$) against an unchanged peripheral resistance. This suggests that during one-legged exercise, where $\dot{Q}$ is not maximal, $\dot{V}O_2$ max before training may be limited by the inability of the muscle to accept the available blood supply. After training, improvements in the central circulation leading to an increased $\dot{Q}$ may, as Clausen and his coworkers suggest, allow an increased $\dot{Q}$ in the absence of a decreased peripheral resistance. Clausen and his coauthors attributed this ability to an increased systemic arterial pressure leading to an increased perfusion pressure and blood supply to the limited muscle mass. This may provide an explanation for the increased $\dot{V}O_2$ max during exercise with the UTL found in the present investigation. However, it must not be forgotten that the transfer reported by Clausen and coworkers occurred as a result of training a large muscle mass. Under such circumstances, $\dot{Q}$ has been found to increase in excess of the pre-training absolute value (Clausen et. al., 1973) demonstrating improvement in the central circulation. This increase in excess of the
absolute pre-training value has not been found, even after a period of training, during exercise with a small muscle mass, e.g. one leg (Gleser, 1973; Saltin et. al., 1976). This may explain why the transfer effects reported from trained legs to untrained arms are more numerous than those reported from trained legs to untrained legs.

Other factors contributing to the increase in \( \dot{V}O_2 \) max during exercise with the UTL may include an overlap of the involved musculature. In this study the arms and postural muscles were being used during exercise with the TL and the UTL, therefore the increase in \( \dot{V}O_2 \) max during exercise with the UTL may partly be explained by local adaptations in these muscles. In addition, the stabilizing effect of the UTL resulted in some activity in the quadricep muscles of this leg. It is possible that such activity, together with associated metabolic changes in the muscle, may have contributed to the increased \( \dot{V}O_2 \) max found during exercise with the UTL after training. It is suggested that such a contribution may be only small because the stabilizing activity of the UTL is likely to be insignificant when compared with the daily activities of the subjects.

The size of the exercising muscle mass is a critical factor influencing \( \dot{V}O_2 \) max (Åstrand and Rodahl, 1977, p.305). The motivation levels of the subjects may have increased as the training programme progressed, resulting in the subjects relying to a greater extent on the postural, arm and resting leg muscles to continue the exercise when they would otherwise have had to stop. An increase in the exercising muscle mass may have contributed to the improvement in \( \dot{V}O_2 \) max during exercise with the UTL.

Despite the above alternative explanations, the increased \( \dot{V}O_2 \) max during exercise with the UTL was accompanied by a decreased heart rate during submaximal exercise with this leg after training. This suggests that improvements in the central cardiovascular system played the major contribution in increasing \( \dot{V}O_2 \) max during exercise with the UTL.

No change was found in maximum ventilation after training. Increased activity of the respiratory muscles would not appear to have contributed
to the increase in \( \dot{V}O_2 \) max during exercise with the UTL after training.

**Summary**

The present study and those reported in the literature demonstrate that the increases in \( \dot{V}O_2 \) max during exercise with the UTL are small when contrasted with improvements during exercise with the TL. Improvements in \( \dot{V}O_2 \) max during exercise with the UTL have, in this and other studies (Saltin et al., 1976), been mainly attributed to improvements in the central cardiovascular system. An overlap of the involved musculature during one-legged exercise and to a lesser extent, the stabilizing activities of the UTL during exercise with the TL, may also have contributed to the small increase in \( \dot{V}O_2 \) max found during exercise with the UTL after training.

**Factors contributing to an increased \( \dot{V}O_2 \) max during exercise with the trained leg (TL)**

The results of this investigation suggest that changes in the peripheral musculature were mainly responsible for the increased \( \dot{V}O_2 \) max during exercise with the TL. If central factors were responsible for the increase, the same improvement in \( \dot{V}O_2 \) max would have been found during exercise with the UTL. Nevertheless, the small 4.4% increase in \( \dot{V}O_2 \) during exercise with the UTL indicates that some central improvement occurred which probably contributed to the total increase in \( \dot{V}O_2 \) max during exercise with the TL.

As mentioned above, two factors result in an augmentation of \( \dot{V}O_2 \) max. These are an increased maximum cardiac output (\( \dot{Q} \) max) and an increased arterio-venous oxygen difference (\( a-\dot{V}O_2 \) diff). Evidence in the literature suggests that both these factors contribute to an increased \( \dot{V}O_2 \) max during exercise with the TL after a one-legged training programme.

Gleser (1973) provides evidence for the importance of an increased \( \dot{Q} \) max. The maximal \( \dot{Q} \) during one-legged exercise has been shown to be 80 to 90% of the value obtained during two-legged exercise (Gleser, 1973).
Even after a period of one-legged endurance training this value, although greater, did not exceed the pre-training absolute value, while $\dot{V}O_2$ max increased by 12.8% during exercise with the TL. This increase in $\dot{V}O_2$ max was linked to both an increased $Q$ max and a decreased peripheral resistance to blood flow. Gleser attributed the increased ability of the muscles to accept the greater flow, to an improved ability of the muscle vasculature to dilate, or to an augmentation in the effective area of the muscle vasculature.

Although $Q$ max was not measured in the present investigation, the increase in $\dot{V}O_2$ max of 11.2% during exercise with the TL may be due to improved peripheral vasodilation. However, the small increase in $\dot{V}O_2$ max during exercise with the UTL of 4.4% found in the present study, together with the large increase in stroke volume reported by Gleser after his one-legged training programme, makes it impossible to completely ignore central circulatory changes. Such changes may, as stated above, have contributed at least in part to the increased $\dot{V}O_2$ max during exercise with the TL. These changes may include hypertrophy of the heart muscle, improved contractility, and an increase in blood volume.

One-legged training has been found to increase the oxidative potential of the skeletal muscle in the TL (Henriksson, 1977). This enhanced oxidative capacity may enable the muscle to extract more oxygen from the blood. This is clearly a factor that may explain the greater increase in $\dot{V}O_2$ max found during exercise with the TL when compared with the UTL.

Evidence supporting this is provided by Clausen and coworkers, who found a significant increase in the $a-\dot{V}O_2$ difference at the maximum level in response to arm training (Clausen et. al., 1973). They also found that leg training did not alter the $a-\dot{V}O_2$ difference during exercise with the untrained arms. This demonstrates that peripheral adaptations in the muscles are the major factors responsible for an increased oxygen extraction during maximal exercise with a limited muscle mass.
As stated above, an increased oxidative capacity may be responsible for improved oxygen extraction, but an increased capillary muscle density may also enhance extraction (Andersen and Henriksson, 1977). Andersen and Henriksson (1977) showed that training increases the ratio between the number of capillaries and the number of muscle fibres. Although no evidence has been reported in the literature regarding muscle capillarization before and after one-legged training, the changes are likely to be the same as those found after two-legged training. An increase in the number of capillaries increases the capillary surface area, enhancing the exchange of oxygen and carbon-dioxide and increasing the ability of the muscle to accept blood flow. An increase in muscle myoglobin after training (Pattengale and Holloszy, 1967) will also enhance the diffusion of oxygen into the myofibrils.

The above illustrates the importance of local adaptations in the muscle for increasing $\dot{V}O_2$ max during exercise with the TL after a period of one-legged endurance training. Further evidence for the importance of peripheral factors has been provided by the work of Davies and Sargeant (1974; 1975).

Davies and Sargeant (1974) reported the physiological responses to one-legged ergometry, breathing air and a high oxygen mixture (45% $O_2$ in $N_2$). Breathing 45% oxygen failed to increase one-legged $\dot{V}O_2$ max. These findings, together with the evidence that $\dot{Q}$ max is not reached during one-legged exercise (Gleser, 1973), suggests that one-legged $\dot{V}O_2$ max is limited by the inability of the exercising muscle mass to cope with the available blood supply and to extract oxygen from it, and not by the oxygen transport system.

Davies and Sargeant (1975) provided further evidence for the importance of local factors on $\dot{V}O_2$ max during one-legged exercise. They trained both legs, using one-legged exercise for 5 to 6 weeks. The $\dot{V}O_2$ max values increased during exercise with both the right and left legs by 14%. However, during two-legged exercise, where the muscle mass was effectively doubled, the increase in $\dot{V}O_2$ max was only 4.7%. These findings suggest that local factors are responsible for
the increases in $\dot{V}O_2$ max found after training during exercise with a limited muscle mass.

Summary

The $\dot{V}O_2$ max values increased by 11.2% ($p < 0.001$) during exercise with the TL and by 4.4% ($p < 0.05$) during exercise with the UTL after 5 weeks' one-legged endurance training. The larger increase in $\dot{V}O_2$ max during exercise with the TL (6.8%), despite a common cardiovascular system, suggests that this increase was the result of local adaptations in the muscle. Although local adaptation was marked, some improvements occurred in the central circulation which could be transferred to the UTL. It may be possible to attribute 4.4% of the increase in $\dot{V}O_2$ max during exercise with the TL to central factors, and 6.8% of the 11.2% increase during exercise with the TL to local factors.

Increases in $\dot{V}O_2$ max may be attributed to an increased $\dot{Q}$ max and an increased $a-VO_2$ difference. Both may have contributed to the improvement in $\dot{V}O_2$ max during exercise with the TL, but the increase in $\dot{V}O_2$ max during exercise with the UTL was probably the result of changes only in $\dot{Q}$ max.

Improvements in $\dot{V}O_2$ max during exercise with the UTL have in this and other studies reported in the literature (Saltin et. al., 1976) been mainly attributed to adaptations in the central cardiovascular system. Such changes may include increased myocardial contractility, myocardial hypertrophy, an increased blood volume and an increase in the total amount of haemoglobin (Clausen, 1977).

An overlap of the involved musculature and to a much lesser extent the stabilizing activities of the UTL during the training programme, may also have contributed to the small (4.4%) increase in $\dot{V}O_2$ max during exercise with the UTL after training.

Improvements in $\dot{V}O_2$ max during exercise with the TL may be due partly to central adaptations but would appear to be mainly the result of local changes in the muscle.
Local adaptations in the muscle, resulting in an increased ability to accept a higher blood flow after training, may be the result of an increased ability of the muscle vasculature to dilate, an increase in the effective cross-sectional area of the muscle vasculature (Gleser, 1973) or an increased capillarization (Andersen and Henriksson, 1977). The increased oxygen supplied to the muscle as a result of this decrease in the total peripheral resistance may have contributed to the increased $\dot{V}O_2$ max found during exercise with the TL in the present study.

Local adaptations resulting in an increased oxygen extraction by the trained muscles may also explain the increased $\dot{V}O_2$ max during exercise with the TL. Such factors include an enhanced oxidative capacity (Henriksson, 1977), an increased capillarization (Andersen and Henriksson, 1977), and an increased myoglobin content (Pattengale and Holloszy, 1967). The relative importance of the above factors is unknown, but improvements in the oxidative capacity after training one leg are large (Henriksson, 1977). It is possible that the larger increase in $\dot{V}O_2$ max during exercise with the TL is mainly the result of enhanced oxygen extraction by the trained muscles, due to an increased oxidative potential and an increased capillarization.

The above findings suggest that the adaptive response of the skeletal muscles for oxygen extraction are greater than that of the cardiovascular system for oxygen transport.

Endurance test and one-legged training

One-legged training and submaximal heart rate (HR)

Heart rate decreased during exercise with the TL and the UTL after training by 10.3% ($p < 0.001$) and 6.0% ($p < 0.001$) respectively. Although there was a decrease in HR during exercise with the TL and the UTL after training, the magnitude of the fall was greater for the TL by 4.3%. In addition, the HR response to prolonged submaximal exercise differed during exercise with the TL and UTL (figure 6.11).
This figure illustrates that during exercise with the TL in the post-training endurance test, HR increased during the first 16 minutes of exercise after which it remained unchanged for the rest of the exercise period. During exercise with the UTL, however, HR increased progressively as the exercise continued. The levelling off in HR, after 16 minutes during exercise only with the TL, suggests that local adaptations in this leg resulted in the improved HR response to prolonged submaximal exercise.

The decrease in HR during exercise with the TL and the UTL after training during the endurance test, is consistent with the decreases reported above during exercise with the TL and UTL during the 4 minute continuous loading oxygen uptake test (figures 6.3 and 6.4). During this test HR decreased only at the higher work loads (98 watts and above). The work load at which HR showed the greatest decrease (98 watts) corresponded closely to the mean training work load (103 watts) for the group.

The fall in HR during exercise with the UTL demonstrated that the training of one leg results in changes in the central circulation which can be transferred to the UTL during submaximal exercise. This suggests that a one-legged endurance training programme provides a sufficient stimulus to the cardiovascular system, resulting in improvements in the central circulation. This is supported by the improvement in \( \dot{V}O_2 \) max also found during exercise with the UTL after training. The high heart rate values recorded during training (170 - 180 b.min\(^{-1}\)) provide evidence of the considerable stress being placed on the cardiovascular system during this type of exercise.

The reduction in HR during exercise with the UTL was of the same magnitude as the fall in pre-exercise HR which decreased by 9 b.min\(^{-1}\) after training. In the post-training endurance test HR was 10 b.min\(^{-1}\) lower than the value measured in the pre-training endurance test at the same time. Therefore, the increase in HR in excess of the pre-exercise value was the same before and after training. The larger decrease in HR of 16 b.min\(^{-1}\) during exercise with the TL resulted in
an increase in HR over the pre-exercise value after training that was less pronounced. The same changes in HR during exercise with the TL and the UTL were found at the work load of 98 watts during the 4 minute continuous loading test, i.e. at this work load HR decreased by 10 and 16 b.min⁻¹ during exercise with the UTL and the TL respectively.

This fall in HR during exercise with the UTL, which was of the same magnitude as the fall in pre-exercise HR, is consistent with the findings of Clausen and coworkers. They demonstrated that after leg training the reduction in HR during exercise with the untrained arms was of the same magnitude as the fall in basal HR (Clausen et. al., 1973).

The fall in HR during exercise with the UTL may, as stated above, be largely due to improvements in the central circulation, e.g. improved myocardial contractility. A second explanation for the fall in HR during exercise with this leg may be the result of a lower output of catecholamines. During the pre-training endurance test the subjects may have been fairly anxious despite their familiarization with the task. Under such stress impulses received by the hypothalamus increase the activity of the sympathetic nervous system which increases the sympathetic neural discharge to the heart and the output of catecholamines from the adrenal medulla. This increases HR and may therefore result in an unnecessarily high HR during exercise at a given submaximal work load. With greater experience at the task, the subjects became less anxious resulting in decreased sympathetic activity and a lower secretion of catecholamines.

This decrease in the activity of the sympathetic nervous system, together with improvements in the central circulation, may also account for some of the fall in HR during exercise with the TL. However, the larger fall in HR during exercise with this leg (16 b.min⁻¹ compared with 10 b.min⁻¹ during exercise with the UTL) confirms that at least part of the decrease in HR was confined to exercise with the trained muscles. Adaptations in the muscle which may combine to reduce the stress placed on the heart include: an improved oxygen extraction; a decreased muscle blood flow; a decreased peripheral resistance and an
increased capillarization. Evidence for the above have been found during two-legged exercise after two-legged training and therefore it is likely that these adaptations also occur in response to a one-legged training programme.

The findings in the present investigation concerning a decrease in HR during exercise with the TL and the UTL are similar to the limited findings reported in the literature.

Saltin and coworkers reported that HR decreased by 8% and 4% during exercise with the TL and the UTL respectively after 4 weeks' one-legged endurance training. Although HR decreased during exercise with the TL and the UTL, the fall only reached the level of statistical significance during exercise with the TL. From their findings, the authors suggested that the decrease in HR during exercise only with the TL was related to marked local adaptations in the muscles (Saltin et al., 1976). They suggested that the decrease may be the result of a "less active peripheral drive" or a "less marked cortical activation". Such factors may help to explain the larger fall in HR found in the present investigation during exercise with the TL. Despite the significant fall in HR during exercise only with the TL in the study by Saltin and coworkers, the fall of 4% during exercise with the UTL suggests, as in this study, that the training of one leg provides a stimulus to the cardiovascular system, which results in improvements in the central circulation (Saltin et al., 1976).

Henriksson (1977) found that although HR decreased by 8.3% after training during exercise with the TL, this change was not significant. No change in HR was found during exercise with the UTL. The lower relative work load (70% one-legged VO$_2$ max) at which his subjects trained, may provide an explanation for the absence of a fall in HR during exercise with the UTL. This work load may not have provided a sufficient stimulus for central cardiovascular adaptation. In addition, although the author stated that the HR values were obtained during steady-state exercise, he obtained the values from two measurements made in the 5th and 6th minutes of exercise. From the results obtained
in the present investigation regarding oxygen uptake, steady-state had not been reached after 6 minutes of exercise. The measurements made by Henriksson (1977) may not therefore have been determined during steady-state submaximal exercise. Nevertheless, he demonstrated a fall in HR during exercise with the TL which, although not significant, may be the result of local adaptations in the muscles.

Summary

Although training reduced HR during exercise with the TL and the UTL, the magnitude of the fall was greater during exercise with the TL. This suggests that at least part of the decrease in HR was confined to exercise with the TL.

The fall in HR during exercise with the UTL, which was proportional to the decrease in pre-exercise HR after training, may be due to central adaptations, e.g. improved myocardial function, which can be transferred to this leg during submaximal exercise. In addition, the decrease in HR during exercise with the UTL may be due to a decreased sympathetic discharge and catecholamine secretion as a result of experience with the task.

Central adaptations together with a decreased sympathetic activity and output of catecholamines may also explain some of the fall in HR during exercise with the TL. The larger decrease in HR during exercise with this leg suggests however, that local adaptations in the muscles reduce the stress placed on the heart during one-legged exercise. These may include an improved oxygen extraction, a decreased blood flow, a decreased total peripheral resistance and in increased capillarization.

The fall in HR during exercise with both the TL and the UTL suggests that local and central factors may operate together to decrease HR. This is summed up by Saltin and coworkers who stated that "there appears to be a very close interplay between the central circulation and the peripheral adaptation in the regulation of the heart rate response."

(Saltin et. al., 1976).
Finally, the fall in HR during exercise with the UTL suggests that a one-legged endurance training programme provides a sufficient stimulus to the cardiovascular system which results in improvements in that system.

