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TRAINING INDUCED ADAPTATION OF SKELETAL MUSCLE AND METABOLISM DURING SUBMAXIMAL EXERCISE

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SUMMARY

1. Six subjects were trained using a one-leg bicycle exercise for 2 months. The untrained leg served as control. After the training period, muscle oxidative capacity, determined as succinate dehydrogenase activity, was 27 % higher in the trained (as opposed to the control) leg ($P < 0.05$).

2. When the subjects in this situation performed a 1 h two-legged submaximal bicycle exercise bout (150–225 W), determinations of $\dot{V}_{O_2}$ of the single leg (leg blood flow $\times$ $(A\text{–}V)_{O_2}$ difference) revealed that they appeared to choose to work harder with their trained than with their untrained leg, so as to make the relative loads for the two legs the same.

3. Determinations of O_2 and CO_2 on femoral arterial and venous blood demonstrated that the R.Q. was lower in the trained as compared to the untrained leg, 0·91 cf. 0·96 (10 min) and 0·91 cf. 0·94 (50 min) ($P < 0.05$).

4. That metabolism of fat was more pronounced in the trained leg was further supported by the finding of a significant net uptake of free fatty acids in this leg only. Moreover, a lower release of lactate from the trained leg was demonstrated.

5. It is suggested that the shift towards a more pronounced metabolism of fat in the trained leg is a function of an increased muscle oxidative capacity.

INTRODUCTION

A large number of studies, both in animal and man, have established a marked adaptive increase in skeletal muscle oxidative potential in response to an increased level of physical activity (Holloszy & Booth, 1976). The physiological significance of this local adaptation is subject to discussion. In an earlier study, evidence has been presented that the oxidative potential of skeletal muscle is not the limiting factor deter-

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mining the capacity of the whole body to utilize oxygen ($\dot{V}_{O_2}$ max.) (Henriksson & Reitman, 1977). It has been suggested (Holloszy and Booth, 1976) that a high muscle oxidative potential may be of greater importance during submaximal exercise, contributing to the increased metabolism of fat relative to carbohydrate, as reported earlier for trained individuals (Christensen & Hansen, 1939; Saltin & Karlsson, 1971). In humans, this hypothesis has been tested by Saltin *et al.* (1976), but a definite relationship between oxidative capacity of leg muscle and metabolism during submaximal exercise was not found. The reason behind this may have been that the differences in oxidative capacity, in this study, were too small.

In general, there are few studies available giving a complete picture of human skeletal muscle metabolism during work, and especially in response to training. In order to collect more data on this, with special emphasis on the role of local adaptive processes, a modification of the one-leg training model of Davies & Sargeant (1975) and Saltin *et al.* (1976) has been used. Six subjects were trained with a one-leg endurance exercise on a bicycle ergometer during a 2 month period in order to improve the oxidative capacity of only one leg. As an indicator of oxidative capacity, the activity of succinate dehydrogenase in the thigh muscle was determined. Thereafter, the metabolism of both legs during a two-leg submaximal exercise bout was studied, using arterial and venous catheterization in addition to muscle biopsy sampling.

METHODS

Subjects

Six healthy male subjects completed the study, four performing military service (office work) and two being medical students. Their av. age was 22·2 (20–24) yr, ht. 179 (173–184) cm, and wt. 68·5 (61–76) kg. The variation in body wt. during the study did not, in any of the subjects, exceed 2 kg. Only one of the subjects had ever been involved in athletics, and none of them had performed any regular training during the preceding 6 months. Their initial maximal oxygen uptake during two-legged bicycle exercise averaged 3·6 (3·0–4·9) $l.min^{-1}$ or 52 (47–64) $ml.kg^{-1}.min^{-1}$.

Each subject was informed about the procedure and the risks involved in the experiment before giving an oral consent. The subjects were informed that they were free to leave the study at any time.

Experimental details

In the experiments, an Elema bicycle ergometer was used, whereas both Elema and Monark bicycles were used during the training. The pedal rate was always 60 rev/min. For the one-legged bicycling the exercising foot was fastened to the pedal with a toe-clip and a rubber band around the heel. The other foot was placed on a chair beside the bicycle. Care was taken to keep the resting leg as inactive as possible but, as pointed out by Ahlborg, Hagenfeldt & Wahren (1975), even with

this precaution, some muscular activity and metabolic alterations in the non-exercising leg cannot be avoided.

