EFFECTS OF HIGH-INTENSITY INTERVAL TRAINING ON VO_{2MAX} AND POST-EXERCISE FAT CONSUMPTION IN RECREATIONALLY ACTIVE ADULTS COMPARED TO STEADY-STATE RUNNING

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ABSTRACT

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Introduction. HIIT has a long history in athletes' training. In the recent decades numerous studies have been published of its influence in health and fitness also among sedentary and recreationally active individuals. HIIT is shown to induce health related positive peripheral and central adaptations, such as enhanced aerobic capacity and improved fat oxidation. The aim of the current study was to examine 1) effects of 8 weeks of high intensity interval running (HIIR), high-intensity interval circuit training (HIICT) and steady-state running (SSR) on peak oxygen uptake (VO_{2peak}), fat consumption and the rate of fat oxidation, and 2) compare effects of three different training groups on post-ex fat consumption and the rate of fat oxidation. **Methods.** 24 recreationally active males and females were randomly assigned to three different training groups: HIIR (N=8), HIICT (N=8) and SSR (N=8). They implemented 24 training sessions in eight weeks (3 x/week). HIIR consisted of 8-10 x 1 min intervals (85-95 % of HR_{max}) separated by 30 s of active recovery whereas HIICT group performed 8-10 x 1 min own-body weight and plyometric exercises (as many reps as possible in 1 min) separated by 30 s active recovery. SSR consisted of 40-60 min of moderate intensity continuous running. Respiratory gases were analyzed from the first and the last exercise 15-30 min post-training. VO_{2peak} was tested in a cycle ergometer before and after the training period. **Results.** No significant differences were found in VO_{2peak} either post-training period or between-groups comparisons. The highest magnitude of post-exercise fat consumption and the rate of fat oxidation were achieved in HIICT group before eight weeks of training. Significant differences were found in the post-exercise values in the pre-training measurement between HIICT and SSR: Respiratory exchance ratio (RER) 0.73/0.87 (p=0.018), % of carbohydrates used 8/56 (p=0.012), % of fats used 92/44 (p=0.012), energy used in carbohydrates 2/12 kilocalories (p=0.026), energy used in fats 21/9 kilocalories (p=0.011), rate of carbohydrate oxidation (carbohydrates used g/min) 0.03/0.20 (p=0.030) and rate of fat oxidation (fats used g/min) 0.15/0.06 (p=0.011. The rate of fat oxidation was significantly higher in HIICT (0.12 g/min) compared to SSR (0.06 g/min) (p=0.043) also in the post-training measurement. Additionally a significant difference was found in the rate of carbohydrate oxidation (g/min) in the pre-measurement between HIICT and HIIR 0.03/0.18 (p=0.027). **Conclusion.** Persons aiming to increase post-exercise fat oxidation, may benefit from low volume high-intensity circuit training more than higher volume steady-state running.

Key words: high-intensity interval training, high-intensity interval running, high-intensity interval circuit training, steady-state running, VO_{2peak}, fat consumption, rate of fat oxidation

TIIVISTELMÄ

Stenman, Mari (2016). Korkeatehoisen intervalliharjoittelun vaikutukset maksimaaliseen hapenottokykyyn ja harjoituksen jälkeiseen rasvan kulutukseen liikunnallisesti aktiivisilla aikuisilla verrattuna tasavauhtiseen juoksuun. Liikuntabiologian laitos, Jyväskylän yliopisto, liikuntafysiologian pro gradu -tutkielma, 61 sivua, 4 liitettä.

Johdanto. Korkeatehoista intervalliharjoittelua on käytetty jo pitkään urheilijoiden valmennuksessa. Lisäksi viime vuosikymmeninä on julkaistu useita tutkimuksia harjoitusmuodon vaikutuksesta sekä vähän liikkuvien että kuntoliikkujien terveyteen ja fyysiseen kuntoon. Korkeatehoisen intervalliharjoittelun on todettu aiheuttavan positiivisia sentraalisia ja perifeerisiä muutoksia, kuten kohonnut aerobinen kunto ja tehostunut rasvan oksidointikyky. Tämän tutkimuksen tavoitteena oli tutkia 1) 8 viikon korkeatehoisen intervallijuoksun (HIIR), korkeatehoisen intervallikuntopiirin (HIICT) ja tasavauhtisen juoksun (SSR) vaikutuksia maksimaaliseen hapenottokykyyn sekä harjoituksen jälkeiseen rasvan kulutukseen ja rasvan oksidointinopeuteen, ja 2) verrata eri harjoitusmuotojen vaikutusta harjoituksen jälkeiseen rasvan kulutukseen ja rasvan oksidointinopeuteen. **Menetelmät.** 24 vapaaehtoista liikunnallisesti aktiivista miestä ja naista satunnaistettiin kolmeen harjoitusryhmään: HIIR (N=8), HIICT (N=8) ja SSR (N=8). Koehenkilöt toteuttivat 24 harjoitusta 8 viikon aikana (3 x/vko). HIIR-ryhmä juoksi 8-10 x 1 min intervallia (85-95 % HR_{max}) 30 s aktiivisilla palautuksilla. HIICT-ryhmän harjoitus sisälsi 8-10 x 1 min oman kehon painolla tehtyjä lihaskunto- ja plyometrisiä harjoituksia (mahdollisimman monta toistoa/1 min) 30 s aktiivisilla palautuksilla. SSR-ryhmän harjoitus koostui 40-60 min pituisesta kohtuutehoisesta tasavauhtisesta juoksusta. Hengityskaasut mitattiin ensimmäisen ja viimeisen harjoituksen jälkeen ja analysoitiin 15-30 minuutin ajanjaksolta. Maksimaalinen hapenottokyky (VO_{2peak}) mitattiin polkypyöräergometrillä harjoitusjaksoa ennen ja sen jälkeen. **Tulokset.** Maksimaalisessa hapenottokyvyssä ei ollut eroja harjoitusjakson seurauksena eikä ryhmien välisessä vertailussa. Suurin harjoituksen jälkeinen rasvojen käyttö energiana ja rasvojen oksidointinopeus tapahtui korkeatehoisen intervallikuntopiirin jälkeen ennen kahdeksan viikon harjoitusjaksoa ja tottumista harjoitteluun. Harjoitusjaksoa edeltävässä mittauksessa oli useita HIICT- ja SSR-ryhmien välisiä tilastollisesti merkitseviä eroja: Hengitysosamäärä (RER) 0.73/0.87 ($p=0.018$), hiilihydraattien (CH) kulutus 8/56 % ($p=0.012$), rasvojen (F) kulutus 92/44 % ($p=0.012$), CH kulutus 2/12 kcal ($p=0.026$), F kulutus 21/9 kcal ($p=0.011$), CH oksidointinopeus 0.03/0.20 g/min ($p=0.030$) ja F oksidointinopeus 0.15/0.06 g/min ($p=0.011$). Lisäksi rasvan oksidointinopeus oli merkitsevästi suurempi myös harjoitusjakson jälkeen HIICT-ryhmällä (0.12 g/min) verrattuna SSR-ryhmään (0.06 g/min) ($p=0.043$). Ainoa HIICT ja HIIR -ryhmien välinen ero oli CH oksidointinopeudessa ennen harjoitusjaksoa 0.03/0.18 g/min ($p=0.027$). **Yhteenveto.** Harjoituksen jälkeinen rasvan käyttö energiana on suurempaa yhteensä 12 minuuttia kestävän korkeaatehoisen intervallikuntopiirin jälkeen verrattuna 40 minuutin tasavauhtiseen juoksuun.

Avainsanat: Korkeatehoinen intervalliharjoittelu, korkeatehoinen intervallijuoksu, korkeatehoinen intervallikuntopiiri, tasavauhtinen juoksu, VO_{2peak}, rasvan kulutus, rasvan oksidointinopeus

ABBREVIATIONS

AMP	Adenosine monophosphate
BF	Breathing frequency (1/min)
BLa	Blood lactate concentration
CH	Carbohydrates
EQ	Respiratory equivalent
F	Fats
FA	Fatty acids
FABPpm	Plasma membrane fatty acid binding protein
FAT/CD36	Fatty acid translocase
HbO_2	Oxyhemoglobin
HIIT	High-intensity interval training
HIIR	High-intensity interval running
HIICT	High-intensity interval circuit training
HR	Heart rate
KCAL	Kilocalories
RER	Respiratory exchange ratio
RER-pre	Pre-training period RER
RER-post	Post-training period RER
RPE	Rated perceived exertion
SSR	Steady-state running
VCO_2	CO_2 consumption (ml/min)
VE	Ventilation (l/min)
VO_2	O_2 consumption (ml/min)
VO_{2peak}	Peak oxygen uptake
1RM	Repetition maximum
%CH	% of kcals derived from carbohydrates
%F	% of kcals derived from fats
ΔRER	Change in RER after 8 weeks of training
ΔVO_{2peak}	Change in VO_{2peak} after 8 weeks of training

CONTENTS

APPENDIXES

1 INTRODUCTION

Background of HII training method. High-intensity interval training (HIIT) has reached huge popularity among press and recreationally active individuals during the last two decades. However, it is not an unheard or a novel training method, since athletes have applied HIIT from the beginning of the 20th century. Incredible examples are Finnish middle- and long-distance runners Hannes Kolehmainen (Triple Olympic gold medallist in Stockholm 1912) and Paavo Nurmi (9-fold Olympic Champion in different Olympic games between 1920-1928). They used interval training by running intervals close to their competition velocities. Three-fold Olympic champion in the Helsinki Olympic Games 1952 Emil Zatopek, was probably the one who popularized interval training. Czechoslovakian runner ran daily up to 100 x 400 meters altered by 200 meters recovery at the intensity corresponding competition velocities between 800 and 5000 meters. (Tschakert & Hofmann 2013.)

Reindell and Roskamm wrote the first scientific article about interval training in 1959, even though the training method had been applied in competitive sport decades earlier. A year later (1960) Swedish research team, Åstrand, Åstrand & Christensen, published studies on HIIT. At the beginning HIIT research concentrated on athletes' performance and mainly on endurance sport competitors. Nevertheless, during the last 20 years HIIT research has expanded among team sport players as well as non-competitive sport enthusiasts. During that period the researchers have demonstrated that the benefits of high intensity interval training are similar in recreationally active people as in competitive athletes. (Tschakert & Hofmann 2013.) Moreover, throughout the last decade HIIT has been applied in individuals suffering from a variety of chronic diseases, such as cardiovascular problems and type II diabetes (Wisloff et al. 2007).

Traditionally HIIT researches have used mainly sprint interval training, which requires all-out effort from the participants. However, in recent years, aerobic HIIT has become more popular and a number of studies have used different training modes with sub-maximal intensities. Aerobic HIIT, where energy is produced mainly aerobically and intervals are longer in duration, can be considered as a compromise between time-consuming endurance training and highly demanding sprint interval training (Perry

2008). Moreover, less intense intervals are considered safer and more practical for the majority of the population (Gibala & McGee 2008).

Benefits of HIIT. Strong evidence presently exists that HIIT has remarkably health benefits affecting both centrally and peripherally. Cardiovascular and skeletal muscle related adaptations have been obtained in a relatively low volume training and thus, HIIT can be considered as a time efficient training method. (Gibala et al. 2012.) Simultaneously the lack of time is reported to be the main reason not to exercise. Time efficiency combined with health benefits may be the most important character, which makes HIIT as a tempting and interesting training strategy for all population. (Gibala & McGee 2008.)

HIIT is shown to induce both acute responses and long-term adaptation in the body. One bout of HII exercise is known to significantly increase heart rate, some hormones (norepinephrine, epinephrine, growth hormone and cortisol), blood lactate concentration and glucose as well as glycerol levels. On the contrary, HIIT acutely decreases parasympathetic reactivation and induces depleted ATP, phosphocreatine and glycogen stores. The chronic adaptations to HIIT (two weeks or more training) include improved maximal oxygen uptake, enhanced anaerobic capacity, beneficial skeletal muscle adaptations, improved fat oxidation and decreased fasting insulin and insulin resistance. (Boutcher 2011.)

VO_{2max}. Up to date knowledge suggests that high-intensity interval training is likely to be superior in order to improve maximal oxygen uptake compared to traditional continuous aerobic training. Significant improvements have been achieved with both supramaximal (intensity > 100 % of VO_{2max}) and aerobic submaximal HIIT (intensity ~ 85 – 95 % of VO_{2max}). The results have been obtained in active as well as in sedentary individuals and in relatively short period of time. (Harris & Wood 2012.) Even though different training protocols (duration, intensity and work to rest ratio) seem to result in similar responses, interval training with longer intervals and submaximal intensity, might be more practical, easier and safer to perform, and thus recommended for non-athletes (Gibala & McGee 2008).

Lipid oxidation. A number of studies have demonstrated improved lipid oxidation after a period of high intensity interval training (Harris & Wood 2012). Moreover a spectrum of studies suggest that HIIT may be superior in order to improve fat oxidation in both subcutaneous and abdominal fat depots compared to moderate intensity exercise. The physiology behind the efficacy is related to several skeletal muscle adaptations, such as mitochondria capacity and activity, as well as hormonal responses to high-intensity exercise. Enhanced lipid oxidation related to HIIT may partly result in long term fat loss and weight reduction. (Boutcher 2011.) With regards to today’s problems, sedentary lifestyle and lack of time to exercise combined with overweight, HIIT might serve as a part of the solution. Furthermore, the body’s enhanced capacity to oxidize fat is essential not only for the individuals attempting to lose fat and improve their body composition, but also for athletes aiming to spare carbohydrates in competition (Talanian et al. 2007).

The purpose of the current study was to examine effects of eight weeks of HII training (high-intensity interval running HIIR and high-intensity interval circuit training HIICT) compared to continuous steady-state running (SSR) on VO_{2peak} and post-exercise fat consumption. Additionally the aim was to compare influences of three different training modes (HIIR, HIICT and SSR) on post-exercise fat consumption and the rate of fat oxidation.

2 HIIT AS A TRAINING METHOD

2.1 Determination of HIIT

High-intensity interval training (HIIT) is considered as an alteration of short high-intensity training periods and active or passive recovery periods (Harris & Wood 2012; Helgerud et al. 2007; Tschakert & Hofmann 2013). A diversity of variables exists in HIIT; one can vary intensity, number of intervals, duration of intervals as well as duration of recovery (Gibala et al. 2012). Tschakert & Hofmann (2013) also consider mean workload and recovery load as HIIT variables. Moreover Buchheit and Laursen (2013) add an exercise modality (e.g. running or cycling) to the list. As seen above, high intensity interval training can be executed in a number of ways. However, the effect of manipulation of different variables on physiological responses is not known. Despite of the large number of HIIT studies published in the recent years, a standardized and consistent description of the training method does not exist (Tschakert & Hofmann 2013).

One approach to determine HIIT is to divide it in two different categories based on the intensity. In a number of studies *high-intensity sprint training* consists of supramaximal work periods (intensity › 100 % of VO_{2max}) with the duration of 30 seconds or less. The recovery periods have been approximately 4 minutes in the most of the studies. *Submaximal high-intensity training,* in turn, has been performed at the intensity of approximately 85 – 95 % of VO_{2max}. Duration of working periods has altered between 30 seconds to 4 minutes while active recovery periods have typically lasted 30 seconds to 3 minutes. (Harris & Wood 2012.) Figure 1 presents a suggested model of HIIT determination by Tschakert & Hofmann (2013).

