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The Nature of the Training Response; Peripheral and Central Adaptations to One-Legged Exercise

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Abstract

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3 male subjects were studied and placed in 3 groups. Each group exercised one leg with sprint (S), or endurance (E) training and the other leg oppositely or not at all (NT). Oxygen uptake ($\dot{V}o_2$), heart rate and blood lactate were measured for each leg separately and for both legs together during submaximal and maximal bicycle work before and after 4 weeks of training with 4–5 sessions per week. Muscle samples were obtained from the quadriceps muscle and assayed for succinate dehydrogenase (SDH) activity, and stained for myofibrillar ATPase. In addition eight of the subjects performed after the training two-legged exercise at 70% $\dot{V}o_2$ max for one hour. The measurements included muscle glycogen and lactate concentrations of the two legs as well as the blood flow and the a–v difference for O_2, glucose and lactate.

The improvement in Vo_2 max, the lowered heart rate and blood lactate response at submaximal work levels were only found when exercising with a trained leg (E or S). Part of the variables studied were markedly more changed with E as compared with S-training. Although muscle fibre composition did not change a pronounced muscle adaptation took place with the training with enhancement of the SDH activity of the S and E legs while the NT-leg did not change. Blood flow and oxygen uptake were similar in NT and S–E legs while femoral vein oxygen content was slightly lower in the trained as compared to the NT-leg. Glycogen utilization was lowest in the trained leg with similar glucose uptake in all legs regardless of training status. Moreover, lactate was only continuously released from the NT-leg. It is concluded that training induces marked local adaptations which not only affects the metabolic response to exercise but also are of importance eliciting an improved cardiovascular function.

The extent to which local and more general factors participate in the adaptations to physical training is still an unsolved problem. Studies in which the response to exercise with both trained and untrained limbs (Clausen *et al.* 1973, 1974, 1975, Gleser 1973, Davies and Sargeant 1975) suggest that the central circulatory response to training and work capacity is at least partially a function of whether the limb muscles performing the exercise also are trained. Since the "local factor" appears to be crucial we felt it of interest to study simultaneously both the adaptation of the skeletal muscles with training and adaptation of central

...ections. We attempted to distinguish between local and more general effects of ...g with different training procedures, as well as between subject differences by using one-legged bicycle exercise during a 4-week training period.

Subjects

hirteen healthy male medical or fine arts students participated in the study. They averaged 21.7 (19-25) ars in age, 181 (172–191) cm in height, and 71.1 (59–94) kg in weight. Mean body weight did not change ıring the study, and in no case there was an individual variation above 2 kg. Measurements of body dimen- ıns and skinfold (Hermansen and von Döbeln 1971) did not change indicating no apparent changes in dy composition during the training period.

None of the subjects had ever trained for competition, and none had engaged in any regular training sport activity in the months before this study. Maximal oxygen uptake ($\dot{V}O_2$ max) during two-legged ercise averaged 3.3 (2.9–3.9) l/min or 46 (37–54) ml/kg × min at the start of the study. These values are hin 5% of normal values for this age group in Sweden (Saltin and Sjögaard, unpublished data). All ıjects underwent a physical examination before participating in the study. On this occasion each subject s informed of the procedure to be used and the discomfort and risks—both acute and chronic—with se procedures. An oral consent was obtained from each subject entering the study, and they were in- med that they were free to leave a test or the whole study at any point.

Since the subjects were reasonably homogenous in regard to previous physical activity and $\dot{V}O_2$ max, y were allowed to express their preference for one of the following training regimens: A) training one leg endurance (E) (continuous bicycle exercise for 30–50 min) and the other leg with sprint (S) training peated all-out efforts for 30–40 s with 1 1/2 min of rest between exercise bouts); B) training one leg with S program and the other leg remaining untrained; and C) one leg E trained and the other untrained. nitially five subjects entered each group with no subject being forced into a group he did not select. Unfortunately, two subjects in group C) did not complete the training or the post-training studies. One of se subjects became ill during the first week of training and could not complete the training. The other ıject completed the training but elected not to complete the final tests.

Methods, protocol, and training

ercise capacity. Oxygen uptake was determined by the Douglas bag technique. Gas volumes were meas- d in a Tissot spirometer and fractions of O_2 and CO_2 determined with the Haldane or Scholander ıniques. Gas collection in the submaximal exercise was made after 5 min of exercise and during maximal k during the last 1½ to 2 min of exercise. Air was collected in each bag for at least 30 s. Heart rate was nted from ECG recordings made at frequent intervals during each work load.

he bicycle ergometer was used both for testing (Krogh or Elema) and for training (Monark). The jects were allowed to familiarize themselves with one- and two-legged submaximal and maximal work ls of the bicycle before any measurements reported in this study were made. The only special arrange- ıt for one-legged exercise was to secure the foot on the pedal with a toe clip and elastic band around the . The foot of the nonworking leg was rested on a small chair placed beside the bicycle.

xygen uptake and heart rate relationships were used to establish the work load before the training ted with each subject exercising on 3–4 occasions at different days. Each day different combinations of ıaximal and maximal one- and two-legged exercise loads were tried. In this way, the levelling-off erion for $\dot{V}O_2$ max could be established for each leg separately as well as for the two-legged exercise. It easier to obtain reproducible results after the training period; therefore, at that time only selected submaximal and maximal work rates were used. However, after training each subject also exercise at least e different days to establish the levelling-off criteria for $\dot{V}O_2$ max.

oth Gleser (1973) and Davies and Sargeant (1974 and 1975) have reported difficulties in establishing levelling-off criteria for maximal oxygen uptake in one-legged exercise. This was related to a gradual ering of the apparent mechanical efficiency at heavy work intensities. We did not experience these culties. On the other hand our subjects had a higher oxygen uptake at all levels of submaximal exercise ng one-legged work.

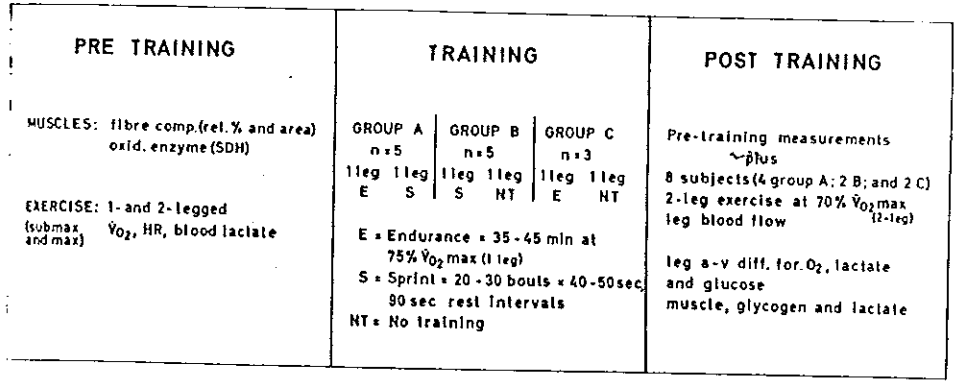


Fig. 1. A schematic illustration of the experimental protocol and training groups.