Measurements of oxygen uptake were performed with the Douglas bag technique. The volume of expired air was measured using a Tissot spirometer and fractions of O_2 and CO_2 were analysed with the Haldane or the Scholander technique. During the pre-exercise and post-exercise tests, air was collected from 5–6·5 min of submaximal exercise; at maximal work loads two to four bags (30s) were collected during the last 1·5–2 min of exercise.

Heart rates were monitored with an electrocardiograph; during submaximal exercise steady-state heart rate was defined as the mean value of the heart rates at the 5th and the 6th minute of exercise.

Muscle biopsy analyses

All muscle biopsies were obtained from the lateral vastus of the quadriceps femoris muscle, 12–16 cm above the patella, using the needle biopsy technique (Bergström, 1962). From the pre-training and post-training biopsies, one part was immediately homogenized and analysed for succinate dehydrogenase activity by the method of Cooperstein, Lazarow & Kurfess (1950). The other part was mounted in embedding medium and treated for subsequent freeze-sectioning, staining and fibre typing. Fibres were classified as type I or type II (Engel, 1962), based on the stain for myofibrillar ATPase, with a modification of the method of Padykula & Herman (1955). From the biopsies obtained during the post-training metabolic study, the main part was frozen immediately in liquid nitrogen and stored at $-80°$ C for subsequent analysis of glycogen, glucose, glucose-6-phosphate and lactate as described by Karlsson (1971). The remaining pieces of the muscle were used for histochemical identification of fibre types and glycogen depletion pattern (Gollnick, Piehl & Saltin, 1974).

Blood analyses

Glucose was analysed in whole blood using the glucose oxidase reaction (Hugett & Nixon, 1957). Lactate, pyruvate, and glycerol were determined in whole blood by enzymatic, fluorometric methods (Lowry & Passonneau, 1973). The finger-tip blood obtained after the pre-exercise and post-exercise tests was analysed for lactate by an enzymatic method described by Scholz, Schmitz, Buecher & Lampen (1959). Free fatty acids in plasma were analysed by a colorimetric micromethod according to Laurell & Tibbling (1967). Oxygen and carbon dioxide content of blood were analysed using the Van Slyke technique.

Training programme

The subjects underwent an 8 week training programme consisting of one-leg bicycle exercise for 45 min/day for an average of 3 days/week. Work loads represented approximately 70% of the value of the one-legged $\dot{V}_{O_2}$ max. The training was supervised and heart rates were recorded. The leg which was to be trained was chosen at random; three subjects trained their left leg and three trained their right leg.

Pre-exercise and post-exercise tests

Before and after the training period, a resting muscle biopsy for determination of succinate dehydrogenase activity and fibre-type distribution was taken. The subjects then exercised on different submaximal and maximal one-legged and two-legged workloads. With this procedure, which also was used by Saltin *et al.* (1976), it was possible to establish $\dot{V}_{O_2}$ max. for one-legged exercise with right and left leg,

as well as for two-legged exercise. In addition, steady-state oxygen uptake, pulmonary ventilation and heart rate were determined for fixed submaximal one-legged and two-legged exercise loads. Immediately after each submaximal and maximal exercise bout, blood for lactate analysis was obtained from a finger-tip. Before any pre-training measurements were performed, the subjects were familiarized with the technique of one-leg bicycle exercise. All pre-exercise and post-exercise studies were completed within the week preceding or following the training period.

Post-training metabolic study

The subjects reported to the laboratory in the morning after an over-night fast. Teflon catheters were inserted percutaneously into both femoral arteries and veins at the groin using the Seldinger technique (Seldinger, 1953). The catheters were introduced to a distance of 8 cm proximal to the puncture at the groin and were fixed in this position with adhesive tape during the whole experiment. The subjects were allowed to rest (1 h) before the experiment started. Then they performed a two-leg exercise bout (1 h) on the bicycle ergometer at a load representing an average of 67% (range 58–79) of their actual two-leg $\dot{V}_{O_2}$ max.

Simultaneous arterial and bilateral femoral venous blood samples for metabolite analysis were obtained at rest, and after 3 min (for lactate analysis only), 10, 30, and 50 min of exercise. On the samples obtained after 10 and 50 min of exercise, O_2 and CO_2 content were also determined. At the same time as the samples for metabolite determinations were taken (except at 3 min), blood flow to both legs was measured with the dye dilution technique of Jorfeldt & Wahren (1971), simultaneously with measurements of pulmonary oxygen uptake, heart-rate and pedal-force. The force exerted on the pedals was recorded by means of strain-gauges fitted to each pedal (Hoes, Binkhorst, Smeekes-Kuyl & Vissers, 1968). The force measurements were expressed as integrated values per pedal thrust (mean of five values). Before, after 3 min of exercise, and immediately after the exercise bout, muscle biopsies were taken.

