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High-intensity interval eccentric cycling: Acute and chronic effects

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PhD Thesis

High-intensity interval eccentric cycling: acute and chronic effects

This thesis is presented for the award of
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ABSTRACT

Eccentric cycling training has been prescribed in continuous and low intensities protocols, based on concentric cycling parameters. While the lower metabolic demand of eccentric than concentric cycling is advantageous for clinical or 'at-risk' populations, it is a disadvantage for cardiovascular and pulmonary adaptations. High-intensity interval protocols may increase both, strength and endurance. Thus, this research project compared i) an incremental concentric and eccentric cycling test until exhaustion for the relationship between power output and physiological parameters <**Study1**>; ii) interval and continuous eccentric cycling protocols for oxygen consumption, perceived exertion and enjoyment <**Study 2**>; and iii) aerobic performance, muscle morphology and function after 8-week interval eccentric versus concentric cycling training <**Study 3**>. **Study 1:** Nine men and two women (20-48 y) performed an incremental concentric and eccentric cycling test. Peak power output (PPO) was 53% greater ($P<0.001$) for eccentric (449 ± 115 W) than concentric cycling (294 ± 61 W), and peak oxygen consumption was 43% lower ($P<0.001$) for eccentric (30.6 ± 5.6 $ml \cdot kg \cdot min^{-1}$) than concentric (43.9 ± 6.9 $ml \cdot kg \cdot min^{-1}$), but maximal heart rate was similar between eccentric (175 ± 20 bpm) and concentric cycling (182 ± 13 bpm). For training prescription, concentric PPO could be an alternative reference parameters to heart rate, but optimally eccentric PPO should be used. **Study 2:** The same subjects as those of Study 1 performed continuous cycling at 60% of PPO for 20 min at 60 rpm, and 13.2 min at 90 rpm (CONT13@60%), 4 x 4 min intervals at 75% of PPO with 2 min rest, 12 x 1 min at 100% of PPO with 1 min rest and 10 x 1 min at 150% of PPO with 1 min rest (INT1x10@150%). Total VO_2 was the largest ($p<0.0001$) during INT1x10@150% (382 ± 73 $ml.kg^{-1}$) and smallest ($p<0.0001$) during CONT13@60% (146 ± 27 $ml.kg^{-1}$). The interval protocols resulted in greater VO_2 ($P<0.0001$) than continuous protocols, and thus interval eccentric cycling could increase mechanical and metabolic load more than continuous eccentric cycling. **Study 3:** Eighteen men (19-56 y) performed either eccentric (EC, n=9) or concentric cycling (CC, n=8) twice a week for 8 weeks on an isokinetic cycling ergometer. Intensity was matched for perceived effort, started at 30% and 45%, and increased to 36% and 70% of concentric sprint PPO (10s) for CC and EC, respectively, and progressively increased from 5 x 2 min with a 1-min rest to 7 x 2 min with 30-s rest. The magnitude of increases in quadriceps cross-sectional area, concentric sprint PPO, countermovement and squat jump was greater ($P<0.05$) for EC than CC, while there were no significant differences for VO_{2peak}, incremental concentric PPO, 6-min walking distance and maximal isometric knee extension strength. It appears that interval eccentric cycling can increase strength and endurance

simultaneously. The three studies have highlighted parameters and procedures for eccentric cycling training prescription, and metabolic advantages of high-intensity interval protocols. Interval eccentric cycling training with a progressive periodisation of intensity and volume increased strength, power, and oxygen consumption, which should be considered in future application of eccentric cycling.

DECLARATION

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List of Abbreviations

1RM	1 repetition maximum
6MW	6-min walk test for distance
ANOVA	Analysis of variance
AUC	Area under the curve
B_f	Breathing frequency
CC	Interval concentric cycling training group in study 3
CMJ	Countermovement jump
CON	Concentric
CON-T	Incremental concentric cycling test in study 1
CSA	Cross-sectional area
EC	Interval eccentric cycling training group in study 3
ECC	Eccentric
ECC-T	Incremental eccentric cycling test in study 1
FL	Fascicle length
g	Hedges' g
HIT	High-intensity interval training
HR	Heart rate
ISOM	Isometric
MVC	Maximal voluntary isometric contraction
PA	Pennation angle
PPO	Peak power output
PPO_{10s}	Peak power output during a 10 s sprint
PPO_{inc}	Incremental peak power output
RPE	Rating of perceived exertion

SD	Standard deviation
SJ	Squat jump
VO_2	Oxygen consumption
VO_{2peak}	Maximal oxygen consumption
V_E	Minute ventilation
V_t	Tidal volume

List of Publications

Some chapters found in this thesis have been published, submitted to peer-reviewed journals and presented at national or international conferences.

Chapter 4

Lipski M, Abbiss CR, Nosaka K. Cardio-pulmonary responses to incremental eccentric and concentric cycling tests to task failure. Eur J Appl Physiol. 2018 Feb 20;1–11.

Chapter 5

Lipski M, Abbiss CR, Nosaka K. Oxygen consumption, rate of perceived exertion and enjoyment in high-intensity interval eccentric cycling. Eur J Sp Sc. (manuscript in peer-review)

Chapter 6

Lipski M, Abbiss CR, Nosaka K. Effects of high-intensity interval eccentric versus concentric cycling training. Med Sci Sports Exerc (manuscript to be submitted in April 2018)

Additional publications arising from this PhD research

Lipski M, Abbiss CR, Nosaka K. Not all eccentric exercises are the same: characteristics and differences (manuscript to be submitted in June 2018)

Lipski M, Abbiss CR, Nosaka K. The differences in training adaptations between various intensities of eccentric exercise (manuscript to be submitted in August 2018)

Conference presentations

Lipski, M., Abbiss, C.R. & Nosaka, K. Metabolic Demand of Interval versus Continuous Eccentric Cycling Exercise. Science on the Swan Conference. 2016: Perth, Australia

Lipski, M., Abbiss, C.R. & Nosaka, K. Eccentric versus Concentric incremental maximal cycling test. In: Proceedings of the 21st Annual Congress of the European College of Sport Science. 2016: Vienna, Austria.

Lipski, M, Abbiss, C.R. & Nosaka, K. High-Intensity interval eccentric cycling training improves muscle function and aerobic capacity. In: Proceedings of the 22nd Annual Congress of the European College of Sport Science. 2017: Essen, Germany.

3 Minute Thesis (3MT) competition at Edith Cowan University, Joondalup, Australia

Lipski, M. Easy "eccentric" exercise. 2014. 3rd place finish at University level

Lipski, M. Please sit down. 2015. Finalist at University level.

Lipski, M. All in one exercise. 2016. Joint 3rd place finish at University level

CHAPTER ONE

INTRODUCTION

1.1 Background

Three types of contractions are performed by muscles to generate force: isometric (static), concentric (shortening) and eccentric (lengthening). During isometric contractions, muscles produce a force that is equal to an external load thus muscle length remains constant or shortens slightly (1–3). During concentric contractions muscle force exceeds the external load, resulting in muscle shortening (4,5). Conversely, during eccentric muscle actions, the external load is greater than generated muscle force. Thus muscles are lengthened while contracting (4–6). There are two main characteristics that are different between eccentric and concentric contractions. First, as previously shown by the force-velocity relationship (4,5), the force production during eccentric muscle actions can exceed the force produced during isometric and concentric contractions (4). Therefore, the maximal force attainable during eccentric muscle actions is greater than during concentric contractions (6,7), which makes it easier to lower heavier weights during everyday movements. Such movements include simple lowering of shopping bags in comparison to lifting shopping bags or walking down the stairs in comparison to walking up the stairs. Second, eccentric muscle actions require less energy to produce the same amount of work. Abbott et al. (8) investigated this characteristic by using two bicycles connected back to back with a single chain. One individual performed concentric cycling while the other tried to resist the generated backward movement of the pedals thus producing eccentric cycling. Oxygen consumption (VO_2) was 2.4 times lower at 25 rpm during eccentric cycling and increased to 5.2 times lower at 52 rpm than during concentric cycling.

Typical movements that involve eccentric muscle actions include, downhill walking or running, going downstairs, fast changes of direction (9), fall prevention (10) and lowering weights (11). While concentric contractions contribute to propulsion of human movements (12), any movements that require a deceleration of the human body consist of eccentric muscle actions. Although the previously mentioned movements require mainly lower levels of eccentric force production, most studies that investigated eccentric training have utilised intensities above the one repetition maximum of the performed exercise. Such training has been previously termed as “overload” or “accentuated” eccentric training, and was exclusively included in most previous literature reviews on the topic of eccentric training (13–18). The popularity of eccentric overload training is related to the first characteristic of eccentric muscle actions, which is their potential of producing greater forces than concentric contractions (4,6). Other forms of eccentric exercise like downhill walking (13,19), Yo-Yo device based or “isoinertial” eccentric training (20,21), and eccentric cycling (12,22–27) have been shown to be also effective for improving muscle morphology and function. Unfortunately, these

alternative forms are less popular, and only slowly gaining attention (28–33) or specific focus (20,21,34) in literature.