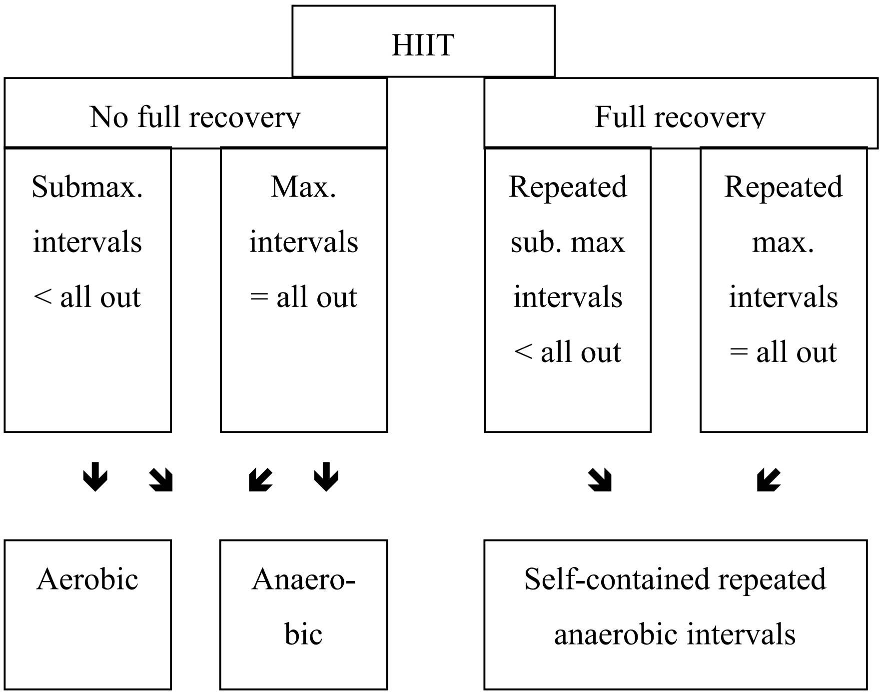

FIGURE 1. Suggestion of Tschakert & Hofmann (2013) of HIIT determination (modified from Tschakert & Hofmann 2013).

2.2 Different modes of HIIT

An abundance of HIIT studies have been conducted with a cycle ergometer or a treadmill (e.g. Astorino et al. 2012; Gosselin et al. 2012 Helgerud et al. 2007; Perry et al. 2010; Talanian et al. 2007; Talanian et al. 2010). However, HIIT can be also applied to resistance training either using weights or own body weight as a resistance. *High-intensity resistance training or a combination of resistance training and cardiovascular training* can furthermore be performed as *high-intensity circuit training.* Circuit training typically combines cardiovascular and resistance training exercises and hence can be considered as a comprehensive training method. High-intensity circuit training (e.g. CrossFit –style exercise) has currently reached high popularity. (Klika & Jordan 2013.)

R.E. Morgan and G.T. Anderson launched the term circuit training in 1953 in England. The exercise mode originally referred to a variety of exercises performed consecutively in 9 to 12 stations for a selected repetitions or duration of time. (Kravitz 1996.) In the original form, the intensity of exercises was moderate (approximately 40 - 60 % of 1RM) and the move to the next station was rather quick without or with only a little recovery. In the recent years it has been popular to increase the intensity of exercises by selecting movements, which particularly elevate heart rate. The modern application of high-intensity circuit training can be considered time-efficient and easy-to-perform aerobic and resistance training exercise. (Klika & Jordan 2013.)

Even though HIIT has widely been applied to different training modalities, at least some discrepancy about the definition of HIIT seems to exist. Some authors (e.g. Gibala & McGee 2008; Savolainen 2013) do not consider resistance training aiming to increase power or hypertrophy as HIIT where as Paoli et al (2012) conducted a study of HII resistance training. Additionally a number of fitness centres offer a variety of HIIT-classes and some of them are clearly based on resistance training and hypertrophy exercises. The next paragraphs illustrate few HIIT studies, which have used other than running or cycling types exercises as a training method.

Paoli et. al (2012) compared the acute effect of high-intensity resistance training and traditional resistance training (TT) on resting energy expenditure and respiratory ratio. The study was conducted as a cross-over-design, where all the subjects performed both high-intensity resistance training and traditional training programs. The high-intensity resistance training was performed with 6RM weights and the duration of the exercise bout was 32 minutes. The intensity of the TT on the other hand, was 70-75 % from the 1RM and the duration of the training period was 62 minutes. Training consisted of typical weight lifting exercises, such as bench press, military press and leg press. Resting periods as well as sets and repetitions varied between the groups. The main finding of the study was that resistance training applied to HIIT principles might increase resting energy expenditure and decrease respiratory exchange ratio (referring to more effective fat oxidation) after exercise more than traditional strength training.

The study of Cook et al. (2014) demonstrated that HIIT applied in a group exercise class (LES MILLS GRIT™) improved VO_{2max} and lean body mass in trained females (elite soccer players). The HII-training was part of the six weeks off-season training program among endurance and strength training as well as soccer playing. The LES

MILLS GRIT™ is a 30 minutes HIIT-workout consisting of explosive plyometric and dynamic strength exercises. Moreover, Gottschall et al. (2014) investigated the effect of HIIT (LES MILLS GRIT™) combined to traditional cardio and strength training compared with cardio and strength training only in healthy adults. The main finding of the study was that HIIT-group improved their VO_{2max}, glucose tolerance, lean body mass as well as reduced body fat mass and triglyceride concentration significantly more than the control group.

2.3 Optimal application of HII-training

As mentioned earlier, high-intensity interval training has a number of variations. The literature has no consensus which application is the most optimal in order to improve health. However, a majority of experts consider submaximal HIIT more suitable and convenient for a larger population compared to high-intensity sprint training. (e.g. Gibala & McGee 2008; Gosselin et al. 2012; Helgerud et al. 2007; Little et al. 2010). The next paragraphs present studies, which have compared different variations of HIIT in order to seek differences between diversity of HIIT protocols.

Gosselin et al. (2012) studied the metabolic and cardiovascular responses of healthy young persons to four different aerobic interval training protocols compared to traditional aerobic training. The HIIT was performed at the intensity of 90 % of VO_{2max} and the work-rest durations were 30/30 (seconds), 60/30, 90/30 and 60/60. The traditional training was done at the intensity of 70 % of VO_{2max}. The purpose of the research group was to identify a safe aerobic HIIT protocol with the maximum health benefits but the minimum time requirements. The most important finding of their study was that altering work-to-rest ratio remarkably alters the metabolic and cardiovascular responses to exercise. The results showed that the higher the work-to-rest ratio, the higher the O_2 consumption. However, no significant difference was found in the post-exercise blood pressure, which suggests that all protocols were safe to perform.

Wood et al. (2015) compared acute physiological changes during two metabolically different modes of HIIT: aerobic high-intensity interval training and sprint interval training. They examined heart rate (HR), blood lactate concentration (BLa), oxygen uptake (O_2) and rating of perceived exertion (RPE) in 12 active adults. Sprint interval training (SIT) consisted of eight all-out intervals at the duration of 30 seconds each and at the workload of 130 % of maximum watts in a cycle ergometer whereas aerobic HIIT group performed eight bouts of 60 seconds cycling at the workload of 85 % of maximum watts. VO_2 and energy expenditure were significantly higher in aerobic HIIT and BLa as well as RPE were significantly lower in aerobic HIIT compared to SIT. Consequently, the authors concluded that the metabolic responses between groups were different, which may induce different long-term adaptations. Moreover, persons aiming to expend more calories with lower perceived exertion should choose aerobic high-intensity interval training as an exercise mode rather than all-out sprints.

Helgerud et. al (2007) compared the effect of four different training groups: 1) continuous long distance running (intensity 70 % of HR_{max}), 2) continuous running at lactate threshold (intensity 85 % of HR_{max}), 3) 15/15 interval running (15 seconds of running at 90 – 95 % of HR_{max} followed by 15 seconds of active rest at the intensity of 70 % of HR_{max}) and 4) 4 x 4 minutes of interval running (4 min at 90 – 95 % HR_{max} and 3 min active rest at 70 % HR_{max}). All groups were matched for energy consumption and thus every training protocol resulted in similar oxygen consumption. VO_{2max} improved significantly more in 15/15 (5.5 %) and 4 x 4 min (7.2 %) groups compared to continuous training groups. However, no significant difference was obtained between the interval groups. (Helgerud et al. 2007.)

Majority of the studies have been conducted at the intensity of at least 90 % of the VO_{2max}. However, Alkahtani et al. (2013) compared high and moderate intensity interval training in obese men. Their study indicated that exercise-induced fat oxidation increased with both protocols without significant differences between the training methods. However, neither of the protocol induced significant changes in body composition.

2.4. Benefits of HIIT

It is well known that high-intensity exercise cause fatigue due to metabolic and neuronal factors. During exercise at high intensities the glycolytic rates are high and consequently lactate levels increase and muscle pH decreases. Intermittent training enables high-intensity exercise for a longer duration compared to continuous training, since oxygen is restored, phosphocreatine is at least partly replenished and some of the muscle metabolites are removed during the recovery periods (Ratel et al. 2003; Tabata et al. 1997). According to the study of Bogdanis et al. (1995) restoration of peak power output and muscle phosphocreatine synthesis after maximal sprint of 30 seconds seems to occur parallel. However, neither one were fully recovered after 6 minutes of exercise bout. The complete restoration of pH and lactate to pre-exercise level might take hours after all-out HII exercise (Boutcher 2011). HbO_2 re-saturation in muscles takes approximately 30 seconds (McCully et. al 1994). As a conclusion, due to physiological restoration during recovery periods between the intervals, HIIT enables to perform higher volume of greater intensity exercise compared to continuous training. Additionally the aim of HIIT can be considered to repeatedly stress central and peripheral systems (Abderrah et al. 2013). As a result of high intensity, the total time committed to exercise can be smaller than in steady-state aerobic training. This is essential in a perspective that lack of time seems to be the main reason not to exercise.

The general opinion typically considers HIIT as an unpleasant mode of exercise that can be implemented only by fit individuals. However, a variety of HIIT studies with unconditioned individuals as well as participants with a disease, such as type II diabetes, have been conducted recently. Jung et al. (2011) evaluated the enjoyment of HIIT (10 x 1 min at the intensity of 90 % of VO_{2max} separated by 1 min recovery) compared to 30 and 60 minutes continuous low-intensity training in type II diabetics. The participants evaluated HIIT greater in terms of perceived exercise enjoyment compared to low intensity continuous training. Furthermore Barlett et al. (2011) compared the perceived enjoyment of HII running (6 x 3 min at the intensity of 90 % of VO_{2max} with 3 min recovery between the intervals) to iso-caloric 50 minutes continuous running at the intensity of 70 % of VO_{2max}. HII running was perceived higher in enjoyment than continuous running.

A numerous amount of studies examining the effect of HIIT on different physiological responses and health variables exist currently (e.g. Burgomaster et al. 2006; Burgomaster et al. 2008; Daussin et al. 2008; Gibala et al. 2008; Helgerud et al. 2007;

Little et al. 2010; Meier et al. 2015; Zhang et al. 2015). A literature review by Gibala et al. (2012) summarized that HIIT is a potential option for a moderate intensity continuous training with a remarkable health benefits. It has a positive effect on both central (cardiovascular) and peripheral (skeletal muscle) adaptations even after a relatively short training period. The body responses to HIIT have been similar or even greater than those achieved with endurance training. Chronic responses to two weeks or more HII training have reported to induce higher resting glycogen content, decreased glycogen utilization and lactate production during exercise, increased lipid metabolism, positive changes in peripheral vascular structure and function, improved performance and anaerobic capacity as well as enhanced VO_{2max} and decreased fasting insulin and insulin resistance. (Boutcher 2011.)

The following chapters concentrate on the effect of HIIT on VO_{2max}/VO_{2peak} as well as on post-exercise lipid consumption and oxidation capacity.

3 HIIT AND VO_{2MAX}

3.1 VO_{2max}

Maximal oxygen uptake (VO_{2max}) describes the maximum amount of oxygen transported from the ambient air to the mitochondria and its utilization for oxidative production of ATP (Levine 2008). A measurement of VO_{2max} is generally accepted to be the best indicator of person's capacity to transport and utilize oxygen and therefore an indicator to define cardiorespiratory fitness (ACSM 2006, 66; Astorino 2009). The definition of VO_{2max} is following (ACSM 2006, 66):

VO_{2max} = the product of maximal cardiac output (L blood/min) and arterial-venous oxygen difference (mL O_2 per L blood)

3.1.1 Factors affecting VO_{2max}

Functional capacity of heart and more specifically cardiac output seems to be the main factor, which effects on maximal oxygen uptake (VO_{2max}) (ACSM 2006, 66). Since maximum heart rate is not affected by the change in VO_{2max}, the change in stroke volume determines the training response in VO_{2max} (Helgerud et al. 2007). VO_{2max} value is expressed either as an absolute rate (L/min) or relative to body mass (ml/kg/min) or lean body mass (ml/kg_{LBM}/min) (McArdle et al. 2010, 241).

A number of factors has an effect on maximal oxygen uptake (McArdle 2010, 237 - 242). Table 1 presents the most significant ones.

TABLE 1. Factors affecting on VO_{2max} (adapted from McArdle et al. 2010, 237 - 242).

Factor affecting on VO_{2max}	**Quantity of effect (%)**	**Details**
Mode of exercise	Variations of VO_{2max} reflects the quantity of muscle mass activated	Generally treadmill running produces the highest values - Bench stepping: similar to treadmill - Cycle ergometer: lower values - Arm crank: 70 % of the treadmill value - Swimming: 80 % of the treadmill value
Heredity	20 – 30 %	Heredity has a significant effect on physiological functions, exercise performance and training responsiveness
State of training	5 – 20 %	Specificity of training
Gender	Women have generally 15 – 30 % lower values compared to men	Difference is greater when expressed in absolute units (L/min^{-1}) compared to relative units ($mL/kg^{-1}/min^{-1}$) due to differences in body composition
Body size and composition	~ 70 %	Affecting factors are the size of the contracting muscle, fat free mass, body mass and surface area
Age	Declines ~ 1 % after 25 years	Boys and girls have about the same value until age of 12. At the age of 14 years boys have approximately 25 % higher values and at the age of 16 around 50 % higher values.

3.1.2 How to improve VO_{2max}?

VO_{2max} can be improved by taken into account four factors: initial level of aerobic capacity, training intensity, training frequency and duration of exercise. Training intensity appeals to be the most significant factor and therefore the optimal work intensities, which cause improvements in maximal oxygen uptake are widely studied. The lowest intensity for improving VO_{2max} seems to be approximately 55 - 65% of maximal heart rate. (McArdle et al. 2010, 470 - 476.) However, studies have shown that high-intensity interval training at the intensity of at least 80 - 90% of VO_{2max} is likely to be superior compared to steady-state training (50 - 75% VO_{2max}) in order to improve maximal oxygen uptake (Abderrahman et al. 2013; Helgerud et al. 2007). In overall, training intensity between 60 - 90 % of HR_{max} is likely to induce positive changes in aerobic fitness. Exercise duration and intensity interacts in their effect on VO_{2max}, since longer duration compensates for reduced intensity and visa versa. Optimal training frequency remains unclear. Nonetheless, it is commonly accepted that two or three times a week is a minimal frequency in order to improve aerobic fitness. The initial level of aerobic fitness has a significant influence on the magnitude of improvement, since sedentary individuals achieve greater positive changes compared to athletes. (McArdle et al. 2010, 470, 475 - 476.)

3.2 Effect of HIIT on VO_{2max}

HIIT has shown to induce positive effects to cardiovascular fitness (Gibala et al. 2012). However, this is not a universal finding, since controversial results also exist (Burgomaster et al. 2008; McKay et al. 2009). Nonetheless, in some studies VO_{2max} have improved even in a greater extend compared to traditional aerobic steady-state training. Similar results have been obtained with both trained and untrained subjects as well as among young and older adults and healthy and unhealthy persons. (Boutcher 2011; Helgerud et al. 2007; Nybo et al. 2010; Talanian et al. 2007; Tjonna et al. 2008.) Boutcher (2011) has summarized the results of 14 HIIT studies and noticed that different types of high-intensity interval exercise protocols lasting from two to 15 weeks improved VO_{2max} from four to 46 %. The meta-analysis by Bacon et al. (2013) analyzed 37 articles (N=334), which had studied the effect of HIIT on VO_{2max} in healthy sedentary or recreationally active males and females. The review revealed that high-intensity interval training improved VO_{2max} by approximately 0.51 L/min. Moreover, HIIT produced slightly higher improvements compared to continuous traditional training.