Conventional statistical methods were used. The significance of intra-individual differences were tested using the paired Student's t test.

RESULTS

Before training, no differences were found for the two legs in the variables studied. The one-legged exercise $\dot{V}_{O_2}$ was slightly higher than the two-legged value at the same submaximal exercise intensity. The oxygen uptake at 100 W with one-leg was approximately equal to that at 126 W during two-leg work (1·9 $l.min^{-1}$). The ratio one-legged to two-legged maximal oxygen uptake was within the range of 0·74–0·92.

Muscle adaptation

During the training period, the succinate dehydrogenase activity of the thigh muscle changed significantly only in the trained leg, from 3·8 to 5·2 $\mu mol.g^{-1}$ (wet wt.).min^{-1} ($P < 0·05$). After training, the average succinate dehydrogenase activity was 5·2 $\mu mol.g^{-1}$ (wet wt.).min^{-1} in the trained, as opposed to 4·1 in the untrained leg, i.e. a difference of 27% ($P < 0·05$). This is shown in Fig. 1.

The percentage distribution of type I and type II fibres did not change with training. There were 39 % (22–53) type I fibres in the trained leg compared to 37 % (24–48) in the untrained leg, following training. No significant differences in sizes of fibres in the two legs could be detected.

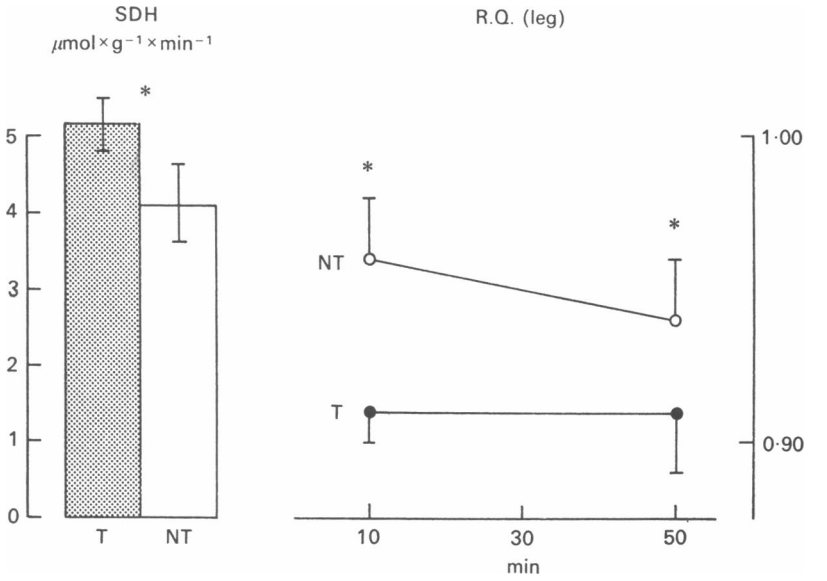

Fig. 1. Succinate dehydrogenase (SDH) activity (μmol.g^{-1}(wet wt.).min^{-1}) in trained (T) and non-trained (NT) leg (left) and R.Q. values for the two legs during the post-training metabolic study (right). Mean ± S.E. of mean. * indicates significant difference between trained and non-trained leg ($P < 0{\cdot}05$).

Training response

One-legged exercise (*Table 1*). At 100 W the oxygen uptake, when working with the trained leg, tended to be somewhat lower after (as compared to before) training (1·72 cf. 1·86 l. min^{-1}; $0{\cdot}05 < P < 0{\cdot}1$). At this load, after the training period, the oxygen uptake was lower, on the average 0·06 l. min^{-1}, when working with the trained (as compared to the untrained) leg ($P < 0{\cdot}05$). With the trained leg $\dot{V}_{O_2}$ max. increased by 11 % from a pre-training value of 3·0 l.min^{-1} ($P < 0{\cdot}01$), and was, following training, significantly higher than $\dot{V}_{O_2}$ max. with the untrained leg ($P < 0{\cdot}05$).