**Oxygen cost and ventilation during one-legged submaximal exercise after training**

The oxygen cost of one-legged submaximal exercise decreased significantly only during exercise with the TL, after a period of one-legged endurance training. The oxygen cost of one-legged submaximal exercise decreased by 12.8% and 1.6% during exercise with the TL and the UTL respectively.

This decrease in the oxygen cost of the exercise combined with the increase in \( \dot{V}O_2 \text{max} \) resulted in the subjects exercising at a lower relative work load after training. From oxygen uptake measurements, the subjects were calculated to be exercising at 69.6% and 78.4% one-legged \( \dot{V}O_2 \text{max} \) with the TL and the UTL after training, compared to 89.2% and 83.2% one-legged \( \dot{V}O_2 \text{max} \) with the TL and the UTL respectively before training.

This decrease in the oxygen cost of submaximal exercise at a given absolute work load has rarely been found during two-legged exercise after training but it is consistent with the findings in the literature regarding exercise with a limited muscle mass. Saltin and coworkers found a decrease in \( \dot{V}O_2 \) during one-legged exercise at the same absolute work load after the training of one leg (Saltin et. al., 1976). Henriksson (1977) also reported a significant decrease in \( \dot{V}O_2 \) during exercise with the TL after a one-legged training programme. Lower \( \dot{V}O_2 \) values have also been reported during exercise with the arms after arm training (Klausen et. al., 1974; McKenzie et. al., 1978; Lewis et. al., 1980).

The presence of such findings after one-legged training and, more rarely, after two-legged training suggests that the unusual nature
of the task may have resulted initially in the use of uneconomical
techniques. As the training programme progressed, the subjects may,
through learning, have improved their original technique. Such an
improvement would result in a better mechanical efficiency of the
exercising muscles. In addition, in the pre-training test the
subjects exercised to exhaustion and, despite repeated instructions
to minimize the use of the postural, arm and resting leg muscles, these
highly motivated subjects did introduce some activity in these muscles.
After training the subjects may not only have learnt how to exercise
more efficiently with one leg, but because the difficulty of the task
was reduced, the subjects may have been able to achieve the same
absolute work load without the aid of added momentum provided by the
above mentioned muscles. After training, therefore, the size of the
exercising muscle mass may have been considerable smaller, resulting
in a lower oxygen requirement.

Another explanation for the lower oxygen cost of one-legged
exercise may be due to the recruitment of a smaller number of motor
units to maintain the tension after training. This would have
occurred if the endurance capacity of the individual muscle fibres
were increased after the training of one leg and would reduce the
oxygen requirement during one-legged exercise.

The ventilation value decreased by 28.8% during exercise with
the TL. Therefore, a fall in the oxygen consumption of the respiratory
muscles may have contributed to the overall decrease in the oxygen cost
of one-legged submaximal exercise with the TL. However, it is
difficult to be conclusive about this because oxygen cost of breathing
information is limited. It is known, however, that at heavy work
loads during exercise with a large muscle mass, the oxygen cost of
breathing may be approximately 10% of the whole body oxygen uptake
(Clausen, 1977). This itself suggests that the oxygen cost of
breathing during submaximal exercise with a limited muscle mass may
be very small.
The ventilation values decreased by 28.8% \( (p < 0.001) \) and by 5.3% during exercise with the TL and the UTL respectively. This suggests that local adaptations in the muscle were responsible for the decrease in \( \dot{\text{V}}E \) during exercise with the TL. This finding is in agreement with the findings reported in the literature regarding the effects of training on a limited muscle mass. Henriksson (1977) reported a significant decrease in \( \dot{\text{V}}E \) only during exercise with the TL. Other authors have also reported significant decreases in \( \dot{\text{V}}E \) which are confined to the trained muscles. (Saltin et. al., 1976; Rasmussen et. al., 1975). The decrease in ventilation has been found to be accompanied by a proportional decrease in blood LA concentration (Klausen et al., 1974). The fall in blood LA, in the present investigation, may explain the decreased ventilation rate. However, blood LA concentration may not, by itself influence \( \dot{\text{V}}E \), since a fall in blood LA concentration was also found during exercise with the UTL but this was not accompanied by a fall in \( \dot{\text{V}}E \).

Pulmonary ventilation is largely dependent upon the hydrogen ion \( (H^+) \) concentration and the partial pressure of carbon-dioxide \( (\text{PCO}_2) \) in the blood (Åstrand and Rodahl, 1977, p.245). Increases above the normal level are detected by the chemoreceptors in both the carotid and aortic bodies, and in the medulla. Messages from these chemoreceptors to the inspiratory centre result in an increased respiratory rate. The greater the \( H^+ \) and \( \text{PCO}_2 \) levels in the blood, the greater this increase will be. Increased ventilation will be maintained until the \( \text{PCO}_2 \) level in the blood returns to normal levels. Endurance training increases aerobic and decreases anaerobic metabolism. The fall in blood LA concentration during exercise with the TL, in the present investigation, is consistent with the above. During aerobic work where less LA is produced, the \( H^+ \) concentration in the blood will be lower, reducing the increase in \( \dot{\text{V}}E \) in excess of the resting level.

The ventilatory equivalent \( (\dot{\text{V}}E.\dot{\text{VO}}_2^{-1}) \) decreased significantly during exercise only with the TL. This decrease was due to the large fall in \( \dot{\text{V}}E \) after training, and was of the magnitude of 16.9%. A small but non-significant decrease in \( \dot{\text{V}}E.\dot{\text{VO}}_2^{-1} \) of 4.4% was found during
exercise with the UTL.

Thus it appears that training produces adaptations in the muscles which, during exercise at a given submaximal work load, reduces the increase in excess of the resting value of $\dot{V}O_2$, $\dot{VE}$ and $\dot{VL}$. Such changes may contribute significantly to the increased endurance capacity of the TL.

One-legged training and submaximal blood lactic acid (LA) concentration

The blood LA (mM) concentration fell significantly during exercise with the TL and the UTL after training, this comparison being made between the pre-training value determined in the last minute of the exercise, and the equivalent time in the post-training endurance test. The blood LA concentration during exercise with the TL decreased by 31.1% ($p < 0.001$) (from 6.95 to 4.65 mM) and during exercise with the UTL by 19.8% ($p < 0.001$) (from 7.53 to 6.04 mM).

Despite the significant decrease in blood LA concentration during exercise with the TL and the UTL after training, the larger fall during exercise with the TL resulted in a significant difference in this parameter between the two legs after training ($p < 0.05$).

Saltin and coworkers demonstrated a significant decrease in blood LA concentration during exercise only with the TL at a given submaximal work load after training. They also reported a fall in blood LA concentration during exercise with the UTL from 7.4 to 6.7 mM, but this decrease did not reach the level of statistical significance. It should be emphasized that these values were obtained from 3 males only, and the absence of a significant decrease in blood LA concentration during exercise with the UTL may be the result of the small sample size (Saltin et. al., 1976).

Henriksson (1977) reported a fall in blood LA concentration only during exercise with the TL after 8 weeks of one-legged endurance training. Although the mean blood LA concentration for the UTL also
decreased, this fall was not statistically significant.

The findings from these two studies reported in the literature (Saltin et. al., 1976; Henriksson, 1977) regarding changes in blood LA concentrations during exercise with trained and untrained legs are similar to those found in the present study. These authors both reported a fall in blood LA concentration during exercise with the UTL but because these falls were not statistically significant they were ignored and no attempt was made to explain them.

A possible mechanism leading to the fall in blood LA concentration during exercise with the UTL after training may be the result of a lower output of catecholamines with experience at the task. This explanation for a fall in blood LA concentration during exercise with the UTL is the same as that given earlier for the fall in HR during exercise with this leg. Adrenalin stimulates glycogenolysis in the skeletal muscles which then proceeds at a faster rate than the muscle cell requires for aerobic metabolism. The excess pyruvate formed is therefore converted to lactate which passes into the blood. With experience at the task, the subjects may respond to the same exercise with a lower secretion of catecholamines. This decreases glycogenolysis and lactate production reducing the amount of lactate passing from the muscle into the blood.

The uptake of muscle lactate by the TL during exercise with the UTL provides an additional possible explanation for the lower blood LA concentration found after training during exercise with this leg. It has been demonstrated that non-exercising muscle plays an important role in the removal of lactate during exercise (Ahlborg, Hagenfeldt and Wahren, 1975). The larger fall in blood LA concentration during exercise with the TL suggests that the oxidative capacity of the TL had been increased by training, resulting in augmented aerobic metabolism in this leg. As a result of this, the ability of the TL (resting leg) to take up lactate may have increased after training explaining the lower blood LA concentration during exercise with the UTL.
This suggestion is supported by the findings of Ahlborg, Hagenfeldt and Wahren (1975) who demonstrated that, during one-legged exercise, the resting leg takes up and utilizes LA. Their finding is in agreement with the earlier work of Freyschuss and Strandell (1968). Further support for the uptake of LA hypothesis is provided by Henriksson (1977). He found that, during two-legged submaximal exercise after a one-legged endurance training programme, the TL demonstrated a tendency towards LA uptake.

A subsidiary experiment included in this investigation (see appendix 1.E) clearly provides supportive evidence for the suggestion that the fall in blood LA concentration during exercise with the UTL is the result of LA uptake by non-exercising muscle. During this experiment, the subjects exercised for 2 hours at approximately 75% one-legged \( \dot{V}O_2 \) max. The exercise was continuous but the exercising leg was changed after 1 hour of exercise. The experiment demonstrated that the first hour of exercise had very little obvious influence on the response of the contralateral limb to the same exercise during the second hour.

During both the first and second hours of the exercise, the blood LA concentration increased during the first 15 minutes of exercise, after which the level decreased during the remainder of the exercise period. The blood LA concentrations during the second hour of exercise were particularly interesting. The blood LA concentrations at the beginning of the second hour and after 15 minutes of exercise were higher than the levels determined at these times during the first hour. However, the falls in blood LA concentration from 15 to 30 and from 30 to 60 minutes of exercise during the second hour were greater than the falls occurring at these times during the first hour. The findings from this experiment, which are reported in more detail in appendix 1.E, provide supportive evidence for the uptake of LA by the non-exercising leg.

As mentioned above, the fall in blood LA concentration during exercise with the TL was of a greater magnitude than that seen in the UTL (31% compared with 20%).
It is suggested that a decrease in catecholamine secretion also accounted in part for the fall in blood LA concentration during exercise with the TL after training. However, the larger fall in blood LA concentration during exercise with this leg compared with the UTL, suggests that at least part of the decrease in blood LA concentration was related to metabolic adaptations in the muscle. It is well established that training increases the oxidative capacity of the muscle (Gollnick et. al., 1973; Henriksson, 1977). An increase of this nature, together with the associated increased capacity for aerobic metabolism, would decrease LA production at a given submaximal work load.

An increase in the oxidative capacity of the muscle is accompanied by an increased ability to oxidize both carbohydrates and fats. In the present study the fall in blood LA concentration during exercise with the TL, without a fall in the RER values after training, suggests that the one-legged training programme increased the ability of the trained muscle to oxidize carbohydrates. These findings compare favourably with those reported by Saltin and coworkers after a one-legged training programme of a similar duration (Saltin et. al., 1976).

Although the RER values did not decrease during exercise with the TL or the UTL after training, the values did show a gradual decrease during the endurance tests as the exercise progressed, thus indicating the shift from carbohydrate to fat metabolism which is a characteristic metabolic response to prolonged submaximal exercise. This was accompanied by a decrease in the blood LA concentration over the exercise period.

**Summary**

Blood LA concentration decreased during exercise with both the TL and the UTL, with the magnitude of the decrease being greater during exercise with the TL.
The decrease in blood LA concentration during exercise with the UTL was attributed to a decreased catecholamine secretion as a result of experience with the task, and an increased uptake of LA by the non-exercising TL after training.

The decrease in blood LA concentration during exercise with the TL was also attributed in part to a smaller output of catecholamines but mainly to the increased oxidative capacity of the muscle.

**One-legged endurance training and perceived rate of exertion (PRE)**

The PRE value decreased during exercise with the TL and the UTL after training, but the magnitude of the change was considerably greater during exercise with the TL, resulting in a significant difference between the PRE values for the two legs after training ($p < 0.001$). Using the Borg (1973) scale (6-20) (Chapter 3, section 3.7), the PRE values during exercise with the TL and the UTL after training were $11.6 \pm 2.1$ and $17.3 \pm 1.6$ respectively. These PRE values were given in response to the degree of pain experienced in the area above the knee because no subject complained of general discomfort. On the Borg (1973) scale 11-12 is associated with "fairly light work" and 17 with "very heavy work".

The fall in the PRE value during exercise with the UTL from 18.8 to 17.3 ($p < 0.01$) may simply be the result of an improved tolerance to a given level of pain. This is supported by statements made by the subjects, who indicated that the type of extremely localized pain in the quadricep muscles experienced prior to training during exercise with the TL and the UTL, was the same after training only during exercise with the UTL. During exercise with the TL, however, the lower PRE value was associated with a definite decrease in these local sensations. All subjects clearly stated that the pain was similar to a dull ache in the general region above the knee, in contrast to a very sharp and more localized pain prior to training. The decrease in the PRE value during exercise with the TL may, therefore, be attributed to a change in the perception of local sensations in the muscles, whereas the small
fall in PRE during exercise with the UTL may be the result of a central learning effect.

Several factors may be responsible for a fall in PRE (Mihevic, 1981). A possible explanation in the present investigation for the decrease in the PRE value during exercise with the TL, may be that the perception of such discomfort is associated with the metabolic conditions in the muscle. Lower blood LA concentrations may be one such factor reducing the very localized discomfort associated with one-legged exercise. However, in one subject, blood LA concentration remained essentially unchanged after training, but the PRE value decreased from 18 to 10 as a result of 5 weeks' training (subject 7).

Central factors may also explain the lower PRE value during exercise with the TL. Saltin and coworkers found that training caused selective hypertrophy of the muscle fibres. They suggested that this may reduce the number of centrally activated motor units that need to be recruited to perform the same absolute submaximal work load (Saltin et al., 1976). As a result of this, a smaller "central nervous command" may be perceived. This hypothesis is supported by the significant decrease in the oxygen cost of one-legged exercise during exercise with the TL. The absence of localised pain enabled the subjects to exercise for longer in the post-training endurance test, since this pain terminated exercise in the pre-training test.

Time course of the adaptive responses to training

A mid-training test, at the pre-training endurance test work load, was performed by the TL to provide insight into the time course of the adaptive responses to training.

The submaximal oxygen cost of one-legged exercise, ventilation, heart rate and the ventilatory equivalent all decreased significantly between the pre- and mid-training tests but despite further decreases in these parameters as the training programme progressed, the falls between the mid- and post-training tests did not reach the level of statistical significance.
The blood LA concentration and the PRE values decreased significantly between the pre- and mid- and between the mid- and post-training endurance tests, but again the greatest reductions occurred in the first half of the training programme.

These findings, showing a rapid adaptation to training after only 2.5 weeks, are in agreement with the findings of Hickson and coworkers. They suggested, on the basis of their findings and previous animal experiments, that cardiovascular and skeletal muscle adaptations occur very rapidly in response to a training programme (Hickson et al., 1981). The authors reported that a further increase in \( VO_2 \max \), or further decreases in the blood LA level and HR after 3 weeks of training, will only occur if the training work load is increased.

Although the work load was increased in the present investigation, at least twice for each subject during the 5 week training programme, the adaptive changes in the second half of the training programme were considerably smaller than those in the first half of the programme. This applied particularly to the oxygen cost of one-legged exercise, ventilation (\( VE \)) and heart rate (HR) (figures 6.14, 6.15 and 6.16).

It is possible, although unlikely, that habituation may have played a part in this process. Davies, Tuxworth and Young (1970) demonstrated that both HR and \( VE \) decreased significantly after only 3 exposures to the exercise. The fall in HR was particularly great. They explained this by stating that "a redistribution of blood flow in favour of the working muscles takes place, thus allowing maximum use of the available cardiac output."

They suggested that the high initial HR values may be the result of venous pooling in the splanchnic and skin regions, and that at least 3 exposures to the task are required before any definitive measurements are made. They also stated that these early changes were most marked in sedentary and laboratory naive subjects. However, in a more recent study they did not find the same effect during the early exposures of their subjects to one-legged exercise (Davies and Sargeant, 1975).
The subjects in the present investigation were all Physical Education students and, therefore, not sedentary and they were all accustomed to the experimental methods necessary for the collection of expired air and the taking of blood samples. In addition, all subjects had previously been exposed to a two-legged $\dot{V}O_2$ max test. Finally, each subject had exercised with both their right and left legs a minimum of 3 times prior to the initial endurance test. On the basis of the above, although habituation may have played a part, it is unlikely that it contributed to any appreciable extent to the early training adaptations.

It is suggested that initial adaptations to training in both the muscles and the central circulation are rapid after which adaptation continues at a slower rate, provided the intensity of the work load is increased.

One-legged training and endurance capacity

The 5 week one-legged training programme produced a 523% ($p < 0.001$) improvement in the ability of the TL to sustain the original pre-training work load. The endurance capacity of the UTL also improved by 119% (NS). The large improvement of the TL compared with the UTL resulted in a significant difference between the post-training endurance times of these two legs ($p < 0.001$). The improvement in endurance capacity of the TL over that seen in the UTL was 404%. When the UTL was used strictly as a control, i.e. the improvement in the endurance capacity of this leg was subtracted from the improvement in the TL, the improvement in the endurance capacity of the TL after training was still highly significant ($p < 0.001$). When calculated in this way a 239% improvement in the ability of the TL to sustain the original pre-training work load was found.

These improvements in the endurance capacity of the TL and the UTL cannot be compared with the findings in the literature because, to the best of the author's knowledge, all other investigators who have trained a limited muscle mass, have not reported changes in endurance capacity.
The results of this study demonstrated again that improvements in \( \dot{V}O_2 \) max are small when contrasted with improvements in endurance capacity and suggest that local adaptations in the skeletal muscles were largely responsible for the improved endurance capacity of the TL after training.

