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Skiing across the Greenland icecap: divergent effects on limb muscle adaptations and substrate oxidation

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Summary

This study investigates the adaptive response of the lower limb muscles and substrate oxidation during submaximal arm or leg exercise after a crossing of the Greenland icecap on cross-country skies. Before and after the 42-day expedition, four male subjects performed cycle ergometer and arm-cranking exercise on two separate days. On each occasion, the subjects exercised at two submaximal loads (arm exercise, 45 W and 100 W; leg exercise, 100 W and 200 W). In addition, peak oxygen uptake ($\dot{V}_{O_2max}$) was determined for both leg and arm exercise. Before and after the crossing, a muscle biopsy was obtained from the vastus lateralis and the triceps brachii muscles prior to exercise (N=3). After the crossing, body mass decreased by 5.7±0.5 kg (in four of four subjects), whereas $\dot{V}_{O_2max}$ was unchanged in the arm (3.1±0.2 l min^{-1}) and leg (4.0±0.1 l min^{-1}). Before the crossing, respiratory exchange ratio (RER) values were 0.84±0.02 and 0.96±0.02 during submaximal arm exercise and 0.82±0.02 and 0.91±0.01 during submaximal leg exercise at the low and high workloads, respectively. After the crossing, RER was lower (in three of four subjects) during arm exercise (0.74±0.02 and 0.81±0.01) but was higher (in three of four subjects) during leg exercise (0.92±0.02 and 0.96±0.01) at the low and high workloads, respectively. Citrate synthase and β-hydroxy-acyl-CoA-dehydrogenase activity was decreased by approximately 29% in vastus lateralis muscle and was unchanged in triceps brachii muscle. Fat oxidation during submaximal arm exercise was enhanced without a concomitant increase in the oxidative capacity of the triceps brachii muscle after the crossing. This contrasted with decreased fat oxidation during leg exercise, which occurred parallel to a decreased oxidative capacity in vastus lateralis muscle. Although the number of subjects is limited, these results imply that the adaptation pattern after long-term, prolonged, low-intensity, whole body exercise may vary dramatically among muscles.

Key words: triceps brachii, vastus lateralis, enzyme activity, fat mass, exercise, muscle, oxygen uptake.

Introduction

In skeletal muscle, regular endurance exercise leads to increased oxidative capacity, capillarisation and glycogen storage, which improves the ability to sustain prolonged exercise (Saltin and Gollnick, 1983; Holloszy and Coyle, 1984). However, during whole body exercise, as in cross-country skiing, both upper and lower body muscles are activated. Upper and lower body muscles demonstrate marked differences in both fibre type and blood flow distribution (Secher et al., 1977). However, there is only sparse information on the adaptation pattern in these different muscle groups after endurance training (Schantz et al., 1983; Turner et al., 1997). One study found that eight weeks intense separate leg and arm endurance training enhanced peak oxygen uptake ($\dot{V}_{O_2max}$) similarly, but, at the tissue level, muscle volume was enhanced only in deltoideus muscle, whereas in vastus lateralis mitochondrial fraction was increased (Turner et al., 1997). Another group studied eight weeks of prolonged, low-intensity, cross-country skiing and found a significant increase in oxidative capacity and capillarisation in triceps brachii muscle but no effect of training on oxidative capacity and capillarisation in vastus lateralis muscle (Schantz et al., 1983). Therefore, these studies suggest that upper and lower body limb muscles may not respond uniformly to endurance training.

We have consistently shown that the diet composition during endurance training markedly influences both substrate utilisation during exercise and skeletal muscle adaptations observed after training (Helge and Kiens, 1997; Helge et al., 2001). During arm or leg exercise performed at the same relative load of $\dot{V}_{O_2max}$, there is a higher muscle glycogen utilisation and a higher lactate output during arm compared with leg exercise (Ahlborg and Jensen-Urstad, 1991).

However, it is not clear how prolonged, whole body, low-intensity training will affect substrate oxidation during submaximal arm or leg exercise. Furthermore, as diet was not controlled in the study by Turner et al. (1997) and was only partially controlled (high carbohydrate in weeks 2 and 3) in the study by Schantz et al. (1983), this may have influenced the adaptive response in leg and arm muscle after the endurance training period.

Crossing the Greenland icecap on cross-country skies pulling heavy sledges demands an extreme load on the human body, where both legs and upper body are engaged. Moreover, although the diet contained a dominance of carbohydrate (CHO), the reliance on lipid oxidation will be very high. The study of people performing the crossing offers a unique opportunity to test the hypothesis that the two factors, moderate but extensive daily exercise combined with a high total fat combustion, elicit an extreme adaptation of limb skeletal muscles, which in turn results in an elevated contribution of fat for energy during exercise. The aim of this study was to investigate the adaptive response in limb muscle and the substrate oxidation during submaximal arm or leg exercise after a cross-country skiing expedition over the Greenland icecap.