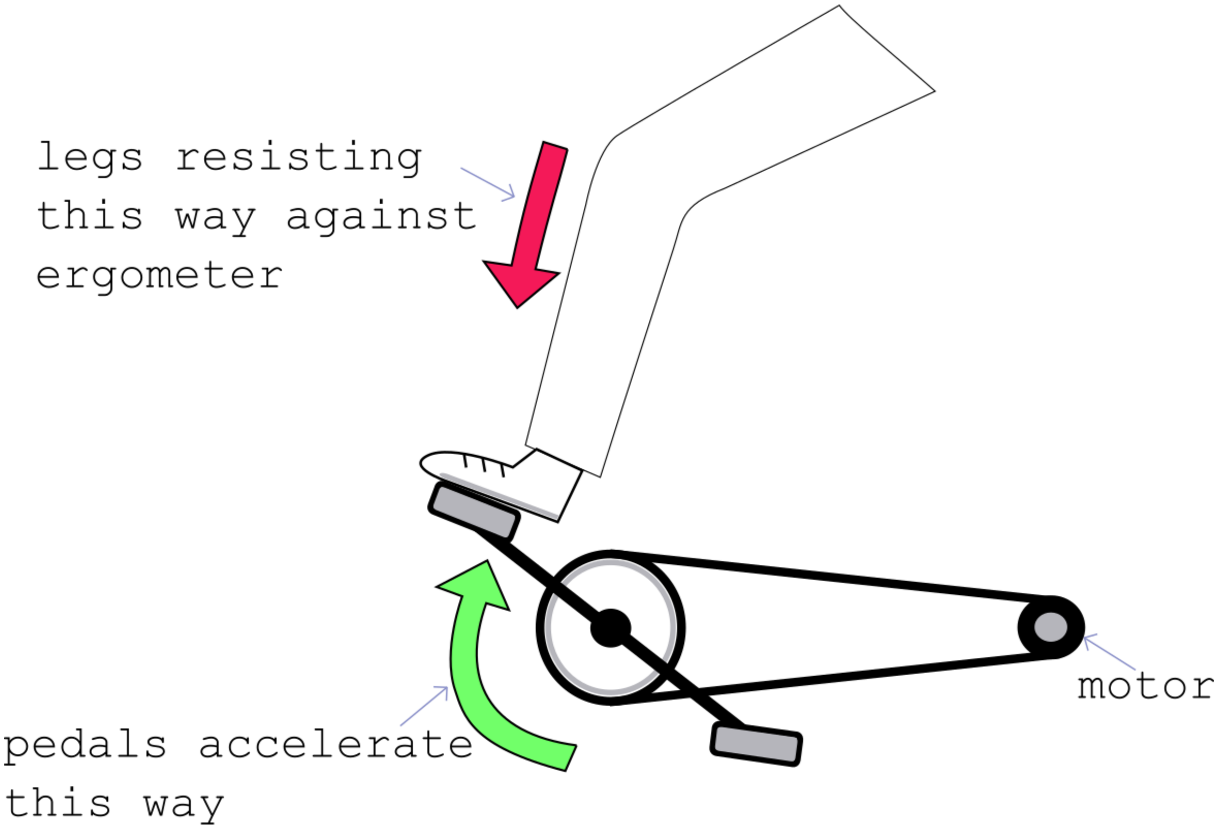
Due to the historical bias towards overload eccentric exercise, there is no clear structure and nomenclature to categorise eccentric exercise. Descriptions of basic training variables such as intensity, volume, or movement velocity vary between studies. There might be other variables that are specific to eccentric muscle actions that have to be considered when prescribing eccentric training. Furthermore, unlike concentric exercise (35), there is also no distinction between the effects of various forms of eccentric exercise and their plethora of variations. As some of the endurance type of eccentric exercise such as downhill walking, eccentric cycling and stepping require less than 30% of the maximal voluntary isometric force of the main muscle group (36), it is necessary to at least compare the effects of the various intensities possible during eccentric training. Such a categorisation will give a better understanding of the differences between various forms of eccentric exercise, as well as promote alternative eccentric training methods, such as downhill or downstairs walking, eccentric cycling or stepping.

Although eccentric exercise could induce greater adaptations in muscle size and strength, it has been previously shown that any form of eccentric exercise can lead to symptoms of muscle damage (36,37). If eccentric exercise consists of very high intensity and large number of eccentric muscle actions, it could lead to myofibrillar disruptions (38,39). However, muscle damage occurs when the muscles are unaccustomed to eccentric exercise, and the magnitude of muscle damage is largely decreased or completely avoided after the repeated bout. It is common that training volume and load are progressively increased, which reduces muscle soreness and muscle damage induced by eccentric exercise (23,24,40,41). Specifically, it has been shown that one single bout of low-intensity eccentric exercise that does not induce any symptoms of muscle damage is effective for reducing the magnitude of muscle damage after higher-intensity eccentric exercise (19,42,43). These precautions always have to be considered when designing eccentric training.

Eccentric cycling and stepping are eccentric exercises in which a large number of repetitive eccentric muscle actions are performed mainly by the knee extensors, and can be further supported by eccentric muscle actions of the ankle and hip extensors (45). Several studies confirmed the results of Abbott et al. (8) with oxygen consumption being 40-80% lower during eccentric cycling (Figure 1) when compared with concentric cycling at the same power output (24,36). In a similar manner, research has also shown that power output at the same oxygen consumption is 3 to 5 times greater during eccentric cycling and arm cranking than

during their concentric equivalents (46–48). As a result of these unique characteristics, eccentric cycling training may result in different neuromuscular and cardiovascular adaptations when compared to concentric cycle training.

Figure 1: Model of an eccentric cycling ergometer. The chain is driven by an electric motor (motor), pedals are accelerated by the motor (green arrow), and the individual has to resist in the opposite direction against the motor. In contrast to common belief, eccentric cycling does not equal cycling backwards and can be performed in both directions.



Following eccentric cycling and stepping training greater adaptations in muscle strength, cross-sectional area (CSA) of muscle fibres, and lean leg mass has been reported when compared with concentric cycling and strength training in healthy populations (22–24,27,49–51). It has also been shown to increase muscle strength (52–60), muscle fibre CSA (61), and muscle thickness and lean leg mass (61–65) in clinical populations. These adaptations seem to lead to improvements in physical performance such as an increase in hopping frequency and jump height in high school basketball players, as well as alpine skiers (10,50), and peak power production in healthy men (25,26). Parameters related to daily living activities for elderly and clinical populations are also improved as indicated by faster completion of stair ascents and descents (22,57,63,66), timed up-and-go test (22,57,60,62,66,67), 6-minute walk test (57,62–66) and increased balance ability (22,57,67) after eccentric cycling or stepping training. This plethora of positive adaptations across several populations consist mainly of parameters related

to muscle strength, morphology and function. Such adaptations are more often observed after strength training interventions consisting of concentric contractions, greater loads and lower total volume of contractions (35). The cyclic nature of eccentric cycling in combination with the low relative intensity is a unique combination that is in strong contrast to the typical concentric focused strength training methods leading to similar adaptations. Furthermore, a comparison to other eccentric training methods like overload training with isokinetic dynamometers or isoinertial eccentric training with Yo-Yo devices has not been performed in the best of this author's knowledge. Such a comparison is necessary to understand the adaptations after various forms of eccentric training better. However, little is known regarding cardiovascular and metabolic adaptations induced by eccentric cycling training.

Contrary to the significant effects of eccentric cycling on muscle strength, size and function, the influence of such exercise on cardiovascular and metabolic adaptations is less clear. Indeed, maximal oxygen consumption in healthy populations has been shown to remain unchanged (51), be slightly reduced (23,68) or in one case increased (70) after 5-8 weeks of eccentric cycling training. However, within clinical populations, continuous eccentric cycling training appears to be beneficial to cardiovascular health and has been shown to increase maximal oxygen consumption by 14-21% (55,71). Furthermore, eccentric cycling training has also shown to result in reduced symptoms of dyspnoea (52) and stabilised oxygen consumption and heart rate (72) during the 6-minute walking distance. These discrepancies between healthy and clinical populations are likely related to the significantly reduced cardiovascular and metabolic capacities in clinical populations before exercise intervention. Several other metabolic factors have been reported to be influenced by eccentric exercise. For example, insulin sensitivity, glucose tolerance, and glycogen have been shown to be decreased after one bout of exercise (73–75). However, it should be noted that after eccentric training, including downstairs walking (40), downhill running (76,77), eccentric quadriceps contractions (41) or isokinetic eccentric muscle actions (78,79), blood lipid profile, insulin sensitivity and glucose tolerance are improved. Furthermore, eccentric cycling has been shown to have no negative impact on glucose tolerance but can increase fat utilisation (80). Patients were also able to perform eccentric cycling training without decreases in insulin sensitivity (54,64). Thus, while in clinical populations eccentric cycling improves cardiovascular and metabolic parameters, in healthy populations adaptations are equivocal. Further research investigating the effects of eccentric cycling training on cardiovascular and metabolic function is warranted.

It has been well demonstrated that concentric high-intensity interval training results in similar or greater physiological adaptations when compared with traditional low to moderate

intensity exercise. Indeed, high-intensity interval training has been shown to improve maximal oxygen consumption (81–87), aerobic enzyme activity (88–91), regulators of mitochondrial biogenesis (86,90–93), the content of glucose transporters (94) and insulin sensitivity (95–97). Despite the high intensity, such exercise has even been adapted for patients with cardiovascular disease (87) or heart failure (98). The factors influencing the effectiveness of an interval training program have recently been reviewed and believed to be dependent mainly on the work to rest ratio, the duration of the work and rest phases and the intensity of the chosen activity (99). Maximising time spent at maximal oxygen consumption is suggested to be the main stimulus increasing oxygen delivery and extraction (100–102). In addition to the often prescribed repeated 30 s Wingate bicycle sprints (90), more tolerable training protocols that do not require “all-out” efforts have also been shown to be effective (103). Popular interval protocols include 10 x 1 min (85,91,104,105) and 4 x 4 min (106–114).

The combination of the increased cardiovascular and metabolic load through interval training and the increased workload during eccentric cycling may, if designed appropriately, be a potent stimulus for simultaneous adaptations in endurance and strength. The low metabolic cost of eccentric cycling is the second major characteristic of eccentric exercise, and an interval design to increase intensity would mainly be taking advantage of the reverse of this second characteristic. Regular continuous eccentric cycling is mainly performed at intensities that are still low relative to a hypothetical eccentric maximum, mainly to take advantage of the low metabolic cost. Of course, in comparison to the intensity at the same metabolic cost of concentric exercise, the intensity of continuous eccentric cycling can be considered high. But performing eccentric cycling in intervals at even greater intensities has potential to increase the already existing stimulation of the neuromuscular system, as well as adding a significant peripheral and central cardiovascular load to maintain high muscle forces. As intensities during interval eccentric cycling will still be far below intensities during overload training methods, it has the potential to be an effective and feasible training method to further stimulate other aspects such as the central nervous system or the different levels of connective tissue in the muscle-tendon unit. It is possible that high-intensity interval eccentric cycling has potential to be an “all in one” exercise.