Only few studies have reported the cardiovascular benefits of circuit training. Kaikkonen et al. (2000) examined the effect of heart rate controlled low resistance (20 % of 1RM) circuit weight training and aerobic endurance training on maximal aerobic power in sedentary adults. They showed that circuit training with low resistance produces equal benefits to cardiovascular fitness compared to same amount of endurance training. Similarly McRae et al. (2012) demonstrated that high-intensity own-bodyweight exercises implemented in the circuit training style was equal to continuous training in order to improve VO_{2max}. Circuit training involved aerobic and own-body weight resistance training exercises such as burpees, mountain climbers and jumping jacks (one set of 8 x 20 s divided by 10 s recovery) . Continuous training consisted of 30 min of treadmill running at the intensity of approximately 85 % of HR_{max}. Both groups completed the exercise session four times a weeks. Aerobic fitness was improved 7 % in continuous training group and 8 % in circuit training group (no significant difference between the groups). (McRae et al. 2012.)

Smith et al. (2013) studied the effect of 10 weeks of crossfit-style high-intensity power training on aerobic fitness and body composition. They used a variety of exercises characterized for high power output and use of multiple joint movements, such as Olympic lifts and gymnastics exercises (e.g.) handstands. They demonstrated that high-intensity power training typically used in Crossfit, improved VO_{2max} significantly (in males from 43.10 to 48.96 ml/kg/min and in females from 35.98 to 40.22 ml/kg/min). (Smith et al. 2013.)

3.2.1 Optimal HIIT duration and intensity

Even though the fact that HIIT increases VO_{2max} significantly is rather commonly accepted, the most effective duration, intensity and work to rest ratio of the exercise for different target groups remain under a debate (Gibala et al. 2012). However, it is assumed that training intensity is more important than volume in order to improve cardiorespiratory fitness (Helgerud et al. 2007). Bacon et al. (2013) suggested that the intervals of 3 - 5 minutes might be the most effective ones in terms of improved exercise capacity. Furthermore the greatest improvement in VO_{2max} has been achieved by combining 3 - 5 minutes interval training bouts to continuous high-intensity training. However, above described training is highly demanding and thus, not recommended to implement for a long period. (Bacon et al. 2013.)

Earlier presented study of Helgerud et. al (2007) compared the effect of four different training groups: 1) continuous long distance running (intensity 70 % of HR_{max}), 2) continuous running at lactate threshold (intensity 85 % of HR_{max}), 3) 15/15 interval running (15 s of running at 90 – 95 % of HR_{max} followed by 15 s of active rest at the intensity of 70 % of HR_{max}) and 4) 4 x 4 min of interval running (4 min at 90 – 95 % HR_{max} and 3 min active rest at 70 % HR_{max}). The absolute value of VO_{2max} improved significantly more in 15/15 (5.5 %) and 4 x 4 min (7.2 %) groups compared to continuous training groups. However, no significant difference was obtained between the interval groups. Stroke volume changed significantly in 15/15 and 4 x 4 min groups without differences between those two groups. Training resulted in no significant changes in blood volume or in lactate threshold. (Helgerud et al. 2007.)

According to the study of Stepto et al. (1999) the highest benefit for 40 km cycling trial in highly trained cyclists were achieved with aerobic intervals (8 x 4 min at the intensity of 85 % of the peak power separated by 90 s rest) as well as with anaerobic intervals (12 x 30 s at the intensity of 175 % of the peak power). 20 cyclists were assigned to one of five different HIIT groups during the period of three weeks. In the addition to HIIT they implemented their normal aerobic base training.

Astorino et al. (2012) studied the effect of short-term high-intensity interval training on VO_{2max} as well as muscle force and other cardiorespiratory functions. Twenty recreationally active males and females completed only 6 session of HIIT over a two weeks period. The training consisted of 4 - 6 repeated Wingate tests. Compared to the previously presented study of Helgerud et al. (2007), the training sessions were conducted with supramaximal intensity (VO_{2max} > 100 %). The results showed that maximal oxygen uptake increased significantly after only 6 training bouts of HIIT. The magnitude of aerobic fitness improvement ranged from 0 to 20 % beeing 6.3±5.4 % on average. However, it is not known if sustained supramaxinal HIIT would continue to induce long-term adaptations. (Astorino et al. 2012.)

The study of McRae et al. (2012) compared the improvements in aerobic fitness and skeletal muscle endurance between low-volume high-intensity whole body training and continuous training after a period of four weeks of training. They implemented circuit type exercise mode for the whole body using movements such as burpees, jumping jacks, mountain climbers and squats. Training protocol was adapted from one of the most popular HIIT researchers Tabata et al. (1996) (one set of 8 x 20 s of a single movement as many repetitions as possible separated with 10 s rest between). The control group conducted 30 min of treadmill running at the intensity of 85 % of HR_{max}. Both groups achieved significant improvements in cardiovascular fitness (8 % in circuit training group and 7 % in continuous running group, respectively) as only circuit training group improved their skeletal muscle endurance. (McRae et al. 2012.)

In the addition to duration and intensity to the working intervals, the characteristics of recovery periods matter. However, the properties of the working intervals are the most relevant in terms of physiological responses to HIIT. The time spent in recovery phase affects the VO_2 value achieved during the recovery. This in turn, influences the time required to achieve the required intensity of the working phase. Moreover, the duration as well as intensity of the recovery have a direct effect on the muscle metabolic recovery, which determines the capacity of the muscles to work in the following work interval. Apparently, blood lactate and muscle H+ decrease as the duration of recovery increases. Consequently the optimal duration of the recovery is affected by the intensity of working phase. Controversy exists which is the optimal intensity of the recovery phase. (Tchakert & Hoffmann 2013.)

Whether active or passive recovery is superior, seem to be dependent on the goal of the exercise (Abderrahman et al. 2013; Buchheit & Laursen 2013; Dupont et al. 2004; Stanley & Buchheit 2014). Abderrahman et al. (2013) demonstrated that the improvement of aerobic capacity was superior with active recovery between intervals compared to passive one. However, the data is somewhat controversial with other researches. Studies of Dupont et al. (2003), Dupont et al. (2004) and Dupont & Berthoin (2004) have revealed that passive recovery allows to exercise longer until exhaustion or complete more high-intensity intervals compared to active recovery. The physiology behind the finding is related to lower metabolic demands during passive versus active recovery. Dupont et al. (2004) showed that passive recovery between high-intensity intervals induced slower decline in oxyhemoglobin compared to recovery at the intensity of 40 % of VO_{2max}. Stanley & Buchheit (2014) indicated that in order to maintain high stroke volume throughout the HII exercise bout, it does not make a substantial difference if the recovery is completed at the intensity of 60 % of VO_{2max}, 30 % of VO_{2max} or passively. Concluding the above presented studies of Dupont et al. (2003 and 2004) and the study of Stanley & Buchheit (2014), reducing the intensity of recovery may allow increased time accumulated at the high stroke volume, which is considered to be important for improving aerobic fitness (Stanley & Buchheit 2014).

3.2.2 Physiology behind HIIT efficacy on VO_{2max}

The physiology behind the improved VO_{2max} followed by HIIT period has been largely discussed and the mechanism regulating the cardiovascular responses of the training method is not fully understood (Gibala et al. 2012). It is commonly known that maximum cardiac output has a close association between maximal oxygen consumption (McArdle et al. 2010, 347). In addition, the high VO_{2max} of elite endurance athletes is mainly explained by high cardiac output resulted by large compliant cardiac chamber. The activity of the cardiac chamber, both myocardium and pericardium, is optimal due to quick relaxation and filling capacity. (Levine 2008.)

According to the study of Helgerud et al. (2007) the improvements in VO_{2max} in their interval training groups were likely resulted by the improvements in cardiac output and more specifically stroke volume. Moreover, blood volume and oxygen-carrying capacity of the blood do probably not explain the increase in VO_{2max}, since there were no significant hematological responses in their study. Bacon et al. (2013) and Boutcher (2011) summarized that VO_{2max} is improved due to increases in cardiac output, stroke volume and cardiac contractility as well as peripheral oxygen extraction. Muscle oxidative adaptations, such as increases in PGC1-α mediated transcription, muscle diffusive capacity and improved mitochondrial oxidative capacity, partly explain the enhanced aerobic power after a HIIT period (Butcher 2011). Nonetheless, the contribution of different factors (stroke volume, blood volume, capillary density, muscle mitochondrial content) might vary on individual basis as well as due to training specificity (Bacon et al. 2013). Rakobowchuk et al. (2008) demonstrated that the compliance of peripheral, but not central, arteries as well as endothelial function of the trained legs are increased due to high-intensity training. Moreover, Butcher (2011) suggests that the major factor explaining aerobic response post-HIIT period is phosphocreatine degradation during exercise. Tchakert & Hofmann (2013) suggest that improved VO_{2max} related to sprint interval training is mostly a consequence of adaptations in muscle oxidative capacity, such as increased mitochondrial enzyme activity and a greater number of mitochondrial content. According to them, the changes in cardiac function would require longer duration (2 - 3 min) of the high-intensity intervals. However, they noted that in the previously summarized study of Helgerud et al. (2007) no significant hematological changes were found in the comparison of different HIIT modes. (Tchakert & Hofmann 2013.)

4 HIIT AND ENERGY METABOLISM

Endurance training induces several physiological benefits including improved metabolic health (Di Blasio et al. 2014; Nordby et al. 2010; Nordby 2015; Sillanpää et al. 2009a; Sillanpää et al. 2009b). Furthermore, studies have discovered that also high-intensity interval training has numerous beneficial effects on skeletal muscle metabolism despite of remarkably smaller volume of exercise compared to traditional endurance training (Alkahtani et al. 2013; Gibala et al. 2008; Gosselin et al. 2012; Little et al. 2010; Paoli et al. 2012; Perry et al. 2008; Talanian et al. 2007; Talanian et al. 2010). Positive HIIT-induced metabolic adaptations have been achieved with sub-maximal training intensity (Alkahtani et al. 2010; Gosselin et al. 2012; Perry et al. 2008; Talanian et. al. 2007; Talanian 2010; Tjonna et al. 2009) as well as with supramaximal intensity (Heydari et al. 2010; MacPherson et al. 2010; Trapp et al. 2009).

4.1. HIIT and energy consumption during and after exercise

Emberts et al. (2013) studied energy expenditure during Tabata-style circuit training workout in sixteen trained individuals. Tabata is often used as a synonym for HIIT in fitness and health centres and it equals the HIIT protocol of 8 x 20:10 (20 seconds all out exercise followed by 10 seconds rest repeated eight times). The concept Tabata is derived from the famous HIIT study of Tabata et al. (1996) where above mentioned HIIT concept with the duration of four minutes was shown to improve VO_{2max} as effective as 60 minutes of moderate intensity (70 % of VO_{2max}) continuous training. Additionally to aerobic fitness, only HIIT improved anaerobic capacity 28 %. The study of Emberts et al. (2013) repeated the four minutes Tabata set four times with a recovery of 1 minute between the sets. They used body-weight and plyometric exercises, such as high knee run, burpees, mountain climbers, push ups and jumping jacks. The mean caloric expenditure was 14.5±2.7 kcal/min whereas the total energy expenditure of the 20 minutes exercise ranged from 240 to 360 kcals.

The study of Scott et al. (2011) investigated the energy expenditure during and after two different resistance training sessions. The other session consisted of endurance type of exercises and the other one included anaerobic strength training (workloads ranging from 37 % of 1RM in endurance exercises to 90 % of 1RM in anaerobic exercises). The endurance type of exercises performed until failure were more effective in terms of total energy expenditure compared to heavy weight lifting. (Scott et al. 2011.) In the future, it would be meaningful to compare the energy expenditure of anaerobic resistance training with heavy weights to own-body weight training completed until muscular failure.

Paoli et al. (2012) compared the acute effect of high-intensity resistance training and traditional resistance training on resting energy expenditure and respiratory exchange ratio. They demonstrated that energy metabolism was significantly greater 22 hours after high-intensity resistance training compared to traditional resistance training. Resting energy expenditure was increased 23 % in the high-intensity group while the increase was only 5 % in the traditional training group.

Chan and Burns (2013) measured post-exercise oxygen consumption and RER in eight healthy males measuring breath-by-breath pulmonary gas exchange. The subjects participated in two trials in separated days: four 30 seconds high-intensity sprints separated by 4.5 minutes recovery on cycle ergometer and equal duration of rest as a control trial. Post-exercise oxygen uptake was significantly higher (43%) after the exercise trial compared to resting trial, reflecting 65 kcal greater energy expenditure. However, the duration of increased oxygen consumption was rather short, lasting only 30 minutes after exercise. (Chan & Burns 2013.)

Excessive post-exercise oxygen consumption (EPOC) represents increased VO_2 and energy expenditure after exercise session. EPOC is known to be the greatest immediately post-exercise and it decreases over time. Studies have shown that both aerobic and resistance training increases EPOC. (Farinatti et al. 2012.) Increased EPOC is due to metabolic restoration back to pre-exercise levels (Boutcher 2011). In terms of weight management EPOC is considered to be beneficial, hence it causes increased total energy expenditure as well as greater fat oxidation (Harris & Wood 2012). According to the study of LaForgia et al. (2006), the contribution of HIIT-related EPOC to total energy expenditure is 14 %. Although the effect of EPOC can be considered rather small, it was greater compared to equated moderate intensity exercise (EPOC 7 % from total energy expenditure). Apparently the greatest energy expenditure comes out during actual exercise and thus, if an elevated post-HIIT EPOC enhances fat loss, requires further research (Boutcher 2011). In theory, the cumulative effect of EPOC with regular exercise routine could have a positive effect on long-term energy balance and hence, facilitate fat loss (Harris & Wood 2012).

LaForgia et al. (2006) compared steady state running (30 min at the intensity of 70 % of VO_{2max}) and HII running (20 x 1 min intervals at the intensity of 105 % of VO_{2max} separated by 2 min recovery). EPOC was significantly greater after HII running nine hours post-exercise. The study of Thorntorn et al. (2011) revealed that either low- or high-intensity work-equated resistance training resulted in similar responses to post-exercise oxygen consumption in overweight African American women. The peak level of EPOC was measured within the first eight minutes following exercise. However, the magnitude of EPOC was rather low and hence, it may not have a relevant influence on weight loss in the long term. (Thorntorn et al. 2011.)

The literature review by Farinatti et al. (2012) suggested that circuit training might increase the magnitude of EPOC more compared to traditional consecutive resistance training sets and therefore be the best method to increase resistance training EPOC. The suggestion is based on the evidence that exercise volume in resistance training may be more essential than intensity alone in terms of greater EPOC. However, the authors stated that further studies are required to confirm the assumption. Furthermore, they concluded that shorter rest intervals (< 60 seconds) between resistance training sets seem to increase the magnitude of EPOC without an effect on total energy expenditure. (Farinatti et al. 2012.)

4.2 HIIT and lipid metabolism

Fat is stored intramuscularly (in skeletal muscle) and extramuscularly (in adipose tissue and liver). Additionally a small amount of fats circulates in the blood. The fuel is used for energy from both sources. Extramuscular fat is mobilized and transported from adipose tissue and liver into the blood and finally to the working skeletal muscle. This process is controlled by neural, endocrine and cardiovascular systems. (Hargreaves & Spriet 2006, 2-3.) The triglycerides stored in adipose tissue are an abundant energy source in the human body consisting approximately 100 000 kcal of energy to be used even in lean adults (Hargreaves & Spriet 2006, 89).

Exercise is known to improve skeletal muscle fat oxidation. During moderate intensity exercise, free fatty acid uptake and oxidation is increased while during high-intensity exercise a body is not able to deliver, uptake and utilize lipids at the same extend. Nevertheless, post-exercise lipid oxidation is greater in high-intensities compared to low or moderate intensity exercise. (Alkahtani et al. 2013.) In the addition to exercise intensity, the fuel availability has an effect on the proportion of the substrate oxidised (Sahlin 2009).

A variety of studies have discovered that HIIT is an effective method to increase muscle and whole body fat oxidation (Burgomaster et al. 2006 and 2008; Talanian et al. 2007 and 2010; Perry et al. 2008). Talanian et al. (2007) studied the acute effect of only 7 sessions of HIIT on fat oxidation in moderately active women. They demonstrated that relatively small amount of high intensity training (7 sessions of 10 x 4 min at the intensity of 90 % of VO_{2peak} with 2 min recovery between) was enough to induce significant increases in lipid oxidation capacity. Whole body fat oxidation increased by 36 % and net glycogen use reduced during 60 minutes cycling trial. In the addition to enhanced whole body fat oxidation, significant skeletal muscle adaptations; increased mitochondrial β-hydroxyacyl-CoA dehydrogenase and citrate synthase as well as total muscle plasma membrane fatty-acid binding protein content, were achieved. (Talanian et al 2007.)