All tests of each subject were completed within a week both before and after the training. This was accomplished by allowing only 1/3 of the subjects to start their training per week.

Metabolic measurements. Muscle samples were obtained from the quadriceps muscle with the percutaneous needle biopsy technique (Bergström 1962). Samples used to determine fibre composition and enzyme activities before and after training were taken at rest in the morning. One part of these samples was immediately weighed, homogenized and used for the determination of succinate dehydrogenase (SDH), (Cooperstein *et al.* 1950). Another part was used for freeze sectioning and stained for myofibrillar adenosine triphosphatase (ATPase), (Padykula and Herman 1955), reduced nicotinamide adenine dinucleotide diaphorase (NADH-diaphorase), (Novikoff *et al.* 1961), and alpha-glycerophosphate dehydrogenase (Wattenberg and Leon 1960). Fibre typing was based on the stain for myofibrillar ATPase. For reasons discussed elsewhere (Gollnick *et al.* 1974, Taylor, Essén and Saltin 1974) we have used the terms slow and fast twitch fibres in stead of the classification of Type I (red) and II (white) fibres, respectively as proposed by Engel (1962). Fibre areas were estimated by integrating the surface area of 20 fibres of each type in a good cross-sectional area of the sample.

In order to evaluate whether the local metabolic changes may have taken place, 8 of the 13 subjects performed two-legged submaximal bicycle exercise at 70% of $\dot{V}O_2$ max (two-legged) *after the training period* (see Fig. 1). Catheters were placed in the two femoral arteries and veins so that blood flow to each leg could be measured at rest and after 10–15 and 50–55 min of exercise (Wahren and Jorfeldt 1973). Arterio-venous differences for lactate and glucose were determined enzymatically at the same time as the blood flows and also after 3 and 30 min of work. Biopsies were taken before, after 3 min, and at the end (60 min) of exercise and used for glycogen and lactate determination (Karlsson, Diamant and Saltin 1971). A piece of the muscle sample obtained before and after the exercise was used for histochemical identification of fibre types and glycogen (see Gollnick, Piehl and Saltin 1974).

A Krogh bicycle ergometer was used for the exercise, and the pedals were fitted with strain-gauges so that the force of each pedal thrust could be evaluated (Hoes *et al.* 1968).

Right versus left leg performance. The response to the one-legged exercise, comparing left and right legs, was evaluated in each subject. In the pre-training examinations, similar results were found for both legs for all variables studied (Table I). Thus, the subjects were allowed to train with either leg. The right leg was chosen for endurance and sprint training by 3 and 5 subjects, respectively, leaving 5 right legs with no training. The number of right and left legs trained were also about equally distributed in groups A, B, and C.

One subject distinguished himself from the group by having only half the maximal isometric leg strength (Karlsson and Ollander 1971) in his left leg as compared with his right. This difference did not influence any of the other measurements. Thus, he was kept in the study (Group C). He trained his "weaker" leg and demonstrated improvements similar to those in the other two subjects of group C. The subject increased the strength of his left leg by 25% with the training.

Training program. The training period lasted for four weeks with an average of five workouts per leg each week (Table II). All training was performed on a bicycle ergometer and was supervised by a physical education teacher. He followed the heart rates during the training sessions and adjusted the work loads according to these measurements. Work loads were chosen to represent approximately 75% (E) and 150%

...values ± S.E. and range for selected variables in the pre-training studies. Measurements ...were performed on the subjects' right and left legs. The submaximal exercise was at 100 W.

Leg	Muscle fibers		SDH mmoles/ kg × min
	%ST	%ST area	
Right	40±2.5	35.5±2.7	3.9±0.2
n=13	28–60	18–54	2.4–5.5
Left	39±2.9	34.2±3.3	3.8±0.2
n=13	26–59	21–57	2.4–5.2

Submaximal and maximal work

Leg	Oxygen uptake (STPD), l/min		Pulm. vent. (BTPS), l/min		Heart rate beats/min		Blood lactate, mmol/l		Leg isometric strength
	Subm	Max	Subm	Max	Subm	Max	Subm	Max	Kp
Right	1.80±0.05	2.74±0.07	45.3±3.01	92.9±5.4	158.8±4.4	186.6±2.2	6.6±0.6	10.3±0.7	103.4±7.6
	1.65–2.10	2.24–3.07	33.2–71.6	69.5–135.6	130–182	174–202	2.2–9.9	6.8–15.5	72–158
Left	1.84±0.07	2.71±0.07	46.1±2.1	92.7±5.7	159.5±5.3	187.5±2.1	6.7±0.5	10.6±0.5	96.0±5
	1.50–2.22	2.19–3.17	36.3–61.2	60.8–142.6	130–181	176–201	3.3–10.0	7.6–15.5	37–146

S) of one-legged $\dot{V}O_2$ max. During the third week repeated measurements of oxygen uptake, heart rate, and blood lactate as well as the $\dot{V}O_2$ max of each leg were made on each subject. The results demonstrated the expected physiological load of the different training regimens.

The work load and duration of each type of training were chosen to give similar total amounts of work in each training bout. In group A, where endurance training of one leg was followed by sprint training of the other leg, 5–10% shorter training periods were used for each leg.

The work performed amounted to approximately 3,000 J per week per trained leg and all groups were within 5–10% of this value. It should be remembered, however, that group A performed about 90–95% more work than group B since both legs were trained. Of note also is that it took up to 90 min per day to complete the sprint training since 60–90 s of rest was allowed between each sprint.

. Mean values ± S.E. for some responses to one-legged bicycle exercise at submaximal (100 W) and maximal (Max) work levels before and after training. The asterisks denote a significant difference between before and after training based on paired t-test ($p < 0.05$).