1.2 Project rationale and purpose

There is limited research examining various intensities during eccentric cycling. Especially the acute and chronic influences of various eccentric cycling protocols on the cardiovascular and neuromuscular systems, as well as on outcome measures of performance are

unknown. It is plausible that eccentric cycling at greater intensities may be effective in simultaneously improving strength and endurance related parameters. Interval training increases cardiovascular and metabolic load during concentric exercise and may provide a model for such increases during eccentric cycling. Even though continuous eccentric cycling has been shown to be effective at improving muscle morphology and function, most training studies have based their training design on parameters from concentric cycling. Thus, this research project focused on high-intensity interval eccentric training, and consisted of three studies. The aim of the first study was to better understand the characteristics of eccentric cycling by comparing the physiological differences between an eccentric and concentric incremental cycling test until task failure. The aim of the second study was to develop a feasible interval eccentric cycling protocol that elicits a high metabolic load. The third study then compared high-intensity interval eccentric and concentric cycling training for changes in parameters of aerobic performance, muscle morphology and function.

1.3 Research questions and hypotheses

Study 1

What is the peak power output, peak oxygen consumption, maximal heart rate, minute ventilation, breathing frequency, during incremental eccentric cycling test till task failure compared to an incremental concentric cycling test till task failure?

- Peak oxygen consumption, maximal heart rate, minute ventilation, breathing frequency will be greater during the incremental concentric cycling test to task failure.
- Peak power output will be greater during the incremental eccentric cycling test until task failure.

Study 2

How different are the total oxygen consumption, the rate of perceived exertion, and enjoyment between interval eccentric cycling and continuous eccentric cycling?

- Interval eccentric cycling will elicit greater total oxygen consumption, the rate of perceived exertion and enjoyment than continuous eccentric cycling.

Study 3

What are the different training effects on peak oxygen consumption, incremental concentric peak power output, 6-minute walk distance, quadriceps cross-sectional area, fascicle length, fascicle pennation angle, maximal voluntary isometric quadriceps strength, concentric sprint peak power output, and jump heights after 8 weeks of high-intensity interval eccentric cycling versus interval concentric cycling?

- Interval eccentric cycling will lead to the greatest adaptations in quadriceps cross-sectional area, fascicle length, fascicle pennation angle, maximal voluntary isometric quadriceps strength, concentric sprint peak power output, and jump heights.
- Interval eccentric and concentric cycling will lead to similar adaptations in incremental concentric peak power output and 6-minute walking distance.
- Interval concentric cycling will lead to the greatest adaptations in peak oxygen consumption.

CHAPTER TWO

REVIEW OF LITERATURE 1

Not all eccentric exercises are the same: characteristics and differences

2.1 Introduction

As mentioned previously in the introduction, research on eccentric exercise and training has largely been focused on eccentric exercise performed at high intensities and percentages of various repetition maxima (16–18,115–117). Although there was some previous indication of the potential of alternative forms of eccentric exercise (10,33), only recently has the discussion on eccentric exercise widened in perspective (29–31,34), with specific focus and attention for rehabilitation and clinical populations (28,118–121). These recent reviews highlight the increasing popularity of other forms of eccentric exercise, yet our understanding of the effects and application of such exercise in the areas of health, fitness and sports is somewhat limited.

Indeed, research on eccentric training has largely focused on performance effects within specific populations, and in comparisons to other methods of strength and muscle training (16,17,117). To date, limited research has directly compared various modes of eccentric training (31), or focused on a single mode of eccentric training (Hoppeler, 2016; Maroto-Izquierdo et al., 2017; Tesch, Fernandez-Gonzalo, & Lundberg, 2017). As a result, the physiological and performance effects of various forms of eccentric exercise across a range of populations is not well understood. Additionally, previous research on eccentric exercise has used varying terminology to describe the exercise task depending on whether the variable of most interest is related to internal or external load. This is important since internal and external load can differ drastically during eccentric exercise and their relationship to each other differ to that observed in concentric exercise (8,36,47,48). For instance, one form of eccentric exercise, eccentric cycling, has been described as "high-force eccentric muscle actions" (28) based on the high power output that can be achieved during eccentric compared with concentric cycling (47). Conversely, the same exercise has been referred to as "submaximal" (122) based on the low metabolic load observed during eccentric (8,36). For most scientists and practitioners unfamiliar with the depth of the research in this area, high-force and submaximal appear contradictory. Such descriptions are not only confusing but also lack specific information important in the categorisation of intensity. As such, it is necessary that basic categories for eccentric exercises are established. Outlining the various characteristics of eccentric exercise, similar to that established for concentric exercise, will improve our understanding of the differences and unique adaptations associated with such exercise.

When compared with eccentric exercise, the characteristics of concentric dominant exercise are typically reported more routinely within the literature, and with a clearer and more systematic distinction between various forms of concentric exercises. Even for more endurance

based and cyclic type of physical activities, there are classifications of exercise into submaximal (below maximal oxygen consumption), maximal (close to maximal oxygen consumption) and supra-maximal (above maximal oxygen consumption). This categorisation is largely based upon the metabolic response to exercise and has resulted in the distinction between low-intensity steady state training (LISS), high-intensity interval training (HIT) and sprint interval training (SIT) (86,99,101,103,123). It is also well accepted that strength, hypertrophy and endurance adaptations from various modes of concentric exercise can be specifically targeted as a result of manipulating various training principles including specificity, loading/intensity, recovery and periodisation (35,124). Indeed, as a result of manipulating such training principles, even exercises with relatively similar movement patterns can result in vastly different adaptations (125). For instance, dominant concentric exercises such as the squat, a machine-based leg extension, a box jump and, a one-legged squat, can lead to vastly different adaptations.

Although there is no clear consensus on the various training principles that are important in eccentric exercise, some studies have examined acute effects of different exercise modalities. Several reviews have attempted to categorise various modes of eccentric exercise based upon the exercising muscle group, exercise intensity or physiological response. For instance, Isner-Horobreti et al. (30) compared the training effects of single joint and multi-joint eccentric exercises. Another research group (34,126) has categorised eccentric exercise as either 'low intensity-high volume' eccentric exercise or 'high intensity-low volume'. High intensity-low volume eccentric exercise utilises a greater external resistance than can be lifted concentrically, while low intensity-high volume eccentric exercise typically consists of a large number of eccentric muscle actions performed at moderate to low intensities. The distinction between high and low intensity appear appropriate as it encompasses the wide spectrum of eccentric exercise typically used. However it limits the classification of eccentric exercise intensity to the two polar ends of the spectrum ignoring other possibilities. Indeed, under such classification eccentric exercise performed at 65 to 85% of concentric one repetition maximum (1RM) could be classified as low-intensity. Clearly, to better understand the effects of eccentric exercise, it is important to clarify and classify the various possible characteristics associated with this mode of exercise.

As a result, the primary aim of this review was to highlight the fundamental differences between various forms of eccentric exercise. The review will outline the differences in various eccentric dominant exercises and categorise them based on several differing characteristics.

Second, it will clarify how the categorisation can showcase major research gaps. Lastly, it will explain how the suggested categorisation is challenging current consensus and directions for future research.

2.2 **Differences in various eccentric dominant exercises – categories for eccentric exercise**

Unlike for concentric exercise, our understanding of the effects various modes of eccentric exercise have on systemic and localised adaptations is not well understood. While there are several important variables typically used to describe and classify concentric exercise (i.e. intensity, duration, volume, velocity), there are also several other important factors in the classification of eccentric exercise typically not described. Therefore, the following variables will be discussed in relation to the classification of eccentric exercise: Intensity of contractions, general motion control, the velocity of contractions, muscle length and range of motion, amount of involved muscles and joints, type of feedback, and general continuity (examples can be found in Appendix A).

2.2.1 Intensity of contractions

The intensity of eccentric exercise can be described based upon the external resistance or load experienced during each contraction or repetition. Given that the history of eccentric exercise is predominantly based in research from resistance training (16,17,117), it seems appropriate to classify eccentric exercise based upon concentric 1RM. However, to date, the majority of literature in eccentric exercise (30,34) has provided limited categories for classification exercise intensity (i.e. high or low). Conversely, we propose four levels for the classification of exercise intensity including very high, high, moderate and low. As eccentric exercise is often performed at an intensity that exceeds the 1RM the first level is termed very high (>100% 1RM). Based on previous research that has shown that maximal eccentric strength can be up to 30% greater than maximal concentric strength (4,5), and that low-intensity eccentric cycling requires up to 30% of maximal voluntary isometric contraction strength of the knee flexors (36), another three levels of intensity were defined: low (0-33% 1RM), moderate (34-66% 1RM) and high (67-99% 1RM). These classifications of exercise intensity may be relatively simple to control within many forms of eccentric exercise including eccentric isokinetic knee extensions, or uninterrupted forms like eccentric cycling or downhill walking. When eccentric exercise involves impact forces typically associated with the deceleration of body mass the quantification of the external load becomes more difficult to control. Such activities may include eccentric squats, drop jumps, depth jumps or downhill walking/running.

As a result, when classifying eccentric exercise intensity, it is important to document whether or not bodyweight and impact forces are involved.