The study of Talanian et al. (2010) discovered that the capacity of muscles to oxidize fat increases after HIIT period. Ten previously untrained females participated to HIIT period during six weeks. Muscle biopsies were taken two and six weeks after training in order to determine sarcolemmal and mitochondrial membrane fatty acid transport protein contents. Their main findings were that post-HIIT period fatty acid transport protein contents were increased in whole muscle (FAT/CD36 and FABPpm) as well as in sarcolemmal (FABPpm) and mitochondrial (FAT/CD36) membranes. Moreover, the increase in transport protein contents occurred rapidly, since no significant difference was found between the results of two and six weeks post-training. (Talanian et al. 2010.)

Perry et al. (2008) demonstrated that aerobic HIIT increased fat and carbohydrate metabolic capacities in skeletal muscle in untrained individuals. The training protocol included aerobic HIIT three times a week during a period of six weeks (10 x 4 min at the intensity of 90 % of VO_{2max} divided by 2 min rest between). They revealed that a broad spectrum of metabolic changes, including increased content of fatty acid transport proteins as well as protein content of five mitochondrial enzymes, increased glycogen content, reduced glycogenolysis and increased fat oxidation, occurred following HIIT protocol. As a summary of their finding, HIIT seems to improve both fat and carbohydrate oxidation capacity in skeletal muscle. (Perry et al. 2008.)

Paoli et al. (2012) investigated the acute effect of short period resistance training compared to traditional resistance training on resting energy expenditure and respiratory exchange ratio 22 hours following a bout of exercise in 18 resistance-trained males. They demonstrated that respiratory exchange ratio was significantly lower 22 hours post high-intensity resistance training compared to traditional resistance training. The result indicates that lipid metabolism is improved after high-intensity exercise. Moreover the increase in resting energy expenditure was 23 % following short but high intensity resistance training session, whereas the increase was only 5 % post traditional training. The significant metabolic effect was consistent to 452 kcal in a day. (Paoli et al. 2012.)

Chan & Burns (2013) compared the rate of fat oxidation after a bout of sprint interval training to the baseline situation as well as to a control trial (rest). They discovered that the rate of fat oxidation (g/min) calculated from RER was 75 % higher two hours post-HIIT than at the baseline situation or after two hours of rest. Moreover RER was significantly lower, reflecting higher usage of lipids, from 30 to 90 minutes post-exercise compared to the baseline values. Additionally Alkahtani et al. (2010) demonstrated significant improvements in exercise-induced fat oxidation based on RER after four weeks (12 sessions) of HIIT in obese men. Nevertheless, the improvement was equal with the group that performed moderate-intensity training with higher volume.

4.3 Physiology behind HIIT-related enhanced lipid metabolism

The most straightforward mechanism underlying behind increased fat oxidation after a session of HIIT might be glycogen re-synthesis. The body is required to remove lactate and H^+ as well as fulfil glycogen stores and thus rather uses lipids as energy. (Boutcher 2011.) However, recent studies have also revealed other mechanisms related to subcellular and hormonal adaptations of training.

Mitochondrial capacity and activity. Studies suggest that one explaining factor for the positive effect on fat metabolism of HIIT is related to mitochondrial capacity and activity (Gibala et al. 2012). PGC-1α is considered one of the most essential regulators of muscle mitochondrial biogenesis (Austin & St-Pierre 2012) and thus, the effect of HIIT on this protein has been studied in the recent years. The intensity of exercise seems to be the main factor affecting the activity of PGC-1α (Gibala et al. 2012). Little et al. (2010) discovered that two weeks of low-volume interval exercise induces mitochondrial biogenesis in skeletal muscle. They found that the nuclear abundance of PGC-1α increased followed by high-intensity interval training. Moreover, the studies of Gibala et al. (2009) and Little et al. (2011) showed that PGC-1α content was elevated by several fold after three hours of Wingate-based exercise bout. However, Laursen (2010) suggest that different mitochondrial signalling pathways, which are related to PGC-1α mRNA transcription, result in the same outcome, improved fat oxidation, in both moderate intensity and high intensity training. In the high intensities mitochondrial oxidative capacities are improved through the AMP-activated protein kinase-pathway. Accordingly, calcium-calmodulin pathways are used in the high-volume moderate intensity exercise. (Laursen 2010.)

Enzymes. Talanian et al. (2007) found significant changes in protein contents, which affect whole body and muscle capacity to oxidize fat, after two weeks of HIIT in women. The skeletal muscle adaptations to HIIT included increased concentrations of muscle β-hydroxyacyl coenzyme A dehydrogenase, citrate synthase and muscle plasma membrane fatty acid binding protein. Gibala et al. (2008 & 2009) have shown that the activity and content of mitochondrial enzymes, such as citrate synthase and cytochrome oxidase, are increased post HII training period.

Fatty acid transport proteins. Talanian et al. (2010) suggest that fatty acid transport protein contents and subcellular localization have an effect on increased skeletal muscle fatty oxidation following HIIT period. It is known that the role of fatty acid transport proteins is important in skeletal muscle fat oxidation. There are a number of sites in the fatty acid transportation process, including plasma, sarcolemma and mitochondrial membranes, where transportation proteins are required. Fat oxidation may be limited by the amount of fatty acid transport proteins on the sites of process regulation. The study of Talanian et al. (2010) research group revealed that the content of fatty acid transportation proteins (FAT/CD36, FABPpm) increased as soon as after two weeks of HII training. Particularly FAT/CD36 (FA translocase) is speculated to be an essential protein when training induced adaptations are concerned. Perry et al. (2008) speculated that signals occurring due to muscle contraction activate a number of signalling pathways, which in turn leads to changes in mitochondrial proteins. The more intense contraction related to HIIT may produce more stimuli compared to moderate intensity training.

Hormonal responses. In the addition to subcellular responses, remarkable hormonal changes have been reported during and acutely after high-intensity exercise. Catecholamines (norepinephrine and epinephrine) concentration increases essentially during maximal intensity exercise (figure 2). (McArdle et al. 2010, 415.) At the intensities higher than 75 % of VO_{2max}, epinephrine and norepinephrine concentrations are reported to be even 17 to 20 times greater compared to resting situation (Borer 2013, p. 110). Gratas-Delamarche et al. (1994) and Vincent et al. (2004) reported significant elevation of catecholamines after Wingate test in physically active men and women. The hormonal responses of other HIIT protocols than Wingate have also been studied. Trapp et al. (2007) and Bracken et al. (2009) demonstrated significant increases in epinephrine and norepinephrine concentration after HII cycling exercise bout. Trapp et al. (2007) used two different 20 minutes cycling exercise; 8 s sprint/12 s recovery and 12 s sprint/24 s recovery) whereas Bracken et al. (2009) had a protocol of 10 x 6 s sprint with 30 s recovery between. Above-mentioned hormonal responses of HIIT are in contrast to low-to-moderate intensity endurance training, which results in none or minor elevation of catecholamines (figure 2).

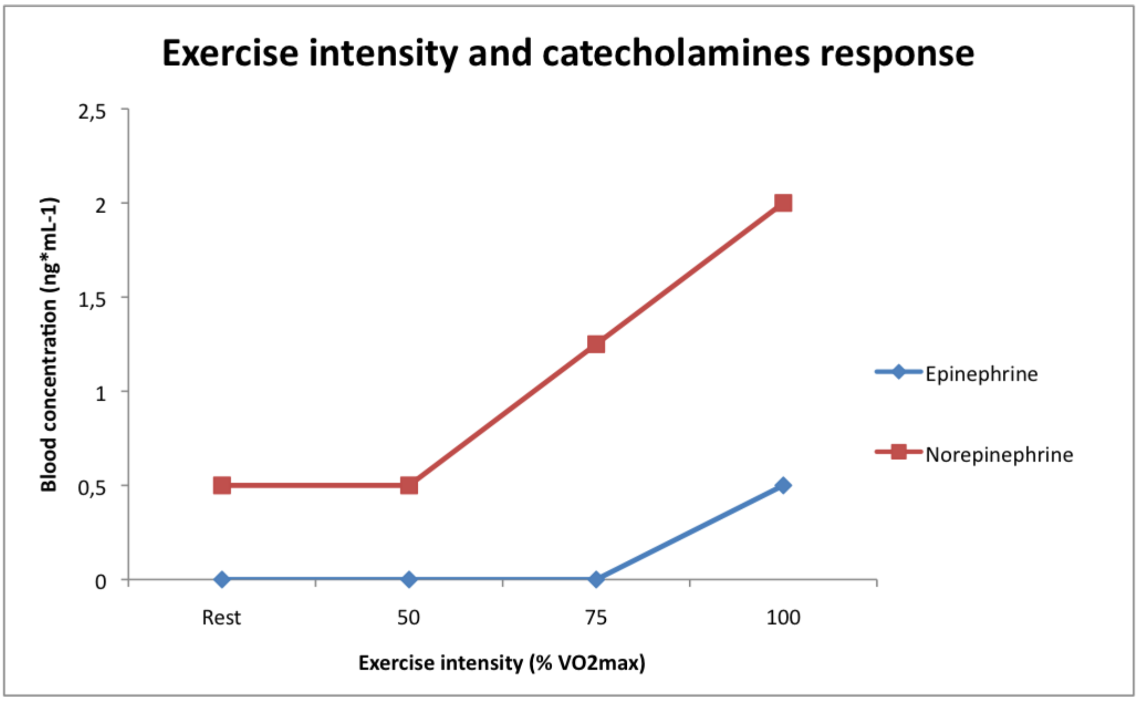

FIGURE 2. The effect of exercise intensity on catecholamine response. Adopted from McArdle et al. (2010, 415).

Pullinen et al. (1999) investigated plasma catecholamine responses to four different resistance exercises in adult men and women. The subjects performed bilateral knee flexion-extension exercise until exhaustion with four different training loads: 80 %, 60 %, 40 % and 20 % of the personal 1RM. Each participant conducted all four exercises separated by at the minimum of three days of recovery. The results indicated that plasma noradrenaline response was the highest with the longest exercise duration (load 20 % of 1RM, respectively), with the greatest total integrated muscle activity and with the highest blood lactate concentration. Plasma adrenaline response was higher in 20 % of 1RM exercise compared to 80 % of 1RM exercise, although it not differed from the 40 % 1RM and 60 % 1RM. The difference between the exercises in adrenalin response was smaller compared to noradrenalin. No significant difference in catecholamine response were observed between men and women. (Pullinen et al. 1999.)

The importance of catecholamine response is related to more effective fat oxidation. Lipolysis is negatively controlled by insulin and activation of α adrenergic receptors. Accordingly, it is positively controlled by the action of catecholamine on β adrenergic receptors as well as growth hormone and ANP (atrial natriuretic peptide). The secretion of catecholamine results in inhibition in insulin secretion by stimulating α adrenergic receptors on pancreatic cells. Insulin in turn inhibits lipid oxidation and thus a decline of insulin is a stimulus for fat oxidation. (Borer 2013, pp. 100-108.)

Specifically epinephrine enhances lipolysis and has a major role in lipid release from both subcutaneous and intramuscular fat stores (Boutcher 2011). The rate of fat oxidation in different regions of adipose tissue is related to the distribution of α and β adrenergic receptors in the adipose tissue. The α adrenergic receptors are found more in subcutaneous adipose tissue, as several β adrenergic receptors are found in visceral fat. (Borer 2013, pp. 100-108.) HIIT may enhance abdominal lipid oxidation, since a greater amount of lipolytic β_1 and β_2 -adrenergic receptors have reported to be in an abdominal area compared to other fat depots (Borer 2013, p. 111; Boutcher 2011). Both subcutaneous and visceral abdominal fat stores are highly responsive to lipolysis driven by catecholamines. However, the amount of circulating free fatty acids in visceral adipose tissue is rather small (5 – 20 %) compared to the amount circulating in subcutaneous abdominal fat stores. (Borer 2013, pp. 111-112.)

Further to epinephrine and norepinephrine, the concentrations of growth hormone have reported to increase after a bout of HIIT, which has a positive effect on energy expenditure and lipid oxidation (Boutcher 2011). Growth hormone serves as a lipolytic hormone by most probably suppressing protein oxidation during exercise (Borer 2013, p. 108, 112). Additionally, it stimulates the muscle protein synthesis, facilitates the release of free fatty acids as well as inhibits the action of anti-lipolytic insulin (Harris & Wood 2012). Moreover, growth hormone has reported to enhance post-exercise fat oxidation in subcutaneous abdominal adipose tissue (Borer 2013, p. 108, 112). In the study of Wee et al. (2005) the peak effect of growth hormone concentration was achieved two hours after an exercise bout with an intensity of 70 % of VO_{2max} and duration of 20 minutes.

5 PURPOSE OF THE STUDY AND STUDY QUESTIONS

The purpose of the study was to examine 1) effects of eight weeks of high-intensity interval running (HIIR), high-intensity interval circuit training (HIICT) and steady-state running at the continuous phase (SSR) on VO_{2peak} as well as post-exercise fat consumption and the rate of fat oxidation, and 2) to compare effects of three different training groups (HIIR, HIICT and SSR) on post-exercise fat consumption and the rate of fat oxidation in recreationally active adults.

Study questions were the following:

1. How do 8 weeks (24 sessions) of HIIR, HIICT and SSR affect VO_{2peak} and are there differences between the training methods?

2. How do 8 weeks (24 sessions) of HIIR, HIICT and SSR affect post-exercise fat consumption and the rate of fat oxidation and are there differences between the training methods?

Hypotheses based on the previous literature were:

1. Aerobic capacity is improved in all training groups although superior improvements are achieved in HIIR and HIICT compared to SSR (Boutcher 2011; Helgerud et al. 2007; McArdle et al. 2010, 470 – 476; Nybo et al. 2010; Talanian et al. 2007; Tjonna et al. 2008). There is a limitation of studies comparing different high intensity interval training modes and particularly circuit training -style implemented HIIT. Hence, the hypothesis is that the two HII training modes have equal benefits.

2. Post-exercise fat consumption and the rate of fat oxidation are enhanced in all groups although superior improvements are achieved in HIIR and HIICT compared to SSR. Post-exercise fat consumption and the rate of fat oxidation are greater both pre-training period and post-training period in HIIR and HIICT compared to SSR (Alkahtani et al. 2013; Di Blasio et al. 2014; Gibala et al.

2008; Gosselin et al. 2012; Little et al. 2010; Nordby et al. 2010; Nordby 2015; Paoli et al. 2012; Perry et al. 2008; Sillanpää et al. 2009a; Sillanpää et al. 2009b; Talanian et al. 2007; Talanian et al. 2010). As mentioned above, a limited amount of studies with similar training modes exists. Based on the greater muscle mass involved in HIICT, this training mode may enhance lipid oxidation even more than HIIR.

6 METHODS

6.1 Subjects

20-40 recreationally active volunteers were aimed to recruit as participants of the study. The recruitment was based on voluntariness. After a study info for the volunteers and doctor's examination, which included resting ECG, health questionnaire (Appendix 1), and anamnesis, 24 individuals (20 women, 4 men, aged 21 - 39) were accepted to participate in the study. The subjects were randomly assigned to three different training groups (detailed information below): HIIR (N=8), HIICT (N=8) and SSR (N=8). For different medical and personal reasons, 5 persons dropped out during the training period (three from HIIR and one from HIICT and SSR each). The anthropometric information about the participants is presented in the table 2.

TABLE 2. Anthropometric data of the subjects in each training group presented as pre- and post-measurement values.