The pulmonary ventilation during exercise at 100 W with the trained leg decreased as a result of training, from 51·8 to 44·6 l.min^{-1} b.t.p.s. ($P < 0{\cdot}05$). No such reduction was seen during work with the untrained leg. At maximal work, the pulmonary ventilation was higher after training,

TABLE 1. Physiological responses during pre-training and post-training one-leg exercise tests. Mean ± S.E. of mean is given

Leg	Work level	$\dot{V}_{O_2}$ (s.t.p.d.); l. min^{-1}		Pulm. vent; (b.t.p.s.), l. min^{-1}		Heart-rate; beats.min^{-1}		Blood lactate; mM	
		B	A	B	A	B	A	B	A
Trained	100 W	1·86 ± 0·06	1·72 ± 0·02**†	51·8 ± 3·0	44·6 ± 2·1*†	150·7 ± 8·5	138·2 ± 3·8	5·5 ± 0·6	3·7 ± 1·0*
	max.	3·00 ± 0·22	3·34 ± 0·25*†	105·4 ± 3·6	129·1 ± 7·7*	193·2 ± 3·4	191·0 ± 2·2	11·3 ± 1·5	10·6 ± 1·5
Non-trained	100 W	1·88 ± 0·07	1·78 ± 0·03	51·5 ± 4·4	50·8 ± 3·3	144·4 ± 12·7	143·0 ± 7·9	5·1 ± 1·0	4·7 ± 0·9
	max.	3·02 ± 0·22	3·13 ± 0·27	108·6 ± 4·5	127·4 ± 10·0*	189·8 ± 4·5	188·3 ± 1·5	9·8 ± 1·5	9·4 ± 0·8

* ($P < 0·05$) and ** ($0·05 < P < 0·1$) denote significant difference, B = before, A = after, training.
† ($P < 0·05$) denote significant difference, trained cf. non-trained leg.

both while exercising with the trained and the untrained leg ($P < 0{\cdot}05$). The ventilatory equivalent ($\dot{V}_E/\dot{V}_{O_2}$) was unchanged with training. No significant reductions in submaximal heart-rate (100 W) with training occurred during work with either leg. However, post-training, five of the six subjects had a lower heart-rate, by 2–14 beats.min^{-1}, when working with their trained (as opposed to their untrained) leg. The maximal heart-rate during one-legged exercise did not change with training.

A reduction in post-exercise blood lactate level at 100 W with training (5·5 to 3·7 mM, $P < 0{\cdot}05$) was found only when working with the trained leg. No changes in blood lactate levels after maximal exercise were seen for either leg.

Two-legged exercise. The oxygen uptake at 150 W (one subject 125 W) was lower after (compared to before) training, 2·09 cf. 2·20 l.min^{-1} ($P < 0{\cdot}01$). All but one subject had a slight increase in two-legged $\dot{V}_{O_2}$ max. with training, the mean change being 8% (not significant). No changes occurred in ventilatory response, heart-rate or blood lactate concentrations, at either submaximal or maximal work intensities.

Post-training metabolic study

During the metabolic study at the end of the training period, the subjects performed two-legged work at an average of 67% (58–79) of the whole body $\dot{V}_{O_2}$ max. for 1 h. The mean work-rate was 175 W (150–225) and mean pulmonary oxygen uptake 2·5 l.min^{-1} (2·2–3·1). No significant changes in pulmonary $\dot{V}_{O_2}$ were observed in the period 10–50 min of exercise. The average respiratory exchange ratios (± S.E. of mean) were 0·91 (± 0·01) in the beginning and 0·93 (± 0·07) at the end of exercise (the difference being non-significant).

Flow of blood to the leg was higher in the trained than in the untrained leg*, the average difference being 8% (2–11) ($P < 0{\cdot}01$) (Fig. 2). The A–V difference for oxygen was 3% higher in the trained (as opposed to the untrained) leg ($P < 0{\cdot}05$). Thus, the mean calculated leg oxygen uptake was 11% higher in the trained leg ($P < 0{\cdot}05$). Neither leg blood flow, $(A\text{–}V)_{O_2}$ difference nor leg oxygen uptake changed during the exercise period. The difference in pedal-force exerted (Fig. 2) by the two legs was in the same direction as the difference in leg oxygen uptake, but no close relationship between individual values for the two variables could be detected.

* The method for measuring leg blood flow, used in this study, is based on the assumption that the flow to both legs is the same. If not, the difference in circulation time to the two legs will give rise to an error in the measurement of recirculating dye concentration. In the present study this may introduce an error of up to 1–2% in the actual leg blood flow determinations.