2.2.2 General movement control

The general movement during eccentric exercise can be controlled externally or internally. Previous research has distinguished between isokinetic, isotonic and isoinertial (18,20) exercise, but the distinction can be simplified into two categories. Internally controlled eccentric exercises are like eccentric squats, drop jumps or any other gravity-based exercise where the individual is controlling the velocity of the movement. Additional load and impact have to be accounted for, as it increases the difficulty of control like for the slow downwards movement during eccentric squats. Externally controlled eccentric exercises are like isokinetic knee extensions or eccentric cycling where dynamometers, ergometers or other external devices are moving the limbs at a pre-set velocity. Independent of how much force an individual will produce against the device, the velocity is always controlled externally.

2.2.3 Velocity of contractions

The velocity of eccentric exercise should be measured and reported as the angular velocity or cadence (rpm or steps per minute). During externally controlled eccentric exercise the angular velocity is usually controlled by the dynamometer and the cadence by the ergometer. However, even for internally controlled exercises like eccentric squats and drop jumps, the movement velocity can be performed in a standardised matter and should then be reported as a cadence. Such standardisation can be achieved by limiting the movement velocity through a metronome rhythm, measuring the range of motion of the major joints involved and then calculating the angular velocities. Internally controlled eccentric exercises have often been performed with an extended time under tension of 3 to 5 s. For example, if an eccentric squat covers 100 degrees range of motion for the knee joint of a 3 s time under tension, it would be equal to an angular velocity of 33.3 degrees per second. Such an angular velocity is similar to studies comparing slow isokinetic eccentric exercise at 30 degrees per second with fast isokinetic eccentric exercise at 180 degrees per second (127,128). Eccentric cycling is often performed at 60 rpm and thus 180 degrees per second at the knee joint (31). For eccentric cycling, the available ergometers allow a cadence from 5 to 110 rpm as a cycling cadence and operate in a constant cadence or isokinetic mode (129). The Cyclus2 eccentric trainer is the only device that can operate at constant Watts, where the amount of applied torque dictates the cadence of the ergometer to match a set power output. But to our knowledge, there is no single study that has utilised this constant power mode. Several movements during sports that include

a stretch-shortening cycle and thus an eccentric phase are performed at a greater velocity than 180 degrees per second. Indeed, the angular velocity of the knee during a countermovement jump reaches an average of 860 degrees per second (130) and the pivot step of a change of direction movement during running is performed with an average of 377 degrees per second at the knee joint (131). Therefore, the velocity of eccentric exercise is categorised into three levels: low (0 – 90 deg/s), moderate (91-180 deg/s) and high (>180 deg/s).

2.2.4 Muscle length and range of motion

The muscle length during eccentric muscle actions depends on the utilised range of motion. It can be reported relative to the range of motion of the major joint is covered during the exercise (where 0% equals full flexion): long (67-100%), medium (34-66%) and short (less than 33%). Although the range of motion is usually reported as the degrees covered by the main joint, it is additionally recommended to access a maximal range of motion and report the relative muscle length used during eccentric exercise. When eccentric exercise is performed across the suggested categories of muscle length, the precise percentage should be noted (e.g. 10-50% of muscle length). Muscle length for most forms of eccentric exercise can be adjusted across wider ranges. For example, drop jumps are usually followed up directly by a vertical jump (132). The vertical jump after the eccentric phase of a drop jump is performed explosively, which requires only a small range of motion and short muscle length of the lower limb muscles. But if modified with a sole focus on the eccentric landing phase of the drop jump it could be performed at longer muscles lengths. Little is known about the acute and chronic effects of eccentric exercise performed at different muscle lengths. It has been shown that eccentric exercise performed at long muscle lengths results in greater increases in muscle damage and soreness (133–135). Isokinetic eccentric training performed at very high intensities has pointed towards potentially greater increases in fascicle length after training at long muscle length (136).

2.2.5 Amount of involved muscles and joints

The exact amounts of involved muscle mass in any particular eccentric exercise is not feasible to measure but can be estimated based on how many joints are involved in the chosen exercise. Based on the number of involved joints it can be categorised into whole-body, multi-joint and isolated eccentric exercise. Whole-body eccentric exercise is where one or more joints for the upper and lower body are used, like during downhill running or downstairs walking. Multi-joint relates to more than one joint for either upper or lower body, like squats or eccentric cycling. Moreover, isolated exercises include all forms with one joint, like isokinetic knee extensions. Unfortunately, to the author’s knowledge there are not studies comparing effects

between eccentric exercise with various amount of involved muscles, e.g. squats, drop jumps and eccentric cycling.

2.2.6 Type of feedback

Although some studies report that feedback was provided during exercise, like the visualisation of force curves during isokinetic knee extension, not all studies choose to report whether feedback was used or not. If no feedback is provided during eccentric exercise, it should be clarified why this approach was chosen. If feedback is utilised, the type of feedback should be reported as detailed as possible. The form of feedback may vary from simple numbers, lines, graphs to sophisticated software design with several parameters reported at once. When providing details about the velocity of the chosen eccentric exercise, the refresh rate of the feedback may differ from the chosen velocity. Thus, the refresh rate of the chosen feedback should be reported as well, especially as eccentric exercise can initially be overwhelming due to its unique character of slowing down against external resistance. For example, during isokinetic knee extensions and eccentric cycling force, torque or power output can be provided instantly or after some delay. Similarly, for drop jumps, the achieved jump height or contact time can be provided, while jump height could be unrelated to how the eccentric landing was performed. Furthermore, force, power output or rate of deceleration could provide further feedback during eccentric exercises like squats or drop jumps. The effects of different type of feedback on eccentric exercise performance and its effects on adaptations are unknown.

2.2.7 General continuity

The general continuity is a characteristic that could be unique to eccentric exercise. It distinguishes between uninterrupted and interrupted eccentric exercise. Interrupted eccentric exercise involves eccentric muscle actions of the agonist's muscle interspersed with either rest or other muscle contraction mode for the same muscle in between. For example, during repeated drop jumps or squats, each eccentric or downward phase of the jump is separated by the concentric phase. When categorising eccentric exercise as interrupted, any other muscle contraction modes (i.e. passive, isometric or concentric contractions) performed before or following the eccentric muscle actions should also be described. Further details about the interruption should be considered, including whether the muscle contraction mode in-between utilises the same or other muscles as during the eccentric muscle action, the time between the contraction modes, as well as the order of contraction modes. Uninterrupted eccentric exercise involves eccentric exercise which is performed without other muscle contraction modes

between contractions. For instance, downhill running or walking (137–140), downstairs walking (141), eccentric stepping, and eccentric cycling (8,23,24,26), are forms of eccentric exercise that are largely performed uninterrupted. For both, interrupted and uninterrupted eccentric exercise, the general programming should be reported as either continuous or interval training with the relevant work to rest ratio. Due to no rests in between eccentric muscle actions during these activities, it is possible that the ability to execute such eccentric exercise for longer periods is limited by specific eccentric coordination or skill. Eccentric cycling, for example, is often performed at a target power output, and the amount of variation of produced power output during exercise to the target was called eccentric coordination. It has been shown that it is the parameter that shows the greatest increases after eccentric cycling training (50,67,142). Therefore, it is possible that there is a large variability in general eccentric skill for interrupted and specifically for uninterrupted eccentric exercise. Unfortunately, the influence of such detailed factors about continuity of eccentric exercise on acute and chronic effects of eccentric exercise is unknown.

2.3 Future directions, and challenging current consensus

The presented characteristics are merely suggestive, and a first framework to provoke more theoretical and practical differentiation between various forms of eccentric exercise in future research and application. Hopefully, future studies will consider the outlined differences and investigate the potential influence of the different variations in characteristics between different forms of eccentric exercise. The suggested characteristics and categories are expected to be edited, deleted, extended and modified to any degree that the extended knowledge at any time in the future allows.

Although previous research has attempted to compare the effects of some of the characteristics specifically within eccentric training only (18,127,136,143), most comparisons are focused on the general differences between eccentric and concentric training (16,17,117). Therefore, as many of the acute and chronic differences between concentric and eccentric exercise are well known, future research should rather focus on the comparison of various forms of eccentric exercise. It has to be clarified that comparing various forms of eccentric exercise could be complicated and has to be designed with great care to detail.

One such comparison that is complicated to execute is between externally and internally controlled exercises. External control eliminates the kinesthetic feedback, such as changes in velocity, which exist during all basic movements and sports. Internally controlled exercises include that kinaesthetic feedback. Control, coordination and movement mechanisms may be

different for both types of training. Unsurprisingly, comparisons of mainly externally (isokinetic) and internally (isotonic) eccentric training have shown that they do lead to different adaptations (18,143). Another complicated comparison is between interrupted and uninterrupted eccentric exercise. Interrupted exercise requires a periodic composition of sets, repetitions and work to rest ratio, while uninterrupted exercises have so far been mainly performed with continuous protocols prescribed at target power output (26,67), % of predicted maximal heart rate (23,144), or rating of perceived exertion (22,27,145). Indeed, many of the unique characteristics of uninterrupted forms of eccentric exercise, as well as the overwhelming evidence for its effectiveness at improving many different outcome measures after training, were the initial reasons for the suggested categorisation.

As previously outlined in the introduction, uninterrupted forms of eccentric exercise, such as downhill walking or running, downstairs walking, eccentric stepping, cycling or arm cranking, have been shown to increase muscle strength, morphology and function (23,26,49–51,140,141,145). Besides being mostly performed in an uninterrupted fashion, several other unique characteristics of these forms of eccentric exercise could be responsible for the outlined increases in outcome measure that are similar in magnitude to previously utilised isokinetic, isotonic and isoinertial eccentric training at high to very high intensities (14,16–18,20). One possibility is the true isokinetic velocity when downhill running or walking is performed on a tread, and eccentric stepping, cycling and arm cranking with a constant cadence. In comparison to isokinetic eccentric training performed on dynamometers, where there is an acceleration and deceleration phase, most uninterrupted eccentric exercise performed with external control, has completely constant movement, and thus contraction velocity. However, the most prominent characteristic of this selective group of eccentric exercise forms is the large volume and very low intensity.