Materials and methods

Subjects

Four moderately trained male subjects (age 40±2 years, height 176±4 cm, mass 79±4 kg and $\dot{V}_{O_2max}$ 4.0±0.1 l O_2 min^{-1}) participated in the study. Subjects were fully informed of the nature and the possible risks associated with the experimental part of the study before they volunteered to participate. One subject had an artificial titanium heart valve and was therefore on lifelong anticoagulant treatment (7.5 mg day^{-1} Marevan, Warfarin). This subject participated in all procedures except for the muscle biopsies. The planning, handling and financial burden of the tour across the icecap was totally organised and controlled by the subjects. The experimental procedure achieved ethical approval and all subjects volunteered to participate and provided ethical consent.

The subjects commenced the crossing from Kangerlussuag on the west coast of Greenland on 2 May 2001 and finished in Isortoq on the east coast on 12 June 2001. The subjects travelled for a total of 42 days. However, 5 days were spent resting in the tents due to harsh weather conditions. The total distance covered was approximately 650 km, and an altitude of 2500 m above sea level was reached. The peak altitude was reached after approximately 430 km and the skiing was, until this point, performed with 'skins' under the skis. In this situation, the friction from the direction of the hairs (mohair or synthetic) on the skin mounted under the ski prevents the ski from sliding backwards. Furthermore, the forward motion of the ski is easier if the ski is slightly lifted during the forward motion. Each subject pulled a sledge weighing initially 120 kg. During the passage, the day temperature ranged between –30°C to 0°C and some wind was experienced. On average, the subjects spent approximately 8–9 h day^{-1} on cross-country skies pulling the sledges. The subjects took turns leading the other members of the expedition, making snow tracks, with a new person taking the lead every 15 min. After each member had taken a turn at the front (approximately 60 min), breaks were taken. Due to the cold conditions, most breaks lasted less than 10 min and only the lunch break was slightly longer (approximately 15–25 min). The food consumed during the passage was pre-packed and carried by the subjects. The diet was a standard high CHO diet consisting of a breakfast, lunch and evening meal and a variety of snacks for consumption during the day. The nutrient composition expressed as a percentage of consumed energy was 9±1% protein, 31±1% fat and 60±1% CHO. During the first part of the passage expedition, the subjects were not able to consume their calculated daily ration. However, during the later part, food intake was increased and subjects were able to consume their full daily ration together with the food that was not consumed during the first part. Based on individual descriptions of mean daily dietary intake, it can be calculated that the mean daily energy consumption was 18.6±1.2 MJ. The consumed amount of CHO provides approximately 8.5±0.6 g CHO kg body $mass^{-1}$.

Experimental protocol

On two consecutive days prior to departure and again five days after the expedition, the subjects came to the laboratory, having fasted for 6–7 h, to perform maximal and submaximal upper and lower limb exercise tests. The subjects were asked to refrain from vigorous physical activity on the day preceding the first testing session. After an initial rest period, a needle biopsy was obtained with suction from the vastus lateralis muscle and from the triceps brachii (lateral head). After this procedure, a catheter was inserted into an antecubital vein for collection of venous blood during the exercise tests. Throughout the exercise testing, the catheter was intermittently flushed with sterile sodium chloride to maintain patency. Prior to exercise, body mass (kg) and skin fold measurements (mm) were performed (Durnin and Womersley, 1974). After a 15 min rest period, a venous blood sample was obtained and exercise initiated. On the first day, subjects performed lower limb bicycle ergometer exercise (Monark 839E; Monark Exercise AB, Vansbro, Sweden) consisting of 10 min at 100 W followed by 10 min at 200 W. On the second day, subjects completed upper limb modified arm cranking exercise involving 10 min at both 45 W and 100 W. The arm ergometer (Monark 884E; Monark Exercise AB) was mounted on an aluminium frame and adjusted to the shoulder height of the subjects. This exercise model requires utilisation of the muscles of the arms and the upper body (Secher et al., 1977). On both days, after the submaximal exercise bouts, a standard $\dot{V}_{O_2max}$ test to exhaustion was performed, where the workload was progressively increased by 40 W min^{-1} and 20 W min^{-1} in leg and arm cycling, respectively. Blood samples were collected during the final 2.5 min of each of the submaximal exercise loads and immediately after termination of exercise. In addition, a blood sample was collected 3 min after termination

of the exercise test. Pulmonary oxygen uptake ($\dot{V}_{O_2}$) and carbon dioxide excretions ($\dot{V}_{CO_2}$) at rest and during exercise were measured by an automated on-line system (CPX; Medical Graphics, Spiropharma, Denmark).

Analytical procedures

Blood was transferred into tubes containing 0.3 mol l^{-1} EDTA (10 µl ml^{-1} blood) and immediately centrifuged at 4°C for 10 min at 23,000 ***g***. A small fraction of the blood was transferred into tubes containing EGTA, and this was later used for the insulin and catecholamine determinations. The plasma was stored at –80°C until analysis. Plasma glucose and lactate were analysed on an automatic analyser (Cobas Fara, Roche, Basel, Switzerland). Plasma glycerol was analysed as described by Wieland (1974), and plasma fatty acid (FA) concentration was measured using a Wako NEFA-C test kit (Wako Chemical, Neuss, Germany); both were determined on an automated analyser (Cobas Fara, Roche, Basel, Switzerland). Insulin in venous plasma was determined using a radioimmunoassay kit (Insulin RIA100; Pharmacia, Stockholm, Sweden). Catecholamines in venous plasma were determined by a radioenzymatic procedure (Christensen et al., 1980). Haemoglobin was determined on a HemoCue (HemoCue AB, Ängelholm, Sweden).