	HIIR (N=5)		HIICT (N=7)		SSR (N=7)	
	Pre	Post	Pre	Post	Pre	Post
Height (cm)	171±7	171±7	173±5	173±5	167±4	167±4
Body mass (kg)	65.7±8.2	65.8±8.3	69.1±9.6	69.3±10.1	63.2±5.5	61.7±4.6
BMI	22.2±1.1	22.0±1.0	22.9±2.4	23.0±2.6	22.7±1.3	22.6±1.3
Fat percent (%)	24.1±3.0	24.6±3.2	25.2±7.5	25.3±7.8	21.8±9.3	22.0±10.5

6.2 Study design and training

The ethical committee of Central Finland Health Care approved the study protocol. Three separate master's thesis were done on the study material: Aino Kari concentrated on body composition and glucose tolerance, Susanna Malmivaara on hormones and blood lipids and the present study aimed to investigate aerobic fitness and fat oxidation.

The duration of the training period was eight weeks, which included one familiarization exercise after the pre-measurement. The aim of the familiarization was, in addition to familiarize, to determine the speed of running groups where the intensity met the aim. The subjects conducted the training by themselves excluding the familiarization exercise and one exercise in the middle of the training period for HIIR and SSR groups, where the running phase was re-determined. The intensity was determined by using heart rate monitors, RPE scale and lactate analysis in order to target the desired HR in the individually adjusted speed (value from HR_{max} achieved from the VO_{2peak} test).

The subjects recorded their diet for three consecutive days two times (altogether six days) and they received diet instructions (appendix 2) in order to standardize nutritional status. The food records were analyzed with Nutri-Flow program (Nutri-Flow Oy, Finland). The participants were also required to record and report their training during the examination period. They were not allowed to do other exercises than those including to the study design. All groups exercised three times a week. The participants were randomly assigned to three different training groups using a simple randomization (Suresh 2011):

1. HIIR (high-intensity interval running)
   - 8 - 10 x 1 min exercise at the intensity of 85 - 95 % of HR_{max} divided by 30 s active recovery at the intensity of 40 - 60 % of HR_{max}
   - The volume increased progressively: weeks 1 - 3 included 8 intervals, weeks 4 - 6 included 9 intervals and finally, weeks 7 - 8 included 10 intervals
   - Treadmill running

2. HIICT (high-intensity interval circuit training)
   - 8 - 10 x 1 min exercise divided by 30 s active recovery at the intensity of 40 - 60 % of HR_{2max}
   - The subjects were instructed to perform as many exercises as possible in one minute
   - The volume increased progressively: weeks 1 - 3 included 8 intervals, weeks 4 - 6 included 9 intervals and finally, weeks 7 - 8 included 10 intervals
   - The exercises included own-body weight and plyometric exercises. Appendix 3 presents a list of the exercises.

3. SSR (steady-state running)
   - 40 - 60 min continuous running at the intensity of 65 – 75 % HR_{max}

- The volume increased progressively: weeks 1 - 3 included 40 min running, weeks 4 - 6 included 50 min running and finally, weeks 7 - 8 included 60 min running
- Treadmill running (some participants were walking on the treadmill at the beginning since the intensity would have been too high in running)

Pre- and post-exercise period measurements were conducted to all subjects:

- Peak aerobic capacity (VO_{2peak}) with indirect calorimeter on a bicycle ergometer (Ergoline bike, Oxygon Mobile and Oxygon Pro, Jaeger, VIASYS Healthcare GmbH)
- DEXA body composition (GE Lunar Prodigy Advance)
- Blood tests for lipid and hormonal concentrations
- Oral glucose tolerance test

VO_{2peak} was measured separately from the other measurements, since the other tests required overnight fasting. The test was started with 5 minutes warm-up at the workload of 50 W. Followed by the warm-up the actual test started with 50 W and the workload was increased by 25 W after each 2 minutes until exhaustion. Blood lactate was obtained from the fingertips, heart rate was monitored with the Polar heart rate monitor (S410, Polar Electro, Kempele, Suomi) and perceived exertion was obtained verbally with the RPE scale at the end of each stage. Respiratory gases were measured with breath gas analyzer (Oxygon Pro and Oxygon Mobile, Jaeger, VIASYS Healthcare GmbH) as 30 seconds means. Additionally, respiratory gases were measured during recovery in sitting position immediately after the first and the last exercise for 30 minutes.

6.3 Calculations

Energy consumption data was calculated based on the RER (respiratory exchange ratio) and thermal equivalents of oxygen for the nonprotein RQ (McArdle et al. 2010, p. 188). Lactate concentration was not measured during the 30 minutes recovery period. RER reflects the macronutrient metabolism in the cell and hence is used to determine substrate use when respiratory gases are measured at the mouth. RER is considered rather reliable indicator of oxidative metabolism in steady-rate conditions. However, in anaerobic conditions lactate is buffered by sodium bicarbonate, which finally produces carbon dioxide in the pulmonary capillaries. This buffering-induced extra non-metabolic created carbon dioxide causes RER to increase > 1. RER values < 0.70 or > 1 cannot be considered purely an indicator of oxidative metabolism. Other conditions where carbon dioxide elimination is increased due to other reason than substrate oxidation is hyperventilation. (McArdle et al. 2010, 190.) In order to eliminate unsteady conditions, the first 15 minutes of the post-exercise measurement as well as all values < 0.70 or > 1 were ignored in the calculations. The HIICT group had three participants who had omitted values in the post-training period measurement and hence, the representative sample of RER-post for HIICT is rather small for the proper statistics.

The rate of fat and carbohydrate oxidation (fats and carbohydrates used in grams per min as means during 15 - 30 min post-exercise) were calculated as a following way (Kuo et al. 2005):

$$\text{CHO oxidation } (g \cdot min^{-1}) = [(\%CHO/100)\,(VO_2)\,(5.05\ kcal \cdot L^{-1}O_2)]/(4\ kcal \cdot g^{-1}\ CHO)$$

$$\text{F oxidation } (g \cdot min^{-1}) = [(1 - \%CHO/100)\,(VO_2)\,(4.7\ kcal \cdot L^{-1}O_2)]/(9\ kcal \cdot g^{-1}\ F)$$

6.4 Statistical analysis

The statistical analysis were carried out with SPSS 22.0 Mac OS X. Before the SPSS analyses, the data was compiled with the Microsoft Excel Mac OS X.

The data is presented as means and standard deviation (SD) of three training groups separately. Nonparametric tests were used to analyze the data. The changes between pre- and post-training periods were analyzed with Wilcoxon test. The between groups comparison was done with Kruskal-Wallis test. The p-value was set at 0.05. The five minutes averages were analyzed with Excel using mean values.

7 RESULTS

The main results were significantly higher post-exercise (15 - 30 min) fat utilization and lower carbohydrate consumption in HIICT compared to SSR. Similarly the post-exercise rate of fat oxidation was significantly higher in HIICT compared to SSR and the rate of carbohydrate oxidation significantly lower in HIICT than in either HIIR or SSR. The differences in fuel consumption were significant only before the eight weeks training period whereas the differences in the rate of fat oxidation remained significant after eight weeks of training between HIICT and SSR. Additionally it is noteworthy that the differences between HIICT and HIIR levelled off after 24 training sessions.

Tables 3,4 and 5 present the data (means and SDs) of each training group separately (HIIR, HIICT and SSR). Additionally the results are presented categorically in text and figures: VO_{2peak}, post-exercise respiratory gases and post-exercise fuel utilization.

TABLE 3. Means, SDs (±) and change (Δ) of pre- and post-training period VO_{2peak} (ml/min/kg) values of three training groups (no significant differences found).

VARIABLE	HIIR (N=5)	HIICT (Pre N=7 Post N =4 - 7)	SSR (N=7)
VO_{2peak}-pre	38.6 (±4.1)	40.5 (±5.7)	40.5 (±6.8)
VO_{2peak}-post	39.4 (±4.9)	39.5 (±5.2)	40.7 (±8.7)
ΔVO_{2peak}	0.78 (±2.1)	-1.0 (±5.2)	0.11 (±2.6)

TABLE 4. Means and SDs (±) of pre- and post-training period respiratory gases of three training groups.

VARIABLE	HIIR (N=5)	HIICT (Pre N=7 Post N =4 - 7)	SSR (N=7)
Ventilation-pre (l/min)	11 (±2)	10 (±2)	9 (±2)
Ventilation-post (l/min)	10 (±22)	10 (±2)	8 (±2)
Breathing frequency BF			
BF-pre (1/min)	16 (±3)	18 (±2)***	16 (±3)
BF-post (1/min)	17 (±3)	16 (±3)	14 (±4)
VO_2-pre (ml/min)	348 (±54)	323 (±36)	282 (±52)
VO_2-post (ml/min)	304 (±64)	358 (±75)	261 (±52)
CO_2-pre (ml/min)	288 (±28)	212 (±71)	244 (±66)
CO_2-post (ml/min)	239 (±30)	261 (±41)	229 (±55)
RER-pre	0.83 (±0.07)	0.73 (±0.20)*	0.87 (±0.05)
RER-post	0.79 (±0.08)	0.78 (±0.07)	0.86 (±0.08)
ΔRER	-0.04 (±0.07)	0.10 (±0.21)	- 0.01 (±0.08)
EQ_2-pre	28 (±4)	28 (±4)	29 (±4)
EQ_2-post	28 (±2)	25 (±3)	28 (±3)

* = significant difference between HIICT and SSR, *** = significant difference between pre- and post-training period within the group.

TABLE 5. Means and SDs (±) of pre- and post-training period distribution of energy used and total energy used in three training groups. CH=carbohydrates, F=fats.

VARIABLE	HIIR (N=5)	HIICT (Pre N=7 Post N =4 - 7)	SSR (N=7)
CH-pre (%)	44 (±25)	8 (±9) *	56 (±16)
CH-post (%)	31 (±27)	26 (±26)	55 (±28)
F-pre (%)	56 (±25)	92 (±9) *	44 (±16)
F-post (%)	69 (±27)	74 (±26)	45 (±28)
CH-pre (kcal)	11 (±6) **	2 (±2) *	12 (±6)
CH-post (kcal)	6 (±4)	6 (±6)	11 (±6)
F-pre (kcal)	15 (±9)	21 (±2) *	9 (±4)
F-post (kcal)	16 (±9)	16 (±6)	8 (±4)
CH-pre (g/min)	0.18 (±0.10) **	0.03 (±0.04) *	0.20 (±0.09)
CH-post (g/min)	0.10 (±0.07	0.10 (±0.10)	0.19 (±0.10)
F-pre (g/min)	0.11 (±0.06)	0.15 (±0.02) *	0.06 (±0.03)
F-post (g/min)	0.12 (±0.06)	0.12 (±0.05) *	0.06 (±0.03)
Kcal-pre	25 (±4)	23 (±3)	21 (±5)
Kcal-post	22 (±4)	22 (±2)	19 (±4)

* = significant difference between HIICT and SSR, ** = significant difference between HIIR and HIICT.

VO_{2peak}. None of the training groups had significant change in peak oxygen consumption after eight weeks training period. Moreover there were no significant differences when three training groups were compared. The figure 3 represents VO_{2peak}

and S.D. (ml/min/kg) pre- (blue) and post- (red) training-period and the figure 4 the magnitude of change in VO_{2peak} value compared to pre- and post-training period.

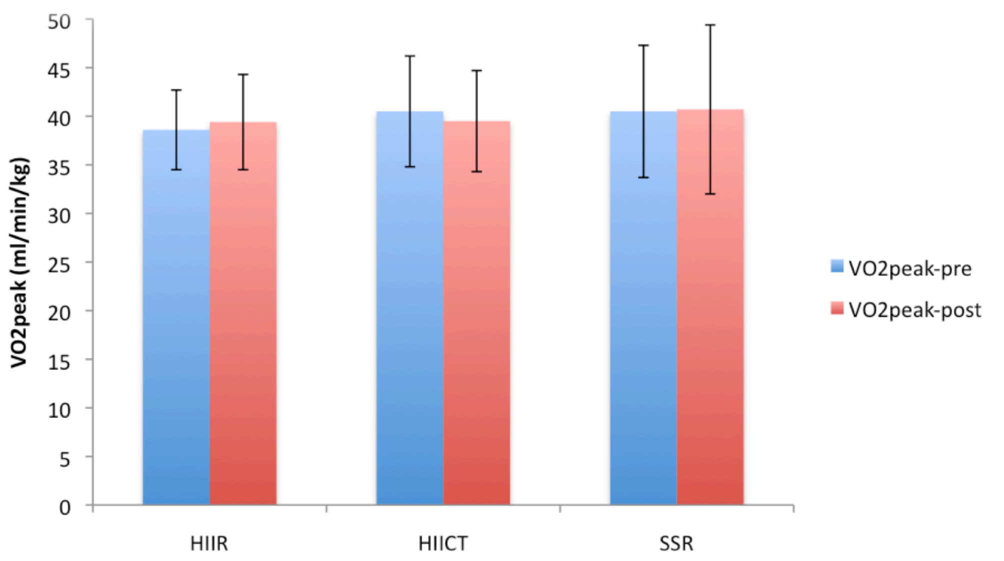

FIGURE 3. Means and SDs (±) of VO_{2peak} (ml/min/kg) pre- and post-training periods in three different training groups.

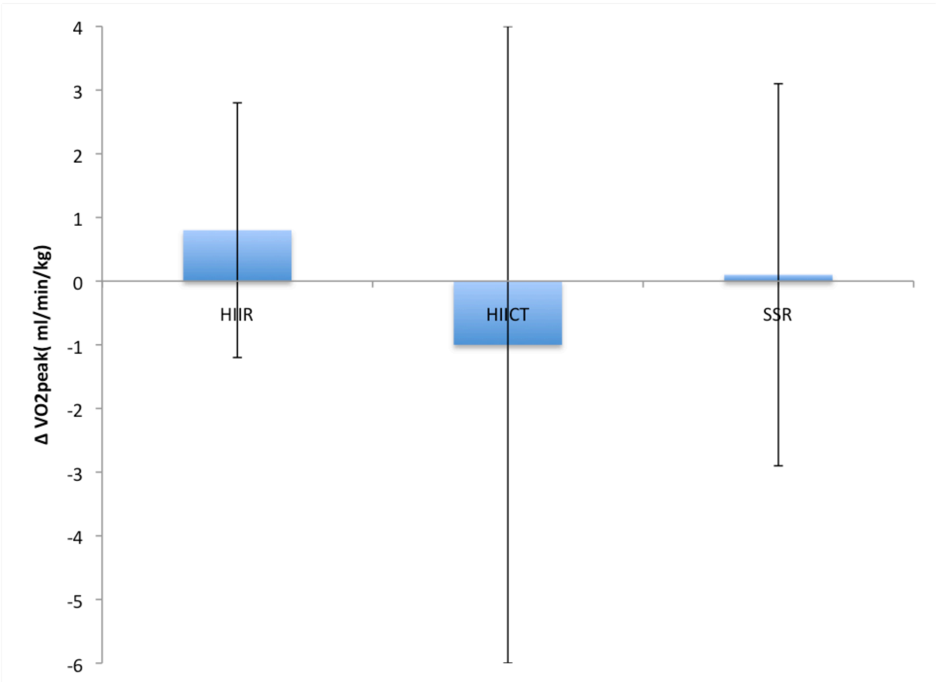

FIGURE 4. Mean changes and SDs (±) in VO_{2peak} (ml/min/kg) after eight weeks of training.

Post-exercise respiratory gases after 8 weeks of training. Breathing frequency (BF) was significantly lower post-training period inside the HIICT group (BF-pre = 18±2, BF-post = 16±3, p = 0.046). However, no significances were found in any group in post-exercise ventilation (VE), oxygen consumption (VO_2), carbon dioxide consumption (VCO_2), respiratory exchange ratio (RER) and in respiratory equivalent for oxygen (EQO_2).

Between-groups comparison in post-exercise respiratory gases. RER of HIICT group (0.73±0.20) was significantly lower than in SSR (0.87±0.05) in pre-training measurements (RER-pre p = 0.018). No other significant differences existed in post-exercise respiratory gases measurement.

Post-exercise fuel utilization after 8 weeks of training. No significant differences existed in fuel (CH and F) consumption when pre-training and post-training periods were compared.

Between-groups comparison in post-exercise fuel consumption. A number of significances were found in the comparison of three different training groups. The % of carbohydrates utilized was significantly lower in HIICT (8±9 %) than in SSR (56±16 %) pre-training period (%CH-pre p = 0.012). Moreover, the relative amount of fat (%) consumed post-exercise was significantly higher in HIICT (92±7 %) than in SSR group (44±16 %) pre-training period. (%F-pre p = 0.012). No significant difference existed between HIIR and SSR or HIIR and HIICT. The figures 5 and 6 present the percentage of fuel utilisation in each group.