It is suggested that the one-legged training programme increased the oxidative capacity of the trained muscles (Henriksson, 1977). An increased oxidative capacity of the trained muscles would increase the ability of the TL to oxidize carbohydrates during prolonged high intensity submaximal exercise reducing the production of lactate in the muscle. In the present study this was reflected by the lower blood lactate concentration and the decreased ventilation found during exercise with the TL. These changes in the muscle may explain the lower perceived rate of exertion reported by the subjects during exercise with this leg after training. The fall in \( VE \) was accompanied by a fall in \( \dot{V}O_2 \) (i.e. the oxygen cost of one-legged submaximal exercise) and a fall in HR during exercise with the TL after training.

The above changes, found in this investigation during exercise with the TL, resulted in a fall in the relative work load. A fall in the exercise intensity would result in a less drastic redistribution of cardiac output (\( Q \)) away from the splanchnic and renal beds, and the skin for thermoregulation (Rowell, 1974).

It is also possible that the one-legged training programme increased capillarization in the trained muscles. Prior to training the exercising leg (above the knee) became noticeably enlarged and the skin temperature very warm. This suggests that an adequate blood supply was provided to the muscle but the muscle was unable to accept the flow. After training this swelling did not occur, suggesting that the muscle was able to extract more oxygen from a reduced blood flow and/or the muscle could accept a larger blood flow as a result of increased capillarization.
The increased oxidative capacity of the trained skeletal muscles leading to an increased ability to oxidize carbohydrates and spare glycogen, and a reduced displacement from the resting values in blood LA concentration, \( \dot{V}E \), \( \dot{V}O_2 \) and HR all combine to lower the intensity of the exercise and to improve the distribution of cardiac output. These factors may therefore underly the improved endurance capacity of the TL after training.

The improvement in the endurance capacity of the UTL, which occurred in 7 of the 8 subjects after training, is difficult to explain. This improvement, although statistically non-significant, may reflect changes in the central circulation which can be transferred to the UTL resulting in an increased endurance capacity. It is possible that the reductions in blood LA concentration and HR during exercise with this leg, which were attributed to a possible decrease in catecholamine secretion as a result of experience at the task, may have also contributed to the small improvement in the endurance capacity of the UTL after training.

6.6

**GENERAL SUMMARY**

1. The one-legged training programme increased \( \dot{V}O_2 \) max during exercise with the TL and the UTL by 11.2% \( (p < 0.001) \) and 4.4% \( (p < 0.05) \) respectively.

2. Endurance capacity increased during exercise with the TL and the UTL by 523% \( (p < 0.001) \) and 119% (NS) respectively. This study indicates again that changes in \( \dot{V}O_2 \) max are small when contrasted with improvements in endurance capacity after training.

3. During the submaximal performance test, \( \dot{V}O_2 \) (i.e. the oxygen cost of one-legged submaximal exercise), \( \dot{V}E \) and \( \dot{V}E.\dot{V}O_2^{-1} \) decreased significantly during exercise only with the TL suggesting that these changes were the result of local adaptations in the muscle.
4. Blood LA concentration decreased during exercise with the TL and the UTL. During exercise with the UTL the fall in blood LA concentration was attributed to a decreased catecholamine secretion and an increased uptake of lactate by the non-exercising TL after training. The larger fall in the blood LA concentration during exercise with the TL was also attributed partly to a lower output of catecholamines but mainly to an increased oxidative capacity of the trained muscles.

5. Heart rate also decreased during exercise with the TL and the UTL after training. The fall in HR during exercise with the UTL was also attributed to a decreased catecholamine secretion and also to improvements in the central cardiovascular system. The larger fall in HR during exercise with the TL was attributed in part to the factors mentioned above but also to changes in the trained muscles e.g. increased capillarization.

6. The respiratory exchange ratio remained unchanged after training during exercise with the TL and the UTL. A longer training programme may therefore be required to lower the RER value and to produce a significant increase in fat metabolism relative to carbohydrate metabolism.

7. The changes at the submaximal level which were predominantly confined to the TL, reduced the intensity of the exercise after training. During exercise with the TL, therefore, there would be a less drastic redistribution of cardiac output away from the splanchnic and renal beds, and the skin.

8. The adaptations to training occurred mainly during the first half of the training programme. It is suggested therefore that the bulk of the improvement in endurance capacity also occurred during the first 2.5 weeks.

9. Although the training adaptations were mainly confined to the TL during exercise, the increase in \( \dot{V}O_2 \) max together with the decrease in
submaximal HR during exercise with the UTL, suggests that the training of one leg may provide a sufficient stimulus to the cardiovascular system leading to improvements in that system. The training of one leg while the other leg is immobilized, e.g. by fractures or even in amputees, may therefore provide a useful method of improving and maintaining cardiovascular efficiency.

Even though previous workers have not included a submaximal performance test in their studies of adaptation to training, they have shown that training increases the oxidative capacity of the skeletal muscle using similar training methods as used in the present study (Henriksson, 1977). Therefore, it can be assumed that similar adaptations occurred in this study. Henriksson (1977) stated that the findings from his one-legged training programme gave rise to the following major question, that is

"Whether an enhanced oxidative potential of skeletal muscle has any significance for metabolism during exercise? Theoretically it may enable the muscle to extract more oxygen from the blood during maximal exercise so as to increase $\dot{V}O_2$ max and it may influence metabolism during submaximal exercise giving rise to a shift towards an increased fat metabolism relative to that of carbohydrate."

(Henriksson, 1977).

It is suggested that this study provides an answer to the above question, since both an increased $\dot{V}O_2$ max and an increased ability to sustain a given submaximal work load were found during exercise with the TL after training. The small increase in $\dot{V}O_2$ max relative to the large increase in endurance capacity suggests that changes in the oxidative capacity of the muscle have a more profound effect on exercise at the submaximal than the maximal level.

The findings of this investigation support the view that improvements in endurance capacity after training are largely the result of adaptations in the skeletal muscles rather than improvements in the central cardiovascular system.
CHAPTER 7

GENERAL DISCUSSION

This study has investigated the relationship between maximum oxygen uptake ($\dot{V}O_2$ max) and endurance capacity and provided further evidence to support the view that $\dot{V}O_2$ max alone does not reflect the endurance capacity of an individual.

More recent studies have concluded that the increase in the oxidative capacity of skeletal muscle is the single most important determinant of endurance capacity (Davies, Packer and Brooks, 1981; Gollnick and Saltin, 1982). While sprint and strength type training may produce small increases in $\dot{V}O_2$ max these increases are not accompanied by improvements in the oxidative capacity of skeletal muscle (Hickson, Rosenkoetter and Brown, 1980; Davies, Packer and Brooks, 1982). Therefore it is unlikely that this latter type of training produces similar improvements in endurance as those which result from an endurance training programme.

Indirect evidence for the dissociation between $\dot{V}O_2$ max and endurance capacity is also to be found in those studies which have included observations before and after training and also after a period of reduced activity, i.e. detraining. Henriksson and Reitman (1977) reported that 6 weeks after an 8 to 10 week training programme which produced a 19% improvement in $\dot{V}O_2$ max, the oxidative capacity of the subjects skeletal muscle had decreased by approximately 35% while $\dot{V}O_2$ max had only decreased by 3%.

Some insight on how a large decrease in the oxidative capacity of skeletal muscle may influence performance is provided by the work of Houston, Bentzen and Larsen (1979). These authors reported that endurance performance at 90% $\dot{V}O_2$ max decreased by 25% after 15 days of detraining which was accompanied by a 24% decrease in the oxidative capacity of skeletal muscle but only a 4% decrease in $\dot{V}O_2$ max.
Improvements in the endurance capacity of an individual as a result of training (Chapters 5 and 6) are reflected by the characteristic reduction of blood lactic acid concentration during a standardized exercise test. This reduction in blood lactic acid concentration after training has been proposed as a useful indicator of the increased oxidative capacity of the muscles and thus aerobic metabolism.

The exercise intensity at which blood lactic acid accumulates has also been a useful indicator of the proportion of \( \dot{V}O_2 \) max which may be endured for prolonged periods. The onset of blood lactic acid accumulation, more commonly referred to as the anaerobic threshold, may therefore also be a more sensitive indicator of improvements in endurance capacity than \( \dot{V}O_2 \) max. Thus the endurance capacity of an individual might be better described by assessing at what percentage of his or her \( \dot{V}O_2 \) max blood lactic acid accumulates rather than by determining \( \dot{V}O_2 \) max alone.

**RECOMMENDATIONS FOR FURTHER RESEARCH**

The improvements in endurance capacity in the present investigation were attributed to changes in the oxidative capacity of the skeletal muscle on the basis of the results of similar one-legged training studies which have not included a performance test (Saltin et al., 1976; Henriksson, 1977). Therefore, it is recommended that a one-legged training study is performed which includes both a submaximal performance test and a closer examination of the adaptations taking place in the skeletal muscles of the trained and untrained legs. For example, a study in which the changes in endurance performance and the changes in the oxidative capacity and capillary density of skeletal muscle are determined. This would provide a more complete description of the adaptations to training than is currently available.
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APPENDICES
APPENDIX 1

EXPERIMENTAL INVESTIGATIONS

1.A

A COMPARISON OF THE CONTINUOUS AND DISCONTINUOUS LOADING OXYGEN UPTAKE TESTS

INTRODUCTION

This study compared a single session 2 minute continuous loading test with a multi-session 4 minute discontinuous loading test for the determination of both maximum oxygen uptake (VO₂ max) and the oxygen uptake (VO₂)/work load relationship.

The tests were compared to answer 2 questions:

1. Do both tests elicit the same VO₂ max?
2. Which test is more accurate for the prediction of a given submaximal work load that will demand a known percentage of an individual's VO₂ max?

The second question is of great importance for the determination of training work loads.

From the findings in Chapter 5, where the training work load was calculated from the maximum work load, i.e. the work load which produced VO₂ max, the subjects were found to be training at work loads ranging from 58 to 94% VO₂ max. The use of this method for the calculation of training work loads is clearly unsatisfactory. The main aim of this study therefore was to examine the use of the above two tests for the prediction of a given relative work load.
METHOD

Eight subjects (6 males and 2 females) participated in the study. Mean age, height and weight ± S.D. were 31.1 ± 10.2 yrs, 178.1 ± 5.6 cms and 71.56 ± 9.67 kg respectively, (table A.1). All subjects were familiar with exercise on a bicycle ergometer. Experimental data was therefore collected on all visits. The time of the tests and the length of time from the last meal were not standardized with these subjects.

The experimental protocol may be summarized as follows:

1. A 2 minute continuous loading VO₂ max test.
2. A 10 minute exercise test at the predicted submaximal work load designed to elicit 75% VO₂ max, as calculated from the continuous loading data.
3. A 4 minute discontinuous loading VO₂ max test.
4. A 10 minute exercise test at the predicted submaximal work load designed to elicit 75% VO₂ max, as calculated from the discontinuous data.

The above tests are fully described in Chapter 3, sections 3.8.1, 3.8.2 and 3.9. The use of the linear regression equation for the prediction of a given submaximal work load that would demand a known percentage of an individual's VO₂ max is described in Appendix 2.E. During both the continuous and discontinuous loading tests the subjects exercised at the same absolute work loads allowing direct comparisons to be made between the two tests.

Data analysis

The t-test for uncorrelated data was used to determine whether any differences existed between the two tests.

In the results section, the 10 minute exercise test derived from the continuous and discontinuous loading data shall be referred to as
the 10 minute "continuous" and "discontinuous" tests respectively. Results are presented as means ± standard deviations (SD).

RESULTS

The mean age, height and weight of the subjects are presented in table A.1.

The two tests produced no differences at the maximum level in the following parameters: \( \dot{V}O_2 \), \( \dot{V}E \), \( \dot{V}E/\dot{V}O_2 \), RER and HR (table A.2). The \( \dot{V}O_2 \) max values as measured by the continuous and discontinuous loading tests were 2.99 ± 0.71 and 3.02 ± 0.63 L.min\(^{-1}\) respectively.

A significant difference was however found between the maximum work loads (watts) produced by the two tests. The work load corresponding to \( \dot{V}O_2 \) max was higher during the discontinuous test (table A.2, \( p < 0.05 \)).

No significant differences were found between the \( \dot{V}O_2 \) and HR values at each of the submaximal work loads during the two tests, the only exception being the HR value at 118 watts (table A.3). Although no differences were found between the HR values produced by the two tests at each submaximal work load, the values recorded during the discontinuous test were all lower than those recorded during the continuous test.

The absence of any differences between the two tests in \( \dot{V}O_2 \) at each submaximal work load suggests that the relationship between \( \dot{V}O_2 \) and work load was the same during both tests.

The predicted work loads for the elicitation of 75% \( \dot{V}O_2 \) max were the same for both tests. The predicted values determined from the continuous and discontinuous loading tests were 183.6 ± 45.1 and 181.7 ± 40.1 watts respectively (table A.4).
During the 10 minute exercise tests, at the predicted 75% work loads determined from the continuous and discontinuous tests, the subjects were calculated to be exercising at 76.6 ± 4.9 and 76.2 ± 2.3 \( \dot{V}O_2 \) max respectively (table A.4). These percentages were obtained from 2 minute expired air collections, i.e. between 4 and 6 minutes of exercise. The mean \( \dot{V}O_2 \) values determined during the "continuous" and "discontinuous" 10 minute tests were 2.28 ± 0.50 and 2.30 ± 0.50 L.min\(^{-1}\) respectively. Although both tests were reasonably accurate at eliciting 75% \( \dot{V}O_2 \) max, the range of values around the mean were greater when the continuous loading test was used. The percentage values obtained during the 10 minute "continuous" test ranged from 71.4 to 84.8%, whereas the values obtained during the "discontinuous" test ranged from 73.3 to 79.7%.

\( \dot{V}O_2 \) and HR values were also determined at 8 to 10 minutes during the two 10 minute tests. These values were significantly higher than the values determined at 4 to 6 minutes during both the "continuous" and "discontinuous" tests. These increases were not accompanied by an increase in the work load, suggesting that the steady-state condition may not have been reached after 4 to 6 minutes of exercise (table A.5).

**DISCUSSION**

Since no differences were found between the two tests at both the maximal and submaximal levels, the predicted work loads for the elicitation of 75% \( \dot{V}O_2 \) max were the same for both tests. Although the two tests would appear to be of equal accuracy for predicting a given relative work load, the smaller range of percentage values found during the 10 minute test derived from the discontinuous test data, suggests that this test may have an advantage over the continuous test for the calculation of training work loads. The discontinuous protocol, however, has the disadvantage of being very time consuming as it involves several visits to the laboratory.

The elicitation of the steady-state condition is important for the accurate measurement of oxygen cost at each submaximal work load.
Astrand and Rodahl (1977, p.337) stated that at least 5 minutes was required to elicit this condition. The findings of this study, however, suggest that a longer period, i.e. 8 to 10 minutes may be required. Therefore the \% \textit{VO}_2\textsuperscript{max} calculated from the information obtained during the 2 minute continuous loading test will underestimate the exercise intensity at which the subjects are working during prolonged periods of exercise. A discontinuous 10 minute loading test may be more accurate for the determination of training work loads but the time involved is rarely practical.

As a result of the small differences between the tests, it was decided to adopt the faster continuous loading protocol. On the basis of the findings in this study, the 2 minute continuous loading test was increased to a 4 minute continuous loading test. The time at each work load cannot be increased beyond this because if \textit{VO}_2\textsuperscript{max} is to be reached considerable motivation would be required. In addition, fatigue may terminate the test before \textit{VO}_2\textsuperscript{max} is obtained.
### TABLE A.1

Physical characteristics of the subjects

<table>
<thead>
<tr>
<th>SUBJECT</th>
<th>AGE yrs</th>
<th>HEIGHT cms</th>
<th>WEIGHT kg</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>24.6</td>
<td>178.0</td>
<td>65.90</td>
</tr>
<tr>
<td>2</td>
<td>39.6</td>
<td>176.0</td>
<td>73.05</td>
</tr>
<tr>
<td>3</td>
<td>51.6</td>
<td>181.7</td>
<td>82.85</td>
</tr>
<tr>
<td>4</td>
<td>22.4</td>
<td>171.0</td>
<td>59.25</td>
</tr>
<tr>
<td>5</td>
<td>34.6</td>
<td>170.8</td>
<td>63.05</td>
</tr>
<tr>
<td>6</td>
<td>23.2</td>
<td>178.0</td>
<td>64.85</td>
</tr>
<tr>
<td>7</td>
<td>26.9</td>
<td>182.5</td>
<td>78.95</td>
</tr>
<tr>
<td>8</td>
<td>25.6</td>
<td>187.1</td>
<td>84.55</td>
</tr>
<tr>
<td>MEAN</td>
<td>31.1</td>
<td>178.1</td>
<td>71.56</td>
</tr>
<tr>
<td>S.D.</td>
<td>10.2</td>
<td>5.6</td>
<td>9.67</td>
</tr>
<tr>
<td>PARAMETER</td>
<td>CONTINUOUS TEST</td>
<td>DISCONTINUOUS TEST</td>
<td></td>
</tr>
<tr>
<td>-----------------</td>
<td>-----------------</td>
<td>--------------------</td>
<td></td>
</tr>
<tr>
<td>( \dot{V}O_2 ) L.min(^{-1} )</td>
<td>2.99 ± 0.71</td>
<td>3.02 ± 0.63</td>
<td></td>
</tr>
<tr>
<td>( \dot{V}O_2 ) ml.kg(^{-1})min(^{-1} )</td>
<td>41.22 ± 7.03</td>
<td>41.79 ± 6.02</td>
<td></td>
</tr>
<tr>
<td>VE L.min(^{-1} )</td>
<td>109.40 ± 37.90</td>
<td>113.90 ± 29.00</td>
<td></td>
</tr>
<tr>
<td>RER</td>
<td>1.30 ± 0.07</td>
<td>1.24 ± 0.09</td>
<td></td>
</tr>
<tr>
<td>VE.VO(_2) L(^{-1} )</td>
<td>32.3 ± 7.5</td>
<td>35.5 ± 5.2</td>
<td></td>
</tr>
<tr>
<td>HR</td>
<td>181.0 ± 18.6</td>
<td>179.4 ± 12.4</td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>250.3 ± 52.2</td>
<td>270.7 ± 45.7</td>
<td></td>
</tr>
</tbody>
</table>

Level of significance between the two tests:

* \( P < 0.05 \)
TABLE A.3

Oxygen uptake ($\dot{V}O_2$ L.min$^{-1}$) and heart rate (b.min$^{-1}$) values determined during the continuous and discontinuous loading tests (means ± SD)

<table>
<thead>
<tr>
<th>WORK LOAD (WATTS)</th>
<th>OXYGEN UPTAKE</th>
<th>HEART RATE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CONTINUOUS TEST</td>
<td>DISCONTINUOUS TEST</td>
</tr>
<tr>
<td>59</td>
<td>0.90 ± 0.16</td>
<td>0.99 ± 0.03</td>
</tr>
<tr>
<td>118</td>
<td>1.54 ± 0.13</td>
<td>1.62 ± 0.03</td>
</tr>
<tr>
<td>177</td>
<td>2.18 ± 0.14</td>
<td>2.24 ± 0.05</td>
</tr>
<tr>
<td>235</td>
<td>2.84 ± 0.19</td>
<td>2.87 ± 0.09</td>
</tr>
<tr>
<td>265 (n=4)</td>
<td>3.23 ± 0.24</td>
<td>3.22 ± 0.08</td>
</tr>
</tbody>
</table>

Level of significance between the heart rate values determined during the two tests:
* $P < 0.05$
Comparison of the continuous and discontinuous tests for the prediction of a given submaximal work load (75% \( \dot{V}O_2 \max \)) (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>CONTINUOUS TEST</th>
<th>DISCONTINUOUS TEST</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predicted 75% ( \dot{V}O_2 ) max value (L.min(^{-1}))</td>
<td>2.23 ± 0.56</td>
<td>2.26 ± 0.47</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1})) at 4-6 min</td>
<td>2.28 ± 0.50</td>
<td>2.30 ± 0.50</td>
</tr>
<tr>
<td>Predicted 75% work load (W)</td>
<td>183.6 ± 45.1</td>
<td>181.7 ± 40.1</td>
</tr>
<tr>
<td>Work load at 4-6 min (W)</td>
<td>183.4 ± 45.5</td>
<td>182.0 ± 40.6</td>
</tr>
<tr>
<td>% ( \dot{V}O_2 ) max at 4-6 min</td>
<td>76.6 ± 4.9</td>
<td>76.2 ± 2.3</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1})) at 8-10 min</td>
<td>2.38 ± 0.53</td>
<td>2.36 ± 0.47</td>
</tr>
<tr>
<td>Work load at 8-10 min (W)</td>
<td>184.7 ± 45.7</td>
<td>181.5 ± 41.7</td>
</tr>
<tr>
<td>% ( \dot{V}O_2 ) max at 8-10 min</td>
<td>79.9 ± 4.9</td>
<td>78.3 ± 2.04</td>
</tr>
</tbody>
</table>

NB Predicted values and values determined during the 10 minute exercise tests are included.
TABLE A.5

Oxygen uptake and heart rate values determined at 4-6 and 8-10 minutes during the 10 minute exercises tests, derived from the continuous and discontinuous tests (means ± SD)

<table>
<thead>
<tr>
<th>TEST</th>
<th>PARAMETER</th>
<th>4 - 6 MIN</th>
<th>8 - 10 MIN</th>
<th>PERCENTAGE INCREASE</th>
</tr>
</thead>
<tbody>
<tr>
<td>CONTINUOUS</td>
<td>$\dot{V}O_2$ (L.min$^{-1}$)</td>
<td>2.28 ± 0.53</td>
<td>2.38 ± 0.53</td>
<td>4.4%</td>
</tr>
<tr>
<td>DISCONTINUOUS</td>
<td>$\dot{V}O_2$ (L.min$^{-1}$)</td>
<td>2.30 ± 0.50</td>
<td>2.36 ± 0.47</td>
<td>2.6%</td>
</tr>
<tr>
<td>CONTINUOUS</td>
<td>HR (b.min$^{-1}$)</td>
<td>149.6 ± 18.8</td>
<td>158.3 ± 18.1</td>
<td>5.8%</td>
</tr>
<tr>
<td>DISCONTINUOUS</td>
<td>HR (b.min$^{-1}$)</td>
<td>148.8 ± 17.5</td>
<td>157.0 ± 17.0</td>
<td>5.5%</td>
</tr>
<tr>
<td>CONTINUOUS</td>
<td>% $\dot{V}O_2$ max</td>
<td>76.6 ± 4.9</td>
<td>79.9 ± 4.9</td>
<td>4.3%</td>
</tr>
<tr>
<td>DISCONTINUOUS</td>
<td>% $\dot{V}O_2$ max</td>
<td>76.2 ± 2.3</td>
<td>78.3 ± 2.0</td>
<td>2.8%</td>
</tr>
<tr>
<td>CONTINUOUS</td>
<td>W (watts)</td>
<td>183.4 ± 45.5</td>
<td>184.7 ± 45.7</td>
<td>0.74%</td>
</tr>
<tr>
<td>DISCONTINUOUS</td>
<td>W (watts)</td>
<td>182.0 ± 40.6</td>
<td>185.1 ± 41.7</td>
<td>1.70%</td>
</tr>
</tbody>
</table>

Levels of significance between the two values:
* $P < 0.05$
*** $P < 0.001$
A 4 MINUTE CONTINUOUS LOADING OXYGEN UPTAKE TEST DURING ONE-LEGGED ERGOMETRY WITH BOTH THE RIGHT AND LEFT LEGS

INTRODUCTION

Exercise intensity is the most important factor influencing the training response (Davies and Knibbs, 1971, Pollock, 1973). During any training programme therefore, the prediction of a given submaximal work load that will demand a known percentage of an individual's \( \dot{V}O_2 \) max, is of crucial importance to ensure that all subjects are training at approximately the same relative work load.

The most common procedure is to use percent maximum HR as the criterion reference point (Davies and Knibbs, 1971). In the present investigation, however, the use of percent maximum oxygen uptake (\( \% \dot{V}O_2 \) max) was adopted as the method for equating the exercise intensity between subjects. Although many investigators state the exercise intensity at which their subjects trained, very few have included information regarding the calculation of the training work load. This is particularly the case in one-legged training studies. Saltin and coworkers, for example, stated that "work loads were chosen to represent approximately 75% one-legged \( \dot{V}O_2 \) max" and from expired air collections made in the third week of training the subjects were found to be exercising at "the expected physiological load" (Saltin et. al., 1976).

The present study, therefore, set out to investigate the accuracy of the 4 minute continuous loading oxygen uptake test for the calculation of a given relative work load for both the right and left legs. This test was repeated twice on each leg to examine test-retest reliability. A discontinuous test was also included to establish and confirm the \( \dot{V}O_2 \) max values obtained during the continuous test.
METHOD

Five male subjects participated in the study. Mean age, height and weight ± SD were 29.4 ± 7.4 yrs, 180.2 ± 3.4 cms, and 78.56 ± 4.19 kg respectively (table A.6).

A preliminary visit to the laboratory was made by all subjects to familiarize them with one-legged bicycle ergometry. During this visit a 2 minute continuous loading test was carried out on each leg up to maximal levels. This allowed the subjects to experience one-legged exercise at both the submaximal and maximal levels, and provided the experimenter with an indication of the exercise capacity of each subject to perform one-legged work. During this test the work load was increased from 29 watts and by 29 watts every 2 minutes until subjective exhaustion was reached. It was found that the inability of the subjects to turn the pedal terminated the exercise. For this reason, at a work load of 118 watts, the work load increments were reduced to 15 watts every 2 minutes. This allowed the subjects to continue exercising for a longer period. To assess the effects that this might have on VO\textsubscript{2} max measurements, the 2 minute continuous loading tests with the different work load increments were performed on 3 of the 5 subjects. The protocol with the smaller work load increments at the higher work loads is described in Chapter 3, section 3.8.1.

During the first visit to the laboratory the saddle height for each subject was determined. The subjects dictated this setting by indicating which height was most comfortable. This resulted in the selection of a height that resulted in noticeable upper body movement and considerable contribution from the plantar flexors. On subsequent occasions, therefore, the saddle height was set by the experimenter in an attempt to ensure that the angle at the knee was approximately 90° when the pedal was in its lowest position. This reduced upper body movement, local sensations of pain at the knee joint and the contribution of the plantar flexors.

All subjects in the study were used to two-legged bicycle ergometry at submaximal and maximal levels during which VO\textsubscript{2} max had been determined.
They were all therefore accustomed to the experimental procedure necessary for the collection of expired air.

**Experimental protocol**

The experimental protocol may be summarized as follows:

1. A 2 minute continuous loading test to familiarize the subjects with one-legged exercise.
2. A 2 minute continuous loading test during which expired air was collected at the higher work loads (n=3).
3. The test performed by the 3 subjects during visit 2 was repeated with the smaller work load increments at the higher work loads.
4. A 4 minute continuous loading oxygen uptake test on both the right and left legs (described in Chapter 3, section 3.8.1).
5. The 4 minute continuous loading test was repeated by both the right and left legs.
6. A 4 minute discontinuous oxygen uptake test performed by both the right and left legs (described in Chapter 3, section 3.8.2).
7. A 10 minute exercise test with either the right or left leg at the predicted work load designed to elicit 75% one-legged $\dot{V}O_2$ max (Chapter 3, section 3.10).
8. The test performed during visit 7 was repeated on the other leg.

During all visits (excluding visit 1) oxygen uptake, respiratory and heart rate values were determined.

**Data analysis**

The t-test for uncorrelated data was used to compare the right and left legs. The t-test for correlated data was used to compare measurements made on the same leg on different occasions. Significance
was accepted at the .05 level. Results are presented as means ± standard deviations -(SD).

RESULTS

The mean age, height and weight of the subjects are presented in table A.6.

During the 2 minute continuous loading test where the work load was increased by 29 watts every 2 minutes, the measured mean \( \dot{V}O_2 \) max value for the 3 male subjects was significantly lower than the value obtained during the test where the work load increments were reduced at the higher work loads (p < 0.05). The \( \dot{V}O_2 \) max values determined during these 2 tests were 2.30 ± 0.12 and 2.49 ± 0.07 L.min\(^{-1}\) respectively. The work load required to elicit the higher value of 2.49 L.min\(^{-1}\) was significantly higher than the load which elicited the lower value of 2.30 L.min\(^{-1}\) (p < 0.05).

No differences were found between the maximum values produced by the continuous and discontinuous loading tests for both the right and left legs. Despite this the \( \dot{V}O_2 \) max values elicited by the discontinuous test were higher (table A.7).

No differences were found between the right and left legs at the maximum level (table A.7). The \( \dot{V}O_2 \) max values for the two legs were 2.68 ± 0.39 and 2.74 ± 0.39 L.min\(^{-1}\) respectively. (The highest measured value from the continuous and discontinuous tests was taken.)

No differences were found between the \( \dot{V}O_2 \) and HR values at each of the submaximal work loads between the right and left legs (table A.8).

When the 4 minute continuous loading test was repeated by the right leg, no differences were found at both the maximal and submaximal levels between the oxygen uptake, respiratory and heart rate values determined during the two tests. This was also the case for the left
leg (tables A.9, A.10 and A.11). Figure A.1 illustrates the similarity between the \( \dot{V}O_2 \) values determined on two occasions for the right leg.

Since the relationship between \( \dot{V}O_2 \) and work load was not linear as in two-legged exercise, the linear regression equation was not used for the prediction of the work load that would demand 75% one-legged \( \dot{V}O_2 \) max. The work load was estimated from each subject's \( \dot{V}O_2 \)/work load relationship. The estimated work load for the elicitation of 75% one-legged \( \dot{V}O_2 \) max was the same for both the right and left legs. The work loads for the right and left legs were 121.1 ± 14.8 and 119.8 ± 13.7 watts respectively (table A.12).

From the expired air collections made at 4 to 6 minutes during the 10 minute exercise tests, the subjects were calculated to be utilizing 75.7 ± 3.0% and 72.9 ± 3.2% of their right and left leg \( \dot{V}O_2 \) max values respectively (table A.12).

The \( \dot{V}O_2 \) and HR values determined at 8 to 10 minutes were higher than the values determined after 4 to 6 minutes during the 10 minute test. The differences however were not significant, possibly as a result of the small sample size (n = 5).

**DISCUSSION**

The main aim of this investigation was to assess the accuracy of the 4 minute continuous loading oxygen uptake test for the calculation of a given relative work load. During the 10 minute tests, designed to investigate the accuracy of the load calculation, the subjects were found to be exercising at 75.7 ± 3.0 and 72.9 ± 3.2% with the right and left legs respectively. Since the desired work load was 75% one-legged \( \dot{V}O_2 \) max, the 4 minute continuous loading test was considered to be of sufficient accuracy for the determination of training work loads. In addition, as can be seen from the small standard deviations, the range of values around each mean were small.
This study showed that no differences were found at the maximum level between the continuous and discontinuous oxygen uptake tests. The results also indicated that there were no differences between the right and left legs at both the maximal and submaximal levels.

Finally, the continuous loading test with the smaller work load increments at the higher work loads (Chapter 3, section 3.8.1) allowed the subjects to exercise for a longer period of time resulting in a higher measured $\dot{V}O_2$ max. This protocol was adopted during all subsequent one-legged exercise tests.
### Physical characteristics of the subjects

<table>
<thead>
<tr>
<th>SUBJECT</th>
<th>AGE (yrs)</th>
<th>HEIGHT (cms)</th>
<th>WEIGHT (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>24.6</td>
<td>185.5</td>
<td>84.60</td>
</tr>
<tr>
<td>2</td>
<td>33.8</td>
<td>178.5</td>
<td>78.55</td>
</tr>
<tr>
<td>3</td>
<td>39.4</td>
<td>178.0</td>
<td>73.50</td>
</tr>
<tr>
<td>4</td>
<td>28.5</td>
<td>181.5</td>
<td>80.05</td>
</tr>
<tr>
<td>5</td>
<td>20.8</td>
<td>177.5</td>
<td>76.10</td>
</tr>
<tr>
<td><strong>MEAN</strong></td>
<td><strong>29.4</strong></td>
<td><strong>180.2</strong></td>
<td><strong>78.56</strong></td>
</tr>
<tr>
<td><strong>S.D.</strong></td>
<td><strong>7.4</strong></td>
<td><strong>3.4</strong></td>
<td><strong>4.19</strong></td>
</tr>
</tbody>
</table>
**TABLE A.7**

Maximum values determined during the continuous and discontinuous tests, for the right and left legs (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>CONTINUOUS TEST</th>
<th>DISCONTINUOUS TEST</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RIGHT LEG</td>
<td>LEFT LEG</td>
</tr>
<tr>
<td></td>
<td>RIGHT LEG</td>
<td>LEFT LEG</td>
</tr>
<tr>
<td>(\dot{V}O_2) (L.min(^{-1}))</td>
<td>2.59 ± 0.29</td>
<td>2.61 ± 0.41</td>
</tr>
<tr>
<td>(\dot{V}O_2) (ml.kg(^{-1}).min(^{-1}))</td>
<td>34.65 ± 3.67</td>
<td>32.72 ± 3.89</td>
</tr>
<tr>
<td>(\dot{V}E) (L.min(^{-1}))</td>
<td>99.48 ± 22.68</td>
<td>89.17 ± 26.68</td>
</tr>
<tr>
<td>(\dot{V}CO_2) (L.min(^{-1}))</td>
<td>3.08 ± 0.21</td>
<td>2.91 ± 0.51</td>
</tr>
<tr>
<td>RER</td>
<td>1.19 ± 0.08</td>
<td>1.18 ± 0.12</td>
</tr>
<tr>
<td>(\dot{V}E).(\dot{V}O_2)(^{-1})</td>
<td>38.41 ± 7.92</td>
<td>35.06 ± 7.89</td>
</tr>
<tr>
<td>HR(b.min(^{-1}))</td>
<td>167.2 ± 13.1</td>
<td>162.6 ± 19.8</td>
</tr>
<tr>
<td>W (watts)</td>
<td>150.4 ± 12.5</td>
<td>148.7 ± 12.3</td>
</tr>
</tbody>
</table>
TABLE A.8

Oxygen uptake (\(\dot{V}O_2 \text{ L.min}^{-1}\)) and heart rate (b.min\(^{-1}\)) values determined during the continuous loading test, for the right and left legs (means ± SD)

<table>
<thead>
<tr>
<th>WORK LOAD (watts)</th>
<th>RIGHT LEG (\dot{V}O_2)</th>
<th>LEFT LEG (\dot{V}O_2)</th>
<th>RIGHT LEG HR</th>
<th>LEFT LEG HR</th>
</tr>
</thead>
<tbody>
<tr>
<td>29</td>
<td>0.64 ± 0.11</td>
<td>0.63 ± 0.06</td>
<td>84.4 ± 8.9</td>
<td>88.2 ± 6.8</td>
</tr>
<tr>
<td>59</td>
<td>1.08 ± 0.10</td>
<td>1.02 ± 0.06</td>
<td>97.4 ± 6.7</td>
<td>103.2 ± 8.5</td>
</tr>
<tr>
<td>88</td>
<td>1.50 ± 0.09</td>
<td>1.46 ± 0.13</td>
<td>118.4 ± 9.4</td>
<td>123.2 ± 17.4</td>
</tr>
<tr>
<td>118</td>
<td>2.12 ± 0.14</td>
<td>2.02 ± 0.12</td>
<td>144.4 ± 18.1</td>
<td>149.2 ± 21.8</td>
</tr>
<tr>
<td>132(n=4)</td>
<td>2.46 ± 0.10</td>
<td>2.41 ± 0.07</td>
<td>159.3 ± 21.2</td>
<td>159.5 ± 22.9</td>
</tr>
<tr>
<td>147(n=3)</td>
<td>2.77 ± 0.11</td>
<td>2.95 ± 0.21</td>
<td>163.7 ± 6.4</td>
<td>164.3 ± 12.7</td>
</tr>
</tbody>
</table>
Maximum values, determined during the 4 minute continuous loading test repeated on two occasions, for the right and left legs (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>RIGHT LEG</th>
<th>LEFT LEG</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TEST 1</td>
<td>TEST 2</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1}))</td>
<td>2.59 ± 0.29</td>
<td>2.42 ± 0.29</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) (ml.kg(^{-1}).min(^{-1}))</td>
<td>34.65 ± 3.76</td>
<td>32.78 ± 5.13</td>
</tr>
<tr>
<td>( \dot{VE} ) (L.min(^{-1}))</td>
<td>99.48 ± 22.68</td>
<td>88.00 ± 21.88</td>
</tr>
<tr>
<td>( \dot{V}CO_2 ) (L.min(^{-1}))</td>
<td>3.08 ± 0.20</td>
<td>3.01 ± 0.48</td>
</tr>
<tr>
<td>RER</td>
<td>1.19 ± 0.08</td>
<td>1.16 ± 0.11</td>
</tr>
<tr>
<td>( \dot{VE}.\dot{V}O_2 ) (L)</td>
<td>38.41 ± 7.92</td>
<td>35.95 ± 6.74</td>
</tr>
<tr>
<td>HR (b.min(^{-1}))</td>
<td>167.2 ± 13.1</td>
<td>164.0 ± 16.4</td>
</tr>
<tr>
<td>W (watts)</td>
<td>150.4 ± 12.6</td>
<td>148.3 ± 14.7</td>
</tr>
<tr>
<td>Exercise time (min)</td>
<td>20.9 ± 3.6</td>
<td>21.1 ± 4.13</td>
</tr>
</tbody>
</table>
Oxygen uptake (\(\dot{V}O_2 L.min^{-1}\)) values, determined during the 4 minute continuous loading test repeated on two occasions, for the right and left legs (means ± SD)