The muscle tissue was frozen in liquid nitrogen within 10–15 s of sampling. Before freezing, a section of the samples was cut off, mounted in embedding medium and frozen in isopentane, cooled to its freezing point in liquid nitrogen. Both parts of the biopsy were stored at –80°C until further analysis. Before biochemical analysis, muscle biopsy samples were freeze-dried and dissected free of connective tissue, visible fat and blood using a stereomicroscope. Myosin heavy chain composition was analysed as described by Andersen and Aagaard (2000). Muscle capillary density was analysed, visualised and quantified as described by Qu et al. (1997). In the serial transverse muscle sections, fibre types were stained for myofibrillar ATPase as described by Brooke and Kaiser (1970). The fibre type determined from the myosin heavy chain (MHC) composition was in agreement with the fibre type distribution quantified by traditional histochemistry both before and after the expedition (histochemical fibre type data are not included).

The maximal activity of the enzymes β-hydroxy-acyl-CoA-dehydrogenase (HAD), citrate synthase (CS), phospho-fructo-kinase (PFK) and lactate dehydrogenase (LDH) were determined fluorometrically according to Lowry and Passonneau (1972). Hormone-sensitive lipase activity (HSL) was assayed as described by Langfort et al. (1998). For the determination of LDH isozymes, identified as LDH_1, LDH_2, LDH_3, LDH_4 and LDH_5, muscle homogenates were prepared by centrifugation at 190 000 ***g*** for 90 min at 4°C, and LDH activity was measured in the supernatant (Brooks et al., 1999). After protein content determination with a bovine serum albumin (BSA) standard (DC protein assay; BioRad, Hercules, CA, USA), 1.5 µg of protein was loaded onto 1% agarose gels and separated for 45 min at 90 V using a Bio-Rad Sub-Cell system. LDH isozymes were revealed colorimetrically with a commercial kit (procedure no. 705-EP; Sigma Diagnostics, St Louis, MO, USA). Gels were fixed in 5% acetic acid and scanned. Band densities were quantified by software analysis with SigmaGel (SPSS Science Software GmbH, Munchen, Germany).

Calculations

Body density was determined from the skin fold measurements, and, subsequently, body fat (%) was calculated from the body density according to the method of Siri (1961). The LDH isozyme results were expressed as a proportion of the H or M subunits (H-LDH and M-LDH, respectively). H-LDH and M-LDH were estimated as follows (Linossier et al., 1997):

$$\text{H-LDH} = LDH_1 + 0.75\times LDH_2 + 0.5\times LDH_3 + 0.25\times LDH_4,$$

$$\text{M-LDH} = LDH_5 + 0.75\times LDH_4 + 0.5\times LDH_3 + 0.25\times LDH_2.$$

The HOMA insulin resistance index, described originally by Matthews et al. (1985) and modified recently by Jenkins et al. (2000), was calculated according to the latter. In brief, fasting plasma insulin and fasting plasma glucose values were used to calculate an index of insulin resistance (HOMA-R_{mod}; Jenkins et al., 2000). There is a direct correlation between the insulin resistance index and insulin resistance as measured by the euglycemic clamp technique (Jenkins et al., 2000).

Statistics

Results are given as means ± S.E.M., if not otherwise stated. As the number of subjects was so small, formal statistics are not applied to discriminate changes due to the intervention. However, to underline the major changes, we have added the general direction of change after the intervention (for example, ‘three of three subjects’ implies the same directional change in all three subjects). In addition, Pearson correlation was applied to the dataset (SigmaStat 2.0, SPSS Science Software, Erkrath, Germany, Germany).

Results

The body mass, body mass index, lean body mass and content of body fat were lower (four of four subjects) after the passage (Table 1). On average, the subjects had a mean mass loss of 5.7±0.5 kg, of which 78±7% was fat and the remainder lean body mass. The $\dot{V}_{O_2max}$ was unchanged for arm exercise (Table 1) but was lower in three of four subjects for leg exercise. There was an approximately 100% higher content of MHC IIA and MHC IIX fibres in triceps brachii than in vastus lateralis. However, muscle fibre type distribution given as a percentage of MHC composition was not changed in either vastus lateralis or triceps brachii after the passage (Table 1). The capillarisation expressed as capillaries per type I or type II fibre was slightly increased (three of three subjects) in the triceps brachii after the passage but remained unchanged in the vastus lateralis (Fig. 1A). After the passage, the type II and

Table 1. *Anthropometric, maximal oxygen uptake and fibre type data before and after crossing the Greenland icecap on cross-country skis*