Type of train-ing	Work level	Oxygen uptake (STPD), l/min		Pulm. vent. (BTPS), l/min		Heart rate, beats/min		Blood lactate, mmol/l	
		Before	After	Before	After	Before	After	Before	After
Sprint	100	1.87±0.11	1.80±0.05	23.2±3.3	25.7±2.1	159.6±8.1	147.8±6.5*	6.2±1.2	5.2
	Max	2.86±0.11	3.18±0.17*	95.2±9.3	128.1±6.5*	184.6±3.3	189.0±1.5	11.8±1.3	13.3
End	100	1.86±0.05	1.79±0.03	23.4±1.6	24.5±0.9	160.2±6.8	143.1±4.1*	5.9±1.0	4.3
	Max	2.79±0.11	3.33±0.17*	92.8±7.8	122.5±7.2*	185.4±3.3	188.2±2.9	11.4±1.1	12.3
Sprint	100	1.76±0.09	1.71±0.06	43.3±4.9	42.1±3.3	158.2±8.5	152.4±8.4	6.8±0.8	4.3
	Max	2.75±0.07	3.18±0.11*	96.4±11.6	114.8±8.2*	191.8±3.3	194.2±3.9*	10.1±0.7	12.2
No train	100	1.78±0.08	1.75±0.07	45.2±7.0	48.7±5.6	157.0±8.0	154.8±7.8	6.4±0.7	6.0
	Max	2.76±0.06	2.80±0.06	96.0±10.2	107.6±5.8	188.8±4.4	190.4±4.2	10.2±0.7	10.1
End	100	1.87±0.16	1.79±0.03	51.4±3.0	45.6±0.5	165.3±8.3	152.2±5.5*	7.5±1.2	4.4
	Max	2.43±0.13	3.01±0.12*	83.8±13.7	111.3±6.3*	184.7±4.4	188.3±4.3*	9.2±0.4	9.4
No train	100	1.81±0.10	1.82±0.06	52.2±2.3	54.2±3.2	164.3±10.1	157.0±5.6	7.4±1.2	6.7
	Max	2.47±0.14	2.64±0.13*	87.5±8.9	111.2±10.2	183.0±4.9	187.0±3.5	9.0±1.1	10.6

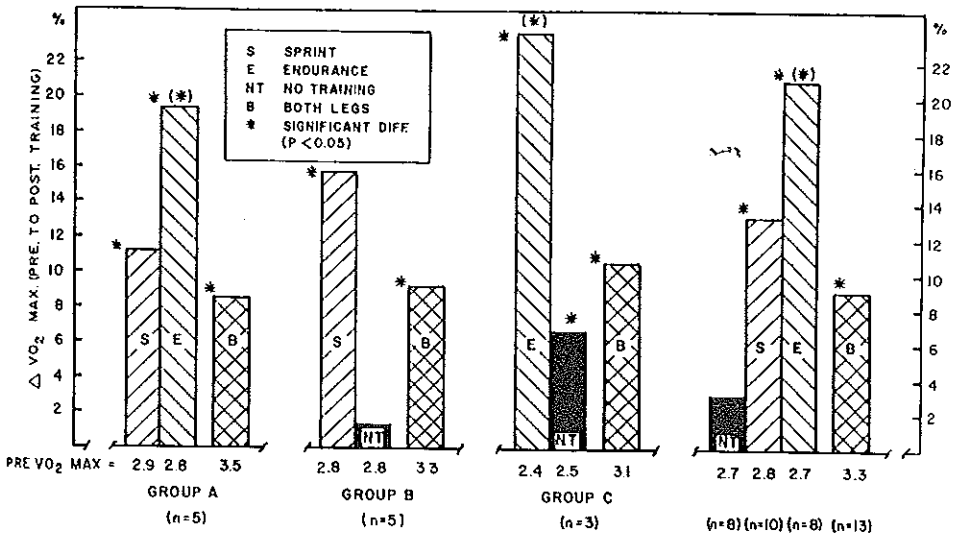


Fig. 2. Mean values for changes in per cent in maximal oxygen uptake in the groups A–C. Below each bar is the pretraining Vo_2 max given in l/min. The four bars to the right give the mean values for all untrained sprint- or endurance-trained limbs as well as for two-legged exercise regardless of group belonging. The star within parenthesis denotes a significant difference between sprint- and endurance-trained leg.

A schematic summary of the basic features of the protocol is given in Fig. 1.

Conventional statistical methods were applied. Intra-individual differences were evaluated using Student's t-test (Fischer 1946).

Results

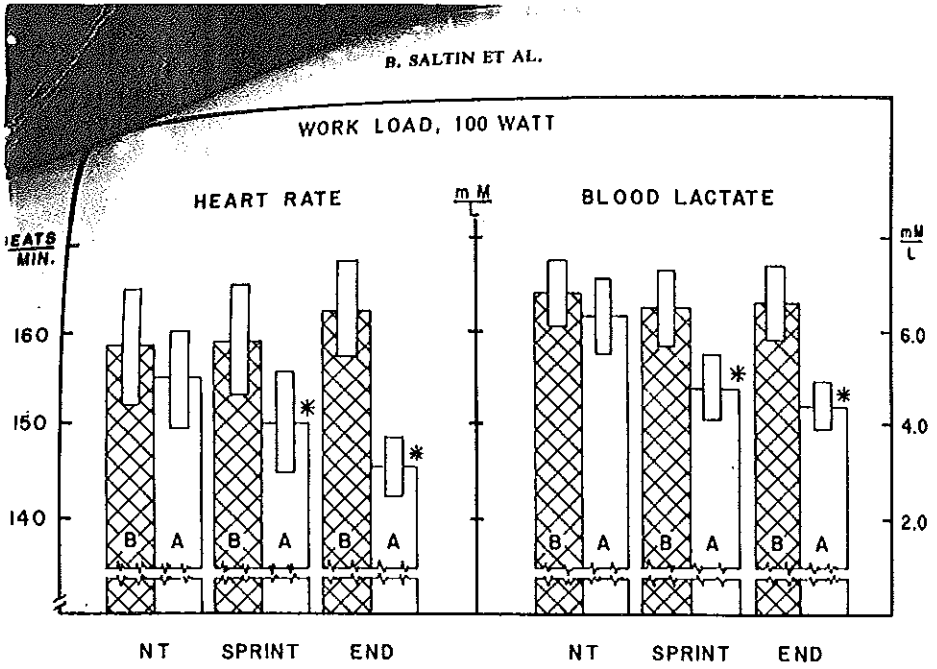
Pretraining studies (Table I)

In the control experiments before training started none of the variables studied were significantly different comparing right and left leg. One-legged exercise V_{O_2} is slightly higher than two-legged when working at submaximal intensities. Thus, the oxygen uptake at 100 W with one leg approximated that at 125 W during two-legged work (1.8 l/min). The ratio for one- to two-legged exercise maximal oxygen uptake averaged 0.78–0.84 in our subjects, but only 0.71–0.77 in the studies of Glesen (1973), Davies and Sargeant (1975). Only small variations were seen among the groups. Our values agree closely with those reported previously when a similar arrangement was used for one-legged exercise. (Pernow and Saltin 1971).

