

# Impact of Exercise Intensity on Body Fatness and Skeletal Muscle Metabolism

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The impact of two different modes of training on body fatness and skeletal muscle metabolism was investigated in young adults who were subjected to either a 20-week endurance-training (ET) program (eight men and nine women) or a 15-week high-intensity intermittent-training (HIIT) program (five men and five women). The mean estimated total energy cost of the ET program was 120.4 MJ, whereas the corresponding value for the HIIT program was 57.9 MJ. Despite its lower energy cost, the HIIT program induced a more pronounced reduction in subcutaneous adiposity compared with the ET program. When corrected for the energy cost of training, the decrease in the sum of six subcutaneous skinfolds induced by the HIIT program was ninefold greater than by the ET program. Muscle biopsies obtained in the vastus lateralis before and after training showed that both training programs increased similarly the level of the citric acid cycle enzymatic marker. On the other hand, the activity of muscle glycolytic enzymes was increased by the HIIT program, whereas a decrease was observed following the ET program. The enhancing effect of training on muscle 3-hydroxyacyl coenzyme A dehydrogenase (HADH) enzyme activity, a marker of the activity of  $\beta$ -oxidation, was significantly greater after the HIIT program. In conclusion, these results reinforce the notion that for a given level of energy expenditure, vigorous exercise favors negative energy and lipid balance to a greater extent than exercise of low to moderate intensity. Moreover, the metabolic adaptations taking place in the skeletal muscle in response to the HIIT program appear to favor the process of lipid oxidation.

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**I**N SEVERAL STUDIES, exercise training has been shown to induce a substantial reduction in body fatness in overweight or obese individuals without a concomitant dietary restriction.<sup>1-4</sup> However, in other studies the decrease in adiposity resulting from regular exercise was low,<sup>5,6</sup> and other investigators have even reported a small weight gain in obese women.<sup>7,8</sup> These studies also tend to show that fat loss is increased in response to a large volume of exercise. With respect to exercise intensity, the optimal prescription to maximize fat loss has not been clearly established and still remains a matter of ongoing debate.

The common belief among health professionals is that low-intensity, long-duration exercise is the most appropriate type of program for the obese.<sup>9</sup> Beyond the fact that this is a safe exercise prescription, low-intensity exercise is also recommended because the proportion of lipid in the fuel mix oxidized under these circumstances is greater than during a high-intensity effort.<sup>10</sup> However, we have recently reported, based on a large sample size, that for a given level of energy expenditure, individuals engaging in vigorous activities are leaner than those participating in less intense activities and inactive people.<sup>11</sup> This suggests that increasing exercise intensity may favor negative energy balance, which exceeds that resulting from a low-intensity exercise. The present study was aimed at reevaluating this hypothesis by comparing the impact on body fatness of a program including only aerobic exercise of moderate intensity versus a high-intensity exercise program. In an attempt to provide a mechanistic explanation for the potential difference in fat

loss between the two exercise programs, we have investigated their effects on skeletal muscle metabolism.

## SUBJECTS AND METHODS

### Subjects

Twenty-seven subjects (13 men and 14 women) aged 18 to 32 years gave their written consent to participate in this study, which was approved by the Laval University Medical Ethics Committee. None had previously engaged in exercise-training programs or regularly participated in sports or other physical activities. A total of 17 subjects (eight men and nine women) completed a 20-week endurance-training (ET) program, and the other 10 subjects (five men and five women) completed a 15-week high-intensity intermittent-training (HIIT) protocol. The subjects of the two studies were healthy, and none of them were obese.

### Training Programs

Subjects of the ET group were submitted to a 20-week ergocycle ET program consisting of uninterrupted cycling four times a week and increasing to five times a week. The duration of the sessions was 30 minutes at the beginning of the protocol and progressively increased to 45 minutes. The initial intensity of exercise corresponded to 60% and increased to 85% of the maximal heart rate reserve. During each training session, heart rate was monitored every 2 minutes to maintain the predetermined exercise intensity and to ensure that subjects were all submitted to the same standardized training stimulus.