			Before	After	
BMI (kg m^{-2})			25.6±0.6	23.7±0.5	*(4 of 4)
Mass (kg)			79.2±3.9	73.6±3.4	*(4 of 4)
Fat (%)			22.4±1.4	18.2±1.1	*(4 of 4)
LBM (kg)			61.3±2.0	60.3±2.0	*(4 of 4)
$\dot{V}_{O_2max}$ (l min^{-1})		Arm	3.1±0.2	3.0±0.1	
		Leg	4.0±0.2	3.6±0.1	*(3 of 4)
Blood haemoglobin (mmol l^{-1})			9.3±0.3	9.4±0.4	
Fibre type (%)	Arm	MHC I	27.6±3.9	23.7±5.3	
		MHC IIA	50.9±4.5	53.8±4.3	
		MHC IIX	21.5±7.3	22.5±9.0	
Fibre type (%)	Leg	MHC I	63.3±2.9	62.9±3.3	
		MHC IIA	25.9±2.9	27.0±8.7	
		MHC IIX	10.7±3.2	10.0±5.6	

Values are means ± S.E.M.
Abbreviations: BMI, body mass index; LBM, lean body mass; MHC: myosin heavy chain; $\dot{V}_{O_2max}$, peak oxygen uptake.
*Number of subjects in which the change is observed, compared with the pre-test, followed by the total number of subjects.

type I fibre area in the triceps was increased (three of three subjects), whereas no change in mean fibre type area was found in the vastus lateralis (Fig. 1B). The capillarisation expressed per fibre area remained unchanged in triceps brachii (537±87 capillaries mm^{-2}) and vastus lateralis (692±43 capillaries mm^{-2}). In the triceps brachii, the lack of change in capillaries per fibre area is a reflection of the observed increase in both number of capillaries and fibre area.

Muscle citrate synthase activity was decreased (three of three subjects) in vastus lateralis but remained unchanged in triceps brachii after the passage (Table 2). The β-hydroxy-acyl-CoA-dehydrogenase activity was lower in two of three subjects in vastus lateralis after the passage, whereas no change was apparent in triceps brachii after the passage (Table 2). Hormone-sensitive lipase activity was not changed in either vastus lateralis or triceps brachii after the passage (Table 2). Phospho-fructo-kinase activity was decreased (three of three subjects) in both muscles after the passage (Table 2). The lactate dehydrogenase activity was not altered after the passage in either triceps brachii or vastus lateralis (Table 2). By contrast, the expression of muscle-type-specific LDH (M-LDH) was decreased (three of three subjects) in vastus lateralis after passage, whereas it remained unchanged in triceps brachii (Table 2). The M-LDH expression was approximately 80% higher in triceps brachii than in vastus lateralis (Table 2). When all sample points are included, i.e. arm and leg muscle, before and after the passage, a very strong correlation is shown between LDH activity and % M-LDH expression ($r_{Pearson}$=0.84, P<0.001, N=3).

During the initial exercise test, the $\dot{V}_{O_2}$ during arm exercise was 1.1±0.1 l min^{-1} and 2.4±0.1 l min^{-1} at 45 W and 100 W, respectively, and during leg exercise was 1.6±0.1 l min^{-1} and

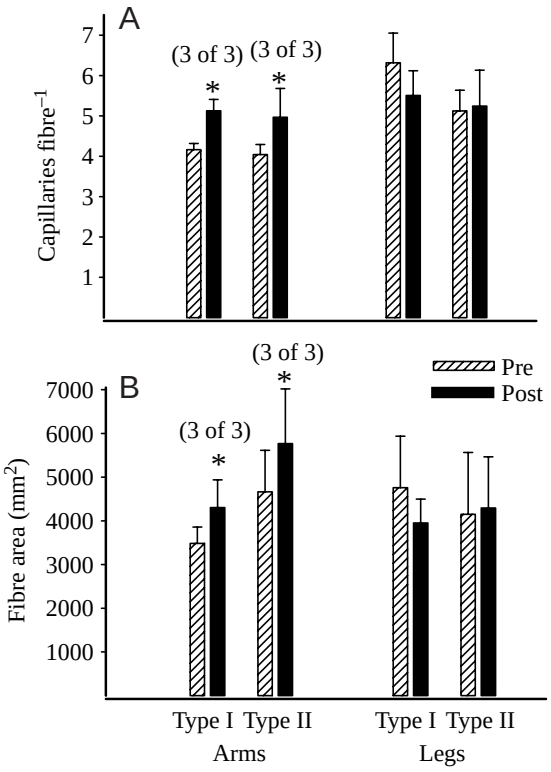

Fig. 1. Capillarisation (A) and fibre area (B) in triceps brachii and vastus lateralis before and after crossing the Greenland icecap on cross-country skies. The asterisks represent the number of subjects in which the change is observed, compared with the pre-test, followed by the total number of subjects.