Training response

1. *One-legged exercise*

A. Analysis by groups (Fig. 2, Table II). Oxygen uptake at the submaximal one-legged exercise work loads was in most instances somewhat lower after as compared with before training. The differences, however, were insignificant in all groups and within 0.1 l/min. Depending upon the training procedure, the post-training measurements varied greatly. In group A, $\dot{V}_{O_2}$ max increased from a pre-training value of 2.8 l/min by 11% (4–24) and 20% (10–31)



g. 3. Mean values ± 1 S.D. for heart rates and blood lactate concentration at 600 kpm/min exercising th one-leg before (B) and after (A) training. The star denotes a significant ($p < 0.05$) difference comparing e-post training results (Student's t-test).

the sprint and endurance trained legs, respectively. In group B each leg also had a pre-aining $\dot{V}_{O_2}$ max of approximately 2.8 l/min. Sprint training resulted in a 15% (3–30) in-ease whereas the inactive leg did not change more than 3% (2–5). In group C, where pre-aining $\dot{V}_{O_2}$ max was 2.4 and 2.5 l/min for the two legs, respectively, endurance training oduced a 24% (21–30) enhancement of $\dot{V}_{O_2}$ max. The nontrained leg exhibited an increase 6% (5–8) ($p < 0.05$).

The greater the increase in $\dot{V}_{O_2}$ max that occurred with training, the more marked was the duction in heart rate during submaximal one-legged exercise. It may be of note, however, at minor variations from this general finding existed. At a work rate of 100 W, heart rate as 17 and 13 beats/min lower in groups A and C, respectively, after endurance training ith the posttraining heart rates in these groups being 143 and 152 beats/min (Table III). print-training resulted in a 13 beat/min drop in group A ($p < 0.05$) and 6 beat/min drop in roup B ($p < 0.05$) in heart rate. Thus, submaximal heart rate response was more markedly fluenced in group A where both legs had been trained. Of note also is the observation in roup B and C that with the untrained leg only a very small reduction in the heart rate (2–6 eats/min) was observed in spite of a significant reduction in the heart rate when exer-ising with the trained leg at the same absolute work level. The five subjects who trained both gs (one E and the other S) had the lowest heart rate when exercising with the endurance-ained leg.

B. Analysis by training procedure (Fig. 2, 3, 4 and 5). From the results presented above, it ppears as though the training of one leg affected the response to exercise of the other leg

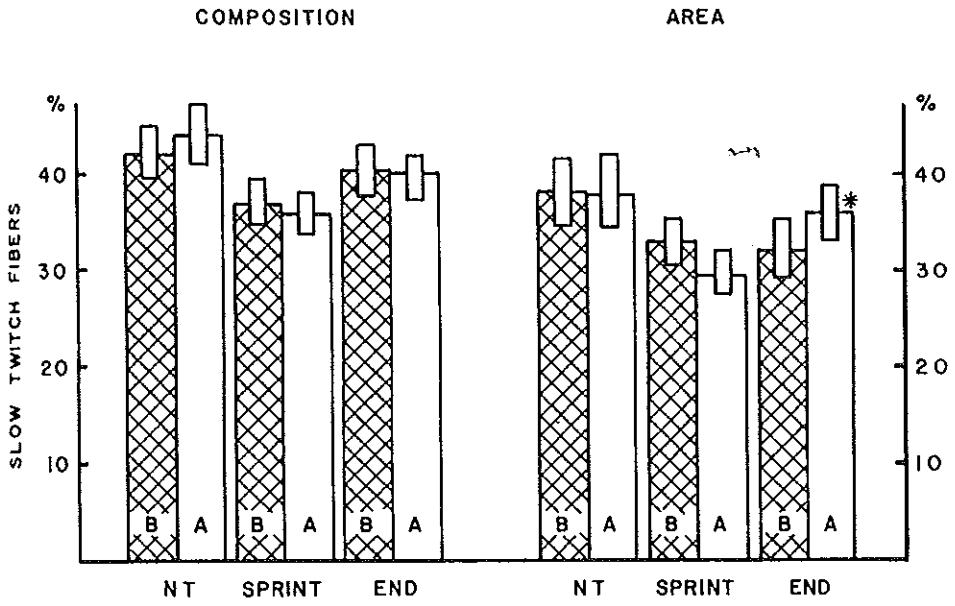


Fig. 4. Mean values ± 1 S.D. for the percentage of slow twitch fibres and area before and after the training period.

only to a minor extent. An approach which may facilitate a further analysis of the responses to the various procedures of training would then be to combine the observations for the non-trained, sprint-trained (S), and endurance-trained (E) legs regardless of which training group the subject belonged to.

Significant reductions in heart rate response during submaximal exercise (100 W) existed for both sprint- and endurance-trained legs, but not for the untrained leg (Fig. 3). The larger

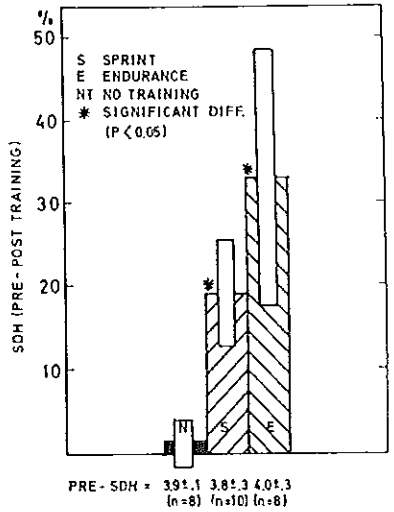


Fig. 5. Mean change in per cent for succinate dehydrogenase activity (SDH) of vastus lateralis with the different training procedures. Note that the mean values ± 1 S.D. for the absolute activities for each leg before the training started are given under each bar.

observed for the endurance as compared with the sprint-trained leg was not significant. At maximal one-legged (NT, E, and S) exercise, heart rate was 2–4 beats/min higher in the tests after training with the difference for the S-trained leg being significant ($p < 0.01$).

The $\dot{V}_{O_2}$ max measurements in relation to training procedure also gave a very clear picture (Fig. 2). The insignificant whereas the sprint- and endurance-trained legs both improved significantly.