The HIIT group performed 25 30-minute sessions of continuous exercise at 70% of the maximal heart rate reserve, ie, at an intensity comparable to that imposed in the ET program. In addition, they performed 19 short- and 16 long-interval sessions over a period of 15 weeks. The distribution of the sessions was planned in such a way that half of the continuous sessions were completed by the fifth week of the program to expose subjects progressively only to high-intensity-interval sessions. Each high-intensity-interval session began with a 5-minute warm-up at an intensity of 50% maximal oxygen uptake ( $\dot{V}O_{2max}$ ). The short-interval work consisted of initially 10 and later 15 bouts of 15 seconds' increasing to 30 seconds' duration, whereas the long-interval work included four to five bouts of 60 seconds' increasing to 90 seconds' duration. These bouts were separated by recovery periods allowing the heart rate to return to 120 to 130 beats per minute. The intensity of the short exercise bouts was initially fixed at 60% of the maximal work

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output in 10 seconds, and that of the long exercise bouts corresponded to 70% of the individual maximal work output in 90 seconds. The intensity of the short- and long-interval exercises was increased by 5% every 3 weeks. The dropout rate was approximately the same in the two programs and corresponded to 25% to 30% of the initial sample.

**Maximal Physical Work Tests**

$\dot{V}O_2$ max was measured by a progressive cycle ergometer test to exhaustion before and after the two training programs, according to previously described procedures.<sup>12</sup> Briefly, the initial work load was 50 W, and it was increased by 20 W in women and 25 W in men every 3 minutes until exhaustion. Oxygen uptake ( $\dot{V}O_2$ ) and carbon dioxide production ( $\dot{V}CO_2$ ) were measured using an open-circuit indirect calorimetry system, (Beckman MMC, Schiller Park, IL). Maximal ergocycle work output during 10, 30, and 90 seconds was also assessed before and after the HIIT program using the methodology reported by Simoneau et al.<sup>13</sup>

**Energy Cost of Exercise Training**

The total energy cost of each training program was estimated by referring to  $\dot{V}O_2$ max and maximal work-output measurements. The energy cost of the ET program was based on heart rates obtained in each exercise session and on the assumption that  $\dot{V}O_2$  at the given power-output level was the same as during the  $\dot{V}O_2$ max test. The mean  $\dot{V}O_2$ max measured before and after this training program was used as the reference value for this calculation. The energy equivalent of  $\dot{V}O_2$  was assumed to be 20.5 kJ/L  $O_2$ .

The energy cost of the continuous exercise, including warm-up and recovery during high-intensity-interval sessions, performed in the HIIT program was estimated using the same procedure as for the ET program. The specific energy cost of the interval work was determined according to the following procedure: for interval exercise of 10 to 15 seconds, we referred to the work output, expressed in joules, observed in the 10-second maximal ergocycle performance; for interval exercise of 20 to 30 seconds and 60 to 90 seconds, the reference values for calculation of the work output were those obtained in the 30-second and 90-second maximal exercise performance tests, respectively. As for the calculation of the energy cost of continuous exercise, the mean power output measured before and after training was used as the reference value. To convert values of mechanical work into their physiological equivalents, we assumed that energy efficiency during high-intensity-interval exercise was 21%. The total energy cost of the HIIT program was finally determined by summing the energy cost of continuous and interval exercise. All the energy-cost-of-exercise values include resting energy expenditure, and no attempt was made to correct for this component, which was likely comparable in the two groups of subjects.

**Anthropometric Measurements**

Six subcutaneous fat skinfolds (biceps, triceps, calf, subscapular, suprailiac, and abdomen) were measured on the left side of the body using a Harpenden skinfold caliper and following the recommendations of the International Biological Program.<sup>14</sup> The value obtained at each site was the mean value of three valid measurements.

**Muscle Biopsies and Biochemical Assays**

Muscle needle biopsies were performed in the middle portion of the vastus lateralis muscle according to the methodology described by Simoneau et al.<sup>15</sup> Detailed procedures for the enzyme activity measurements of hexokinase ([HK] EC 2.7.1.1), phosphofructoki-

nase ([PFK] EC 2.7.1.11), malate dehydrogenase ([MDH] EC 1.1.1.37), and 3-hydroxyacyl coenzyme A dehydrogenase ([HADH] EC 1.1.1.35), as well as their reproducibility derived from repeated human skeletal muscle samples, were previously published.<sup>16</sup>

**Statistical Analyses**

Student's *t* test was used to analyze the effect of each training program on body weight, subcutaneous skinfolds, and skeletal muscle enzyme activities. The same test was applied to compare changes induced by the two training programs on each variable.