Table 2. *Muscle enzyme activity in vastus lateralis and triceps brachii before and after crossing the Greenland icecap on cross-country skis*

	Arm			Leg		
	Before	After		Before	After	
CS activity ($\mu mol\,g^{-1}\,min^{-1}$)	25±5	26±2		39±2	28±5	*(3 of 3)
HAD activity ($\mu mol\,g^{-1}\,min^{-1}$)	17±3	18±1		31±3	22±6	*(2 of 3)
PFK activity ($\mu mol\,g^{-1}\,min^{-1}$)	190±31	136±56	*(3 of 3)	164±8	95±40	*(3 of 3)
HSL activity ($\mu mol\,g^{-1}\,min^{-1}$)	1.03±0.37	0.39±0.08		0.32±0.06	0.32±0.07	
LDH activity ($\mu mol\,g^{-1}\,min^{-1}$)	860±126	680±98		470±90	370±118	
H-LDH (%)	15±4	22±3		47±9	63±2	*(3 of 3)
M-LDH (%)	85±4	78±3		53±9	37±2	*(3 of 3)

Abbreviations: CS, citrate synthase; HAD, β-hydroxy-acyl-CoA-dehydrogenase; PFK, phospho-fructo-kinase; HSL, hormone-sensitive lipase; LDH, lactate dehydrogenase; H-LDH, heart-type-specific LDH; M-LDH, muscle-type-specific LDH.

Values are means ± S.E.M. N=3.

*Number of subjects in which the change is observed, compared with the pre-test, followed by the total number of subjects.

2.7±0.1 l min^{-1} at 100 W and 200 W, respectively. When the subjects returned and performed the submaximal exercise at the same absolute workload, the $\dot{V}_{O_2}$ was similar to that measured in the initial test. The relative exercise intensity ($\%\dot{V}_{O_2max}$) remained unchanged during the pre- and post-tests (35±2% and 43±3% at the lower submaximal work loads in arm and leg, respectively; 73±3% and 72±2% at the higher submaximal work loads in arm and leg, respectively). After the expedition, the respiratory exchange ratio (RER) was lower during arm exercise at both the lower (four of four subjects) and the higher (three of four subjects) submaximal workload compared with the initial test (Fig. 2A). By contrast, the RER was higher during leg exercise at the lower (four of four subjects) and the higher (three of four subjects) submaximal workload (Fig. 2B). During the initial test, the expiratory ventilation ($\dot{V}_E$) during arm exercise was 29±2 l min^{-1} and 66±6 l min^{-1} at 45 W and 100 W, respectively, and during leg exercise was 43±3 l min^{-1} and 72±4 l min^{-1} at 100 W and 200 W, respectively. When the subjects returned and performed the submaximal exercise at the same absolute workload, the $\dot{V}_E$ was similar to that observed in the initial test. The ratio between $\dot{V}_E$ and $\dot{V}_{O_2}$ ($\dot{V}_E/\dot{V}_{O_2}$) during arm exercise was similar before and after crossing: 27±2 l air l $oxygen^{-1}$ and 32±4 l air l $oxygen^{-1}$ at 45 W and 100 W, respectively. By contrast, the $\dot{V}_E/\dot{V}_{O_2}$ during leg exercise was increased (four of four subjects) from 22±2 l air l $oxygen^{-1}$ and 24±2 l air l $oxygen^{-1}$ before the crossing to 27±2 l air l $oxygen^{-1}$ and 27±1 l air l $oxygen^{-1}$ after the crossing at 100 W and 200 W, respectively.

Prior to departure, haemoglobin concentrations were 9.3±0.3 mmol l^{-1}, and, although an altitude of 2500 m was reached during the crossing, no increase in haemoglobin concentration was observed after returning (9.4±0.4 mmol l^{-1}). Prior to exercise, post-absorptive plasma glucose concentration was similar on the four experimental days (Fig. 4A). However, plasma insulin was slightly higher (three of four subjects) after the passage (Fig. 3A), as was a calculated HOMA insulin resistance index (three of three subjects; Fig. 3B). Plasma glucose concentration was unchanged across the different exercise intensities or in recovery (Fig. 4A). Plasma lactate concentration at rest was similar on the four experimental days (Fig. 4B). As expected, plasma lactate concentration increased (four of four subjects) when exercise intensity was increased (Fig. 4B). During arm