The blood lactate concentration at submaximal and maximal exercise also changed according to the different training regimens (Fig. 3). Thus, endurance training caused the most marked reductions in blood lactate concentration at 100 W, sprint-training the second largest reduction ($p < 0.001$), with an insignificant change in the untrained leg. Of note is the observation that blood lactate concentration after one-legged maximal exercise was significantly increased only with sprint-training, with mean values of 10.1 before and 12.2 mM after training.

Muscle fibre composition in the thigh varied slightly among the subjects, with mean values for ST fibres of 42 (NT), 38 (S), and 40 (E) % (Fig. 4). As the ST fibres occupied a somewhat smaller area than the FT fibres, the relative area of the ST fibres was 38 (NT), 34 (S), and 37 (E) % before the training (Fig. 4). Although the training caused no changes in the percent of ST fibres, their relative area varied with the type of training. In endurance training, the ST fibre area appeared to be increased ($p < 0.05$). With sprint-training both the FT and ST fibres increased in size, but as the FT fibres increased more, there was a tendency for a reduction in the relative ST area ($p < 0.05$).

SDH activity in the thigh muscles averaged 3.9 (NT), 3.8 (S), and 4.0 (E) mmol·(kg · min)$^{-1}$ before training. No significant change was observed in the inactive leg, but in the sprint- and endurance-trained legs an increase in SDH activity of 19% (1–40), and 33% (8–61), respectively, occurred (Fig. 5). No significant correlations were found between changes in SDH activity and $\dot{V}_{O_2}$ max when evaluated for each training procedure separately. However, when based on all three groups, this relationship becomes significant ($p < 0.05$). The stains for NADH-diaphorase and α-glycerophosphate dehydrogenase were more intense after training, but the staining pattern was not consistent enough to clearly demonstrate any differences in response to the different training regimens or between fibre types.

II. *Two-legged exercise*

A. Work capacity (Fig. 2, Table III). The two-legged pre-training maximal $\dot{V}_{O_2}$ was 3.1, 3.3, and 3.5 l/min for groups C, B, and A, respectively. The mean increase in these groups was 10, 9, and 8% or approximately 0.3 l/min in each group. In the pre-training studies, the ratio between one- and two-legged $\dot{V}_{O_2}$ max was 0.81. This ratio increased to 0.83 in the post-training measurements ($p < 0.05$). The changes in pulmonary ventilation generally followed the oxygen uptake both in one- and two-legged exercise. Thus, no major variation was found in the ventilatory equivalent for oxygen ($\dot{V}_E/\dot{V}_{O_2}$) in response to training.

Submaximal heart rate during two-legged exercise (125 W) was reduced by 18 (A), 11 (B), and 18 (C) beats/min after training (Table III). Max. heart rate were 194–201 beats/min both in the pre- and post-training tests.

Table III. Mean values ± S.E. to two-legged bicycle exercise at a submaximal (125 W) and maximal work levels before (B) and after (A) training. An asterisk denotes significant difference ($p < 0.05$) based on paired t-test

Groups (N)	Work level Kpm/min	Oxygen uptake (STPD), l/min		Pulm. vent. (BTPS), l/min		Heart rate, beats/min		Blood lactate, mmol/l	
		B	A	B	A	B	A	B	A
A	125	1.92±0.08	1.81±0.09	41.2±2.3	40.4±0.4	148.6±5.9	130.6±4.9*	6.3±0.4	5.0
n=5	Max	3.51±0.14	3.81±0.18*	109.4±8.4	130.4±9.4*	200.8±3.2	199.2±2.6	12.8±0.7	14.0
B	125	1.77±0.03	1.74±0.02	47.4±4.4	40.8±1.7	139.8±7.5	129.2±5.8*	5.5±0.6	4.5
n=5	Max	3.34±0.15	3.64±0.16*	104.5±5.3	120.7±3.6*	196.1±2.6	200.1±1.4	11.9±0.7	13.2
C	125	1.87±0.02	1.81±0.03	42.6±2.4	45.7±3.7	157.7±4.3	140.1±6.7*	6.3±0.6	4.9
n=3	Max	3.11±0.16	3.44±0.2*	99.3±6.2	130.3±14.7*	193.7±0.4	193.7±3.3	11.8±1.3	12.6

B. Blood flow studies, (Fig. 6 and 7). After the training period eight of the subjects performed "ordinary" two-legged exercise for 1 h at 70% (66–76) of $\dot{V}_{O_2}$ max. Individual values for the absolute work rates varied between 150–215 watts (mean = 180 watt) and pulmonary oxygen uptake after 12 min of exercise varied between 2.1–2.9 l/min (mean = 2.4 l/min). A further increase of 0.1 l/min was observed during the 60 min of exercise ($p < 0.05$). With very similar relative work intensities inter-subjects difference in heart rate were small with mean heart rates of 169 and 183 beats/min after 10 and 60 min of exercise, respectively ($p < 0.05$). The respiratory exchange ratios were 0.95 in the beginning and 0.93 at the end of the exercise ($p < 0.05$).

The whole body reaction observed in the blood flow experiment gives a composite picture as each subject exercises with both legs; one trained and one untrained or one endurance- and one sprint-trained, respectively. A more informative comparison would be to compare the response of each leg to the two-legged exercise. This can be done since the blood flow and arterio-venous differences (O_2, CO_2, lactate, and glucose) were established for each leg during the two-legged exercise.

Leg blood flow was very similar in the untrained and trained legs of the subjects, as well as in the endurance – compared with the sprint-trained leg (Fig. 6 A).[1] This was true throughout the one-hour of exercise. The a–v oxygen differences over the exercising legs were also of approximately the same magnitude comparing the sprint- and endurance-trained legs (Fig. 6 B). In the 4 subjects who had one trained and one untrained leg the a–v oxygen difference was slightly higher over the trained leg resulting in a lower oxygen content in the femoral blood returning from the trained leg (Fig. 6 C) ($p < 0.05$). The calculated leg oxygen uptake was thus very similar comparing endurance- and sprint-trained legs, but in some subjects higher in the trained than in the untrained leg (Fig. 6 D) ($p > 0.05$). This was true throughout the prolonged exercise period as leg oxygen uptake did not change significantly. The work performed by each leg as judged by the force development on the pedals was in most subjects rather equally divided between the subjects' legs. At the most the difference

[1] The method used to determine leg blood flow is based on similary flows to the two legs. If there is a difference in circulation time it will result in erroneous measurements of the background dye concentration. In the present study this circumstance may introduce at the most an 1–2% error in the actual values for the flows.