**RESULTS**

The total energy cost of the ET program was  $120.4 \pm 31.0$  MJ (mean  $\pm$  SD), whereas that of the HIIT program was  $57.9 \pm 14.4$  MJ ( $P < .01$ ). Despite the fact that the energy expenditure of exercise was twice as high in the ET as in the HIIT program, the reduction in the sum of six skinfolds tended to be greater after the HIIT program, as shown in Fig 1. Moreover, this figure indicates that when the difference in the total energy cost of the two programs was taken into account, ie, when the decrease in the sum of skinfolds was divided by energy expenditure, the subcutaneous fat loss was ninefold greater in the HIIT program than in the ET program ( $P < .01$ ).

Table 1 shows that there was no significant change in body weight in response to either the ET or the HIIT program. Both programs induced significant reductions in the suprailiac skinfold and the sum of three trunk subcutaneous skinfolds. In addition, a significant decrease in the triceps, biceps, and subscapular skinfolds, as well as the sum of three limb skinfolds and the sum of the six skinfolds, was observed following the HIIT program (Table 1).

The effects of the two training programs on skeletal muscle enzyme activities are presented in Table 2. The two training programs induced a significant increase in MDH activity, whereas they had opposite effects on HK activity. Indeed, the activity of HK was significantly increased by the HIIT program, but was significantly decreased by the ET program. Furthermore, significant increases in PFK and HADH enzyme activities were observed only with the HIIT program. Accordingly, Table 2 also shows that HK, PFK, and HADH activity changes resulting from the HIIT

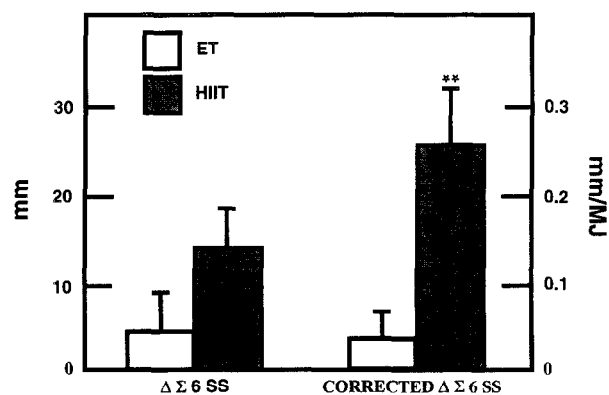


Fig 1. Changes in the sum of six skinfolds ( $\Delta \Sigma 6SS$ ) induced by ET and HIIT. The corrected  $\Delta \Sigma 6SS$  is the change in  $\Sigma 6SS$  divided by the total energy cost of training expressed in macrojoules. \*\* $P < .01$ .

**Table 1. Effects of ET and HIIT on Body Weight and SS Measurements**

Variable	ET		HIIT	
	Before	After	Before	After
Body weight (kg)	60.6 ± 13.4	60.1 ± 12.1	63.9 ± 11.0	63.8 ± 11.5
SS (mm)				
Triceps	11.5 ± 4.4	11.5 ± 5.7	14.5 ± 6.9	12.2 ± 4.9*
Biceps	6.8 ± 3.4	6.8 ± 4.2	8.0 ± 5.2	6.0 ± 3.2*
Calf	10.0 ± 3.8	11.9 ± 7.0	15.6 ± 8.6	14.7 ± 8.3
Subscapular	12.5 ± 6.7	11.7 ± 4.9	15.7 ± 7.8	13.5 ± 5.4*
Suprailiac	19.4 ± 12.0	15.9 ± 8.4*	21.1 ± 12.5	17.0 ± 11.0†
Abdomen	19.0 ± 11.6	16.9 ± 9.5	19.3 ± 12.2	16.9 ± 9.5
Σ limb SS	28.3 ± 10.7	30.2 ± 15.9	38.1 ± 18.8	32.9 ± 15.2†
Σ trunk SS	50.9 ± 27.9	44.6 ± 21.1*	56.1 ± 31.5	47.4 ± 25.2†
Σ 6 SS	79.2 ± 35.1	74.7 ± 34.2	94.2 ± 37.7	80.3 ± 36.0†

NOTE. Values are the mean ± SD.

Abbreviations: Σ, sum; SS, subcutaneous skinfolds; Σ limb SS, triceps + biceps + calf SS; Σ trunk SS, subscapular + suprailiac + abdomen SS.

\* $P \leq .05$ , † $P < .01$ , significant effect of training.

program were significantly different from those induced by the ET program.