When the oxygen uptake of each leg during the two-legged exercise was expressed relative to the maximal oxygen uptake that could be obtained during one-legged work with that leg, the figure for each subject became nearly identical for the two legs, 24·5 % (20·9–27·8) for the trained and 24 % (19·3–28·7) for the untrained leg.

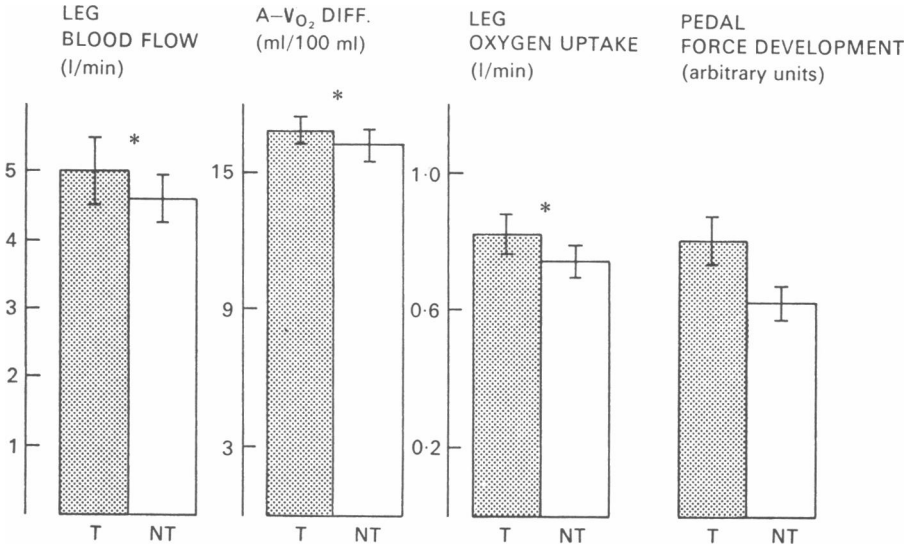

Fig. 2. Blood flow, $(A–V)_{O_2}$ difference and oxygen uptake in the trained (T) and non-trained (NT) leg during the post-training metabolic study. To the right, the pedal force developed with the two legs is given. The bars indicate means for the whole exercise period ± S.E. of mean. * denotes significant difference ($P < 0·05$), T cf. NT leg.

The local R.Q. determinations revealed a lower R.Q. in the trained than in the untrained leg, 0·91 cf. 0·96 at 10 min and 0·91 cf. 0·94 at 50 min of exercise ($P < 0·05$; Fig. 1). The R.Q. in the untrained leg at 10 min was not significantly different from that at 50 min. From the R.Q. values it can be calculated that, on an average, 29 % of the caloric expenditure in the trained leg was derived from the combustion of fat. The corresponding figure for the untrained leg was 16 %. The correlation coefficient between the difference in succinate dehydrogenase activity in the legs and the difference in fat combustion, calculated from the R.Q. values at 10 min of exercise, was 0·79 ($0·05 < P < 0·1$).

A picture of the overall metabolism during the exercise period is given in Fig. 3 and Table 2, where the arterial concentrations and A–V differences for glucose, pyruvate, lactate, free fatty acids, and glycerol are given.

TABLE 2. Arterio-venous differences (mean ± S.E. of mean) for glucose, pyruvate, lactate, free fatty acids, and glycerol (mM) during the post-training metabolic study. T = trained and NT = non-trained leg

		Rest	10 min	30 min	50 min
Glucose	T	0·35 ± 0·10	0·39 ± 0·27	0·33 ± 0·08	0·34 ± 0·15
	NT	0·22 ± 0·10	0·29 ± 0·27	0·23 ± 0·14	0·28 ± 0·09
Pyruvate	T	−0·001 ± 0·001	−0·004 ± 0·022	−0·002 ± 0·004	0·022 ± 0·029
	NT	−0·007 ± 0·004	−0·009 ± 0·011	−0·014 ± 0·005	0·016 ± 0·021
Lactate	T	−0·06 ± 0·04	−0·12 ± 0·37	−0·07 ± 0·28	0·13 ± 0·45
	NT	0·07 ± 0·15	−0·68 ± 0·34	−0·53 ± 0·23	−0·05 ± 0·39
FFA (plasma)	T	−0·110 ± 0·063	0·030 ± 0·039	0·035 ± 0·006	0·068 ± 0·031
	NT	−0·067 ± 0·043	−0·014 ± 0·022	0·048 ± 0·024	0·052 ± 0·042
Glycerol	T	−0·041 ± 0·029	0·002 ± 0·008	0·004 ± 0·013	−0·004 ± 0·006
	NT	−0·036 ± 0·021	−0·007 ± 0·006	0·000 ± 0·009	−0·016 ± 0·007