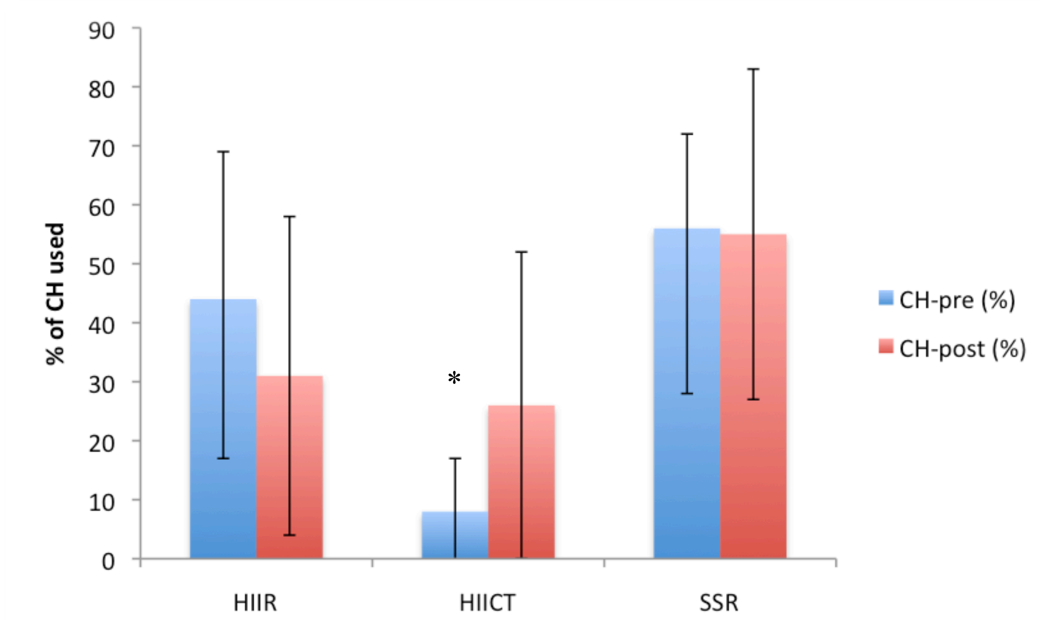

FIGURE 5. Means and SDs (±) of % of carbohydrates used 15 - 30 minutes post-exercise pre- and post-training period. * significantly different from SSR.

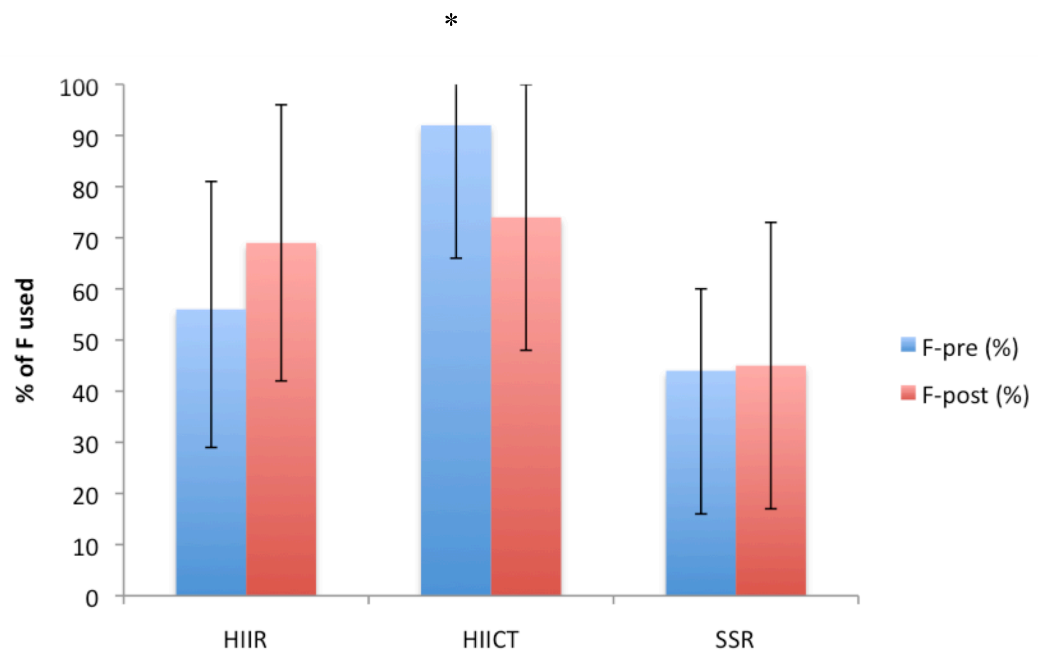

FIGURE 6. Means and SDs (±) of % of fats used 15 - 30 minutes post-exercise pre- and post-training period. * significantly different from SSR.

The total amount of energy derived from carbohydrates was significantly lower in HIICT (2±2 kcal) compared to SSR (12±6 kcal) before eight weeks of training (CH-pre p = 0.026). After the training protocol, no significant differences were found. Furthermore the amount of energy consumed in fats pre-training period was significantly higher in HIICT (21±2 kcal) compared to SSR (9±4 Kcal) (F-pre p = 0.011). The figures 7 and 8 represent the total amount of energy derived from carbohydrates and fats.

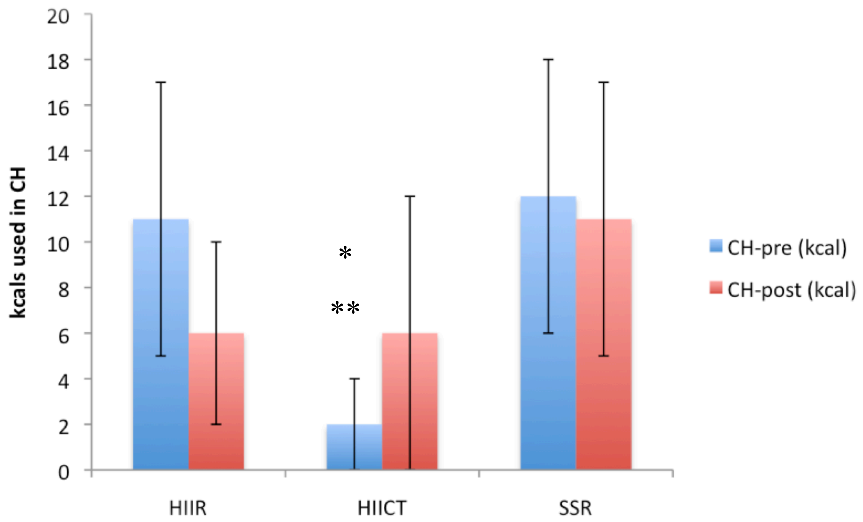

FIGURE 7. Means and SDs of the actual amount of energy from CH 15 - 30 minutes post-exercise pre- (blue) and post-training (red) period. * significantly different from SSR, ** significantly different from HIIR.

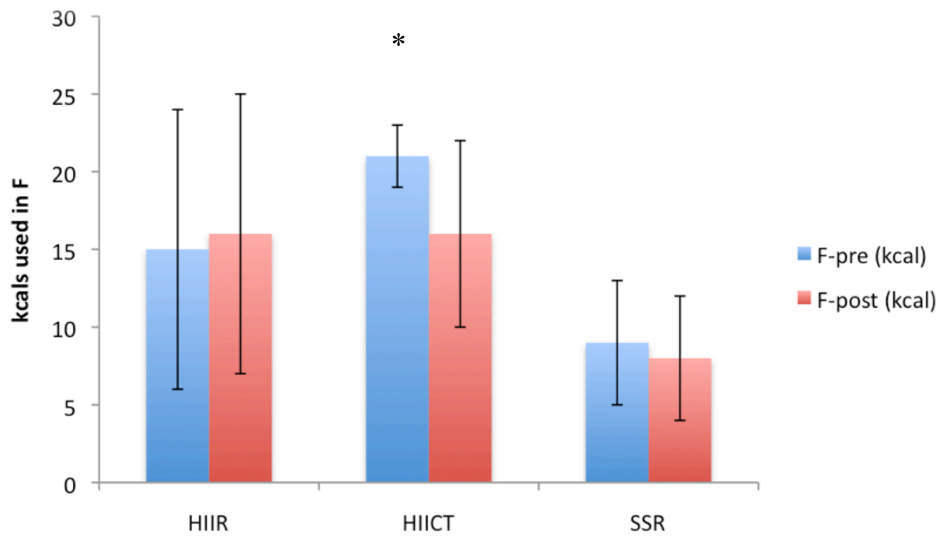

FIGURE 8. Means and SDs of energy from fats 15 - 30 minutes post-exercise pre- (blue) and post-training (red) period. * significantly different from SSR.

When fuel distribution was examined in absolute amounts (grams per minute) representing the rates of carbohydrate and fat oxidation, similar differences between the groups were observed (figures 9 and 10). The rate of carbohydrate oxidation (g/min) was significantly lower in HIICT (0.03±0.04) compared to HIIR (0.18±0.10) and SSR (0.20±0.09) before the training protocol (HIICT/HIIR p = 0.027, HIICT/SSR p = 0.03). After eight weeks of training no significances were found. Correspondingly the rate of fat oxidation was significantly higher in HIICT (0.15± 0.02 and 0.12±0.05) compared to SSR (0.06±0.03 and 0.06±0.03) both pre- and post-training session (Fgmin-pre p = 0.011, Fgmin-post p = 0.043).

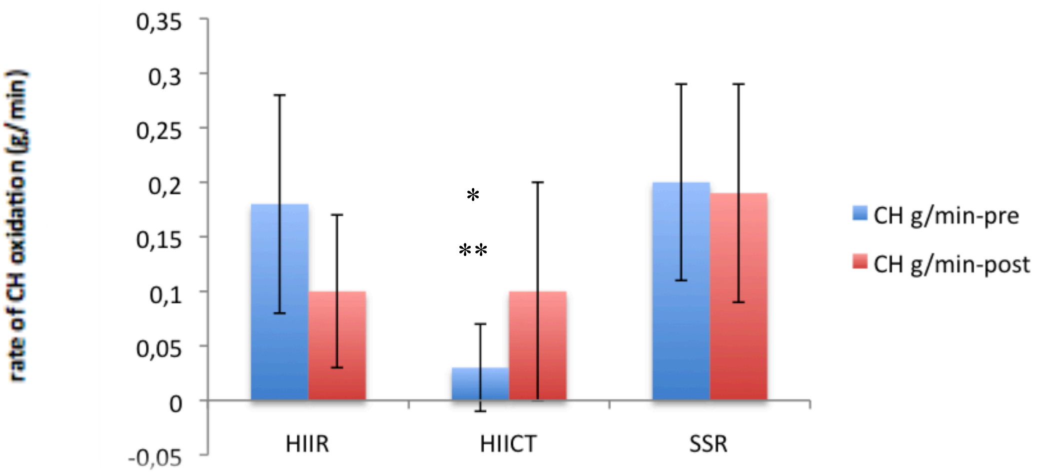

FIGURE 9. Means and SDs of the rate of CH metabolism during 15 - 30 minutes after the cessation of exercise bout pre- and post- training periods. * significantly different from SSR. ** significantly different from HIIR.

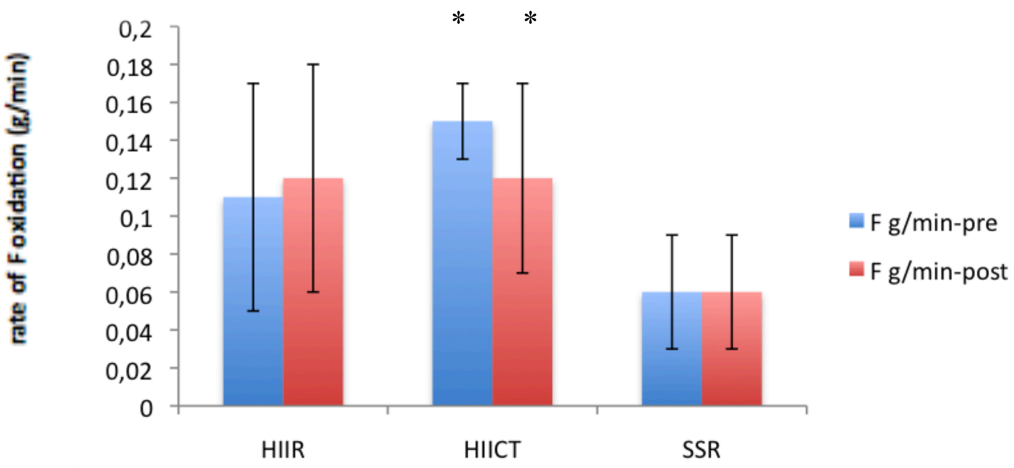

FIGURE 10. Means and SDs of the rate of fat metabolism during 15 - 30 minutes post-exercise pre- and post- training periods. * significantly different from SSR.

The amount of kilocalories used during 15 - 30 minutes after the cessation of exercise bout were calculated in Kcalories per liter of oxygen and in absolute amount of kilocalories. The only significant difference was observed between HIICT and SSR when Kcals per liter of O_2 was calculated (HIICT 4.7, SSR 4.9, p = 0,012).

The calculations and study results are based on the measurements during 15 - 30 minutes post-exercise when respiration and metabolism have at least at some extend stabilized. However, The data was also observed in five minutes averages during 0 – 30 minutes after a workout bout. The figures in the appendix 4 demonstrate the deepest curve in HIICT group when post-exercise fuel utilization transforms from carbohydrates to fats.

8 DISCUSSION

The main finding of this study was that post-exercise fat consumption and the rate of fat oxidation was significantly higher in high-intensity interval circuit training group (HIICT) compared to steady state running group (SSR) (15 - 30 min after the cessation of workout). Fat consumption was significantly higher only before eight weeks of training whereas the rate of fat oxidation remained higher also after the training period. Correspondingly carbohydrate consumption was significantly lower post-exercise in HIICT compared to SSR and the rate of carbohydrate consumption was significantly lower in HIICT compared to both SSR and HIIR. The significant differences in carbohydrate utilization existed only before eight weeks of training.

VO_{2peak}. None of the training groups improved their VO_{2peak} significantly after eight weeks of training, which is contrast with previous studies (e.g. Gromley et al. 2008; Helgerud et al. 2007; Nemoto et al. 2007; Nybo et al. 2010; Schjerve et al. 2008; Tabata et al. 1996; Tjonna et al. 2008). However, like this study, also other studies exist where the improvement of VO_{2peak} in HIIT group is smaller than in the control group (Burgomaster et al. 2008) or the difference between the groups is not significant (Berger et al. 2007; Gibala et al. 2006: Esfarjani et al. 2007; McKay et al. 2009; Trapp et al. 2008). HIIR and SSR had a minor improvement expressed as group means (HIIR 0.78 ml/min/kg, SSR 0.11 ml/min/kg) while in the HIICT group, maximal O_2 consumption decreased 1.04 ml/min/kg. However, the largest standard deviation was in HIICT (5.18 ml/min/kg) as the other groups had smaller distribution in the values (HIIR 2.10 ml/min/kg, SSR 2.58 ml/min/kg). One participant in circuit training group improved VO_{2max} 6.9 ml/min/kg in 8 weeks while one's VO_{2peak} decreased 7.3 ml/min/kg. The initial level of maximal oxygen consumption (ml/min/kg) was rather similar in all groups (HIIR 38.6 ±4.1, HIICT 40.5±5.68, SSR 40.54±6.84). This finding can be explained by individual differences principle, which states that the response to exercise varies between individuals. Even though the same exercise regimen is implemented for the rather homogenous group, not all achieve the same fitness improvement. The baseline level of fitness and genetic factors have an effect on training response. (McArdle et al. 2010, 456-457.)