As expected, each training program provoked a significant increase in  $\dot{V}O_2\text{max}$  (ET before,  $36.6 \pm 7.9$ , after,  $48.2 \pm 7.7$  mL/kg/min,  $P < .01$ ; HIIT before,  $38.7 \pm 8.8$ , after,  $48.6 \pm 7.0$  mL/kg/min,  $P < .01$ ). Maximal ergocycle performance (J), which was measured only during the HIIT program, was also considerably increased by this program (10-second before,  $5,082 \pm 1,988$ , after,  $6,176 \pm 1,941$ ,  $P < .01$ ; 30-second before,  $11,032 \pm 4,034$ , after,  $14,025 \pm 4,108$ ,  $P < .01$ ; 90-second before,  $19,196 \pm 7,031$ , after,  $25,963 \pm 7,848$ ,  $P < .01$ ).

## DISCUSSION

The rationale underlying this study was that for a given energy expenditure of activities, individuals engaging regularly in vigorous activities are leaner than those not practicing such activities. This observation was derived from the data of an epidemiological study in which participation in physical activities was recorded in a large sample of subjects using a diary.<sup>11</sup> In the present study, one aim was to verify whether this finding could be confirmed under controlled experimental conditions in which exercise intensity was

monitored, thus allowing a reasonable estimation of the energy expenditure of exercise. Furthermore, we were also interested in the problem of exercise intensity and substrate utilization, and their implications for energy balance. Indeed, it is well established that the relative contribution of carbohydrate to energy metabolism is increased with increasing exercise intensity, whereas the fraction of energy expended as lipid is proportionally reduced.<sup>9</sup> Recent data have also established that a negative energy balance is necessarily equivalent to a lipid deficit.<sup>17,18</sup> In practical terms, the question was how high-intensity exercise favoring carbohydrate oxidation can contribute to a body lipid deficit.

We subjected young healthy adults displaying comparable initial morphological characteristics ( $P > .1$  for all subcutaneous fat indicators) to either a 20-week exercise-training program of moderate intensity or a 15-week training program including mainly high-intensity-interval exercise. Despite the fact that the energy cost of the ET program was more than twice that of the HIIT program ( $120.4$  v  $57.9$  MJ), its impact on subcutaneous adiposity was lower than that of the HIIT program. Moreover, since experimental evidence<sup>19,20</sup> suggests that there is a positive association between exercise duration and weight loss, it appeared reasonable to correct changes in subcutaneous fat for the total energy cost of training. This was performed by expressing changes in subcutaneous skinfolds per megajoule energy expended in each program. As depicted in Fig 1, results showed that the decrease in subcutaneous adiposity relative to the energy cost of training was ninefold greater in the HIIT program than in the ET program. We believe that this finding represents a convincing confirmation of our previous observation<sup>11</sup> that for a given energy expenditure of activity, fat loss is greater when exercise intensity is high.

As a first step to investigate the metabolic determinants of this effect of high-intensity exercise, we focused on the response of skeletal muscle to training. The biochemical adaptations of skeletal muscles to ET have been intensively investigated since Holloszy<sup>21</sup> demonstrated that this type of training increases mitochondrial enzyme activities in rat

**Table 2. Effects of ET and HIIT on Skeletal Enzyme Activities (U/g wet weight)**

Enzyme	Before	After	Change
ET			
HK	1.08 ± 0.23	0.93 ± 0.19*	-0.15 ± 0.24
PFK	100.4 ± 30.9	90.6 ± 35.1	-9.9 ± 30.8
MDH	123.2 ± 29.2	179.8 ± 27.8†	56.6 ± 41.9
HADH	3.61 ± 1.10	4.26 ± 1.20	0.65 ± 1.45
HIIT			
HK	1.00 ± 0.16	1.31 ± 0.15†	0.31 ± 0.27§
PFK	108.8 ± 27.2	129.3 ± 28.6*	20.5 ± 27.7†
MDH	128.0 ± 11.9	190.6 ± 25.3†	62.6 ± 20.9
HADH	3.49 ± 0.76	5.59 ± 1.65†	2.10 ± 1.29§

NOTE. Values are the mean ± SD.

\* $P < .05$ , † $P < .01$ , significant effect of training.