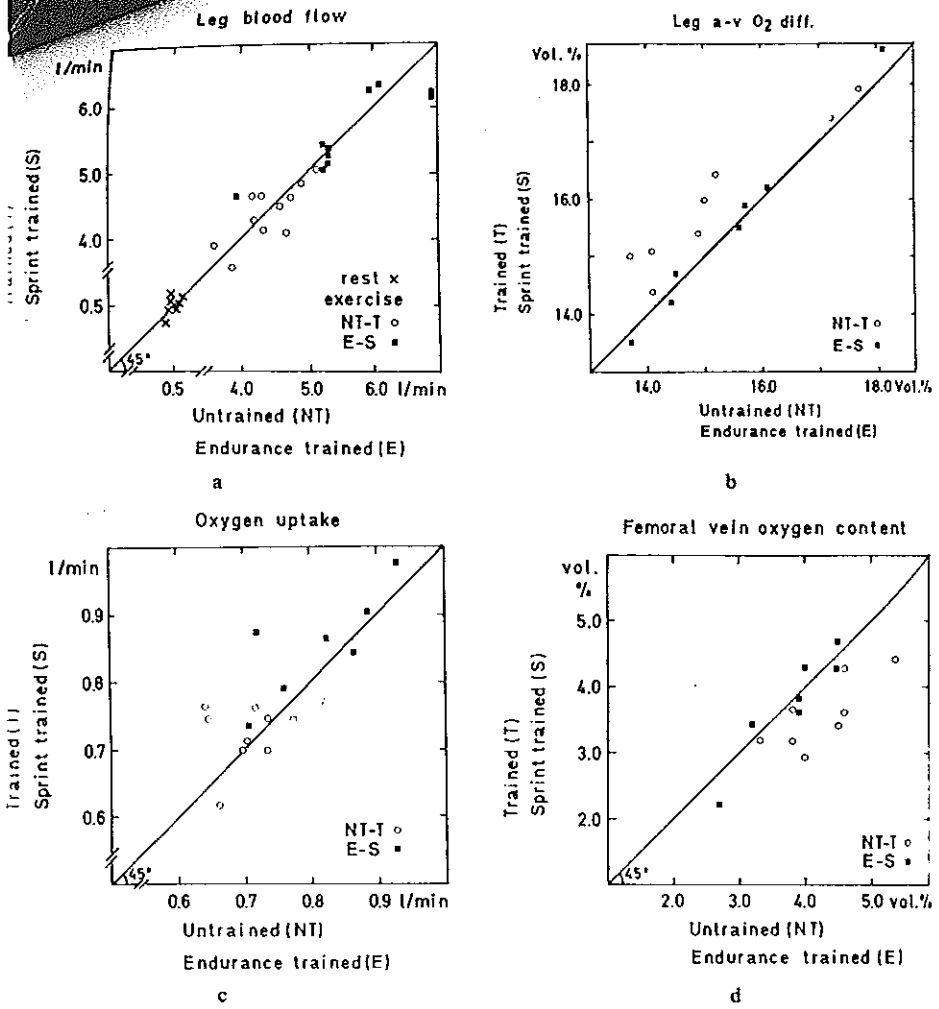


Fig. 6. The 4 panels (a–d) illustrate leg blood flow (a), a–v oxygen difference (b), leg oxygen uptake (c), and femoral vein oxygen content (d), comparing the response of the two legs of the subjects performing the two-legged exercise for one hour at 70% $\dot{V}O_2$ max. Comparisons are made between four subjects' untrained (NT) and trained (T; endurance- or sprint-trained) legs. Comparisons are also made between the four subjects who had trained one leg with the endurance regimen and the other with sprint type training included in the panels are measurements after 10–15, 30–35, and 50–55 min of exercise. For none of the variables did a significant change occur with time. However, in several subjects $\dot{V}O_2$ and femoral vein oxygen content did increase and a–v oxygen difference and RQ did drop.

amounted to 12% but the observed mean differences of 4 (S *vs.* E) and (T *vs.* NT) 7% were insignificant. Moreover any direct relationship between uneven pedal force development and difference in oxygen uptakes between legs was not apparent. The RQ measurements on the blood perfusing the leg did drop from around 0.98 in the beginning to 0.92 at the end of the one-hour exercise ($p < 0.05$). A comparison between legs revealed no difference between the untrained and the trained legs, whereas the sprint-trained leg in three subjects exhibited definitely lower RQ values than the endurance-trained leg.

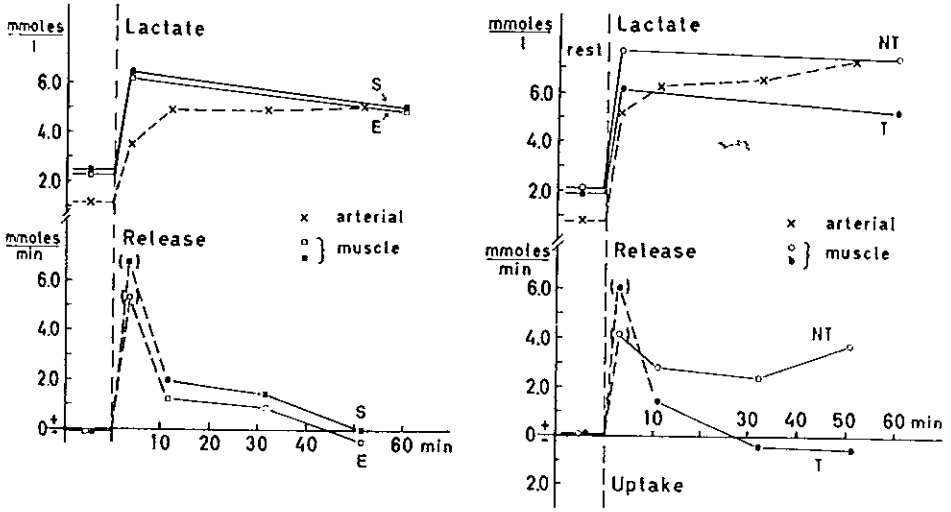


Fig. 7. Mean values for muscle and arterial lactate concentration as well as uptake or release (a–v difference for lactate × leg blood flow) for the untrained and trained legs during the two-legged prolonged submaximal exercise. Comparisons are made in the upper panel between sprint- and endurance-trained legs of the same individuals. In the lower panel the same comparisons are made but for trained (sprint or endurance) as compared to the untrained legs. Observe that both panels give mean values for 4 subjects who belonged to training group A (upper panel) and B or C (lower panel). The differences between untrained and trained legs in muscle lactate concentration and release of lactate are significant (lower panel).