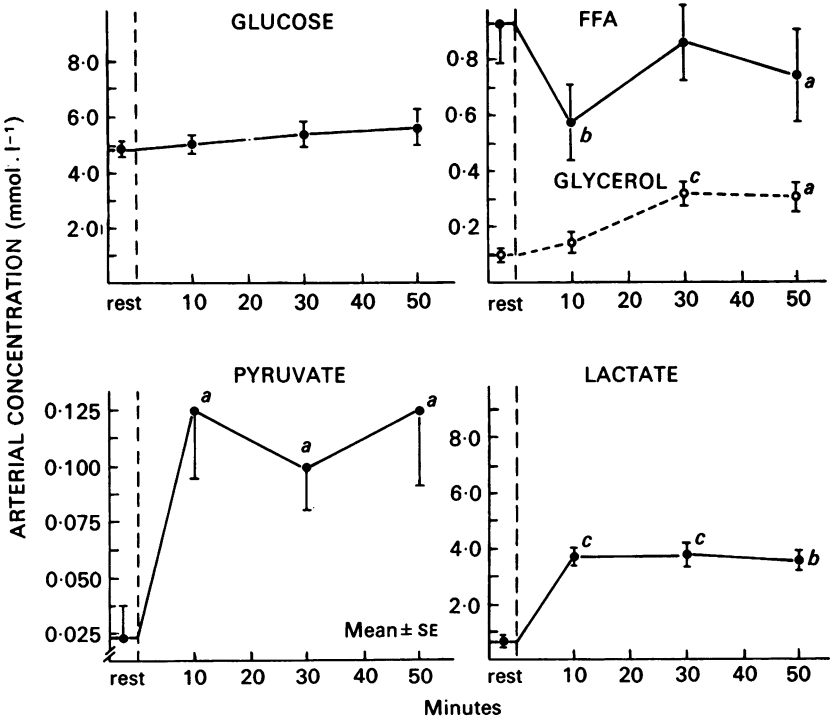

Fig. 3. Arterial concentrations of glucose, pyruvate, lactate, glycerol (whole blood) and free fatty acids (FFA) (plasma) during the post-training metabolic study. Mean ± S.E. of mean is given. Significant differences from resting values are indicated (*a*, $P < 0{\cdot}05$; *b*, $P < 0{\cdot}01$; *c*, $P < 0{\cdot}001$).

The release of lactate from the untrained leg tended to be higher than that from the trained leg, the difference being significant at 10 min of exercise (Fig. 4) ($P < 0{\cdot}05$). At 50 min of exercise, a small uptake of lactate was noticed in the trained leg. Release/uptake of pyruvate and uptake of glucose were not significantly different in the two legs. During the exercise period, the thigh muscle glycogen content decreased from 101 (82–112) to 66 (43–81) mmol.kg^{-1}(wet wt.) in the trained leg, and from 95 (72–120) to 54 (17–70) mmol.kg^{-1}(wet wt.) in the untrained leg (Table 3). No significant differences between the glycogen depletion in the trained and the untrained legs could be detected.