The study of McRae et al. (2012) used similar whole-body high-intensity exercises (burbees, jumping jacks, mountain climbers, squat thrusts etc.) as was used in the current study. Moreover, the protocols had similarities with the exercise instructions as in the both studies the participants were asked to do as many repetitions as possible in the given time without a iso-caloric equalisation with the control group. Albeit the exercise selection and instructions were similar to the recent study, the training design of McRae et al (2012) mimicked the Tabata (1996) protocol using one set of 8 x 20 seconds of a single exercise separated by 10 seconds of rest. The control group conducted 30 minutes of continuous treadmill running with the aerobic intensity. Contrary to the recent study, both groups achieved improvements in aerobic fitness although only circuit training group improved their skeletal muscle endurance as well. Since the baseline level of VO_{2max} of the participants was relatively similar compared to the current study, the initial level of fitness does not explain contradictory results. Rather different metabolic stress induced by Tabata-style workout and individual differences in training responses might be the explaining factors. This study did not examine the muscle endurance or strength and hence, this could be an area of research in the future studies.

Post-exercise fat utilization. The novel finding of the study was that high-intensity interval circuit type training, where whole body is challenged, seems to stimulate fat oxidation more than high-intensity interval running or moreover, steady state running. Even though there were no significant difference in most variables between HIICT and HIIR, the results suggest that post-exercise fat utilization is more effective after HIICT than HIIR. That is demonstrated with the significant difference between HIICT and SSR, but not between HIIR and SSR. Furthermore, the significant difference was found in the pre-training measurement in the rate of carbohydrate oxidation (g/min) between HIICT and HIIR as well as SSR.

The significantly increased lipolytic effect of HIICT may be explained by a variety of ways. The most classical explanation seems to be that glycogen stores are filled and glucose is moreover spared to further oxidation. Consequently fats serve as a primary energy source. (Paoli et al 2012.) The other explanations are related to mitochondrial capacity and activity as well as enzyme and hormonal functions. AMP-activated protein kinase activation is increased after high-intensity exercise (Gibala 2009), which leads to decreased acetyl CoA Carboxylase activity. As a result, the rate of the synthesis of MalonylCoA is decreased leading to release of inhibition of CPT1 (carnitine palmitoyltransferase) activity. The outcome of the above-described reactions is increased lipid metabolism. (Paoli et al. 2012.) Furthermore, ANP (atrial natriuretic peptide) is shown to increase the rate of lipolysis and the production of this enzyme is related to the magnitude of oxygen consumption (Souza et al. 2011). Additionally HIIT is reported to increase the capacity of mitochondria. It is known that PGC-1α is the main regulator in mitochondria biogenesis and exercise intensity in turn, seems to be the most important factor inducing increased PGC-1α activation in skeletal muscles. (Gibala et al. 2012.)

Hormonal responses related to enhanced fat oxidation after HIIT are mainly caused by increased concentrations of catecholamines and growth hormone. Circulating levels of adrenalin and noradrenalin increases significantly in high intensities. (McArdle et al. 2010, 434.) The importance of catecholamine response is related to more effective fat oxidation. Lipolysis is negatively controlled by insulin and activation of α adrenergic receptors. Accordingly, it is positively controlled by the action of catecholamine on β adrenergic receptors as well as growth hormone and ANP (atrial natriuretic peptide). The secretion of catecholamine results in inhibition in insulin secretion by stimulating α adrenergic receptors on pancreatic cells. Insulin in turn inhibits lipid oxidation and thus a decline of insulin is a stimulus for fat oxidation. Also growth hormone serves as a lipolytic hormone. (Borer 2013, pp. 100-108.)

A number of significant differences were demonstrated in between-groups comparison. However, contrary to the hypothesis, relevant changes were not found when pre- and post-training period was compared. This is in controversy with previous studies where lipid oxidation was enhanced after a period of HII-training. E.g. Whyte et al. (2010) reported significantly higher fat oxidation rate after 6 sessions of high-intensity sprint interval training in obese/overweight men. Moreover, Talanien et al. (2007) reported significantly increased whole body fat oxidation (36 %) after two weeks training period with submaximal HIIT (10 x 4 min with 2 min recovery). However, the small amount of participants in the recent study as well as RER values collection only until 30 minutes post-exercise may have had an influence on the results. Since the ventilation was apparently not normalized and lactate buffering was ongoing in some of the HIICT group participants, three of seven RER values were discarded. Considering that all the substrate metabolism calculations were based on RER, the amount of numbers analyzed was rather small for the proper statistical analysis. Nonetheless, this had an effect only on the RER-related pre -and post-training period comparison, which was just a part of the study. Between-group comparison in pre-training period as well as not RER-related results were achieved successfully.

The difference between HIIR and HIICT in distribution of fuel usage. There were only one significant difference between two high-intensity interval training groups (the rate of CH oxidation in the pre-measurement). Nonetheless, the closer observation to the results revealed that the difference shown in the pre-measurement narrowed in the post-measurement. Therefore, the numbers in the post-measurement between HIIR and HIICT were rather close to each other possibly indicating a stronger adaptation to training in HIIR. The average difference in RER-pre between HIIR and HIICT was 0.10 while RER-post difference was only 0.01. Moreover, the difference between distribution of energy used followed the same pattern. The participants of HIIR utilized 36 % more CH pre-training period compared to HIICT. However, after eight weeks of training the HIIR group consumed only 5 % more carbohydrates than the subjects in HIICT group. Correspondingly, the subjects of HIIR consumed 36 % less fats pre-training period compared to HIICT. Nonetheless, the difference leveled off after the training period whereas HIIR group used only 5 % less fats than HIICT participants.

When the energy distribution difference was observed in kilocalories, HIIR consumed 8,7 kilocalories more from CH and 6,3 kilocalories less from F compared to HIICT pre-training. Post-training HIIR consumed only 0.1 kilocalories more from CH and 0.3 kilocalories less from F.

The difference between HIIR and HIICT levelled off also in the rate of fuel oxidation. Similar pattern was observed in the rate of fat oxidation. The results implies that the improvement of fat oxidation may be higher in submaximal high-intensity interval running compared to whole-body challenging high-intensity interval circuit training after 8 weeks of training. The improved fat oxidation capacity was expected after a HII training period and is in line with the previous studies (Astorino et. al 2013; Haff 2009; Perry et al. 2008; Talanian et al. 2007). However, why HIIR seemed to be more effective than HIICT in training-induced increasing of fat metabolism, remains unsolved.

In the post-measurement, the HIIR group consumed less carbohydrates and more fat, still not significantly, compared to pre-training. However, the total amount of kilocalories consumed was lower post-training (21.8±3.5) compared to pre-training (25.3±3.5). The result may imply to an improvement in running economy, which refers to the energy demand for a given pace of submaximal running (Barnes & Kilding 2015).

Energy expenditude. No significant differences were found in post-exercise oxygen consumption either in total kilocalories consumed. However, the absolute values were higher in interval training groups both pre and post 8 weeks of training compared to SSR: O_2 (ml/min) consumed HIIR 348/304, HIICT 323/358, SSR 282/261; KCal consumed HIIR 25/22, HIICT 23/22, SSR 21/19. When energy consumption was observed as kilocalories per liter of O_2, there was a significant difference in pre-training measurement between HIICT and SSR (HIICT 4.7±0.03 kcal/LO_2 and SSR 4.9±0.06 kcal/LO_2). The study of Chan & Burns (2013) compared the oxygen uptake and energy expenditure after a bout of high intensity sprint training and rest. Both values were significantly elevated after an exercise bout compared to rest. However, the positive effect was rather short-lived lasting only 30 minutes post-exercise. This is in line with the results of the other study, which indicated that a single bout of high intensity sprint training does not effect on resting metabolism measured during 23 hours post-exercise, but has an influence on total daily energy expenditure (+ 950 kJ) (Sevits et al. 2013). Due to a short measurement period as well as an absent data of the baseline situation of the current study, it is not known if there has been a long-term effect. Future studies should determine what is the effect of high intensity circuit training on total daily energy expenditure.

Study design. One factor explaining the difference between HIIR and HIICT results may be related to study design. The intensity of the exercise was not the same in these two groups. The velocity of treadmill running was fixed to be comparable to approximately 90 % of the HR_{max}. Consequently, the intensity was submaximal and stable. However, in the HIICT the exercise was implicated in a different manner. Firstly, the intensity was not stable due to the exercise selection, but it varied through to movements being smaller in some exercises, e.g. plank, and higher in some, e.g. jumping lunges. Secondly the participants were instructed to perform as many repetitions as possible in one minute. As a result they ended up to exhaustion and failure. The similar aspects of the exercises were time committed (warm-up and 10 times 1 minute with 30 seconds rest between) and high intensity of the exercise bouts. The HIIR protocol was similar than Gibala et al. (2012) have used (10 x 60 seconds at the intensity of 90 % HR_{max} with 60 seconds rest between the sets) except the recovery phase was only 30 seconds in our study reducing the total time commitment.

A variety of studies researching lipid oxidation have used biopsy samples from muscles (e.g. Talanian et al. 2007 and Talanian et al. 2010). However, some researches (e.g. Chan & Burns 2013) including this study measured respiratory gases in order to evaluate metabolism. Respiratory exchange ratio (RER) was used to estimate the source of substrate used and together with oxygen uptake value, the overall rate of energy consumed. RER values are ranging between 0.70 (100 % lipids, 0 % carbohydrates) – 1.0 (0 % lipids, 100 % carbohydrates) indicating a macronutrient utilization distribution. RER is known to evaluate rather well oxidative metabolism in steady-state conditions. However, some circumstances may invalidate the RER validity. Hyperventilation may increase the RER value over 1.0 and hypoventilation in turn, might decrease it under 0.7. In these conditions RER illustrates the state of respiration as well as substrate metabolism and thus, is not a valid indicator of oxidative metabolism alone. (Duncan & Howley 1999.) Moreover, RER more than 1.0 or under 0.7 may reflect lactic acid buffering by sodium bicarbonate causing carbon dioxide elimination and retention (Chan & Burns 2013). This condition might exist after an intensive exercise bout as in the current study. Consequently, the values measured during the first 15 minutes post-exercise as well as values over 1.0 or under 0.7 were omitted in the result calculations.

Future studies. Future research should continue to compare and study different modes of HIIT (running, cycling, circuit training, stair climbing etc.), since the present studies have primarily used cycling or running as training modes. Studies should also investigate the acute post-exercise responses e.g. 1, 8, 16, 24 and 48 hours after an exercise bout. Additionally future research could study the long-term effect of increased post-HIICT lipid oxidation on body weight and composition. The study of Kari (2015) used the same data as was used in the current study examining the effect of 8 weeks of HIIR, HIICT and SSR on body composition. As a contrary what would be expected based on the increased fat utilization reported in this study and a spectrum of researches, the interval training groups did not have significant changes in body weight or most of the body composition parameters. However, the fat mass of the arms decreased significantly in HIICT groups, which is correspondent with the fact that the training program was relatively loading for the arms. These to some extent controversial results are in line with the study of Alkahtani et al. 2013, where moderate intensity interval training and high intensity interval training resulted in increased post-exercise fat oxidation without changes in body composition.

The most relevant finding of the current study was the enhanced lipid oxidation after high intensity circuit type training. In order to research only the post-exercise substrate metabolism in the future studies, the study design should be different. The training period is not necessary and consequently it might be easier to recruit greater amount of participants. However, the examination of lipid oxidation was not the only purpose of the recent study and hence, the training period was reasonable. In the future studies, the researchers should concentrate on to equalize the O_2 or energy consumption of different training modes. The limitation of the recent study was that the intensity was not equal in HIIR and HIICT groups. For example, Tjonna et al. (2008) compared HIIT and continuous aerobic exercise using study protocols with matched energy expenditure. Moreover, in the future studies the post-exercise gas collection could begin later and last longer, e.g. 30 – 120 minutes post-exercise.

Practical applications. The findings of the study are interesting in terms of weight reduction and moreover fat loss. The circuit training type exercise, which can be performed practically anywhere in a relatively short time might be tempting for busy individuals aiming to lose weight. Even though a high motivation is required to perform the exercise to the point of exhaustion and failure, some studies suggest that HIIT might be even more enjoyable than traditional training methods (Bartlett et al. 2011). However, due to the amount of different movements (e.g. squats, push-ups and planks), the exercise is more complicated compared to running. Proper execution of the movements is required in terms of safe training. (Klika & Jordan 2013.)

The HIICT exercise method that combines aerobic HIIT and body weight resistance exercises can be considered time-efficient way to improve metabolism. This might be an exercise protocol that includes and combines the guidelines recommendations (such as UKK-instituutti liikuntapiirakka) for aerobic and strength training in a time sparing manner. This is essential in the society where lack of time is the main reason not to exercise and simultaneously the problems related to sedentary lifestyle, such as overweight, are extensive. The results of the current study are promising concerning the metabolic effect of HIICT. However, further investigations are required to demonstrate overall health benefits (e.g. aerobic fitness, muscle mass and strength, bone mineral density) of circuit training type high-intensity interval training.

From the physiological point of view, the combination of HIIT and traditional endurance training might be the most effective in order to reduce specifically abdominal fat. Compared to subcutaneous fat depots, abdominal fat is reported to be more numerous in lipolytic β-adrenergic receptors. Epinephrine and norepinephrine binds to before mentioned receptors. Keeping in mind that HIIT is an effective to increase the plasma concentration of catecholamines (epinephrine and norepinephrine) in contrast of low- or moderate intensity exercise, HIIT has the potential to target especially to abdominal fat. (Boutcher 2011.) Moreover, Riviere et al. (1989) reported that endurance-trained women had enhanced sensitivity of β-adrenergic receptors and decreased sensitivity in anti-lipolytic α-adrenergic receptors. Consequently, in theory HIIT combined to endurance training may improve the reduction of abdominal fat.

Conclusion. High-intensity interval circuit training was superior in fat consumption 15 - 30 minutes post-exercise compared to equal duration high-intensity interval running or longer duration moderate intensity continuous running. This finding between HIIR and HIICT existed only when the exercises were new to the participants. After eight weeks of training the differences between HIICT and HIIR levelled off. HIICT also induced higher rate of fat oxidation compared to SSR before the training period of eight weeks. No significant differences between three training groups were found in the improvement of maximal aerobic capacity after eight weeks of training.

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APPENDIX 1: HEALTH QUESTIONNAIRE (IN FINNISH)

TERVEYSKYSELY

On tärkeää, että tiedämme terveydestäsi, elintavoistasi ja liikuntatottumuksista ennen tutkimuksen alkamista ja siihen liittyviä testejä. Vastaa seuraaviin kysymyksiin huolellisesti. Ota tämä lomake mukaan jo varsinaista tutkimusprojektia edeltävään lääkärintarkastukseen, jossa yhteydessä voidaan keskustella tarvittaessa mahdollisista terveysongelmista tai oireista.

Nimi__________________Syntymäaika____________Paino_______Pituus________

Ei Kyllä

1. Onko sinulla todettu hengitys-, sydän-, tai verenkiertoelimistön sairauksia? □ □
   Mitä?_______________________________________
2. Onko sinulla todettu verenpainetautia? □ □
3. Onko sinulla todettu korkea kolesteroli? □ □
4. Onko sinulla muita sairauksia? □ □
   Mitä?_______________________________________¨
5. Onko joku läheinen sukulainen (isä, äiti, veli, sisko) kokenut sydänkohtauksen tai hänelle on tehty sydänkirurginen toimenpide ennen ikää 50? □ □
6. Käytätkö säännöllisesti lääkkeitä? □ □
   Mitä?_____________________________________
7. Onko sinulla ollut rintakipuja tai hengenahdistustuntemuksia
   a. levossa? □ □
   b. rasituksessa? □ □
   Miten usein ja millaisia?__________________________
8. Onko sinulla ollut rasituksen aikana rytmihäiriöitä, huonovointisuutta tai tajuttomuuskohtauksia? □ □
9. Onko sinulla selkävaivoja tai muita tuki- ja liikunta-elinten pitkäaikaisia tai usein toistuvia vaivoja? □ □
   Mitä?____

10. Oletko viimeisen kahden viikon aikana sairastanut □ □
jotakin tulehdustautia (flunssa, kuumetauti)?
11. Oletko raskaana? □ □
12. Onko sinulla kehossasi elektronisia laitteita (esim sydämen □ □
tahdistin) tai metallisia esineitä (esim. ruuveja)?
13. Tupakoitko? □ □
Jos kyllä, montako savuketta/vrk?____________
Jos olet lopettanut tupakoinnin, milloin (vuosi)?___________
14. Koska olet viimeksi nauttinut alkoholia?_____________Kuinka
paljon?___________
15. Mikä on nykyisen työsi fyysinen rasittavuus?
-toimistotyö tai vastaava □
kevyt ruumiillinen työ □
raskas ruumiillinen työ □
16. Miten kuljet työmatkasi?_________________ Työmatkan kesto
_________min/päivä
17. Kuinka usein olet harrastanut liikuntaa viimeisen kolmen kuukauden aikana?
-en lainkaan □
-kerran viikossa □
-2-3 krt viikkossa □
-säännöllisesti yli 4 kertaa viikossa □
Mitä liikuntaa olet harrastanut?
____
18. Arvio oma kuntotasosi asteikolla 1=heikko, 2=välttävä, 3=keskitasoinen,
4=hyvä, 5=erinomainen
Kuntoarvio:__________________

Vakuutan antamani tiedot oikeiksi, tunnen testaustavan ja osallistun siihen omalla vastuullani.