Previous research has established the consensus that eccentric training needs to be performed at greater intensities and workloads than concentric training to be more effective (14,16,17,117,146). Similarly, there is still a widespread believe that these greater forces have to be accompanied by great increase in muscle damage and soreness, although it has been repetitively shown how through progressive increases in volume and load, and the repeated bout effect, it can be completely avoided (147–149). Low-intensity eccentric exercise like eccentric cycling, which requires about 30% of the maximal isometric strength (36), has proven that neither of these consensuses are true. Various studies have shown that great increases in muscle strength, morphology and function can be achieved at low intensities of eccentric

exercise, and without major reports of muscle damage or soreness (19,27,49,140,150). Thus, it is possible that in relation to outcome measures, the details of how eccentric training is prescribed are of great importance. It is possible that a certain threshold level of loading exists, that can be either surpassed by increases in intensity or volume. Indeed, in a recent review on concentric strength training it has been concluded that low intensity strength training is as effective at increasing muscle strength as high intensity strength training (151).

2.4 Conclusions

The suggested categorisation clarifies that there are many differences between various modes of eccentric exercise. A first categorisation was suggested here based on 7 characteristics of eccentric exercise: the intensity or load of each repetition, the general movement control, the velocity of each repetition, the muscle length and range of motion, the type of feedback during exercise, the amount of involved muscles and joints, and the general continuity. Initial thoughts about the potential influence of these characteristics on relevant outcome measures have been derived from this categorisation. It has been clarified how these characteristics could result in different acute characteristics and chronic effects of various form of eccentric exercise. It has been shown how established statements about eccentric exercise can be challenged when several of the suggested characteristics are analysed in more detail. There are many questions unanswered about eccentric exercise that have to be addressed in the future. Future research should focus more on establishing knowledge around the influence of these characteristics for eccentric exercises first, before venturing into comparing with other muscle contraction modes. Furthermore, vastly variable parameters during eccentric training like intensity, volume, and contraction velocity should be reviewed based on previous research to provide a summary on the current state of knowledge. A better understanding of adaptations due to different characteristics of eccentric exercise will provide detailed knowledge of how and when to apply what form of eccentric exercise. To achieve the best possible outcomes, future research should focus on providing practitioners with as much detail about the characteristics and effects of various forms as possible.

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CHAPTER THREE

REVIEW OF LITERATURE 2

The differences in training adaptations between various intensities of eccentric exercise

3.1 Introduction

Previous reviews on eccentric exercise have covered a vast depth of topics: general physiological characteristics, acute and chronic responses (30,32,152), morphological, cellular and molecular responses (16,117,153,154), the validity and significance of eccentric exercise in aging and diseased skeletal muscle (120), as well as for rehabilitation (28,118). Additionally, other reviews have focused on the potential molecular mechanisms (126,155–157), neural characteristics of eccentric muscle actions (115,116), as well as mechanisms of the repeated bout effect (147,148). Only one previous review has highlighted potential differences in exercise intensity during eccentric exercise (34). In chapter two a categorisation for 7 characteristics of eccentric exercise has been suggested. It was clearly outlined how despite the large variation in possible exercise intensity (30-130% of concentric 1RM), it appears that increases outcome measures of muscle strength, morphology and function are independent of the chosen training intensity. Despite a large interest in eccentric exercise, no previous study has systematically investigated the effect of training intensity on selected outcome measures of muscle strength, morphology, and on performance parameters.

Thus, this review aimed to analyse whether training intensity has a significant effect on adaptations of muscle strength, muscle morphology, and related performance parameters. Special focus was attributed to studies utilising eccentric cycling and how they can be classified in comparison with other forms of eccentric training regarding adaptations.

3.2 Methods

3.2.1 Literature search

The computerised search of the literature was performed in the electronic databases PubMed, Google Scholar and Web of Science. Original research, reviews, conference abstracts, poster presentations and proceedings, letters to editors and comments related to eccentric training were included in the findings. The literature search was performed until the 30th of September, 2017 and had no restricted time frame for studies published in the past. English was the language of the search and the search strategy focused on general keywords that are related to eccentric training. The first search included the terms “eccentric training”, “eccentric strength training” and “eccentric exercise”. The more specific second search included the terms “lengthening contractions”, “eccentric muscle actions” and “negative muscle work”. Finally, the third search consisted of the terms “overload training”, “isoinertial training”, “flywheel training”, “eccentric cycling”, “eccentric stepping”, “downhill running”, “downhill walking”, “downstairs walking”, “descending stair walking”, and “drop jump training”. Additionally, the

reference list of all studies was inspected to find further studies that were not identified in the first three searches. If the full-text of a study was not accessible, it was attempted to receive the necessary information from the abstract. In case that the abstract did not provide enough information, the study was excluded from the review.

3.2.2 Inclusion and exclusion criteria

The articles had to meet the following criteria to be included:

1. The study investigated the effects of eccentric training on parameters related to muscle strength, morphology, or to performance
2. Participants of either gender had to be healthy
3. A training protocol was utilised that consisted of more than two training sessions

A study was excluded if:

1. The participants had any pathology or existing musculoskeletal injury
2. English was not the language of the article
3. The necessary information was not identifiable from the full text or the abstract

3.2.3 Categories of training intensity

Based on the intensity categories suggested in chapter two the studies were divided in to very high (>100% concentric 1RM), high (67-99% 1RM), medium (34-66% 1RM) and low intensity (0-33% 1RM). In studies that consisted of several groups of eccentric training with different characteristics (e.g. movement velocities), each group was treated as a separate study. If training intensity was not stated as the % of concentric 1RM, it was assumed that eccentric 1RM is 30% greater than the concentric 1RM. As common for concentric training (158), eccentric training intensity was then calculated based on the maximum amount of repetitions performed relative to the assumed 130% of concentric 1RM. This method was assumed to be adequate, as many eccentric training studies have utilised a training design of maximal effort for a certain range of repetitions. To provide an overview on the effects of training intensity on strength, muscle morphology, as well as performance parameters, an average % change from pre to post intervention was noted or calculated for each study. Thus, some author's names and the publication date have an additional small alphabetical letter in the figures. If several measures for the same strength, morphology, or performance parameter were performed, results were averaged across all sub-measures.

3.2.4 Statistical Analysis

A one-way ANOVA was used to compare differences in adaptations between categories of velocity, contraction mode, and training intensity. In case of significance, a Tukey´s post hoc test was performed for multiple comparisons. The significance level was set at $P < 0.05$. All statistical analyses were performed using statistical software (GraphPad Prism version 7.02, GraphPad Software, La Jolla California, USA).

3.3 Distribution of all studies between intensity categories

A total of 220 studies that have investigated the effects of various forms of eccentric exercise was identified. There was 84 (38%) that have used very high intensities of eccentric exercise. For the high-intensity category, there was a total of 67 (30%) studies. The medium intensity was utilised in 36 (16%) studies. The low-intensity category was represented by 33 (15%) studies. Thus, 151 out of 220 studies (68%) have utilised training intensities from 67 to 130% of concentric 1RM, which confirms the previously assumed bias in literature towards high-intensity eccentric training.

3.4 Strength adaptations

Out of 220 studies that were identified, a total of 192 studies investigated changes in isometric, concentric and eccentric strength. There were 72 studies that utilised very high intensities (Figure 1), 59 investigations that used high intensities (Figure 2), 34 studies at medium intensities (Figure 3), and 27 at low intensities (Figure 4).

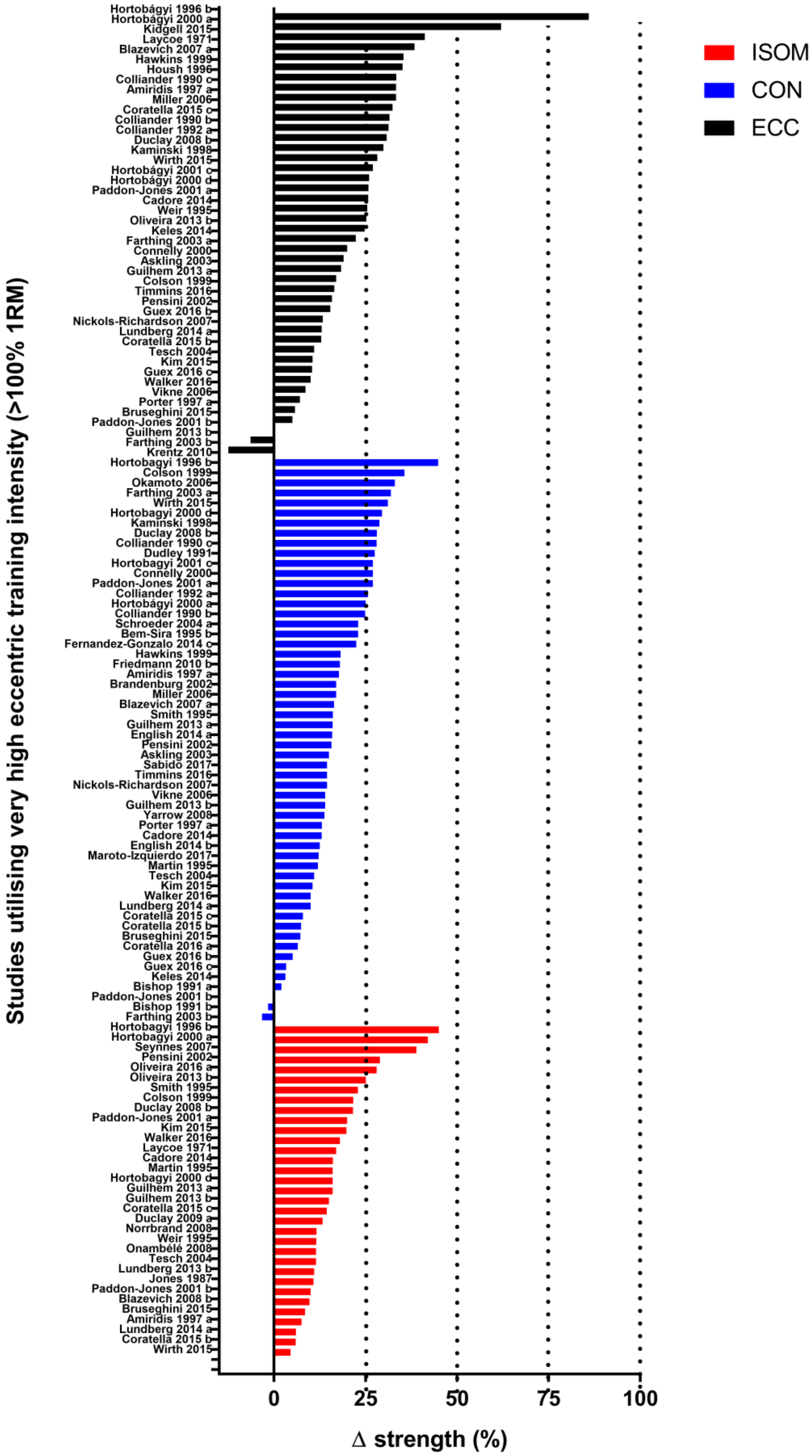

Figure 2: Average % change in isometric (ISOM, red bars), concentric (CON, blue bars) and eccentric (ECC, black bars) strength in studies utilising very high eccentric training intensity (>100% concentric 1RM) (20,127,128,136,143,159–215)