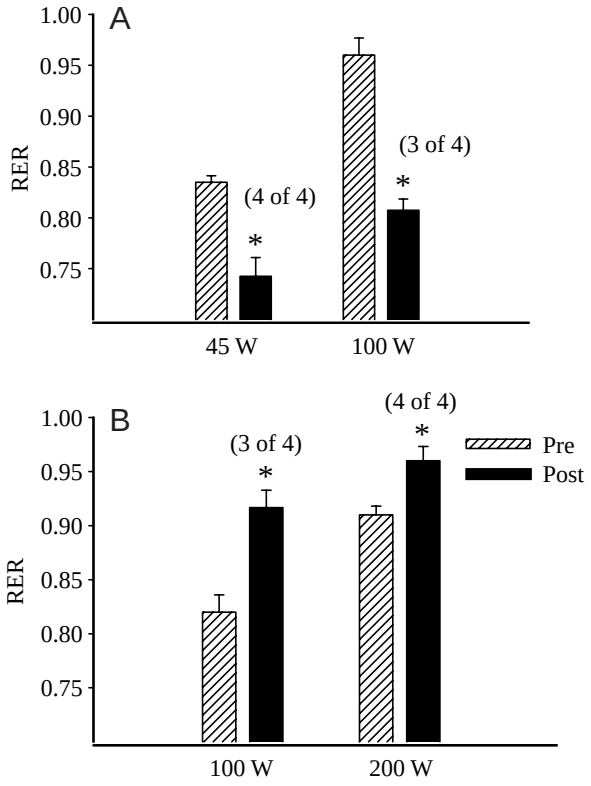

Fig. 2. Respiratory exchange ratio (RER) at two submaximal exercise loads during arm (A) or leg (B) ergometer exercise before and after crossing the Greenland icecap on cross-country skies. The asterisks represent the number of subjects in which the change is observed, compared with the pre-test, followed by the total number of subjects.

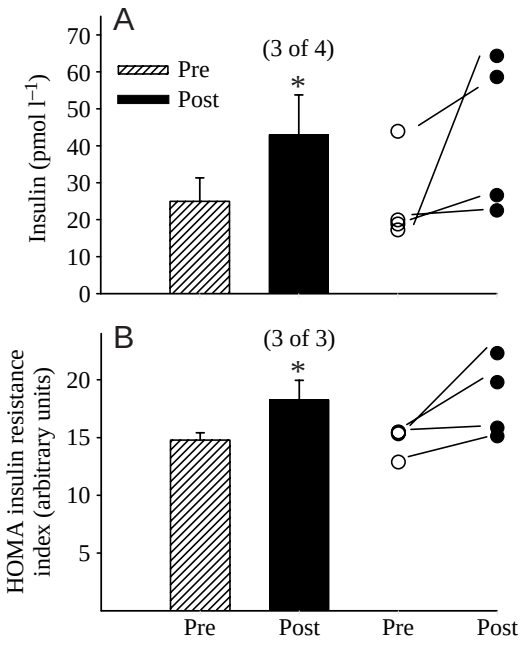

Fig. 3. Fasting insulin concentration (A) and calculated HOMA insulin resistance index (B) before and after crossing the Greenland icecap on cross-country skies. Individual values are represented by circles and mean values are represented by bars. The asterisks represent the number of subjects in which the change is observed, compared with the pre-test, followed by the total number of subjects.

exercise, both at submaximal and maximal workloads, plasma lactate concentration was slightly higher (four of four subjects) than when leg exercise was performed at comparable relative workloads (Fig. 4B). Prior to departure for Greenland, plasma fatty acid (FA) concentration at rest was similar on the two experimental days (Fig. 4C). Interestingly, plasma FA concentration at rest was markedly decreased (four of four subjects) on both experimental days when the subjects returned from Greenland. During submaximal exercise in the pre-testing, both during arm and leg exercise, plasma FA was lower (four of four subjects) as exercise intensity increased. By contrast, there was no effect of exercise intensity, in either arm or leg exercise, on the plasma FA after the passage (Fig. 4C). Prior to exercise, fasting glycerol concentration was similar on the four experimental days (Fig. 4D). In the two arm exercise tests, before and after passage, plasma glycerol concentration increased (four of four subjects) similarly as exercise intensity was increased. By contrast, plasma glycerol concentration was lower (four of four subjects) at the different exercise intensities after the passage when leg exercise was performed (Fig. 4D).

Prior to exercise, venous adrenaline and noradrenaline concentrations were similar on the two experimental days: 2.5±0.4 nmol l^{-1} adrenaline and 0.5±0.15 nmol l^{-1} noradrenaline. At the different exercise intensities at the pre-tests, both during arm and leg exercise, the venous adrenaline and noradrenaline concentrations increased (four of four subjects) similarly and to the same level (40±8 nmol l^{-1} and 8.6±2.9 nmol l^{-1} at max, respectively) as exercise intensity increased. After the passage, the venous adrenaline and noradrenaline concentrations increased (four of four subjects) as exercise intensity was increased and, compared with the pre-passage values, the values after passage were 25±3% lower overall.

Discussion

A major finding of this study is that the higher fat oxidation observed during submaximal arm exercise after prolonged, low-intensity, whole body training and consumption of a carbohydrate-rich diet was present despite only a minor increase in the capillarisation and no change in the oxidative capacity in triceps brachii. The very marked increase in fat oxidation during arm exercise, occurring despite a high carbohydrate intake, resembles the dramatic shift in fuel utilisation seen during migration in birds, and we suggest that our current understanding of the arm muscle adaptation pattern after prolonged, low-intensity, whole body training may need some reconsideration.