<table>
<thead>
<tr>
<th>WORK LOAD (watts)</th>
<th>RIGHT TEST 1</th>
<th>RIGHT TEST 2</th>
<th>LEFT TEST 1</th>
<th>LEFT TEST 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>29</td>
<td>0.64 ± 0.11</td>
<td>0.62 ± 0.05</td>
<td>0.63 ± 0.06</td>
<td>0.60 ± 0.06</td>
</tr>
<tr>
<td>59</td>
<td>1.08 ± 0.10</td>
<td>1.04 ± 0.08</td>
<td>1.02 ± 0.06</td>
<td>1.03 ± 0.05</td>
</tr>
<tr>
<td>88</td>
<td>1.50 ± 0.09</td>
<td>1.47 ± 0.10*</td>
<td>1.46 ± 0.13</td>
<td>1.45 ± 0.06</td>
</tr>
<tr>
<td>118 (n=4)</td>
<td>2.12 ± 0.14</td>
<td>1.94 ± 0.11</td>
<td>2.02 ± 0.12</td>
<td>2.01 ± 0.20</td>
</tr>
<tr>
<td>132 (n=4)</td>
<td>2.46 ± 0.10</td>
<td>2.33 ± 0.13</td>
<td>2.41 ± 0.07</td>
<td>2.43 ± 0.10</td>
</tr>
<tr>
<td>147 (n=3)</td>
<td>2.77 ± 0.11</td>
<td>2.55 ± 0.04</td>
<td>2.95 ± 0.21</td>
<td>2.73 ± 0.16</td>
</tr>
</tbody>
</table>

Level of significance between tests 1 and 2: * P < 0.05
FIG. A.1  OXYGEN COST OF ONE-LEGGED CYCLING DETERMINED DURING EXERCISE WITH THE RIGHT LEG ON TWO OCCASIONS

( ) no. of subjects when less than whole group
TABLE A.11

Heart rate (b.min⁻¹) values, determined during the 4 minute continuous loading test, repeated on two occasions for the right and left legs (means ± SD)

<table>
<thead>
<tr>
<th>WORK LOAD (watts)</th>
<th>RIGHT LEG TEST 1</th>
<th>RIGHT LEG TEST 2</th>
<th>LEFT LEG TEST 1</th>
<th>LEFT LEG TEST 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>29</td>
<td>84.4 ± 8.9</td>
<td>82.4 ± 5.5</td>
<td>88.2 ± 6.8</td>
<td>85.8 ± 9.9</td>
</tr>
<tr>
<td>58</td>
<td>97.4 ± 6.7</td>
<td>96.6 ± 6.0</td>
<td>103.2 ± 8.5</td>
<td>101.0 ± 9.8</td>
</tr>
<tr>
<td>88</td>
<td>118.4 ± 9.4</td>
<td>117.2 ± 11.7</td>
<td>123.2 ± 17.4</td>
<td>121.6 ± 12.9</td>
</tr>
<tr>
<td>118</td>
<td>144.4 ± 18.2</td>
<td>142.4 ± 20.2</td>
<td>149.2 ± 21.8</td>
<td>146.6 ± 21.7</td>
</tr>
<tr>
<td>132(n=4)</td>
<td>159.3 ± 21.2</td>
<td>159.3 ± 21.7</td>
<td>159.5 ± 22.9</td>
<td>156.8 ± 23.1</td>
</tr>
<tr>
<td>147(n=3)</td>
<td>163.7 ± 6.4</td>
<td>160.0 ± 11.4</td>
<td>164.3 ± 12.5</td>
<td>158.7 ± 11.0</td>
</tr>
</tbody>
</table>
TABLE A.12

Predicted and actual values determined during the 10 minute exercise tests designed to elicit 75% \( \dot{V}O_2 \) max, for the right and left legs (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>RIGHT LEG</th>
<th>LEFT LEG</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predicted 75% work load (watts)</td>
<td>121.1 ± 14.8</td>
<td>119.8 ± 13.7</td>
</tr>
<tr>
<td>Work load (watts) at 4-6 min</td>
<td>121.1 ± 15.4</td>
<td>120.0 ± 13.6</td>
</tr>
<tr>
<td>Predicted 75% ( \dot{V}O_2 ) max value (L.min(^{-1}))</td>
<td>2.03 ± 0.28</td>
<td>2.09 ± 0.36</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1})) at 4-6 min</td>
<td>2.06 ± 0.34</td>
<td>2.03 ± 0.32</td>
</tr>
<tr>
<td>% ( \dot{V}O_2 ) max at 4-6 min</td>
<td>75.7 ± 3.0</td>
<td>72.9 ± 3.2</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1})) at 8-10 min</td>
<td>2.04 ± 0.30</td>
<td>2.06 ± 0.32</td>
</tr>
<tr>
<td>% ( \dot{V}O_2 ) max at 8-10 min</td>
<td>75.0 ± 3.7</td>
<td>74.3 ± 2.6</td>
</tr>
</tbody>
</table>
TEST-RETEST RELIABILITY DURING ONE-LEGGED CYCLING

INTRODUCTION

The purpose of this study was to investigate the test-retest reliability of oxygen uptake, respiratory and heart rate values determined during exercise of increasing intensity using one leg only. To examine this, one male subject repeated the discontinuous loading test on four occasions. During each test the subject exercised with his left leg.

METHOD

The subject was a highly experienced laboratory subject and therefore accustomed to both submaximal and maximal levels of exercise and the experimental protocol necessary for the collection of expired air. However before any measurements were made, the subject visited the laboratory on several occasions to familiarize himself with one-legged exercise.

Discontinuous loading one-legged oxygen uptake test

During this test the load was progressively increased from 29 watts and by 29 watts up to 118 watts after which the load was increased by 15 watts. The subject exercised for 4 minutes at each work load with the rest periods between these being determined by the subject. The highest work load which the subject could sustain for 4 minutes was determined during the first test. During this test the subject completed 4 minutes at 29, 59, 88 and 118 watts. These same work loads were repeated during each subsequent test.

During the test HR was monitored continuously and recorded every minute, and expired air collections were made in the last minute of each 4 minute exercise period. At the two lowest work loads expired air was collected in the last 2 minutes of each 4 minute exercise.
period because of the small expired air volumes produced at these loads during one-legged exercise.

**Data analysis**

The coefficient of variation (V) for each parameter was calculated to determine the variability of the values measured during the 4 tests. Where V was equal to or less than 5%, the values determined during the 4 tests were considered reliable. The investigation was primarily concerned with the reproducibility of the oxygen uptake values. Results are presented as means ± standard deviations (SD).

**RESULTS**

The mean age, height and weight of the subject were 39.4 yrs, 176.0 cms and 73.05 kg respectively.

The means and standard deviations for the oxygen uptake, respiratory and heart rate values are presented in table A.13. The small standard deviations suggest that the values did not vary greatly over the 4 tests. This was particularly the case for the oxygen uptake values (figure A.2).

The coefficient of variation (V) for each parameter at each work load is presented in table A.14. It can be seen that the greatest variability in the values occurred at the lowest and highest work loads.

The two most important parameters under observation were VO₂ and HR. The V values for HR were all under 5%, with the highest value being 2.6% at the highest work load (118 watts).

The values for VO₂ (L.min⁻¹) were again all under 5%, with the exception of the value of 5.2% at 118 watts (table A.14).

**SUMMARY**

The oxygen uptake and heart rate values determined during the 4 minute discontinuous loading test were reproducible.
TABLE A.13

Summary of the data determined during four discontinuous loading oxygen uptake tests performed by one subject (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>WORK (watts)</th>
<th>LOAD (watts)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>29</td>
<td>59</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1}))</td>
<td>0.56 ± 0.03</td>
<td>0.92 ± 0.03</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) (ml.kg(^{-1}).min(^{-1}))</td>
<td>7.76 ± 0.28</td>
<td>12.27 ± 0.32</td>
</tr>
<tr>
<td>( \dot{V}E ) (L.min(^{-1}))</td>
<td>16.81 ± 1.57</td>
<td>22.97 ± 1.19</td>
</tr>
<tr>
<td>RER</td>
<td>0.85 ± 0.06</td>
<td>0.92 ± 0.04</td>
</tr>
<tr>
<td>( \dot{V}E.\dot{V}O_2 ) (^{-1})</td>
<td>29.66 ± 3.39</td>
<td>25.05 ± 1.16</td>
</tr>
<tr>
<td>HR(b.min(^{-1}))</td>
<td>68.0 ± 0.8</td>
<td>83.3 ± 0.5</td>
</tr>
</tbody>
</table>
FIG. A.2 OXYGEN COST OF ONE-LEGGED CYCLING DETERMINED DURING A DISCONTINUOUS LOADING EXERCISE TEST FOR ONE MALE ON FOUR OCCASIONS
Coefficients of variation for the oxygen uptake, respiratory and heart rate values determined during four discontinuous loading tests performed by one subject

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>WORK</th>
<th>LOAD</th>
<th>(watts)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\dot{V}O_2$(L.min$^{-1}$)</td>
<td>29</td>
<td>59</td>
<td>88</td>
</tr>
<tr>
<td>4.7%</td>
<td>3.1%</td>
<td>0.4%</td>
<td>5.2%</td>
</tr>
<tr>
<td>$\dot{V}O_2$(ml.kg$^{-1}$.min$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3.6%</td>
<td>2.6%</td>
<td>0.9%</td>
<td>5.4%</td>
</tr>
<tr>
<td>$VE$ (L.min$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9.3%</td>
<td>5.2%</td>
<td>6.3%</td>
<td>18.1%</td>
</tr>
<tr>
<td>RER</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6.5%</td>
<td>4.4%</td>
<td>6.7%</td>
<td>7.4%</td>
</tr>
<tr>
<td>$VE.\dot{V}O_2^{-1}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11.4%</td>
<td>4.6%</td>
<td>6.3%</td>
<td>13.6%</td>
</tr>
<tr>
<td>HR(b.min$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.2%</td>
<td>0.5%</td>
<td>0.8%</td>
<td>2.6%</td>
</tr>
</tbody>
</table>
THE REPRODUCIBILITY OF BLOOD LACTATE CONCENTRATIONS DURING ONE- AND TWO-LEGGED EXERCISE

INTRODUCTION

This study set out to investigate the reproducibility of the lactate/work load relationship during both one- and two-legged exercise. Different protocols and blood sampling sites were included to examine the advantages and disadvantages of the various protocols. From such information the best method for both the subjects and the experimenter could be adopted.

METHOD

The subject performed the following exercise tests during which blood samples were collected for the determination of lactic acid levels:--

1. A two-legged 2 minute continuous loading test on a free wheel ergometer.
2. Test 1 repeated on a fixed wheel ergometer.
3. A one-legged 2 minute continuous loading test.
4. A one-legged 5 minute discontinuous loading test. The blood sampling site being an ear lobe and not the thumb as in all other tests.
5. A one-legged 5 minute discontinuous loading test with a controlled 12 minute rest period.
6. Test 5 repeated but with longer uncontrolled rest periods.

The above tests are described in Chapter 3, sections 3.8.1 and 3.8.2.

All one-legged exercise was performed on a fixed wheel ergometer with the left leg. During the discontinuous tests the blood samples were taken 4 minutes after exercise and during the continuous test the samples were taken at the end of each 2 minute exercise period. The lactate concentrations were expressed in relation to both absolute and
relative (% \( \dot{V}_O_2 \) max) work loads.

**RESULTS**

The blood lactate (LAMM) and % \( \dot{V}_O_2 \) max values at each of the work loads are presented in table A.15.

The LA levels, at each of the work loads over the 4 one-legged tests, vary from ± 0.21mM at the lowest work load (29 watts) to ± 0.84mM at the highest work load (118 watts). During two-legged ergometry the variation in the LA levels at each of the work loads is again smallest at the lowest work load and greatest at the highest work load. The variations at these two work loads being ± 0.01mM and ± 0.71mM respectively.

The blood LA concentrations at 2mM and 4mM are often used as reference levels in the Exercise Physiology literature. The absolute and relative work loads at these two concentrations are presented in table A.16. At 2mM, the % \( \dot{V}_O_2 \) max values all fell in the sixties, ranging from 62.0 to 67.0% \( \dot{V}_O_2 \) max (the only exception being 72.0% during the one-legged test with a controlled rest period). At 4mM, the % \( \dot{V}_O_2 \) max values during both types of exercise were all in the eighties, ranging from 80.0 and 86.5% \( \dot{V}_O_2 \) max. It should be pointed out that the relative work loads during the one- and two-legged exercise tests were calculated from their own \( \dot{V}_O_2 \) max values.

**DISCUSSION**

The blood LA concentrations determined at each work load during both the one- and two-legged exercise tests showed only small variations between the different tests despite the use of various protocols. The smallest variation was found at the lowest work load and the largest variation at the highest work load.

The findings indicate the LA/work load relationship for one subject may consistently be reproduced.
The use of the ear lobe as a sampling site was not adopted because the taking of blood from this area was difficult for the experimenter. The use of the thumb was therefore adopted in this and all other experiments in the investigation.

The discontinuous test, where a steady-state condition may have been reached, would normally be adopted in preference to the 2 minute continuous loading test. However, due to the very small variation between the two tests, the faster continuous loading test was employed.

Unfortunately the LA/work load relationships for the trained and untrained legs in the one-legged training programme could not be determined before and after training due to insufficient time. This data could not therefore be used for the purpose for which it was designed. However, these results indicate the good reproducibility of the blood lactate measurements determined at various work loads. This would suggest that the blood lactate measurements made throughout the investigation were reproducible.
### TABLE A.15

Blood lactate and % \( V\text{O}_2 \text{ max} \) at each work load (W) determined during the different test protocols

<table>
<thead>
<tr>
<th></th>
<th>LACTATE (mM)</th>
<th>% ( V\text{O}_2 \text{ max} )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TEST</td>
<td>29W</td>
</tr>
<tr>
<td>ONE-LEGGED</td>
<td>2 min cont.</td>
<td>0.85</td>
</tr>
<tr>
<td>EXERCISE</td>
<td>5 min discont. (ear sample)</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>5 min discont. (12 min rest)</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td>5 min discont. (uncontrolled rest)</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td>MEAN</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>S.D.</td>
<td>0.21</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>LACTATE (mM)</th>
<th>% ( V\text{O}_2 \text{ max} )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TEST</td>
<td>59W</td>
</tr>
<tr>
<td>TWO-LEGGED</td>
<td>2 min cont.</td>
<td>1.95</td>
</tr>
<tr>
<td>EXERCISE</td>
<td>(free wheel)</td>
<td>1.94</td>
</tr>
<tr>
<td></td>
<td>2 min cont.</td>
<td>1.95</td>
</tr>
<tr>
<td></td>
<td>(fixed wheel)</td>
<td>0.01</td>
</tr>
</tbody>
</table>

cont. = continuous loading test
discont. = discontinuous loading test
### Table A.16

Percentage $\dot{V}O_2$ max and work load (watts) at the blood lactate concentrations of $2mM$ and $4mM$ during the different tests

**ONE-LEGGED EXERCISE**

<table>
<thead>
<tr>
<th>TEST</th>
<th>$% \dot{V}O_2$ max</th>
<th>WATTS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$2mM$</td>
<td>$4mM$</td>
</tr>
<tr>
<td>2 min cont.</td>
<td>62.5</td>
<td>86.5</td>
</tr>
<tr>
<td>5 min discont. (ear sample)</td>
<td>62.3</td>
<td>84.5</td>
</tr>
<tr>
<td>5 min discont. (12 min rest)</td>
<td>62.8</td>
<td>80.0</td>
</tr>
<tr>
<td>5 min discont. (uncontrolled rest)</td>
<td>72.0</td>
<td>85.5</td>
</tr>
<tr>
<td><strong>MEAN</strong></td>
<td>64.9</td>
<td>84.1</td>
</tr>
<tr>
<td><strong>S.D.</strong></td>
<td>7.3</td>
<td>3.4</td>
</tr>
</tbody>
</table>

**TWO-LEGGED EXERCISE**

<table>
<thead>
<tr>
<th>TEST</th>
<th>$% \dot{V}O_2$ max</th>
<th>WATTS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$2mM$</td>
<td>$4mM$</td>
</tr>
<tr>
<td>2 min cont. (free wheel)</td>
<td>67.0</td>
<td>84.0</td>
</tr>
<tr>
<td>2 min cont. (fixed wheel)</td>
<td>62.9</td>
<td>82.7</td>
</tr>
<tr>
<td><strong>MEAN</strong></td>
<td>64.5</td>
<td>83.4</td>
</tr>
<tr>
<td><strong>S.D.</strong></td>
<td>3.5</td>
<td>0.9</td>
</tr>
</tbody>
</table>

cont = continuous loading test  
discont = discontinuous loading test
THE RESPONSES TAKING PLACE DURING PROLONGED SUBMAXIMAL ONE-LEGGED EXERCISE

INTRODUCTION

The purpose of this investigation was to provide insight into the responses taking place during prolonged submaximal one-legged exercise (~75% one-legged \( \dot{V}O_2 \) max).