Jyväskylässä ___________/_________/2013

Allekirjoitus____

APPENDIX 2: NUTRITIONAL INSTRUCTIONS (IN FINNISH)

RAVITSEMUSOHJE

- Huolehdi riittävästä ja monipuolisesta ravinnon saannista!
- Proteiinin riittävä saanti on tärkeää (esim. liha, kala, kana, raejuusto, maitorahka)
- Rasvojen saannissa kiinnitä huomiota hyvälaatuisten (pehmeiden) rasvojen saantiin, vähennä huonolaatuisia (kovia) rasvoja (hyviä esim. kasviöljyt (rypsi, oliivi tms.), kasvirasvalevitteet)
- Kasviksia, vihanneksia ja hedelmiä runsaasti, vähintään 0,5 kg päivässä
- Pidä ruokailuvälit tasaisena! Ei liian pitkiä ruokailuvälejä, sopiva n. 3-4 tuntia
- 4 – 6 ateriaa päivässä
- Suosi vähärasvaisia tuotteita ja täysjyvävilja tuotteita, vältä liiallista sokerin ja suolan käyttöä
- Juo riittävästi (noin litra päivässä), käytä vettä janojuomana

RAVINTOAINEIDEN SAANTI

RASVAT: Rasvan saannin suositeltava vaihteluväli on 25–35 % energiansaannista. Kovan rasvan osuus olisi hyvä pitää alle 10 %:n.

Nykyään kovaa rasvaa saadaan eniten juustoista, liharuoista ja erityyppisistä ravintorasvoista. Makeista ja suolaisista leivonnaisista kovaa rasvaa saadaan yhtä paljon kuin liharuoista. Suosi vähärasvaisia tuotteita ja leivänpäällä esim. kasvirasvalevitettä.

HIILIHYDRAATIT: Hiilihydraattien osuudeksi suositellaan 50–60 % energiansaannista. Kuitupitoisten hiilihydraattien määrää tulisi lisätä ja puhdistettujen sokereiden osuutta vähentää. Hiilihydraatti- ja kuitusuositus toteutuu käytännössä, kun lisätään täysjyväviljavalmisteiden, erityisesti ruisleivän, ja juuresten, vihanneksien sekä hedelmien ja marjojen osuutta ruokavaliossa ja vähennetään sokerin ja paljon sokeria sisältävien elintarvikkeiden käyttöä.

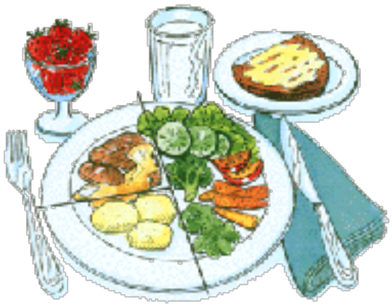
PROTEIINIT: Proteiinin suositeltava saanti on 10–20 % energiansaannista.

Proteiinia saadaan eniten eläinperäisistä elintarvikkeista, lähinnä lihasta ja maidosta. Hyviä proteiinin lähteitä ovat myös pähkinät, siemenet ja palkokasvit, kuten herneet, pavut ja erilaiset soijavalmisteet, jotka ovat myös hyviä proteiinin lähteitä

VITAMIINIT: Riittävällä ja monipuolisella ravinnolla pystytään turvaamaan riittävä vitamiinien saanti normaalisti. Kasviksissa, marjoissa ja hedelmissä on paljon vitamiineja.

ATERIAN KOOSTAMINEN

Lautasmalli hyvä esimerkki!



PÄIVITTÄINEN ENERGIANTARVE

Aktiivisilla miehillä n. 2800 – 3300 ckal ,

aktiivisilla naisilla n.1900 – 2600 ckal

APPENDIX 3: HIICT PROGRAM (MAINLY IN FINNISH)

KUNTOPIIRIOHJE

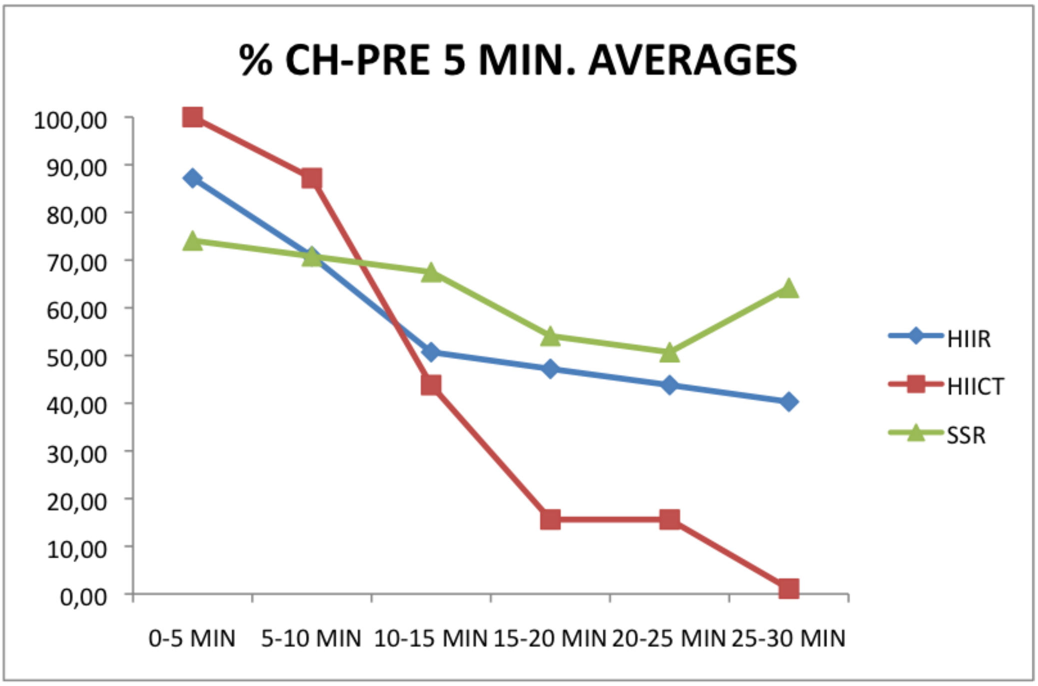
Sinut on arvottu HIIT-kuntopiiriryhmään. Tässä ohjeet harjoituksen toteuttamiseen.

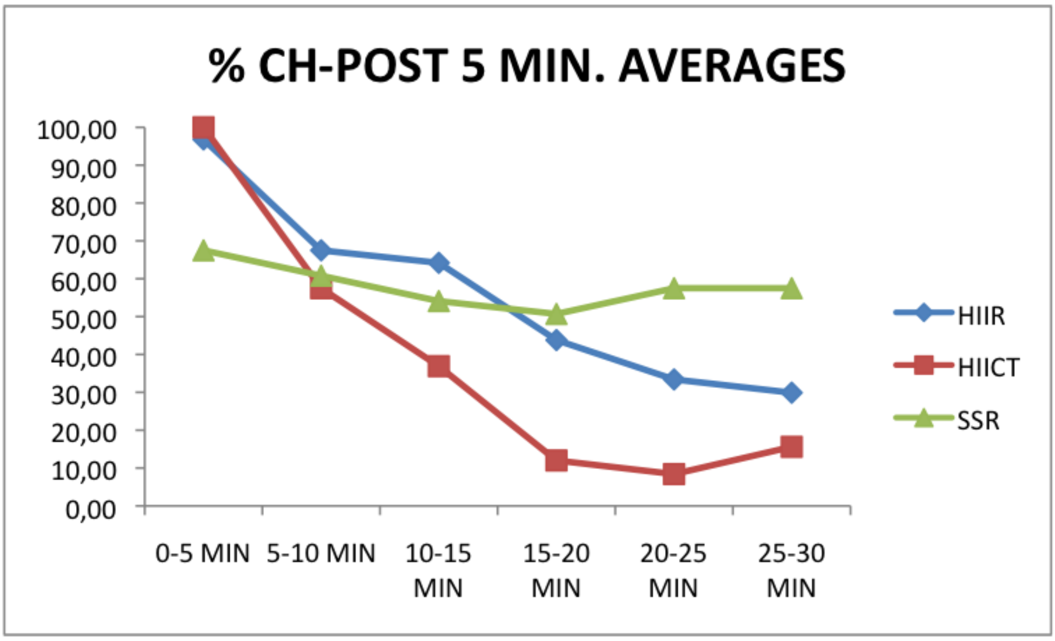
- Tee harjoitus 3 x/vko ja pidä vähintään yksi välipäivä harjoitusten välissä.
- Harjoitusohjelma on nousujohteinen siten, että viikoilla 1-3 teet 8 työosuutta (liikkeet 1-8), viikoilla 4-6 9 työosuutta ja viikoilla 7-8 10 työosuutta
- Tee jokaista liikettä 1 minuutti ja pidä välissä 30 sekunnin palautus
- Tee jokaista liikettä niin monta toistoa kuin pystyt minuutin aikana
- Lämmittele ennen kuntopiiriä omatoimisesti noin 5 minuuttia esim. hölkäten, hypellen, kyykäten ja vartaloa kiertäen
- Harjoituksen voi tehdä missä vain sisätilassa (tarvitset tilaa vähintään noin 2x3m)

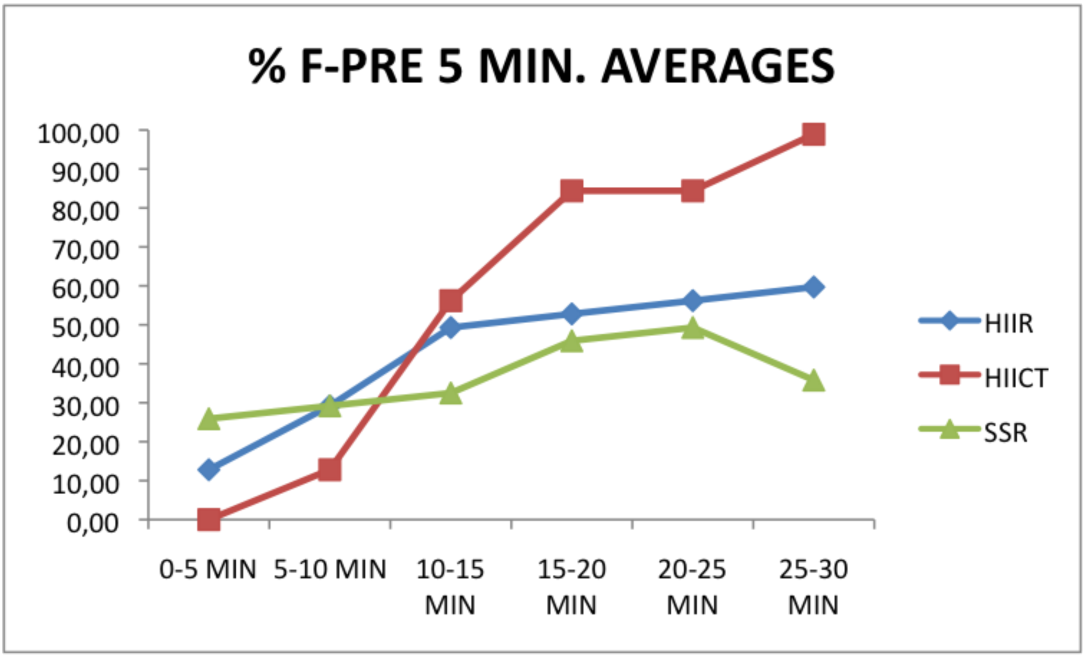
LIIKKEET/EXERCISES

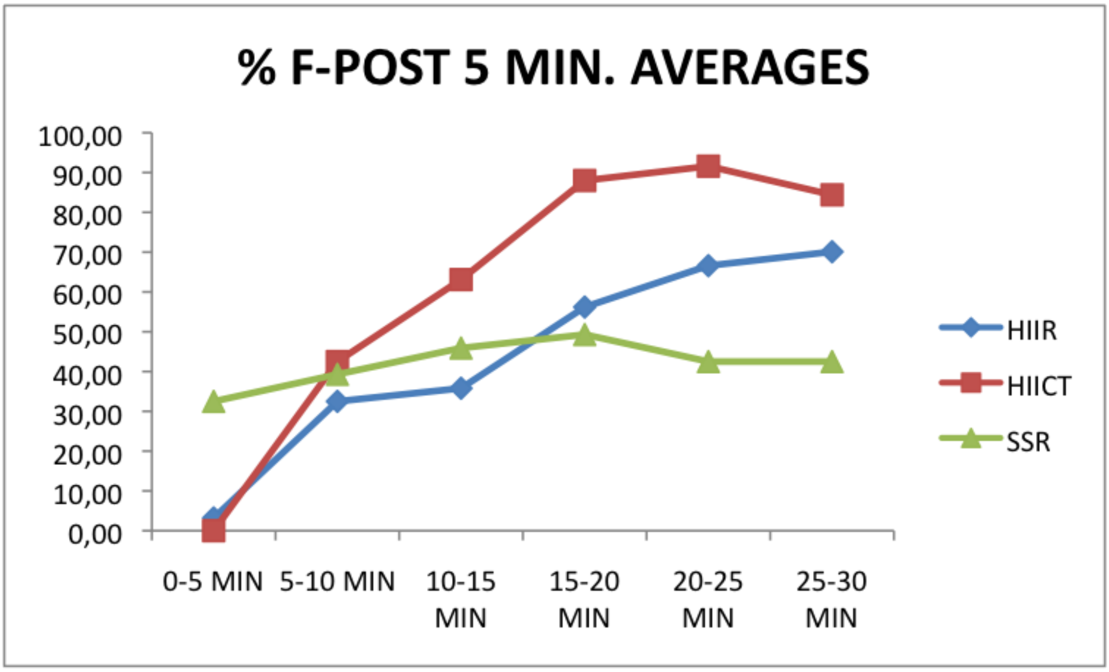
1. Haaraperushyppy (jumping jacks)
2. Haaraperuspunnerrus (push up with a jumping jack in push-up position)
3. Burpee
4. Skorpionipunnerrus (scorpion push-up)
5. Askelkyykkyhyppy (jumping lunge)
6. Lankkukierto (rotational plank)
7. Luisteluhyppy (skating jump)
8. Etunojassa polvennostojuoksu (mountain climber)
9. Vauhditon pituushyppy (long jump from the spot)
10. Kyykky (kosketa sormenpäillä lattiaan ja ojenna kädet ylös suoriksi) (squat)

APPENDIX 4: FUEL DISTRIBUTION IN 5 MIN AVERAGES






% F-PRE 5 MIN. AVERAGES
100,00
90,00
80,00
70,00
60,00
50,00
40,00
30,00
20,00
10,00
0,00
0-5 MIN
5-10 MIN
10-15 MIN
15-20 MIN
20-25 MIN
25-30 MIN
HIIR
HIICT
SSR


% F-POST 5 MIN. AVERAGES
100,00
90,00
80,00
70,00
60,00
50,00
40,00
30,00
20,00
10,00
0,00
0-5 MIN
5-10 MIN
10-15 MIN
15-20 MIN
20-25 MIN
25-30 MIN
HIIR
HIICT
SSR