It is well known that, after a period of endurance training, substrate utilisation during exercise at a given absolute workload is altered towards a larger combustion of lipids at the expense of carbohydrates (Henriksson, 1977; Gollnick, 1985). This alteration in substrate utilisation is thought to occur due to increases in local muscle mitochondrial volume, capillarisation and oxidative enzyme activity, as well as in whole body oxygen uptake capacity (Holloszy and Coyle, 1984; Saltin and Gollnick, 1983). Furthermore, there is evidence that manipulation of dietary intake, primarily the carbohydrate-to-fat ratio, during adaptation to endurance training can also markedly alter substrate utilisation during submaximal exercise after training (Helge et al., 1996, 2001). By contrast, the shift towards a higher fat utilisation during submaximal arm exercise occurred despite a high carbohydrate diet in combination with no change in muscle oxidative enzyme activity and only a minor increase in capillarisation. Apparently, this adaptation is specific to the triceps brachii muscle, since the higher carbohydrate oxidation observed during submaximal leg exercise in the present study is consistent with the decreased oxidative enzyme activity in vastus lateralis and the effect of a high carbohydrate intake on substrate utilisation. The observation of a difference in the adaptation pattern between arm and leg muscles is consistent with the findings of Schantz et al. (1983) and Turner et al. (1997) after whole body training or training of both arms and legs, respectively. However, these studies did not report whether the induced adaptation influenced the limb substrate utilisation during exercise. In the present study, we investigated the triceps brachii and the vastus lateralis, as we considered both of these muscles to be of prime importance for cross-country skiing, particularly as this also included pulling a heavy sledge and using skins though the majority of the crossing. However, although we consider it unlikely, we cannot exclude the possibility that other upper and/or lower