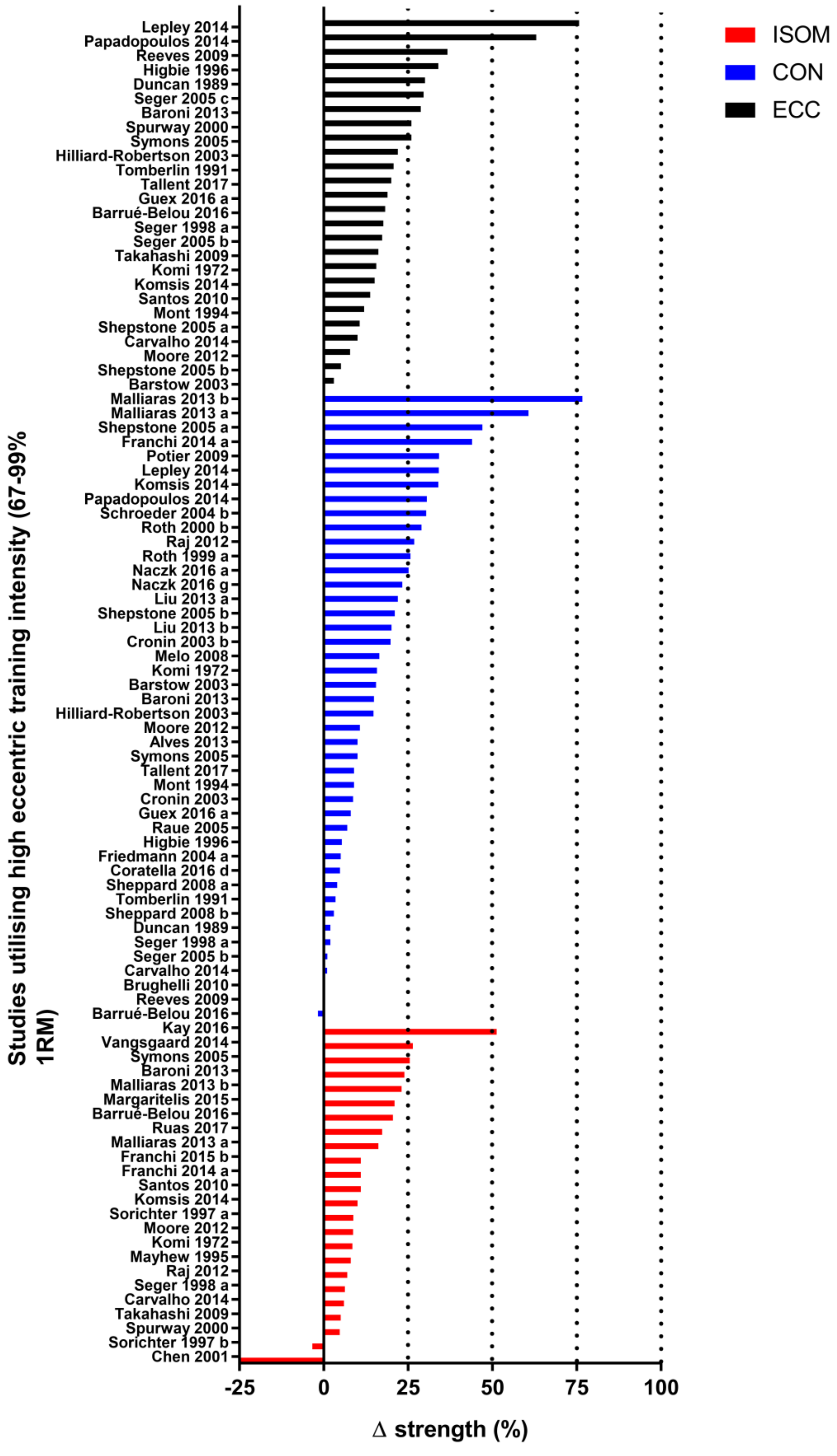

Figure 3: Average % change in isometric (ISOM, red bars), concentric (CON, blue bars) and eccentric (ECC, black bars) strength in studies utilising high eccentric training intensity (67-99% concentric 1RM) (136,199,216–220,220–233,233–263)

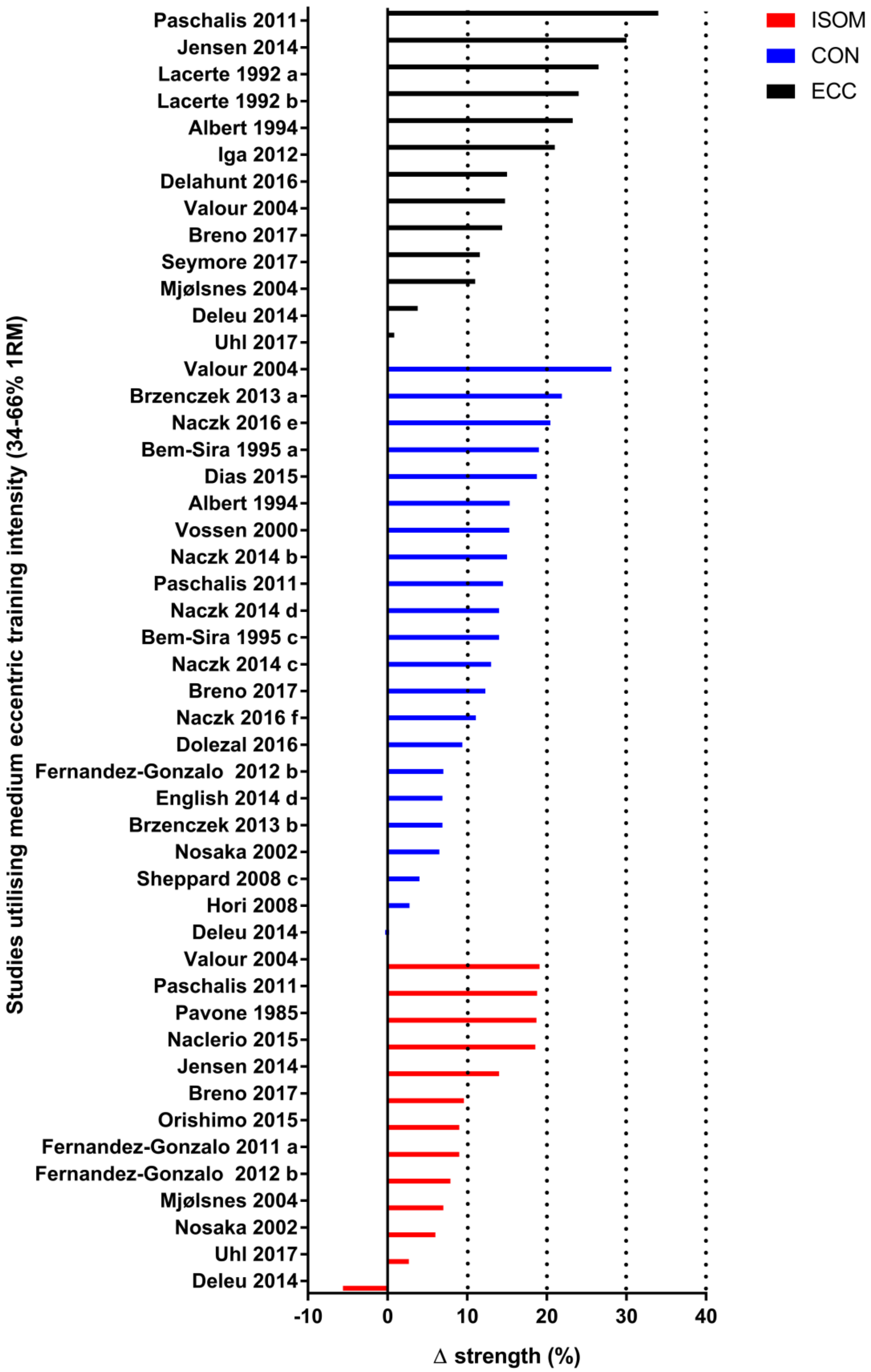

Figure 4:Average % change in isometric (ISOM, red bars), concentric (CON, blue bars) and eccentric (ECC, black bars) strength in studies utilising medium eccentric training intensity (34-66% concentric 1RM) (78,200,205,254,264–266,266–286)