To investigate this, the subjects performed 3 exercise tests. The first was a 1 hour test during which the subjects exercised with their right leg. The second test was also of 1 hour's duration but the exercise was performed with the left leg. Finally, the subjects performed a 2 hour test during which they exercised for 1 hour with their right leg followed by 1 hour with their left leg.

The first two 1 hour tests were included to investigate not only the responses taking place during prolonged one-legged submaximal exercise, but also to determine whether any differences existed between the right and left legs. The 2 hour test was included to examine whether the first hour's exercise influenced the responses taking place during exercise in the second hour with the contralateral limb.

This study was performed because of the lack of information in the literature on prolonged submaximal exercise with a limited muscle mass and because the investigation as a whole was primarily concerned with those factors that lead to an increased ability to sustain high intensity submaximal exercise.

METHOD

The 5 male subjects who participated in the investigation that examined the accuracy of the 4 minute continuous loading oxygen uptake test for the calculation of training work loads during one-legged exercise (see appendix 1.B), also acted as subjects in this investigation. Their
one-legged $\dot{V}O_2$ max values together with the submaximal work loads that demanded 75% one-legged $\dot{V}O_2$ max were determined for both the right and left legs as described in appendix 1.B.

The experimental protocol

The experimental protocol may be summarized as follows:

1. A 1 hour test at 75% one-legged $\dot{V}O_2$ max with either the right or left legs.
2. The 1 hour test was repeated on the other leg.
3. A 2 hour test during which the subjects exercised continuously at 75% one-legged $\dot{V}O_2$ max but changed the exercising leg after 1 hour of exercise.

The 1 hour test

All subjects fasted for 12 hours prior to the test and did not engage in any physical activity during this period. Having ensured (from the 10 minute test described in Chapter 3, section 3.10) that the work load calculation for the elicitation of 75% one-legged $\dot{V}O_2$ max was accurate, the subjects exercised for 1 hour with both the right and left legs. A minimum period of 48 hours separated the testing of the two legs.

During the test heart rate was monitored continuously and recorded every minute. Expired air collections were made at 4-6, 8-10, 14-16, 28-30 and 58-60 minutes. Blood samples for the determination of lactate and glucose concentrations were taken at rest, 15, 30 and 60 minutes.

The 2 hour test

Again, all subjects fasted for 12 hours prior to the test and did not engage in any physical activity during that period. The test followed the exact protocol described above for the 1 hour test. The oxygen uptake, respiratory, heart rate and blood lactate and blood glucose values were therefore obtained at the same times as those in
the 1 hour test.

This test set out to determine whether exercising for 1 hour at a high submaximal work load with one leg influenced the response of the second leg to the same prolonged work. A maximum break of 1 to 2 minutes occurred in the exercise during which the metal plate was transferred from one pedal to the other.

The haemoglobin concentrations were also obtained before and after both the 1 and 2 hour exercise tests.

**Data analysis**

The t-test for uncorrelated data was employed to determine whether any differences existed between the right and left legs.

A one way analysis of variance for repeated measures on one factor was adopted to investigate changes in blood lactate, blood glucose and the respiratory exchange ratio over the exercise periods during the 1 and 2 hour exercise tests. Results are presented as means ± standard deviations (SD).

**RESULTS**

As stated above in appendix 1.B, the estimated work load for the elicitation of 75% one-legged VO₂ max was the same for both the right and left legs.

**1 hour test**

During the 1 hour test no differences were found between the right and left legs at 15, 30 and 60 minutes in the following parameters: blood LA (mM), blood glucose (mM), VO₂ (L.min⁻¹), VE (L.min⁻¹), RER and HR (b.min⁻¹), (tables A.17 and A.18). No differences were found between the right and left leg pre-exercise blood lactate and blood glucose concentrations (table A.17).
Blood LA, blood glucose and RER changed significantly during the course of the 1 hour exercise tests.

The blood LA levels increased significantly during the first 15 minutes of exercise ($p < 0.001$). The right and left leg concentrations increased from $1.52 \pm 0.34$ to $5.55 \pm 2.01$ mM and from $1.36 \pm 0.32$ to $5.10 \pm 1.25$ mM respectively. After 15 minutes the blood LA concentrations decreased with each subsequent measurement made over the 1 hour period (figure A.3). The decrease in blood lactate levels between 15 and 30 minutes were not significant but the decreases from 15 to 60 minutes did reach the level of statistical significance. The LA values decreased from $5.55 \pm 2.01$ to $3.01 \pm 1.14$ mM in the right leg ($p < 0.01$) and from $5.10 \pm 1.25$ to $2.60 \pm 0.68$ mM in the left leg ($p < 0.001$). The decrease in blood LA between 30 and 60 minutes reached the level of statistical significance in the left leg only ($p < 0.01$). A significant difference was also found between the pre-exercise blood LA value and the 60 minute value in the left leg only. This difference found in the left leg but not the right leg was probably due to the greater between subjects variation in the right leg (figure A.3), as opposed to differences in the responses of the two legs to the 1 hour exercise test.

The blood glucose levels decreased significantly during the first 15 minutes of exercise. During exercise with the right leg, the value decreased from $4.86 \pm 0.26$ to $4.11 \pm 0.40$ mM ($p < 0.01$) and during exercise with the left leg, the value decreased from $4.81 \pm 0.17$ to $4.28 \pm 0.17$ mM ($p < 0.05$) (table A.17). After 15 minutes of exercise the blood glucose concentration increased with each subsequent measurement made over the 1 hour period.

The RER values fell throughout the 1 hour exercise tests demonstrating the characteristic shift from carbohydrate to fat metabolism (figure A.4). The decrease in RER between 15 and 30 minutes was significant during exercise with both the right and left legs ($p < 0.05$). The decreases between 15 and 60 minutes were also significant ($p < 0.01$). The values decreased from $1.03 \pm 0.05$ to $0.97 \pm 0.05$ in the right leg and from $1.05 \pm 0.04$ to $0.96 \pm 0.03$ in the left leg (table A.18).
When the $\dot{V}O_2$ and HR values at 15, 30 and 60 minutes were compared no changes were found over the 1 hour period in either leg. During exercise with the right and left leg, however, significant increases occurred in both these parameters from 4-6 to 8-10 minutes (table A.19). $\dot{V}O_2$ increased from 1.96 to 2.04 L.min$^{-1}$ in the right leg ($p < 0.05$) and from 2.01 to 2.06 in the left leg ($p < 0.05$). These increases occurred despite the absence of any change in the work load (watts) suggesting that the steady-state condition may not have been reached after 4 to 6 minutes of exercise.

The 2 hour test

During the 2 hour exercise test no differences were found between the first and second legs (each leg exercised for 1 hour, the exercise being continuous) at 15, 30 and 60 minutes in the following parameters:- blood LA(mM), blood glucose (mM), $\dot{V}O_2$ (L.min$^{-1}$), $\dot{V}E$ (L.min$^{-1}$), RER and HR (b.min$^{-1}$) (tables A.20 and A.21). The pre-exercise LA concentrations for the first and second legs were 1.46 and 2.79 mM respectively and these were significantly different ($p < 0.001$). The blood LA and glucose concentrations together with the RER values changed significantly over the 2 hour period. In the first hour of exercise all three parameters followed the same pattern as described above during the 1 hour exercise test.

Blood LA concentration increased significantly during the first 15 minutes of exercise ($p < 0.001$) and then decreased from 15 to 30 minutes and again from 30 to 60 minutes during the first hour of the 2 hour test. This decrease did not continue during the second hour when the exercising leg was changed. During the second hour the LA concentration again increased significantly during the first 15 minutes of exercise ($p < 0.001$) and also showed a very similar decrease between 15 and 30 minutes and between 30 and 60 minutes (figure A.5). In both legs, i.e. the first and second legs, the decrease in LA concentration from 15 to 60 minutes was significant ($p < 0.001$).
The RER values, like the LA values, followed the same pattern during the first and second hours. The value decreased during the first hour from $1.03 \pm 0.04$ to $0.95 \pm 0.02$ ($p < 0.05$) but this fall did not continue during the second hour when the exercising leg was changed. During the second hour the value decreased from $1.02 \pm 0.03$ to $0.93 \pm 0.02$ ($p < 0.01$) (figure A.6).

Unlike the LA and RER values, however, the blood glucose concentration did not follow a similar pattern during the first and second hours of the 2 hour test. During the first hour the blood glucose concentration decreased significantly during the first 15 minutes of exercise ($p < 0.001$) (table A.20). After 15 minutes the blood glucose concentration increased with each measurement made during the 2 hour test, despite a change in the exercising leg after 1 hour of exercise.

When the $\dot{V}O_2$ and HR values at 15, 30 and 60 minutes were compared, no changes were found over the 2 hour exercise period (table A.21). The $\dot{V}O_2$ value did not increase significantly from 4-6 to 8-10 minutes during the first hour but did rise significantly over this period during the second hour ($p < 0.01$) (table A.19). The increase in the second hour is consistent with the findings in the two 1 hour tests. Although the apparent haemoglobin concentration increased after both the 1 hour tests and the 2 hour test, the increases did not reach the level of statistical significance.

DISCUSSION

During the 1 hour test no differences were found between the right and left legs. The LA concentration increased during the first 15 minutes of exercise followed by a decrease with each subsequent measurement made over the 1 hour period. This is in agreement with the one-legged findings of Ahlborg, Hagenfeldt and Wahren (1975). The RER values throughout the hour decreased progressively demonstrating the characteristic shift from carbohydrate to fat metabolism.
The LA and RER values showed the above described response during both the first and second hours of the 2 hour test, despite a change in the exercising leg. These findings demonstrate that the fuel utilization during the second hour of the 2 hour test was possibly similar to that used in the first hour. The shift from carbohydrate to fat metabolism seen during the first hour did not continue during the second hour, i.e. there was no carry over effect. This suggests that one-legged exercise is extremely local in nature in that there was little obvious influence of the preceding 1 hour's exercise on the response of the contralateral limb to the same exercise. It is interesting to note that the subjects complained of discomfort in the quadriceps between 15 and 20 minutes after which the discomfort decreased. The onset and level of pain followed the same pattern in the second hour during exercise with the contralateral leg.

After 15 minutes, \( \dot{V}O_2 \) and HR remained stable during the rest of the exercise period. The significant increase in \( \dot{V}O_2 \) and HR from 4-6 to 8-10 minutes suggests that the steady-state condition had not been reached after 4 to 6 minutes of exercise. The significant increase in \( \dot{V}O_2 \) between the 4 to 6 and the 8 to 10 minute values in the second hour of the 2 hour test again points to the importance of local factors during one-legged exercise. This is supported by the fact that none of the subjects complained of central cardio-respiratory discomfort.

The above findings clearly indicate the importance of local factors during one-legged exercise. This was most clearly seen from the results of the 2 hour test where the first hour of exercise appeared to have little effect on the response of the contralateral leg to the same prolonged exercise.
TABLE A.17

Blood lactate and blood glucose concentrations determined during the 1 hour test with both the right and left legs (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>TIME (min)</th>
<th>RIGHT LEG</th>
<th>LEFT LEG</th>
</tr>
</thead>
<tbody>
<tr>
<td>LACTIC ACID (mM)</td>
<td>0</td>
<td>1.52 ± 0.34</td>
<td>1.36 ± 0.32</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>5.55 ± 2.01</td>
<td>5.10 ± 1.25</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>4.73 ± 2.24</td>
<td>4.33 ± 1.09</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>3.01 ± 1.14</td>
<td>2.60 ± 0.68</td>
</tr>
<tr>
<td>GLUCOSE (mM)</td>
<td>0</td>
<td>4.86 ± 0.26</td>
<td>4.81 ± 0.17</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>4.11 ± 0.40</td>
<td>4.28 ± 0.17</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>4.16 ± 0.56</td>
<td>4.39 ± 0.24</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>4.32 ± 0.59</td>
<td>4.58 ± 0.40</td>
</tr>
</tbody>
</table>
FIG. A.3  BLOOD LACTATE CONCENTRATIONS FOR THE RIGHT AND LEFT LEGS DETERMINED DURING A 1 HOUR EXERCISE TEST
FIG. A.4 THE RESPIRATORY EXCHANGE RATIO (RER) VALUES
FOR THE RIGHT AND LEFT LEGS DETERMINED
DURING A 1 HOUR EXERCISE TEST
Oxygen uptake, respiratory and heart rate values determined during the 1 hour tests with both the right and left legs (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>TIME (min)</th>
<th>RIGHT LEG</th>
<th>LEFT LEG</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\dot{V}O_2$ (L.min$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>2.03 ± 0.26</td>
<td>1.96 ± 0.28</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>1.99 ± 0.21</td>
<td>1.96 ± 0.24</td>
<td></td>
</tr>
<tr>
<td>60</td>
<td>2.08 ± 0.22</td>
<td>2.00 ± 0.27</td>
<td></td>
</tr>
<tr>
<td>% $\dot{V}O_2$ max (one-legged)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>78.6 ± 2.5</td>
<td>75.1 ± 2.9</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>77.0 ± 2.8</td>
<td>75.9 ± 3.8</td>
<td></td>
</tr>
<tr>
<td>60</td>
<td>80.5 ± 3.5</td>
<td>77.3 ± 4.3</td>
<td></td>
</tr>
<tr>
<td>VE (L.min$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>51.78 ± 6.88</td>
<td>50.11 ± 5.67</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>50.69 ± 7.45</td>
<td>50.99 ± 6.24</td>
<td></td>
</tr>
<tr>
<td>60</td>
<td>52.01 ± 7.24</td>
<td>51.28 ± 6.82</td>
<td></td>
</tr>
<tr>
<td>RER</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>1.03 ± 0.05</td>
<td>1.05 ± 0.04</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>0.99 ± 0.06</td>
<td>0.99 ± 0.03</td>
<td></td>
</tr>
<tr>
<td>60</td>
<td>0.97 ± 0.05</td>
<td>0.96 ± 0.03</td>
<td></td>
</tr>
<tr>
<td>HR (b.min$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>144.8 ± 18.0</td>
<td>141.4 ± 25.5</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>144.2 ± 20.9</td>
<td>144.6 ± 27.1</td>
<td></td>
</tr>
<tr>
<td>60</td>
<td>145.6 ± 22.5</td>
<td>144.8 ± 26.7</td>
<td></td>
</tr>
<tr>
<td>WORK LOAD (watts)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>119.2 ± 12.8</td>
<td>116.2 ± 12.2</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>116.5 ± 12.9</td>
<td>116.8 ± 12.2</td>
<td></td>
</tr>
<tr>
<td>60</td>
<td>120.2 ± 13.7</td>
<td>115.9 ± 12.3</td>
<td></td>
</tr>
</tbody>
</table>
\( \dot{V}O_2 \), % one-legged \( \dot{V}O_2 \) max and HR values determined at 4-6 and 8-10 minutes in the right and left legs during the 1 hour test and in the first and second exercising legs during the 2 hour test (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>LEG</th>
<th>4-6 MIN</th>
<th>8-10 MIN</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1}))</td>
<td>RIGHT</td>
<td>1.96 ± 0.28</td>
<td>2.04 ± 0.30</td>
</tr>
<tr>
<td></td>
<td>LEFT</td>
<td>2.01 ± 0.38</td>
<td>2.06 ± 0.32</td>
</tr>
<tr>
<td></td>
<td>FIRST</td>
<td>2.08 ± 0.32</td>
<td>2.08 ± 0.31</td>
</tr>
<tr>
<td></td>
<td>SECOND</td>
<td>1.94 ± 0.28</td>
<td>2.02 ± 0.31</td>
</tr>
<tr>
<td>% one-legged ( \dot{V}O_2 ) max</td>
<td>RIGHT</td>
<td>72.3 ± 2.1</td>
<td>75.0 ± 3.7</td>
</tr>
<tr>
<td></td>
<td>LEFT</td>
<td>71.9 ± 1.6</td>
<td>74.3 ± 2.6</td>
</tr>
<tr>
<td></td>
<td>FIRST</td>
<td>74.1 ± 3.2</td>
<td>74.0 ± 2.8</td>
</tr>
<tr>
<td></td>
<td>SECOND</td>
<td>72.7 ± 4.6</td>
<td>75.2 ± 3.4</td>
</tr>
<tr>
<td>HR (b.min(^{-1}))</td>
<td>RIGHT</td>
<td>133.2 ± 10.9</td>
<td>139.6 ± 15.2</td>
</tr>
<tr>
<td></td>
<td>LEFT</td>
<td>129.4 ± 17.5</td>
<td>136.2 ± 22.2</td>
</tr>
<tr>
<td></td>
<td>FIRST</td>
<td>132.0 ± 15.4</td>
<td>137.0 ± 17.8</td>
</tr>
<tr>
<td></td>
<td>SECOND</td>
<td>136.0 ± 22.3</td>
<td>138.6 ± 21.4</td>
</tr>
</tbody>
</table>

Levels of significance between the 4-6 and 8-10 minute values:

* \( P < 0.05 \)

** \( P < 0.01 \)
**TABLE A.20**

Blood lactate and blood glucose concentrations during the 2 hour test in which the exercising leg was changed after 1 hour of exercise (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>TIME (min)</th>
<th>HOUR 1</th>
<th>HOUR 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>LACTIC ACID (mM)</td>
<td>0</td>
<td>1.46 ± 0.45</td>
<td>2.79 ± 0.14</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>5.04 ± 1.00</td>
<td>5.74 ± 1.17</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>4.14 ± 0.66</td>
<td>4.95 ± 1.22</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>2.79 ± 0.14</td>
<td>3.52 ± 0.50</td>
</tr>
<tr>
<td>GLUCOSE (mM)</td>
<td>0</td>
<td>4.77 ± 0.31</td>
<td>4.19 ± 0.27</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>4.06 ± 0.40</td>
<td>4.24 ± 0.23</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>4.12 ± 0.36</td>
<td>4.37 ± 0.23</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>4.19 ± 0.27</td>
<td>4.58 ± 0.24</td>
</tr>
</tbody>
</table>

Levels of significance between the first and second hours of the 2 hour test:

* P < 0.05

*** P < 0.001
TABLE A.21

Oxygen uptake, respiratory and heart rate values determined in the 2 hour test during which the exercising leg was changed after 1 hour of exercise (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>TIME (min)</th>
<th>HOUR 1</th>
<th>HOUR 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\dot{V}O_2$ (L.min$^{-1}$)</td>
<td>15</td>
<td>1.94 ± 0.29</td>
<td>1.88 ± 0.23</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>1.91 ± 0.24</td>
<td>1.92 ± 0.24</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>1.99 ± 0.23</td>
<td>1.95 ± 0.32</td>
</tr>
<tr>
<td>% $\dot{V}O_2$ max (one-legged)</td>
<td>15</td>
<td>72.9 ± 3.1</td>
<td>74.8 ± 2.7</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>71.6 ± 2.9</td>
<td>76.4 ± 4.6</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>74.9 ± 4.5</td>
<td>77.4 ± 4.4</td>
</tr>
<tr>
<td>$\dot{V}E$ (L.min$^{-1}$)</td>
<td>15</td>
<td>51.15 ± 7.62</td>
<td>50.08 ± 6.42</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>50.14 ± 6.60</td>
<td>49.89 ± 6.24</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>51.89 ± 7.74</td>
<td>50.16 ± 6.82</td>
</tr>
<tr>
<td>RER</td>
<td>15</td>
<td>1.03 ± 0.04</td>
<td>1.02 ± 0.0</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>0.98 ± 0.03</td>
<td>0.97 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>0.95 ± 0.02</td>
<td>0.93 ± 0.02</td>
</tr>
<tr>
<td>HR (b.min$^{-1}$)</td>
<td>15</td>
<td>140.6 ± 20.4</td>
<td>141.6 ± 21.7</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>141.4 ± 19.2</td>
<td>143.2 ± 21.2</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>144.0 ± 18.9</td>
<td>144.6 ± 21.6</td>
</tr>
<tr>
<td>WORK LOAD (watts)</td>
<td>15</td>
<td>116.5 ± 16.2</td>
<td>113.7 ± 11.6</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>114.8 ± 14.9</td>
<td>111.0 ± 14.7</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>116.6 ± 16.3</td>
<td>115.7 ± 20.2</td>
</tr>
</tbody>
</table>
FIG. A.5

BLOOD LACTATE CONCENTRATIONS DETERMINED DURING HOUR 1 AND HOUR 2 OF A 2 HOUR EXERCISE TEST

Leg 1.