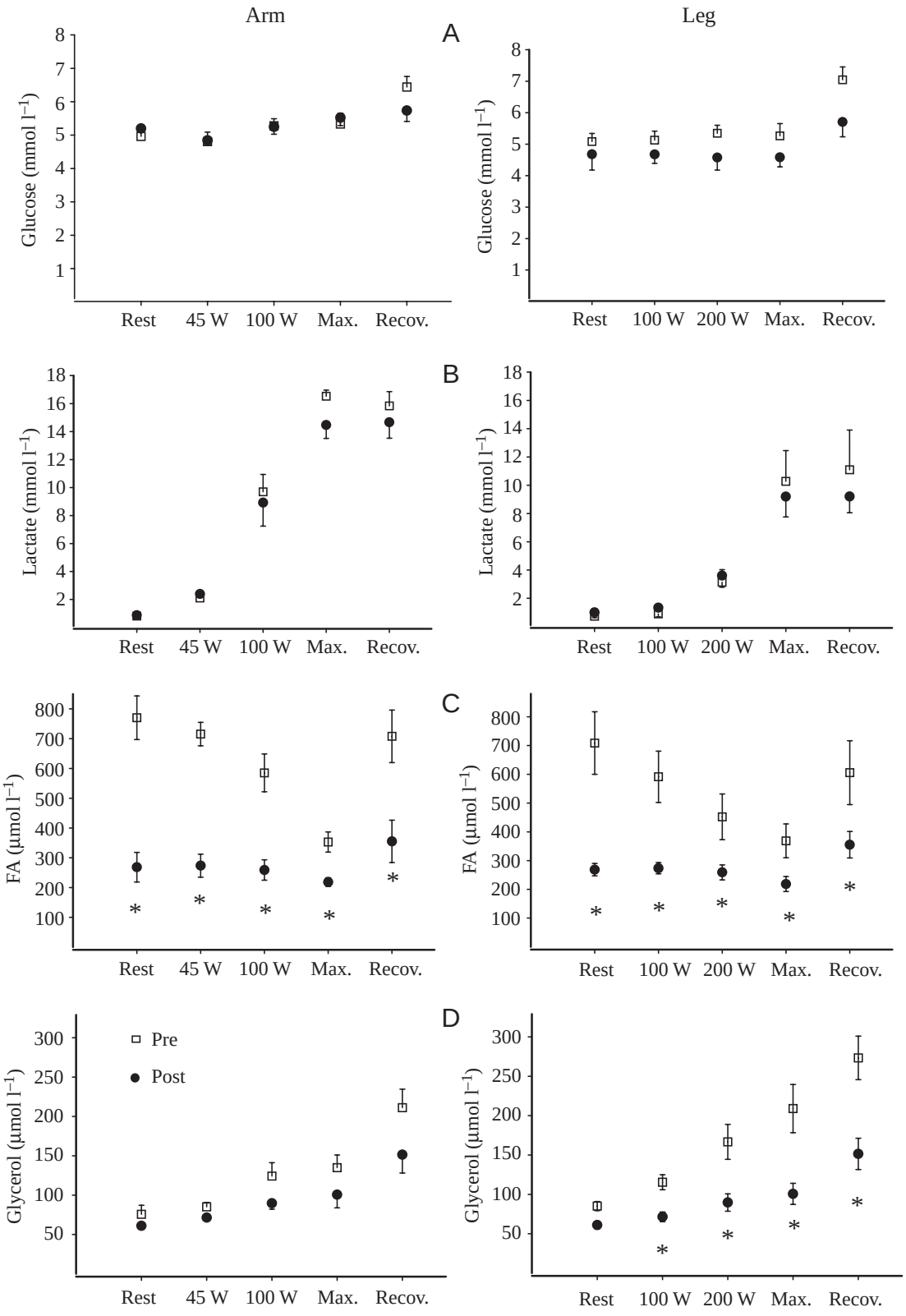

Fig. 4. Blood concentrations of glucose (A), lactate (B), fatty acid (FA) (C) and glycerol (D) at rest, during submaximal exercise (45 W and 100 W), after maximal exercise (max.) and after a 3 min recovery period (recov.) in arms and legs before and after crossing the Greenland icecap on cross-country skies. * In 4 of 4 subjects.

body muscles may exhibit an adaptation pattern that is different to that observed in triceps brachii and vastus lateralis.

In the present study, the crossing resulted in a loss of 5.7 kg of body mass, the majority of which was body fat, indicating the presence of an overall energy deficit (approximately 5 MJ day^{-1}) during the crossing. It is not clear how this energy deficit affected substrate utilisation during exercise and rest but, inevitably, it must have stimulated utilisation of body fat reserves. As reported by Stroud et al. (1997), two explorers crossed Antarctica, under very strenuous conditions, on cross-country skies pulling very heavy sledges and consuming a high fat diet (57% fat, 35% carbohydrate). Based on the doubly labelled water technique and calculated energy balance data, it can be estimated that their average daily energy deficit ranged between 3 MJ and 27 MJ. Over the 95 days, the two subjects lost approximately 25% of their body mass and, when the crossing was stopped on health grounds, there was almost no body fat present (Stroud et al., 1997). No attempt was made to quantify exercise substrate utilisation during or after the Antarctic crossing. However, it is clear that energy for the exercise performed must, to a large extent, have come from fat. In both subjects, muscle oxidative capacity in vastus lateralis and maximal whole body oxygen uptake was significantly declined after the crossing (Stroud et al., 1997), indicating that skeletal muscle under strenuous conditions and severe energy deficit has a large capacity to metabolise fat. Further support for this comes from a study of migrating Great Knots (*Calidris tenuirostris*), which were studied before and after a 5400 km migration and compared with a group of captured birds that were fasted for a fortnight (Battley et al., 2001). Using this model, it was demonstrated that migrating birds were able, to a large extent, to sustain flight primarily using fat as substrate and, furthermore, to keep lean tissue loss to a minimum (Battley et al., 2001). In the present study, the fibre type area of both type I and type II fibres tended to be increased in the triceps brachii after the crossing, which suggests that extra muscle protein was added despite the energy deficit. Overall, this implies that there is some similarity between the adaptation patterns in arm muscle after prolonged, low-intensity exercise and the adaptation pattern observed in migrating bird flight muscle.

Due to the design and conditions of the present study, we could not assess changes in muscle substrate stores immediately before or after the crossing. However, one possible explanation for the high fat oxidation during arm exercise is that intramuscular triacylglycerol stores become located, to a higher degree, around the mitochondria (Vock et al., 1996), which makes the FA, recruited *via* breakdown of triacylglycerol, more accessible for oxidation. Unfortunately, due to large inter-individual variations, our measurement of hormone-sensitive lipase does not allow us to expand on this. However, the finding of an unchanged venous glycerol response at the different arm exercise intensities, contrasting to the significantly decreased glycerol response during leg exercise, gives some support to utilisation of intramuscular triacylglycerol, particularly as venous plasma FA concentrations were very low throughout the different exercise intensities.

Interestingly, we observed an increased plasma insulin concentration at rest and an increased insulin resistance after the subjects had completed the expedition. This is a noteworthy observation considering the amount of physical activity that these subjects endured during the crossing. However, a large part of the carbohydrates consumed during the crossing were simple sugars (approximately 50–55%), which in several studies, both epidemiological (Liu and Manson, 2001) and interventional (Jeppesen et al., 1997; McLaughlin et al., 2000), have been linked to an adverse outcome in relation to insulin resistance. Furthermore, there was, in fact, a slight decrease in lean body mass after the passage, which is consistent with the observation of an increased insulin resistance. Thus, the finding of an increased insulin resistance index despite the arduous physical stress endured emphasizes the need to consider both diet intake and physical activity in order to combat insulin resistance.

In conclusion, a major finding in the present study is the marked increase in fat oxidation during submaximal arm exercise after a 42-day cross-country skiing expedition involving prolonged, low-intensity, whole body endurance training. This occurred despite only a minor increase in capillarisation and no change in oxidative capacity in triceps brachii muscle after training. The marked increase in fat oxidation during arm exercise, occurring despite a high carbohydrate intake, and an increase in muscle fibre type area do resemble the dramatic shift in fuel utilisation seen during migration in birds. Thus, with due respect to the limited number of subjects, we suggest that our current understanding of the effect of prolonged, low-intensity, whole body training on the arm muscle adaptation pattern needs reconsideration.

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