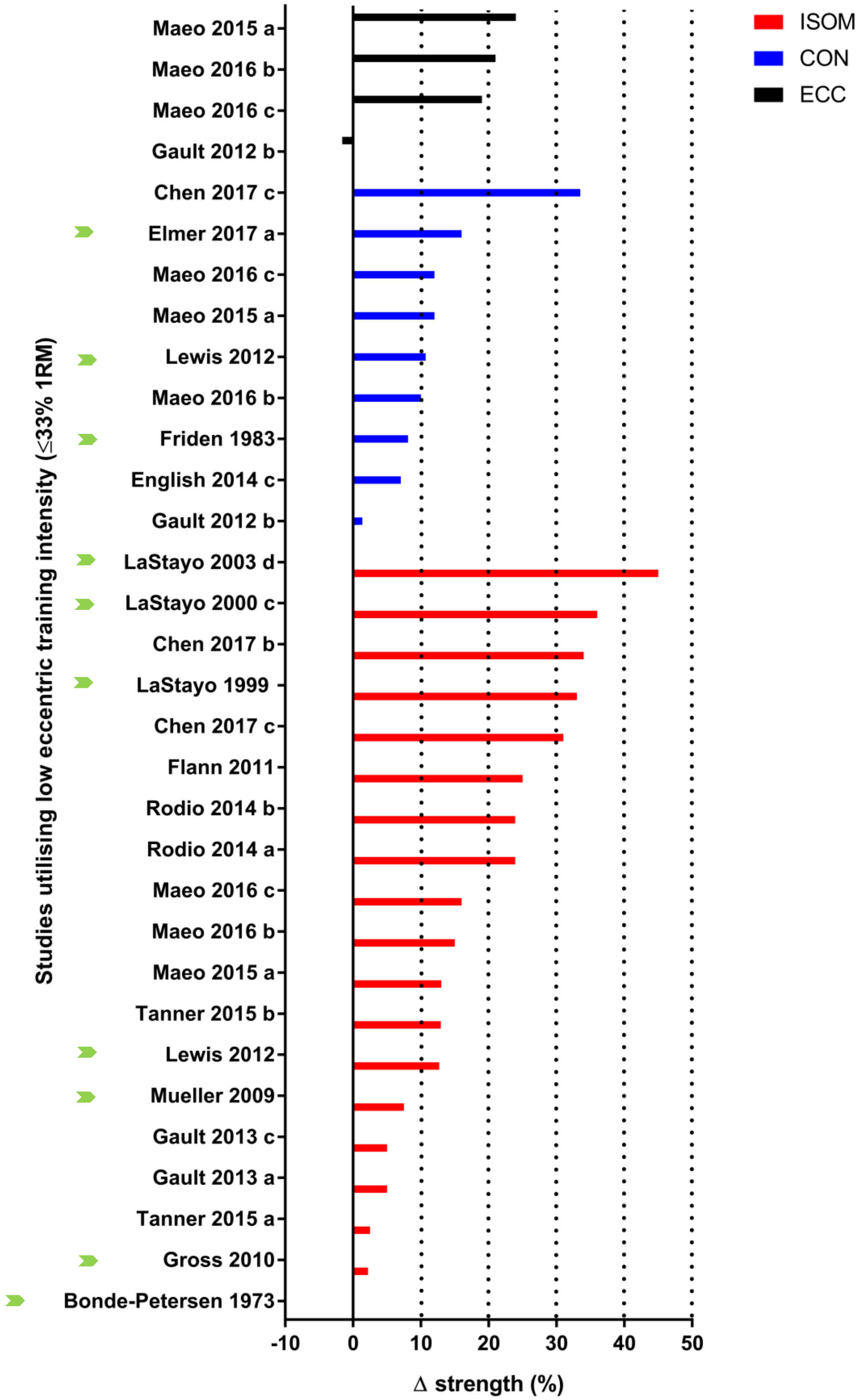

Figure 5: Average % change in isometric (ISOM, red bars), concentric (CON, blue bars) and eccentric (ECC, black bars) strength in studies utilising low eccentric training intensity (≤33% concentric 1RM). Eccentric cycling studies are indicated by the green arrow. (19,22–24,27,41,50,51,67,69,140,141,144,205,287–290)

3.4.1 Effect of contraction velocity on strength adaptations

Although contraction velocity has been suggested in the previous review as one of the 7 main characteristics of eccentric exercise, 97 out of 192 (50%) studies that investigated strength adaptations did not report contraction velocity in any form. For the studies that did report contraction velocity or standardised movement velocity via time under tension, 25 performed eccentric muscle actions at 60 degrees per second, 12 at 30 degrees per second, 7 at 180 degrees per second, 6 at 90 degrees per second, 4 at 20 degrees per second, 4 at 15 degrees per second, 3 at 25.71 degrees per second, and 2 studies at several velocities ranging from 10 to 430 degrees per second. Based on the categories for contraction velocity for the main joint from the first review (slow at 0 – 90 deg/s, moderate at 91-180 deg/s and fast at greater than >180 deg/s), there were 78 studies in the slow category, 13 studies in the moderate category, and only 3 studies that performed training at fast velocities. This distribution clarifies that it is complicated to draw clear conclusions about the effects of contraction velocity during eccentric training. Out of this selection of studies, no study from the fast category measured changes in isometric strength, 3 measured concentric strength and only 1 measured eccentric strength. Nevertheless, there were no significant differences between any of the velocity categories ($P \geq 0.2768$) (Figure 5).

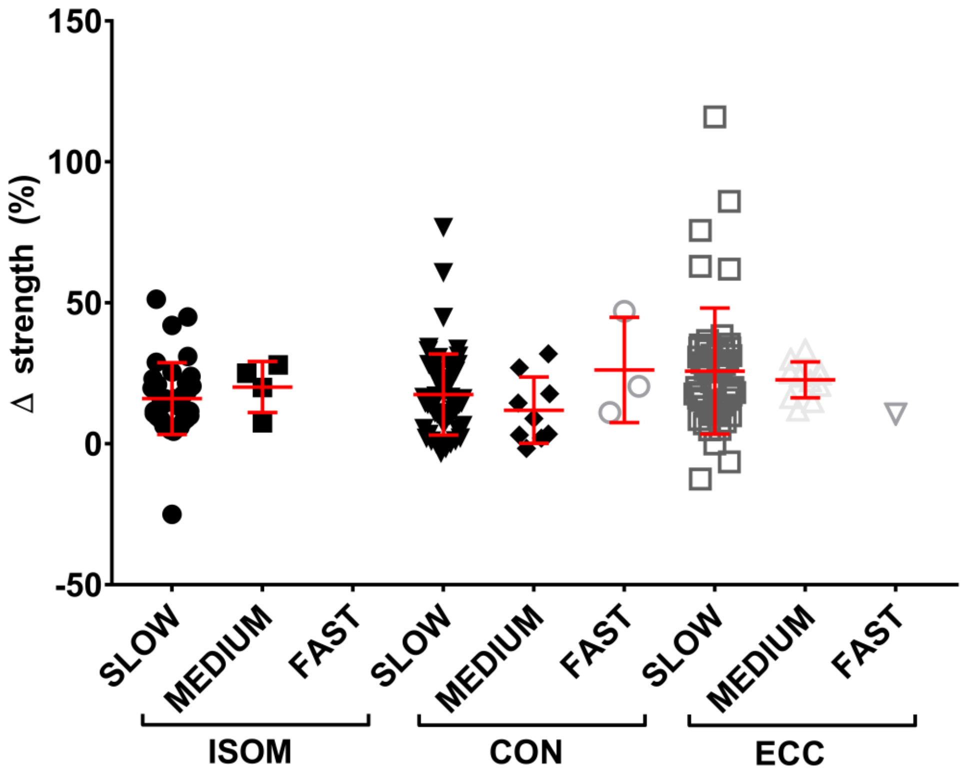

Figure 6: Average % change in isometric (ISOM), concentric (CON) and eccentric (ECC) strength between eccentric training at slow (≤90 deg/s), medium (91-180 deg/s) and fast (≥181 deg/s) eccentric muscle actions velocities. There were no significant differences

3.4.2 Specificity of contraction modes

In relation to the specificity of contraction mode, it has been previously concluded that eccentric training increases eccentric strength to a greater degree than concentric or isometric strength (17). Across all intensities isometric strength increased by 15.38% (-25% to +51.3%), concentric strength by 16.23% (-3.3% to +76.7%) and eccentric strength increased by 22.7% (-12.5% to +116%). When compared like this across all categories of training intensity, the changes in isometric strength were not significantly different from the changes in concentric strength (P=0.8998). Conversely, when compared across all intensities, changes in isometric strength (P=0.0019) and concentric strength (P=0.0030) were lower than changes in eccentric strength (Figure 6). From a general perspective, the studies reviewed here show that eccentric strength will specifically increase greater after eccentric training in comparison to isometric or concentric strength.