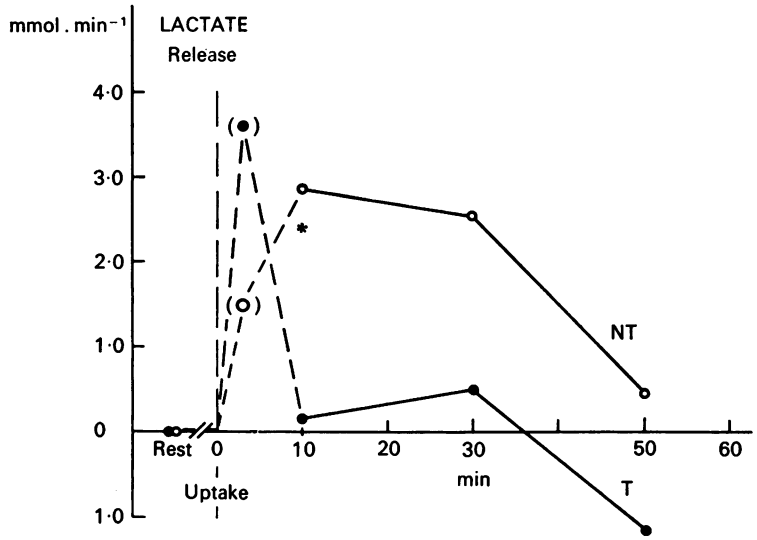

Fig. 4. Release/uptake of lactate from the trained (T) and non-trained (NT) leg during the post-training metabolic study. Values at 3 min are estimations from A–V differences, as blood flow was not determined at this time. * denotes significant difference ($P < 0{\cdot}05$), T cf. NT leg.

The Periodic Acid Schiff stain (PAS) revealed that the most marked glycogen depletion had occurred in the type I fibres. The only difference between the trained and the untrained leg was a tendency towards a greater glycogen depletion of type II fibres in the untrained leg. Of the other muscle metabolites studied, there was a tendency towards a higher concentration of glucose in the trained leg at the end of exercise ($0{\cdot}05 < P < 0{\cdot}1$) (Table 3). No differences were seen in the muscle concentrations of lactate and glucose-6-phosphate.

In most cases, higher A–V differences for free fatty acids were seen for the trained than for the untrained leg. The variation among the subjects

TABLE 3. Muscle metabolites before and at the end of the post-training metabolic study.

Mean ± S.E. of mean is given in mmol. kg^{-1} (wet wt.)

Leg	Glycogen		Glucose		Glucose-6-P		Lactate		
	B	E	B	E	B	E	B	3 min	E
Trained	101 ± 6	66 ± 6*	0·5 ± 0·1	1·5 ± 0·2*†	0·2 ± 0·0	0·1 ± 0·0	2·7 ± 0·3	7·6 ± 1·4*	4·0 ± 0·6**
Fon-trained	95 ± 7	54 ± 9*	0·4 ± 0·1	0·9 ± 0·2**	0·2 ± 0·0	0·2 ± 0·1	2·2 ± 0·2	6·5 ± 1·5**	4·0 ± 0·9**

* ($P < 0·05$) and ** ($0·05 < P < 0·1$) denote significant difference, before (B) cf. at 3 min (lactate) or at the end (E) of exercise.

† ($0·05 < P < 0·1$) denotes significant difference, trained cf. non-trained leg.

was, however, great. A significant net uptake of free fatty acids was only seen in the trained leg. There were no significant differences in A–V for glycerol over the two legs.

DISCUSSION

The regulatory systems for the metabolic adaptation of the body to acute exercise are complex. The model for studying the importance of local adaptive changes used in this work has the advantage that central factors and other variables, for example arterial levels of substrates and hormones are the same, both for the trained and untrained leg. On the other hand, differences in sensitivity to hormones, or a different nervous regulation to the two legs, cannot be excluded. Furthermore, because of the high leg blood flow, even variations in A–V differences within the methodological error may give large fractional changes in calculated uptake or release of substrates.

The major finding of this study was that, during the post-training metabolic study, the degree of fat combustion was higher in the trained than in the untrained leg, and further that this seemed to be linked with the higher oxidative capacity. Despite the fact that the subjects had been instructed to attempt to distribute the work equally between the two legs, the leg $\dot{V}_{O_2}$ measurements revealed that, nevertheless, they actually exercised so much harder with the trained leg as to make the relative loads for the two legs equal. In spite of this, it is remarkable that tendencies towards a different metabolic pattern were seen, and for certain variables, significant differences. Had the absolute workloads for the two legs been the same, even more clear cut differences in metabolism could have been anticipated (Saltin & Karlsson, 1971). Using R.Q. determinations to quantify the proportions of fats and carbohydrates in energy metabolism has possible sources of error (Christensen & Hansen, 1939; Wahren, Ahlborg, Felig & Jorfeldt, 1971). The finding of a significant net uptake of free fatty acids in the trained leg only, together with a higher release of lactate from the untrained leg, provides, however, evidence that the lower R.Q. in the trained leg is indeed indicative of a higher proportion of fat metabolism.

An interesting finding is that, in spite of the difference in lactate release from the two legs, with a tendency towards an uptake of lactate in the trained leg during the last part of the exercise period, muscle lactate concentration was elevated to the same extent in the trained and in the untrained leg, at the end of exercise. This may point to a different lactate metabolism in the trained compared to the untrained leg.