Leg 2.

Lactic Acid (mM)

Time (min.)

0 15 30 60 75 90 120
FIG. A.6  THE RESPIRATORY EXCHANGE RATIO (RER) VALUES DETERMINED DURING HOUR 1 AND HOUR 2 OF A 2 HOUR EXERCISE TEST
PHYSIOLOGICAL RESPONSES TO ONE- AND TWO-LEGGED EXERCISE

INTRODUCTION

This study compared the responses of one and two legs to submaximal and maximal exercise on a bicycle ergometer and was included to provide insight into the nature of one-legged exercise.

To compare one- and two-legged exercise oxygen uptake, respiratory, heart rate and blood lactate determinations were made at both the submaximal and maximal levels.

METHOD

Four male subjects participated in the study. Mean age, height and weight were $36.0 \pm 12.0$ yrs, $180.9 \pm 3.7$ cms, and $74.25 \pm 7.26$ kg respectively (table A.22).

All the volunteers were not only highly experienced laboratory subjects accustomed to exercising at submaximal and maximal levels, but were also familiarized with both one- and two-legged bicycle ergometry.

Both types of exercise were performed on a Monark fixed wheel ergometer and all one-legged measurements were made on the left leg.

A 2 minute continuous loading test was employed during both types of exercise. Heart rate was monitored continuously and recorded every minute and expired air collections were made during the last minute of each 2 minute exercise period. Blood samples, for the determination of lactate concentrations were taken at the end of each 2 minute exercise period. The tests were employed to establish the oxygen uptake, heart rate and blood lactate relationships during one- and two-legged exercise.
Experimental protocol:

The experimental protocol may be summarized as follows:

1. A number of familiarization sessions involving one-legged exercise with both the right and left legs.
2. A 2 minute continuous loading oxygen uptake test during which two-legged exercise was performed.
3. A 2 minute continuous loading oxygen uptake test during which one-legged exercise was performed.

The 2 minute continuous loading test is described in Chapter 3, section 3.8.1.

Data analysis

During the two types of exercise only two work loads (59 and 118 watts) were common to both. Statistical comparisons were therefore only made at these two work loads. The t-test for correlated data was used and significance accepted at the .05 level. Results are presented as means ± standard deviations (SD).

RESULTS

The following parameters were significantly higher during two-compared with one-legged exercise at the maximum level: $\dot{V}O_2\ (L.min^{-1})$, $\dot{V}E\ (L.min^{-1})$, $\dot{V}CO_2\ (L.min^{-1})$, RER, HR, LA and work load (watts), (table A.23). The $\dot{V}O_2$ max values during one- and two-legged exercise were $2.43 \pm 0.36$ and $3.21 \pm 0.27 L.min^{-1}$ respectively, the latter value being significantly higher ($p < 0.001$). The one-legged value was only 76% of the two-legged value. This is consistent with the findings in the literature (Davies and Sargeant, 1974).

Blood lactate concentrations at the maximum level during one- and two-legged exercise were $7.57 \pm 0.72$ and $10.24 \pm 0.88 mM$ respectively. These values are also in agreement with those in the literature. The lactate concentration measured at the maximum level during one-legged exercise is similar to the concentration reported by Saltin and coworkers (Saltin et. al., 1976).
A summary of the oxygen uptake, respiratory, heart rate and blood lactate determinations made during one- and two-legged exercise are presented in tables A.24 and A.25.

Submaximal comparisons between the two types of exercise were restricted to those measurements made at 59 and 118 watts because only these two work loads were common to both one- and two-legged exercise.

At the very low work load of 59 watts, which during one- and two-legged exercise required 32% and 29% $\dot{V}O_2$ max respectively, no differences were found between any of the parameters determined during the two types of exercise (table A.26). The only exception was the blood LA concentration which was significantly higher at this work load during one-legged exercise. The blood LA values were 1.54 ± 0.24 and 1.12 ± 0.16 mM during one- and two-legged exercise respectively.

At the common work load of 118 watts, which during one- and two-legged exercise represented 68% and 51% $\dot{V}O_2$ max respectively, several significant differences were found between the two types of exercise. The following parameters were all significantly higher at this work load during one-legged exercise: $\dot{V}O_2$ (p < 0.05), $\dot{V}E$ (p < 0.05), $\dot{V}CO_2$ (p < 0.05), $\dot{V}E.\dot{V}O_2^{-1}$ (p < 0.05), RER (p < 0.05) and blood LA (p < 0.001) (table A.26). Although the HR value was 25 b.min$^{-1}$ higher during one-legged exercise at this work load, the difference did not reach statistical significance. This was probably due to the large between subjects variance and the small sample size. The HR values at the work load of 118 watts were 146.5 ± 30.6 and 122.0 ± 17.0 b.min$^{-1}$ during one- and two-legged exercise respectively.

The mean blood LA concentrations at the work load of 118 watts were 4.53 ± 0.50 mM during one-legged exercise and only 1.65 ± 0.24 mM during two-legged exercise (p < 0.001).

The mean $\dot{V}O_2$ values at this work load were 1.92 ± 0.15 and 1.61 ± 0.10 L.min$^{-1}$ during one- and two-legged exercise respectively.

Figures A.7, A.8 and A.9 show $\dot{V}O_2$, HR and LA relationships during one- and two-legged exercise. From these illustrations it can be seen that there is a difference in the responses of one and two legs to exercise, with the differences becoming more pronounced at the
higher work loads. Although statistical comparisons between the two types of exercise were not made above a work load of 118 watts, it is reasonable to assume that where a difference was found at this work load there may also be a difference at the higher work loads. Figure A.7 illustrates that during one-legged exercise the relationship between $\dot{V}O_2$ and work load was not linear as in two-legged exercise.

DISCUSSION

The findings of this study are in agreement with similar studies which have compared circulatory and metabolic adaptations during rhythmic exercise with large and small muscle groups. These studies together with the present investigation have demonstrated that the physiological strain and the anaerobic contribution is greater during exercise with small muscle groups (Davies and Sargeant, 1974; Stamford et. al., 1978b).

The lower $\dot{V}O_2$ max value measured during one-legged exercise together with the lower "apparent" mechanical efficiency during this type of exercise supports the findings of Davies and Sargeant (1974). In addition, for a given work load the higher $\dot{V}O_2$, HR and LA values measured during one-legged exercise compared with two-legged exercise also supports the work of Davies and Sargeant (1974).

The relationship between $\dot{V}O_2$ and work load was linear during the two-legged exercise. During one-legged exercise however, $\dot{V}O_2$ increased out of proportion with work load at the higher loads. This is in agreement with the findings of Davies and Sargeant (1975) and Gleser (1973). This is thought to be the result of a decreased "apparent" mechanical efficiency at the higher work loads caused by a change in postural activity.

This study clearly demonstrated that the physiological strain and the anaerobic contribution is greater during one- compared with two-legged exercise.
### Table A.22

Physical characteristics of the subjects

<table>
<thead>
<tr>
<th>SUBJECT</th>
<th>AGE yrs</th>
<th>HEIGHT cms</th>
<th>WEIGHT kg</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>24.6</td>
<td>178.6</td>
<td>66.50</td>
</tr>
<tr>
<td>2</td>
<td>39.5</td>
<td>176.9</td>
<td>73.05</td>
</tr>
<tr>
<td>3</td>
<td>51.3</td>
<td>184.2</td>
<td>83.40</td>
</tr>
<tr>
<td>4</td>
<td>28.4</td>
<td>183.8</td>
<td>84.04</td>
</tr>
<tr>
<td>MEAN</td>
<td>36.0</td>
<td>180.9</td>
<td>74.25</td>
</tr>
<tr>
<td>S.D.</td>
<td>12.0</td>
<td>3.7</td>
<td>7.26</td>
</tr>
</tbody>
</table>
TABLE A.23

Maximum values during one- and two-legged exercise
(means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>TWO LEGS</th>
<th>ONE LEG</th>
<th>1 LEG VALUE AS % OF 2 LEG VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1}))</td>
<td>3.21 ± 0.27</td>
<td>2.43 ± 0.36</td>
<td>75.7% ***</td>
</tr>
<tr>
<td>( \dot{V}E ) (L.min(^{-1}))</td>
<td>122.9 ± 34.33</td>
<td>93.97 ± 28.48</td>
<td>76.5% **</td>
</tr>
<tr>
<td>( \dot{V}CO_2 ) (L.min(^{-1}))</td>
<td>4.31 ± 0.49</td>
<td>3.09 ± 0.49</td>
<td>71.7% ***</td>
</tr>
<tr>
<td>RER</td>
<td>1.34 ± 0.04</td>
<td>1.27 ± 0.07</td>
<td>94.8% *</td>
</tr>
<tr>
<td>( \dot{V}E \frac{\dot{V}O_2}{min} )</td>
<td>35.20 ± 9.38</td>
<td>37.69 ± 10.04</td>
<td>107.1% ***</td>
</tr>
<tr>
<td>HR (b.min(^{-1}))</td>
<td>179.8 ± 23.1</td>
<td>165.3 ± 19.5</td>
<td>91.9% ***</td>
</tr>
<tr>
<td>LA (mM)</td>
<td>10.24 ± 0.88</td>
<td>7.57 ± 0.72</td>
<td>73.9% ***</td>
</tr>
<tr>
<td>W (watts)</td>
<td>268.3 ± 21.2</td>
<td>155.7 ± 24.0</td>
<td>58.0% ***</td>
</tr>
</tbody>
</table>

Levels of significance between the two types of exercise:

* \( P < 0.05 \)
** \( P < 0.01 \)
*** \( P < 0.001 \)
Oxygen uptake, respiratory, heart rate and blood lactate values determined during the two-legged continuous loading oxygen uptake test (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>WORK LOAD (watts)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>59</td>
</tr>
<tr>
<td>(\dot{V}O_2) (L.min(^{-1}))</td>
<td>0.92 ± 0.06</td>
</tr>
<tr>
<td>% (\dot{V}O_2) max</td>
<td>28.9 ± 3.2</td>
</tr>
<tr>
<td>(\dot{V}E) (L.min(^{-1}))</td>
<td>22.65 ± 2.44</td>
</tr>
<tr>
<td>(\dot{V}CO_2) (L.min(^{-1}))</td>
<td>0.89 ± 0.04</td>
</tr>
<tr>
<td>RER</td>
<td>0.97 ± 0.02</td>
</tr>
<tr>
<td>(\dot{V}E.\dot{V}O_2)(^{-1})</td>
<td>24.72 ± 1.89</td>
</tr>
<tr>
<td>HR (b.min(^{-1}))</td>
<td>99.3 ± 14.5</td>
</tr>
<tr>
<td>LA (mM)</td>
<td>1.12 ± 0.16</td>
</tr>
</tbody>
</table>
Oxygen uptake, respiratory, heart rate and blood lactate values determined during the one-legged continuous loading oxygen uptake test (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>WORK LOAD (watts)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>29</td>
</tr>
<tr>
<td>( \dot{V}O_2 ) (L.min(^{-1}))</td>
<td>0.69 ± 0.07</td>
</tr>
<tr>
<td>% ( \dot{V}O_2 ) max</td>
<td>28.9 ± 5.1</td>
</tr>
<tr>
<td>( \dot{V}E ) (L.min(^{-1}))</td>
<td>17.33 ± 1.09</td>
</tr>
<tr>
<td>( \dot{V}CO_2 ) (L.min(^{-1}))</td>
<td>0.59 ± 0.09</td>
</tr>
<tr>
<td>RER</td>
<td>0.86 ± 0.07</td>
</tr>
<tr>
<td>( \dot{V}E.\dot{V}O_2 ) (^{-1})</td>
<td>25.26 ± 1.36</td>
</tr>
<tr>
<td>HR (b.min(^{-1}))</td>
<td>98.3 ± 23.6</td>
</tr>
<tr>
<td>LA (mM)</td>
<td>1.02 ± 0.26</td>
</tr>
</tbody>
</table>

NB % \( \dot{V}O_2 \) max refers to % one-legged \( \dot{V}O_2 \) max
TABLE A.26

Comparison of one- and two-legged values determined at 59 and 118 watts during the continuous loading tests (means ± SD)

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>WORK LOAD (59 watts)</th>
<th>WORK LOAD (118 watts)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TWO LEGS</td>
<td>ONE LEG</td>
</tr>
<tr>
<td>$\dot{V}O_2$ (L.min$^{-1}$)</td>
<td>$0.92 ± 0.06$</td>
<td>$1.01 ± 0.08$</td>
</tr>
<tr>
<td>$Z \dot{V}O_2$ max</td>
<td>$28.9 ± 3.2$</td>
<td>$31.8 ± 3.0$</td>
</tr>
<tr>
<td>$\dot{V}E$ (L.min$^{-1}$)</td>
<td>$22.65 ± 2.44$</td>
<td>$23.90 ± 1.27$</td>
</tr>
<tr>
<td>$\dot{V}CO_2$ (L.min$^{-1}$)</td>
<td>$0.89 ± 0.04$</td>
<td>$0.90 ± 0.15$</td>
</tr>
<tr>
<td>RER</td>
<td>$0.97 ± 0.08$</td>
<td>$0.89 ± 0.12$</td>
</tr>
<tr>
<td>$\dot{V}E.\dot{V}O_2$ $^{-1}$</td>
<td>$24.72 ± 1.89$</td>
<td>$23.66 ± 1.39$</td>
</tr>
<tr>
<td>HR (b.min$^{-1}$)</td>
<td>$99.3 ± 14.5$</td>
<td>$113.3 ± 24.8$</td>
</tr>
<tr>
<td>LA (mM)</td>
<td>$1.12 ± 0.16$</td>
<td>$1.54 ± 0.24$</td>
</tr>
</tbody>
</table>

Levels of significance between the two legs: 

* $P < 0.05$

*** $P < 0.001$
FIG. A.7 OXYGEN COST OF ONE- AND TWO-LEGGED CYCLING

![Graph showing the oxygen cost of one- and two-legged cycling against work load (watts). The graph indicates that the oxygen cost increases linearly with work load. The line for two legs is higher than the line for one leg, indicating a higher oxygen cost for two-legged cycling. The Y-axis represents the oxygen uptake ($V_O_2$, L.min$^{-1}$) and the X-axis represents the work load (watts).]
FIG. A.8 HEART RATE VALUES DETERMINED DURING ONE- AND TWO-LEGGED EXERCISE
FIG. A.9  BLOOD LACTATE CONCENTRATIONS DETERMINED DURING ONE- AND TWO-LEGGED EXERCISE

![Graph showing blood lactate concentrations during exercise.](image-url)

- **Y-axis:** Lactic Acid (mM)
- **X-axis:** Work Load (watts)

Two lines represent:
- **One leg**
- **Two legs**

The graph illustrates the increase in lactic acid concentration with increasing work load.
APPENDIX 2

PROCEDURES FOR CALIBRATION, BLOOD AND GAS ANALYSIS AND WORK LOAD CALCULATIONS

2.A

CALIBRATION PROCEDURES

1. GAS ANALYSERS

The Taylor Servomex oxygen analyser and the Lira Infrared carbon-dioxide analyser were both calibrated at frequent intervals using a null gas (100% nitrogen) and a span gas mixture of a known concentration. The instruments were calibrated with dry gases by passing the gas through a drying agent (silica gel). The instruments were recalibrated at least once an hour and the barometric pressure, temperature and humidity of the atmospheric air were re-determined with each calibration.

2. PARKINSON COWAN GAS METER

This meter was calibrated by the manufacturers. It was also checked periodically in our laboratory by passing through it known volumes ranging from 25 to 150 litres, from a 600 litre Tissot spirometer (Collins Ltd., USA).

3. EDALE THERMOMETER

The instrument contains a built in calibration check, for the temperature range of 0-50°C.