In analyzing the lactate response in the two-legged exercise, only minor differences were found between the endurance- and sprint-trained legs (Fig. 7). There was a tendency for a higher muscle lactate concentration in the sprint-trained leg, and at the end of the one-hour exercise, this leg also released a larger amount of lactate. This evaluation is also based on comparisons between legs performing the same work load.

With the same approach, those subjects who had one trained and one untrained leg exhibited definite differences between the legs (Fig. 7). The non-trained leg not only had the highest lactate concentration but also a significantly greater release of lactate throughout the exercise period. In the trained leg, however, a small uptake of lactate was noticed during latter parts of the exercise.

Consistent with these differences in lactate response, glycogen depletion was also different in the trained versus the untrained leg. Mean glycogen content fell from 101 to 26 mmol/kg in the untrained leg and from 127 to 47 and 116 to 48 mmol/kg for the endurance- and sprint-trained legs, respectively. The difference between trained and non-trained legs was significant. The leg glucose uptake during the hour of exercise was 11.9 (NT), 12.7 (S), and 13.2 (E) g, respectively (NT *vs.* S *vs.* $Ep > 0.05$). ST-fibres had a less marked PAS stain after the exercise than the FT-fibres, with the most pronounced loss of stain taking place in the ST-fibres of the untrained leg. Any differences between training procedures could not be established.

Discussion

any of the results of this study such as lowering of submaximal heart rate and blood lac-
e, increase in $\dot{V}_{O_2}$ max as well as the changes seen in area and oxidative potential of
iscle fibres, are well-known effects of physical conditioning. The major new findings
: related to the observation of the very close interplay between the local and the central
ining response.

uscle adaptation

ercise results in a selective loss of glycogen from muscle fibres, which varies with the inten-
y of the exercise, indicating a special pattern for motor unit recruitment (Gollnick, Piehl,
d Saltin 1974). Generally speaking, submaximal efforts ($\approx 80\ \dot{V}_{O_2}$ max) may mainly involve
T-fibres and more intense work both ST- and FT-fibres. The finding of a significant hyper-
ophy of ST-fibres with the endurance training and of both FT- and ST-fibres with the
rint-training is then a good confirmation of such a selective engagement taking place in
ercise (Gollnick *et al.* 1972, 1973, Edström and Ekblom 1972).

In the present study the oxidative potential of the fibres was enhanced, but based on the
ain for myofibrillar ATPase (Alkaline preincubation pH 10.3), no change in fibre composi-
on occurred with any form of training. In those studies of men where a change in fibre
pe has been found to occur with training, the authors have used an oxidative stain as a
ase for the fibre classification (Morgan *et al.* 1971).

Little is known about why increased physical activity enhances the oxidative enzyme activi-
es of skeletal muscles. Moreover, the role of this increase is not well understood. It is pos-
ible to regard these changes as important either for the tissue's utilization of oxygen during
xercise or for inducing a glycogen saving effect. There is at best only a weak relationship
etween the enhancement in $\dot{V}_{O_2}$ max and skeletal muscle SDH activity (or any other oxida-
ve enzyme) (Gollnick *et al.* 1972, 1973, Holloszy 1975). However, a suggestion that these
nzyme changes play a role in the extraction of oxygen comes from the fact that femoral
ein oxygen content was higher during exercise in the untrained as compared to the trained
g (Fig. 6 D).

Submaximal heart rate response

One of the most challenging findings of the present study is the lowering of the heart rate
t submaximal exercise which was related to the local adaptation; i.e. when exercising with
he trained leg a significant drop in heart rate was induced but this was not the case with the
non-trained leg. In the study by Clausen *et al.* (1973) where one group trained only their
rms and another group only their legs, they found a definite reduction in submaxima
eart rate response after training not only when exercising with the trained, but also with the
non-trained muscles. They suggested that different mechanisms were at play causing the
drop in heart rate in the two situations.

When exercising with the trained muscles, they had indications of a lowered sympathetic
discharge, whereas they explained the drop in heart rate with non-trained muscles after
training as a simple parallel downward displacement of the heart rate–oxygen uptake rela-

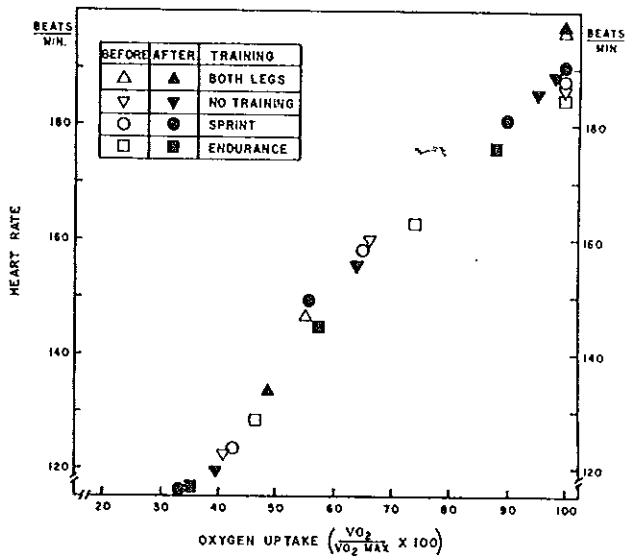


Fig. 8. Heart rate response during one- and two-legged exercise before and after training in relation to the relative work load of the exercising limb (s) work capacity.

tionship. In our study, heart rate corresponded to the improvement in each leg's work capacity in a rather quantitative manner. Thus, relating the heart rates during exercise (one and two-legged; before and after training) to the relative work intensity gives a linear regression with very little scatter (Fig. 8).

In animals and perhaps in man too, cardioacceleration can be elicited both by cortical influence on the vasomotor center and by an afferent inflow of impulses from exercising muscles (Krogh and Lindhard 1913, Hollander and Bouman 1975). Considering the marked local response one could speculate whether the change in submaximal heart rate is related to a less active peripheral drive. However, the same argument can be used in favor of a less marked cortical activation. With the rather selective hypertrophy of muscle fibres observed with the training, the number of centrally activated motor units that have to be recruited to perform a given submaximal work load may be less. Thus, from the present data, no firm conclusion can be drawn on this particular point. This should not distract, however, from the fact 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. Further support for such a statement is found when comparing the results of the subjects in group A with those in groups B and C. The subjects in group A had about twice as much "cardiac" training as any of the subjects in groups B and C. In spite of this especially the increase in $\dot{V}_{O_2}$ max but also submaximal heart rate response were very similar to the E-leg of groups A and C subjects and in the S-leg of groups A and B subjects.