When the total amount of carbohydrates oxidized, as estimated from R.Q. and leg oxygen uptake data, is compared with measured values for

blood glucose uptake, release/uptake of glycolytic end-products (pyruvate and lactate) and degradation of muscle glycogen, the results are more difficult to interpret (Fig. 5). The estimated total amount of carbohydrates (in glucose units) oxidized during the 1 h of exercise is 230 mmol for the trained and 250 mmol for the untrained leg. When blood glucose uptake and release of glycolytic end-products are taken into consideration, the estimated muscle glycogen break-down comes out to 140 mmol.h^{-1} for

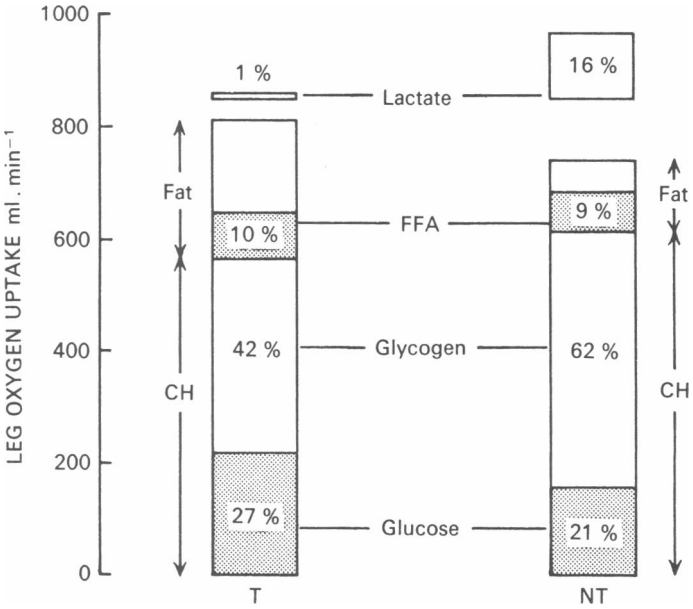

Fig. 5. Contribution of carbohydrate (CH) and fat oxidation to the total leg oxygen uptake in the trained (T) and the non-trained (NT) leg during the post-training metabolic study. The shaded areas indicate leg net uptake of glucose and free fatty acids (FFA) translated to the oxygen uptake needed to combust completely these substrates. The part of the carbohydrate oxidation covered by oxidation of endogenous glycogen is estimated from CH minus blood glucose oxidation. The loss of energy substrates, as released lactate, is indicated by separate bars. Due to the concomitant release of FFA from the leg, the net uptake will underestimate the muscle uptake of free fatty acids. The calculated oxygen uptakes that can be accounted for by FFA oxidation given in this figure are intended only as a comparison between T and NT leg.

the trained and 240 mmol.h^{-1} for the untrained leg. These figures should be compared with the insignificant difference in the measured glycogen break-down of 35 mmol.kg^{-1}(wet wt.).h^{-1} in the trained, and 41 in the untrained leg. Due to the many factors involved, there is, of course, a great deal of uncertainty in estimating total muscle glycogen breakdown; the estimated

difference when comparing the trained and the untrained leg appears, however, to be of a magnitude that should be detectable in the muscle biopsy specimen. One possible explanation for the lack of a difference in the measured muscle glycogen depletion might be a different involvement of the muscles of the two legs. This is suggested by the relatively greater difference in pedal-force (28 %) than in leg oxygen uptake (11 %) in the two legs, indicating a lower mechanical efficiency in the untrained leg.

A major question raised in this study was whether an enhanced oxidative potential of skeletal muscle has any significance for the metabolism during exercise. Theoretically, it may enable the muscle to extract more oxygen from the blood during maximal exercise so as to increase the $\dot{V}_{O_2}$ max. and it may influence the metabolism during submaximal exercise, giving rise to a shift towards an increased fat metabolism relative to that of carbohydrate, as suggested by Holloszy & Booth (1976). In a previous study (Henriksson & Reitman, 1977) evidence was presented that leg muscle oxidative capacity is not the limiting factor determining the $\dot{V}_{O_2}$ max. The significantly higher oxidative capacity of the trained leg in this study was paralleled by significantly lower R.Q. values and a lower release of lactate during submaximal exercise. In conclusion, it is suggested, therefore, that the shift towards a more pronounced metabolism of fat in the trained leg, as indicated by these results, is a function of the increased muscle oxidative capacity.

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