‡ $P < .05$ , § $P < .01$ , significant difference between changes induced by the two programs.

skeletal muscle. Many subsequent studies have confirmed this finding in humans.<sup>22</sup> Results of the present study not only support this observation, but also show that the activity of a citric acid cycle enzyme marker is increased in response to high-intensity training in humans. This effect of HIIT is likely related in part to the fact that repeated exercise bouts during this protocol were interspaced by sufficient recovery periods. It is known that the energy needs for sustaining maximal exercise of very short duration are largely met by the creatine phosphate breakdown such that its concentration decreases to almost zero at the end of maximal exercise leading to exhaustion.<sup>23</sup> An almost complete creatine phosphate recovery is normally observed within rest periods lasting about 4 minutes following repeated maximal exercises of short duration.<sup>24</sup> In contrast, creatine phosphate resynthesis is not possible when the arterial blood flow to the muscle is hindered or blocked.<sup>25</sup> These observations support the concept that the oxidative phosphorylation is essential for creatine phosphate resynthesis in muscle,<sup>26</sup> and may explain why the citric acid cycle enzyme marker of the skeletal muscle was increased in the present study even though subjects were exposed to repeated maximal exercises. In other words, the duration of rest periods may have been a determinant.

The literature pertaining to the adaptive response of human skeletal muscle glycolytic enzymes following exercise training is less consistent. In the present study, the ET program induced a decrease in PFK enzyme activity. This is concordant with the fact that athletes competing in endurance events generally exhibit muscle PFK enzyme activity within the range of sedentary subjects.<sup>27,28</sup> However, the HIIT program resulted in a substantial increase in the activity of the glycolytic enzyme marker. This type of training is known to impose a high demand on the glycolytic energy metabolism so that high muscle lactate concentrations are experienced by subjects exposed to repeated and maximal exercises of short duration.<sup>23</sup>

The issue of the effects of different training modes on enzymes of the  $\beta$ -oxidation pathway still remains unclear. Muscle triglycerides significantly contribute to the energy supply required for prolonged exercises.<sup>29</sup> However, the ET program did not cause any significant increase in HADH enzyme activity. Interestingly, the HIIT program induced a substantial increase in HADH enzyme activity that was

significantly greater than that observed after the end of the ET program. McCartney et al<sup>24</sup> have shown that triglycerides may play a role as a substrate for energy metabolism in repeated 30-second maximal exercise bouts. This greater increase following the HIIT program is compatible with the hypothesis that vigorous exercise may lead to a better lipid utilization in the postexercise state and may thus contribute to a greater energy and lipid deficit.

The results obtained in this study do not allow us to describe what are the effects of exercise intensity on the components of energy balance. However, the recent demonstration in animals that exercise favors anorexia via a stimulation of the corticotropin-releasing factor<sup>30</sup> lends support to the idea that the above-referenced observations might be attributable to an effect on energy intake. Specifically, this may mean that following a vigorous exercise, energy intake is either transiently suppressed or increased to a lesser degree compared with that following an exercise of low to moderate intensity. In addition, it is also possible that vigorous exercise has a greater enhancing effect on postexercise energy expenditure than does moderate exercise.

In summary, the results of the present study show that for a given level of energy expenditure, a high-intensity training program induces a greater loss of subcutaneous fat compared with a training program of moderate intensity. This is probably explained by an enhancing effect of high-intensity exercise on postexercise lipid utilization, which favors a greater body lipid deficit following exercise. From a clinical standpoint, it is obvious that high-intensity exercise cannot be prescribed for individuals at risk for health problems or for obese people who are not used to exercise. In these cases, the most prudent course remains a low-intensity exercise program with a progressive increase in duration and frequency of sessions. However, the data reported here would support the notion that it may be appropriate and useful to prescribe vigorous exercise instead of low-intensity exercise of comparable energy cost when this is compatible with the fitness level of the individual.

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#### REFERENCES

1. Gwinup G: Effect of exercise alone on the weight of obese women. *Arch Intern Med* 135:676-680, 1975
2. Leon A, Conrad JS, Hunninghake DM, et al: Effects of a vigorous walking program on body composition, and carbohydrate and lipid metabolism of obese young men. *Am J Clin Nutr* 32:1776-1787, 1979
3. Woo R, Garrow JS, Pi-Sunyer FX: Voluntary food intake during prolonged exercise in obese women. *Am J Clin Nutr* 36:478-484, 1982
4. Després JP, Pouliot MC, Moorjani S, et al: Loss of abdominal fat and metabolic response to exercise training in obese women. *Am J Physiol* 261:E159-E167, 1991
5. Mackeen PC, Franklin BA, Nicholas WC, et al: Body composition, physical work capacity and physical activity habits at 18-month follow up of middle-aged women participating in an exercise intervention program. *Int J Obes* 7:61-71, 1983
6. Moody DL, Wilmore JH, Girandola RN, et al: The effects of a jogging program on the body composition of normal and obese high school girls. *Med Sci Sports* 4:210-213, 1972
7. Krotkiewski M, Bylund-Fallenius AC, Holm J, et al: Relationship between muscle morphology and metabolism in obese women: The effects of long-term physical training. *Eur J Clin Invest* 13:5-12, 1983
8. Krotkiewski M, Mandroukas K, Sjostrom L, et al: Effects of long-term physical training on body fat, metabolism, and blood pressure in obesity. *Metabolism* 28:650-657, 1979
9. Astrand PO, Rodahl K: *Textbook of Work Physiology*. New York, NY, McGraw-Hill, 1978