4. 'MONARK' ERGOMETERS

These ergometers were calibrated by the manufacturers. Recalibration
was not performed because the oxygen uptake values obtained during the steady-state condition at various work loads for subjects of normal mechanical efficiency agreed with the values obtained by the manufacturers (Monark Ltd.).

5. **FLYWHEEL REVOLUTION/PEDAL REVOLUTION AND SPEEDOMETER RELATIONSHIP ON THE ERGOMETER**

The markers on the speedometer for 60 and 65 pedal revolutions per minute were checked prior to the experiments requiring these pedal rates. The individual on the ergometer pedalled at a constant speed of 21.5 (or 25 km.hr\(^{-1}\) for the one-legged experiments) as indicated by the markers for at least 2 minutes, while the number of flywheel revolutions being measured continuously by the revolution counter were recorded each minute. Whilst the marker was on 21.5 and 25 km.hr\(^{-1}\) the number of flywheel revolutions recorded were 222 and 240 respectively. The ergometer was calibrated so that 222 and 240 flywheel revolutions corresponded to pedal rates of 60 and 65 revs.min\(^{-1}\). That is, for every full pedal revolution the flywheel rotated 3.7 times.

In those experiments where the rate meter described in Chapter 3, section 3.2 was used, an individual pedalled with the meter needle on 60 or 65 (depending upon the type of exercise to be performed) whilst the number of flywheel revolutions per minute were recorded. With the needle on 60 and 65, the number of flywheel revolutions recorded per minute were 222 and 240 respectively.

6. **EPPENDORF PHOTOMETER**

The instrument was calibrated as specified by the manufacturers prior to use and thereafter before each analysis.

7. **avery Weighing Scales and Harpenden Stadiometer**

Both were factory calibrated and rechecked regularly.
2.B GAS ANALYSIS

1. DETERMINATION OF THE OXYGEN AND CARBON-DIOXIDE CONTENT, VOLUME AND TEMPERATURE OF THE EXPIRED AIR

The $O_2$ and $CO_2$ content together with the volume and temperature of the expired air collected in the Douglas Bags were determined as follows:-

a) To prevent the analysis of an unrepresentative sample the air in the Douglas Bag was well mixed before a sample was passed into the $O_2$ and $CO_2$ analysers.

b) The air in the Douglas Bag was extracted for sampling, via the sampling tube, by means of a Hy-flow (Metcalf Industries Ltd.) pump. The rate at which the gas was extracted and passed into the analyser was measured by a Gap-flow meter. The flow rate varied between 0.65 and 0.8 L.min$^{-1}$.

c) The expired air was pumped into the $O_2$ analyser for 60 seconds after calibration and thereafter for 30 seconds during which time the flow rate was recorded for determination of the volume lost during sampling. The flow was stopped and the $% O_2$ read off the meter scale, once the instrument had stabilized.

d) A second sample was passed into the $CO_2$ analyser for 60 seconds after calibration and thereafter for 30 seconds. The flow was stopped and the meter reading recorded once the instrument had stabilized. The meter reading was converted to $% CO_2$ by means of a calibration chart supplied by the manufacturers.

e) The volume and temperature of the expired air was then determined by evacuating the Douglas Bag with a vacuum pump through the dry gas meter. The volume passing through the meter together with the sample volume combined to give the total volume of expired air in litres per minute.

f) The temperature of the air was determined by a thermistor placed in the outlet tube of the gas meter.
2. **OXYGEN UPTAKE**

Oxygen uptake (\(\dot{V}O_2\)) was calculated using standard formulae for the open circuit Douglas Bag method and expressed in L.min\(^{-1}\) or ml.kg\(^{-1}\).min\(^{-1}\). Oxygen uptake is achieved by converting the expired air volumes into inspired air volumes at standard temperature and pressure for dry gases (STPD). Two correction factors were therefore required for the calculation of oxygen uptake:

a) **The correction factor for expressing the volume of the expired air (\(\dot{V}E\) L.min\(^{-1}\)) at standard temperature and pressure for dry gases**

\[
P_B - SWVP \\
760 + (2.8 \times t^°C)
\]

where:

- \(P_B\) = barometric pressure (mmHg)
- \(SWVP\) = saturated water vapour pressure
- \(t^°C\) = expired air temperature
- 2.8 = conversion factor

b) **The correction factor (Haldane Transformation) necessary to convert expired air volumes to inspired volumes**

\[
\frac{\dot{V}_I}{\dot{V}_E} = \frac{\% N_2 \text{ in expired air}}{\% N_2 \text{ in inspired air}} \times \dot{V}E\ STPD \text{ L.min}^{-1}
\]

where:

- \(\dot{V}_I\) = volume of inspired air

The equation for the calculation of oxygen uptake may be summarized as follows:

\[
\dot{V}O_2\ L.min^{-1} = (\dot{V}E\ L.min^{-1}) \left( \frac{F_E N_2}{F_I N_2} \right) \left( \frac{F_O_2}{100} \right) - (\dot{V}E\ L.min^{-1}) \left( \frac{F_E O_2}{100} \right)
\]
where

\( \dot{V}_E = \) volume of expired air

\( \dot{F}_{E N_2} = \% N_2 \) in the expired air

\( \dot{F}_{I N_2} = \% N_2 \) in the inspired air

\( \dot{F}_{I O_2} = \% O_2 \) in the inspired air

\( \dot{F}_{E O_2} = \% O_2 \) in the expired air.

3. **CARBON-DIOXIDE PRODUCTION (\( \dot{V}CO_2 \) L.min\(^{-1} \))**

\[
\dot{V}CO_2 \text{ L.min}^{-1} = (\dot{V}E \text{ L.min}^{-1}) \left( \frac{\dot{F}_{E CO_2}}{100} \right) - (\dot{V}I \text{ L.min}^{-1}) \left( \frac{\dot{F}_{I CO_2}}{100} \right)
\]

where

\( \dot{F}_{E CO_2} = \% CO_2 \) in expired air

\( \dot{F}_{I CO_2} = \% CO_2 \) in inspired air.

4. **RESPIRATORY EXCHANGE RATIO (RER)**

\[
RER = \frac{\dot{V}CO_2 \text{ L.min}^{-1}}{\dot{V}O_2 \text{ L.min}^{-1}}
\]

5. **VENTILATORY EQUIVALENT (\( \dot{V}E \cdot \dot{V}O_2 \) \(^{-1} \))**

\[
\dot{V}E \cdot \dot{V}O_2 \text{ }^{-1} = \frac{\dot{V}E \text{ L.min}^{-1}}{\dot{V}O_2 \text{ L.min}^{-1}}
\]
2.C

BLOOD ANALYSIS

Lactate, glucose and haemoglobin concentrations in the blood were determined from capillary blood samples as follows:-

1. LACTIC ACID ASSAY

Lactic acid levels in the blood were determined by an enzymatic photometric method and expressed in mM.

Procedure.

a) 25μl of blood was deproteinized in 250μl of perchloric acid.
b) The mixture was centrifuged for 3 minutes at 12,000 r.p.m.
c) 50μl of the supernatant was transferred into an acid washed tube.
d) 500μl of the reaction mixture was added and the tube well mixed.
e) An incubation period of 30 minutes followed (at room temperature 21 - 23°C).
f) 500μl of diluent was added and the tube well mixed.
g) The absorbance of the sample was determined at a wavelength of 365nm.

Standards

These were prepared from 10 mM stock solution.

<table>
<thead>
<tr>
<th>10mm stock ml</th>
<th>Distilled water ml</th>
<th>mM</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td>9.0</td>
<td>1.0</td>
</tr>
<tr>
<td>0.75</td>
<td>9.25</td>
<td>0.75</td>
</tr>
<tr>
<td>0.50</td>
<td>9.50</td>
<td>0.50</td>
</tr>
<tr>
<td>0.25</td>
<td>9.75</td>
<td>0.25</td>
</tr>
</tbody>
</table>

A minimum of three standards were used for each assay.
Solutions

a) Perchloric Acid 2.5%
   This was used as the blank against which the absorbances of
   the standards and samples were determined.

b) Hydrazine Buffer (pH 9.15 to 9.2)

c) Diluent 0.07m HCL.

Enzyme Co-factor

LDH supplied by Boehringer Biochemical Corporation (London) Ltd.
NAD supplied by Boehringer Biochemical Corporation (London) Ltd.

Reaction Mixture

Per ml hydrazine buffer - 2 mg NAD
   10 μl LDH

Photometric Wavelength

HG 365 nm

Coefficients of variation

see appendix 2.D.

Reference

Olsen, C. (1971). An enzymatic fluorimetric micromethod for the
determination of acetoacetate, - hydroxybutyrate, pyruvate and lactate

2. GLUCOSE ASSAY

This assay was based on the following principle:
Procedure

a) 25µl of blood was deproteinized in 250µl perchloric acid.
b) The mixture was centrifuged for 3 minutes at 12,000 r.p.m.
c) 20µl of the supernatant was transferred into clean tubes.
d) 1,000µl of the glucose reagent was pipetted into each tube.
e) An incubation period of 30 minutes followed, at room temperature (21 - 23°C).
f) The absorbances of the samples were determined.

Standard (supplied by Boehringer)

\[
glucose \ 9.1 \text{ mg/100ml} \ (= 0.505 \text{ mmol/L})
\]

This solution was used undiluted. One standard was sufficient for each assay.

Buffer/Enzymes/Chromogen (supplied by Boehringer)

- phosphate buffer: 100 mmol/L, pH 7.0
- POD: > 0.8 U./ml
- GOD: > 10 U./ml
- ABTS: 1.0 mg/ml

The contents of the bottle containing the above were dissolved in 300 mls of distilled water and stored at + 4°C in a dark bottle (glucose reagent).

Perchloric Acid 2.5%

This was used as the blank against which the absorbances of the standard and the samples were determined.
Photometric Wavelength

Hg 436 nm

Coefficients of variation

see appendix 2.D.
Reference (from Boehringer)

3. HAEMOGLOBIN CONCENTRATION (Hbg. dl$^{-1}$)

The determination of Hb was based on the cyanmethemoglobin method. The principle of which is as follows:-

haemoglobin $+$ cyanide $+$ ferricyanide $\rightarrow$ cyanmethemoglobin

The combination kit supplied by Boehringer included:

(i) Colour reagent
    phosphate buffer
    potassium cyanide
    potassium ferricyanide

(ii) Detergent
    Drabkins reagent was prepared by
    a) dissolving the contents of the colour reagent into 1,000 mls of distilled water.
    b) adding 2.0 mls of the detergent to the above and mixing well.

Procedure

a) 20$\mu$l of blood was transferred into 5,000$\mu$l of the above reagent and thoroughly mixed.

b) the samples absorbance was read within 4 hours, the incubation temperature being 21 - 23$^\circ$C.
Photometric Wavelength

Hg 546 nm.

Haemoglobin concentration is determined on a regular basis in our laboratory and the following equation has been adopted for converting the photometric reading to Hbg.dl$^{-1}$.

\[ Y = 37.2 \times + 0.06 \]

where

\[ X = \text{the absorbance} \]

\[ Y = \text{Hbg.dl}^{-1} \]

Coefficients of variation

see appendix 2.D.

References (supplied by Boehringer)


Recommendations for haemoglobinometry in human blood.

*Brit. J. Haemat.* 13 (suppl), 71
2.D

COEFFICIENTS OF VARIATION - BLOOD SAMPLE ANALYSIS

Coefficients of variation (V) for repeated measures on one blood sample were derived from the following steps, with the exception of repeated measures on a standard solution.

a) Taking up the blood into 20 or 25μl capillary tubes from venous blood samples.

b) Ensuring that the blood level corresponded with the black mark on the capillary tube which indicated the correct volume.

c) Blowing the blood out of the capillary tube into either Drabkins reagent or perchloric acid depending upon the parameter being measured.

1. LACTIC ACID CONCENTRATION (LA mM)

(i) 8 repeated measures on two standard solutions

<table>
<thead>
<tr>
<th></th>
<th>A - B (1)</th>
<th>A - B (2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td>0.170</td>
<td>0.214</td>
</tr>
<tr>
<td>SD</td>
<td>0.0019</td>
<td>0.0011</td>
</tr>
<tr>
<td>V</td>
<td>1.12%</td>
<td>0.51%</td>
</tr>
</tbody>
</table>

(ii) 8 repeated measures from a resting blood sample

<table>
<thead>
<tr>
<th></th>
<th>A - B</th>
<th>mM</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td>0.015</td>
<td>1.11</td>
</tr>
<tr>
<td>SD</td>
<td>0.00054</td>
<td>0.04</td>
</tr>
<tr>
<td>V</td>
<td>3.60%</td>
<td>3.60%</td>
</tr>
</tbody>
</table>

LA mM was calculated from the linear regression equation determined from four standards and multiplied by eleven because of the dilution factor. The regression equation from the standards in the above assay was:

\[ X = 6.49 \times Y + 0.0060 \]

\[ r = 0.997 \]
(iii) 8 repeated measures from an exercise blood sample

<table>
<thead>
<tr>
<th>A - B</th>
<th>mM</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\bar{X}$</td>
<td>0.116</td>
</tr>
<tr>
<td>SD</td>
<td>0.0015</td>
</tr>
<tr>
<td>V</td>
<td>1.30%</td>
</tr>
</tbody>
</table>

The regression equation from the standards in this assay was:

$$X = 6.27Y + 0.0126$$

$$r = 0.9998$$

(iv) 8 repeated measures also made on a blood sample taken after exercise

<table>
<thead>
<tr>
<th>A - B</th>
<th>mM</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\bar{X}$</td>
<td>0.096</td>
</tr>
<tr>
<td>SD</td>
<td>0.0023</td>
</tr>
<tr>
<td>V</td>
<td>2.4%</td>
</tr>
</tbody>
</table>

The regression equation from the standards in this assay was:

$$X = 6.35Y + 0.019$$

$$r = 0.9999$$

where

- $A = \text{absorbance}$
- $B = \text{blank}$

2. **GLUCOSE CONCENTRATION (mM)**

(i) 8 repeated measures from a resting blood sample

<table>
<thead>
<tr>
<th>A - B</th>
<th>mM</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\bar{X}$</td>
<td>0.287</td>
</tr>
<tr>
<td>SD</td>
<td>0.0043</td>
</tr>
<tr>
<td>V</td>
<td>1.50%</td>
</tr>
</tbody>
</table>

Assay standard = 0.317
All assays together with the haemoglobin determinations in this study were carried out by the author. Assistance in the taking up and blowing down of the blood samples into either Drabkins reagent or perchloric acid was, however, provided during the experiments.

3. **HAEMOGLOBIN CONCENTRATION (Hbg.dl⁻¹)**

(i) **8 repeated measures by the author**

<table>
<thead>
<tr>
<th>A - B</th>
<th>g.dl⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.391</td>
</tr>
<tr>
<td>SD</td>
<td>0.0065</td>
</tr>
<tr>
<td>V</td>
<td>1.66%</td>
</tr>
</tbody>
</table>

(ii) **7 repeated measures by a second experimenter who assisted in the taking of blood samples during the study**

<table>
<thead>
<tr>
<th>A - B</th>
<th>g.dl⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.382</td>
</tr>
<tr>
<td>SD</td>
<td>0.0072</td>
</tr>
<tr>
<td>V</td>
<td>2.02%</td>
</tr>
</tbody>
</table>

(iii) **The above 15 measurements repeated on one blood sample by the two testers**

<table>
<thead>
<tr>
<th>A - B</th>
<th>g.dl⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.387</td>
</tr>
<tr>
<td>SD</td>
<td>0.0082</td>
</tr>
<tr>
<td>V</td>
<td>2.12%</td>
</tr>
</tbody>
</table>

where \( A - B \) = the absorbance of the sample (minus the blank)

The 15 measurements were combined because a major cause of variability in the results is the difference between one tester and another "it is well known that with many haemoglobin methods a single observer can produce more consistent results than a group of observers."

(Macfarlane et. al., 1948).
2. E

WORK LOAD AND RELATIVE WORK LOAD CALCULATIONS

1. WORK LOAD (POWER OUTPUT)

The work done by the subjects was calculated as follows and expressed in watts.

Pedal frequency x circumference of the fly-wheel x load
revs.min⁻¹ (m) (kp)

Therefore at a load of 1 kp and a pedal rate of 60 revs.min⁻¹ the work done is equal to 59 watts.

Work load (power output) = 60 x 0.98 x 1
= 59 watts.

NB. The number of pedal revs.min⁻¹ was calculated as follows:

Pedal rev.min⁻¹ = flywheel revs.min⁻¹

The number of flywheel rotations (3.7) for every pedal revolution were determined by placing a marker on the wheel, counting the number of rotations while one individual slowly turned the pedals through one full revolution and placing a second mark on the wheel at the end of the pedal revolution. This procedure was repeated several times by different experimenters. The relationship was constant and the same for all Monark ergometers in the laboratory.

2. RELATIVE WORK LOAD CALCULATIONS (% VO₂ max)

The regression equation described by Popham and Sirotnik (1973) was used for the calculation of a given submaximal load during two-legged ergometry.

\[ X = a + by \]

where

\[ X = \text{any given value on the } X \text{ axis} \]
\[ Y = \text{any given value on the } Y \text{ axis} \]
\[ a = \text{the point of intercept with the } X \text{ axis} \]
\[ b = \text{the slope of the regression line}. \]
Example:

\[
\begin{align*}
\dot{V}O_2 \max & = 2.5 \text{ L.min}^{-1} \\
\text{equation} & = 3.24 + 51.47Y \\
75\% \dot{V}O_2 \max & = 1.88 \text{ L.min}^{-1} \\
\text{therefore } X & = 3.24 + 51.47 \times 1.88 \\
& = 100
\end{align*}
\]

100 watts is the work load that will demand 75\% of the individual’s \( \dot{V}O_2 \max \).

Assuming a constant pedal rate of 60 revs. min\(^{-1}\) the work load in kiloponds can be determined as follows:

\[
\frac{100}{60 \times 0.98} = 1.69 \text{ kp.}
\]

The load setting for this subject was 1.75 kp (the loads were set to the nearest 0.25 kp).

During one-legged work this equation was not used because of the absence of a linear relationship between \( \dot{V}O_2 \text{L.min}^{-1} \) and work load. The load was determined as above but extrapolated direct from the oxygen uptake/work load relationship.