Peripheral vs. central factors limiting $\dot{V}_{O_2}$ max

Both Gleser (1973) and Davies and Sargeant (1974 and 1975) came to the conclusion that the periphery limited maximal oxygen uptake in one-legged exercise. They based this conclusion on somewhat different grounds. Davies and Sargeant (1974) were unable to demonstrate an

...ement of maximal oxygen uptake in one-legged exercise breathing a high oxygen ...ixture (45% O_2 in N_2), whereas a 10% increase in $\dot{V}_{O_2}$ max was seen in the two-legged ...ercise. Their results are surprising, but we cannot debate them as we did not include any ...nilar measurements.

Gleser (1973) argues that neither before nor after the one-legged training did cardiac out... it reach maximum in one-legged as compared to two-legged exercise. However, the differ...ce between the one- and two-legged maximal cardiac output after training was very small. ...fact, a couple of the subjects had the same cardiac output or higher in the one-legged ...aximal work. Moreover, after the training the stroke volume was the highest during the ...e-legged exercise. Thus, from the data provided by Gleser, it appears more difficult to ...mpletely exclude the central circulation from being the limiting factor also in one-legged ...ercise. A puzzling observation of Gleser's was that the two-legged $\dot{V}_{O_2}$ max was not ...fected by the one-legged training. This was also the case in subjects who showed some ...provements in $\dot{V}_{O_2}$ max for the untrained leg.

In the present study, the non-trained leg had a minor increase in $\dot{V}_{O_2}$ max, especially ...nong those who performed the endurance training. In addition, all subjects in our study ...monstrated an improvement in the two-legged $\dot{V}_{O_2}$ max, producing a very small change ...the ratio between the one- and two-legged $\dot{V}_{O_2}$ max before and after training. The conclu... on from this must then be that the one-legged training caused some improvement of the ...ntral circulation which could be transferred to non-trained muscles. This is in agreement ...ith the findings of Clausen *et al.* (1973), who in leg training did see an enhancement of the ...ork capacity and oxygen uptake of the non-trained arms. The improvement after training ...as related to the capacity of the central circulation to further increase systemic arterial ...ressure, thereby increasing perfusion pressure and blood flow to the arms. Whether their ...ndings should be taken as proof that cardiac factors are also critical in exercise that utilizes ...small percent of the total muscle mass can hardly be settled from data available today. ...he one-legged exercise may, however, be a good model for further studies on this particular ...oint.

...uscle blood flow

...everal studies with the Xenon method have indicated that the muscle blood flow at a given ...ubmaximal load is reduced with training (see Clausen 1975). The results of the present study ...lo not appear to confirm this concept. Our subjects performed two-legged bicycle exercise ...vith each leg having a different work capacity, and we found total blood flow to the lower ...art of the legs to be identical. Whether a big enough difference in flow distribution within ...he leg can explain the difference between our result and those with the Xenon method cannot ...e stated, but it appears to be a remote possibility.

It may be argued that the fact that the subjects did not equally divide the work output be...ween the legs weakens our findings. However, it was the sprint-trained leg which performed "more work" and the $\dot{V}_{O_2}$ max of this leg was not as elevated as that of the endurance-...rained leg. Thus, if there was a way to relate the blood flow of the leg to each leg's relative ...oxygen uptake, it would not come out as in the studies with the Xenon technique. Although ...lood flow was the same to the two legs, this was not always the case for the oxygen uptake.

A-V O_2 difference over the exercising leg was highest for the trained leg for several subjects. This could only partly be attributed to the observation of some asymmetry between the legs performing the two-legged exercise, but as indicated above, it was also related to the training status (SDH activity) of the leg.

Fuel utilization

A "glycogen saving" effect during exercise has been demonstrated to occur with physical training (Karlsson, Nordesjö and Saltin 1974). The design of this study was such that a more detailed analysis of this particular phenomenon was possible. We did find a less marked glycogen breakdown in the trained as compared to the untrained leg during the submaximal two-legged exercise, and we also demonstrated that this was not compensated for by a larger uptake of glucose from the blood stream. In fact, for none of the legs the extramuscular supply of glucose could account for more than 10% of the carbohydrate metabolism (*cf.* Wahren *et al.* 1971). The RQ measurements over the exercising legs did not demonstrate any significant difference between the legs. If anything, the lowest RQ was observed over the sprint-trained leg also when a comparison could be made within the same individual at the same work load. What adds to the confusion are the dissimilarities in the R-measurements over the lungs which are stable throughout the one-hour work period, and the RQ values over the exercising legs being significantly reduced. At present, very little can be said to clarify these observations.

Lactate production

With regard to the lactate response, it is of note that blood concentrations were specifically reduced after the various training regimens that these closely related to improvements in work capacity. Furthermore, sprint-training which was supposed to tax the anaerobic capacity of the subject to a large extent resulted in an increased peak blood lactate concentration. It is true that blood lactate measurements may not adequately reflect production, but under the present circumstances it may be an indication of an enlarged anaerobic capacity of the S-leg. An example of how little information about lactate production may come from muscle and blood lactate measurements can be found in the results of Fig. 7.

When the E and S-legs and the NT and T-legs are compared, only small changes in muscle and blood lactate are seen to occur during the one hour of exercise. That there must be a continuous and rather large lactate production, especially from the NT-leg, appears clear from the marked release of lactate found throughout the exercise. As in fact muscle and arterial lactate concentrations stayed rather constant during the two-legged submaximal work load, the release of lactate from the exercising muscle must then be balanced by a similar magnitude of removal. However, neither the heart nor the liver has been reported to take up as large quantities of lactate as being released (see Rowell 1971, Keul *et al.* 1971, Lassers *et al.* 1971). This points to the importance of tissues like inactive skeletal muscle as being of significance for the lactate to be removed from the blood. Moreover, it should not be overlooked that a net uptake of lactate by exercising muscle may occur (*cf.* Stainsby and Welch 1966, Jorfeldt 1970). In fact this was the case during the later phase of the two-legged exercise for the most trained legs.

In conclusion, it may be said that this study has demonstrated that a training regimen produces a very specific pattern for adaptation, which is partly local in nature. Of special interest is the finding that this local adaptation of the trained skeletal muscles appears essential for being able to elicit the more general adaptation of the central circulation also taking place with the training. This focuses attention on peripheral factors as being at least as essential for the cardiovascular performance during exercise as any central factors. A fact emphasized by Müller already in 1942.

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