10. Bouchard C, Després JP, Tremblay A: Exercise and obesity. *Obes Res* 1:133-147, 1993
11. Tremblay A, Després J-P, Leblanc C, et al: Effect of intensity of physical activity on body fatness and fat distribution. *Am J Clin Nutr* 51:153-157, 1990
12. Lortie G, Simoneau JA, Hamel P, et al: Responses of maximal aerobic power and capacity to aerobic training. *Int J Sports Med* 5:232-236, 1984
13. Simoneau JA, Lortie G, Boulay MR, et al: Test of anaerobic alactacid and lactacid capacities: Description and reliability. *Can J Appl Sport Sci* 8:266-270, 1983
14. Weiner JS, Lourie JA: *Human Biology: A Guide to Field Methods*. Oxford, UK, Blackwell, 1969
15. Simoneau JA, Lortie G, Boulay MR, et al: Skeletal muscle histochemical and biochemical characteristics in sedentary male and female subjects. *Can J Physiol Pharmacol* 63:30-35, 1985
16. Simoneau JA, Lortie G, Boulay MR, et al: Repeatability of fiber type and enzyme activity measurements in human skeletal muscle. *Clin Physiol* 6:347-356, 1986
17. Flatt JP: Dietary fat, carbohydrate balance, and weight maintenance: Effects of exercise. *Am J Clin Nutr* 45:296-306, 1987
18. Schutz Y, Flatt JP, Jéquier E: Failure of dietary fat intake to promote fat oxidation: A factor favoring the development of obesity. *Am J Clin Nutr* 50:307-314, 1989
19. Tremblay A, Després JP, Bouchard C: The effects of exercise-training on energy balance and adipose tissue morphology and metabolism. *Sports Med* 2:223-233, 1985
20. Ballor DL, Keeseey RE: A meta-analysis of the factors affecting exercise-induced changes in body mass, fat mass and fat-free mass in males and females. *Int J Obes* 11:717-726, 1991
21. Holloszy JO: Biochemical adaptations in muscle. Effects of exercise on mitochondrial oxygen uptake and respiratory enzyme activity in skeletal muscle. *J Biol Chem* 242:2278-2282, 1967
22. Saltin B, Gollnick PD: Skeletal muscle adaptability: Significance for metabolism and performance, in Peachy LD, Adrian RH, Geiger RS (eds): *Handbook of Physiology*. Bethesda, MD, American Physiological Society, 1983, pp 555-631
23. Hermansen L: Muscular fatigue during maximal exercise of short duration. *Med Sport* 13:45-52, 1981
24. McCartney NL, Spriet L, Heigenhauser GJF, et al: Muscle power and metabolism in maximal intermittent exercise. *J Appl Physiol* 60:1164-1169, 1986
25. Shenton DW, Heppenstall RB, Chance B, et al: Electrical stimulation of human muscle studied using <sup>31</sup>P-nuclear magnetic resonance spectroscopy. *J Orthop Res* 4:204-211, 1986
26. Sahlin K, Havu M, Karvinen E: Resynthesis of creatine phosphate in human muscle after exercise in relation to intramuscular pH and availability of oxygen. *Scand J Clin Lab Invest* 39:551-558, 1979
27. Gollnick PD, Armstrong RB, Saubert CW, et al: Enzyme activity and fiber composition in skeletal muscle of untrained and trained subjects. *J Appl Physiol* 33:312-319, 1972
28. Costill DL, Daniels J, Evans W, et al: Skeletal muscle enzymes and fiber composition in male and female track athletes. *J Appl Physiol* 40:149-154, 1976
29. Hurley BF, Nemeth PM, Martin WH, et al: Muscle triglyceride utilization during exercise: Effect of training. *J Appl Physiol* 60:562-567, 1986
30. Rivest S, Richard D: Involvement of corticotropin-releasing factor in the anorexia induced by exercise. *Brain Res Bull* 25:169-172, 1990