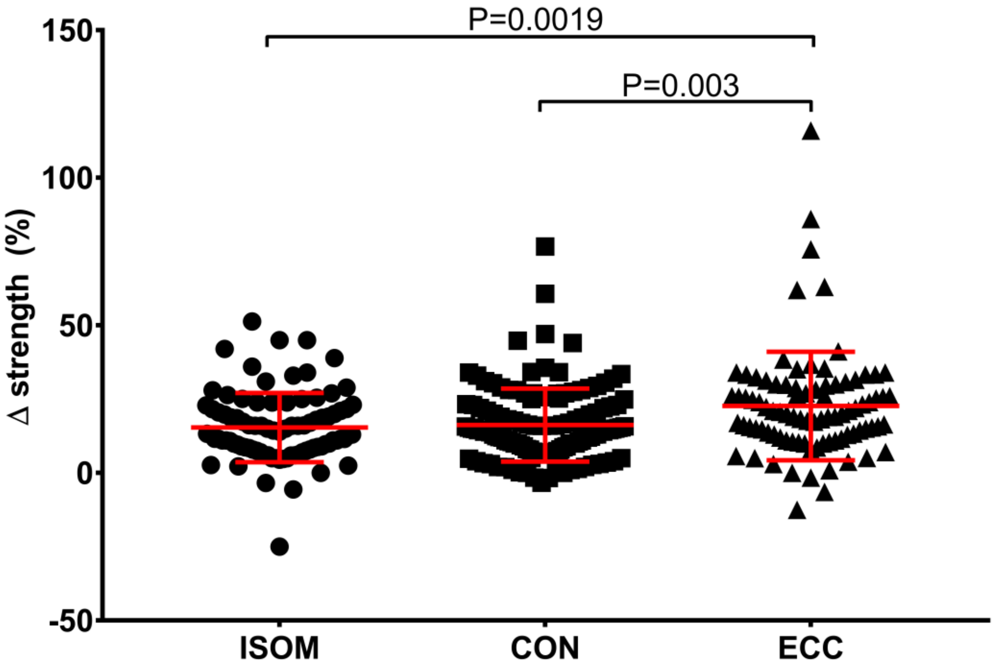

Figure 7: Average % change in isometric (ISOM), concentric (CON) and eccentric (ECC) strength between eccentric training across all eccentric training studies

When the analysis of changes in strength between isometric, concentric and eccentric muscle actions was performed within each intensity category there was no significant difference between contraction modes ($P \geq 0.2287$), and also none between intensity categories ($P \geq 0.9$) (Figure 7). Within the very high intensity, isometric strength increased by 17.63 ± 10.09 % (4.5 to 45%), concentric strength by 17.03 ± 10.06 % (-3.3 to 44.8%), and eccentric strength by 24.69 ± 21.59 % (-12.5 to 116%). Similarly, within the high ($P \geq 0.2891$), medium ($P \geq 0.9755$),

and low (P ≥ 0.9946) intensity category there were no significant differences between the percentage changes of isometric, concentric and eccentric strength. In the high intensity category isometric strength increased by 12.58 ± 13.3 % (-25 to 51.3%), concentric strength by 17.85 ± 16.84 % (-1.7 to 76.7%), and eccentric strength by 22.84 ± 16.24 % (3 to 75.75%). For medium intensity it was 10.37 ± 7.37% (-5.9 to 19.1%) for isometric strength, 12.57 ± 6.79 % (0.2 to 34%) for concentric strength and 17.7 ± 9.84 % (0.85 to 34%) for eccentric strength. For the low intensity it was 18.53 ± 13.08 % (0 to 45%), 12.31 ± 8.9% (1.38 to 33.5%), and 15.6 ± 11.65 % (-1.6 to 24%), respectively. Therefore, a more precise analysis of each training intensity diminished the previously described general greater increase in eccentric strength across all eccentric training studies.

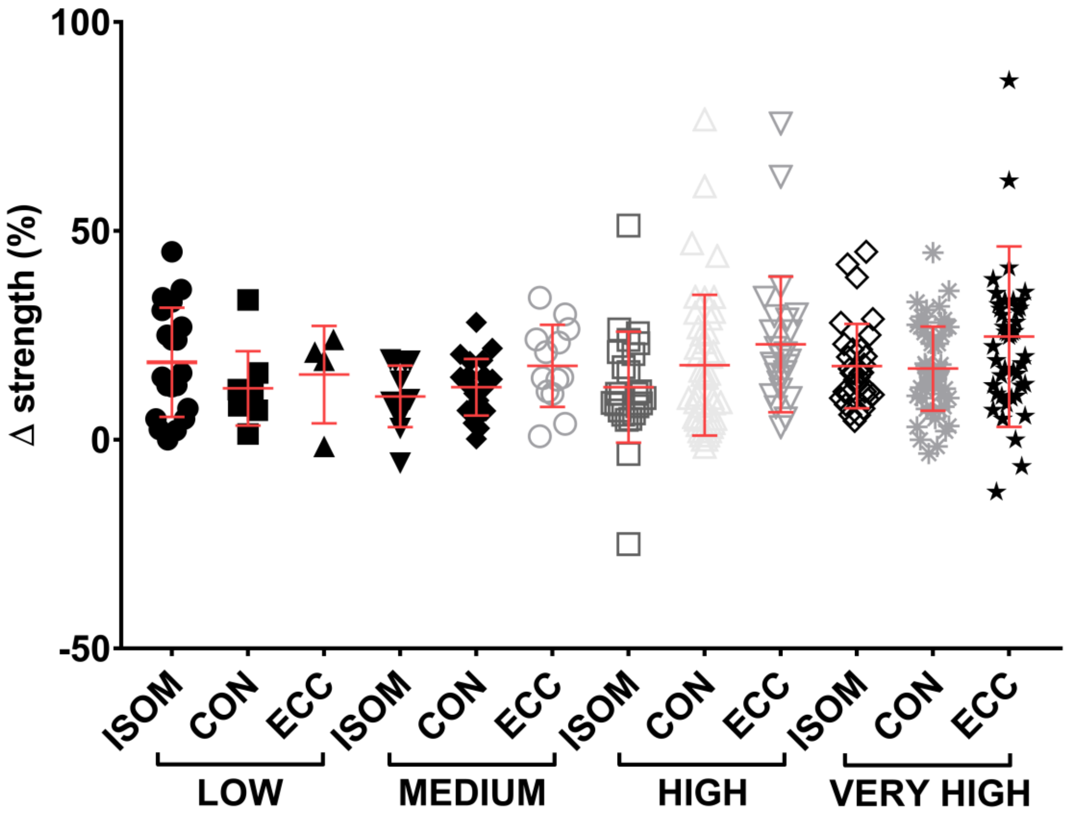

Figure 8: Average % change in isometric (ISOM), concentric (CON) and eccentric (ECC) strength between low (≤33% concentric 1RM), medium (34-66 % concentric 1RM), high (67-99 % concentric 1RM) and very high (≥100% concentric 1RM) eccentric training intensity. There were no significant differences

3.4.3 Isometric strength

Out of 72 studies that have utilised very high-intensity eccentric training, 32 have measured changes in isometric strength. For the high-intensity category it was 25 out of 59 studies, only 13 out of 34 studies in the medium intensity category, and 20 out of 27 studies in the low category. Eccentric strength training performed at very high intensity improved

isometric strength by 17.63 ± 10.09 % (4.5 to 45%), high intensity increased it by 12.58 ± 13.3 % (-25 to 51.3%), medium intensity by 10.37 ± 7.37% (-5.9 to 19.1%), and low intensity by 18.53 ± 13.08 % (0 to 45%). There was no significant difference between intensity categories ($P \geq 0.9$) (Figure 7).

3.4.4 Concentric strength

Concentric strength adaptations after low-intensity training were measured in 9 studies, in 22 after medium intensity training, in 44 after high-intensity training, and in 56 after very high-intensity training. The average increase in concentric strength was 12.31% (1.38 to 33.5%) after low intensity eccentric training, 12.57% (0.2 to 28.13%) after medium intensity, 17.84% (-1.7 to 76.7%) after high intensity, and 17.03% (-3.3 to 44.8%) after very high intensity. There were no significant differences between intensity categories ($P \geq 0.9$) (Figure 7).

3.4.5 Eccentric strength

Out of 192 studies that measured strength changes 88 studies specifically investigated eccentric strength. There were 4 studies for the low-intensity category, 1 study for medium intensity, 26 studies for high intensity, and 45 studies for very high intensity. In respective order, eccentric strength increase by 15.6% (-1.6 to 24%), 23.25%, 22.84% (3 to 75.54%), and 24.69% (-12.5 to 116%). As clarified previously, there was no significant difference between intensity categories ($P \geq 0.9$) (Figure 7).

3.4.6 Summary strength adaptations

In general, there was no difference in increases of isometric, concentric and eccentric strength between training intensities. Despite many different variations of eccentric training that can be used to increase muscle strength 73 studies were performed at a pre-determined set and repetition scheme with every eccentric muscle actions performed maximally. There can be several methodological complications with such an approach to eccentric training. First, quantifying the training load is difficult, as it is impossible to perform each eccentric muscle action at maximal intensity. Second, individual difference in fatigue over each set and training session makes it difficult to plan further training sessions precisely. As such, if the intensity of each eccentric muscle action is not measured, the actual training intensity is unknown. Although the studies in the current review may have collected such data, no study has reported actual intensities and changes over sets or between sessions. It is well known from concentric exercise that clearly structured training that is performed at pre-determined "submaximal" percentages of a maximal lift or strength measurement yields greatest results (35). Thus it is surprising that

most studies would choose a training design where the detailed amount of torque, force and work performed during training is unknown.

Furthermore, as training intensities showed no significant differences in strength changes, it is plausible to assume that in practice one would rather choose an eccentric training form performed at less than very high intensities. Eccentric cycling for example showed an increase in concentric strength across studies of 2.2 to 46 % (22–24,27,50,288,291). While concentric strength was only measured in two studies improved by 8.2 and 10.7% (27,51), unfortunately, no study has measured changes in eccentric strength. However, as the power output or workload during eccentric cycling has been shown to increase by 299-1200% over the course of 6-12 weeks only (22–26,50,51,291), it can be assumed that eccentric strength had improved as well. The eccentric cycling has been performed for 5-20 min, and the power output at the beginning of training ranged from 40 to 225 W (24,26,50,51,291), but 60-80% of predicted maximal heart rate (23,27,69), and average RPE of 9.5-15 (22,24,26,27,69), have also been reported during training. Thus, although on the spectrum of possible eccentric training intensities (30-130% of concentric 1RM) eccentric cycling can be designed to be performed at low to medium intensities, it can stimulate large increases in muscle strength. Such a submaximal form of eccentric exercise could be much easier be performed by a wider population than any range of eccentric repetitions performed maximally.

3.5 Muscle morphology

Out of 220 studies, 78 studies investigated changes in muscle morphology, either as changes in muscle cross-sectional area, muscle thickness, muscle fascicle length or pennation angle. Overall, there were 39 studies at very high intensity (Figure 8), 19 studies at high intensity (Figure 9), 4 studies at medium intensity (Figure 10), and 16 studies used low intensity (Figure 11).

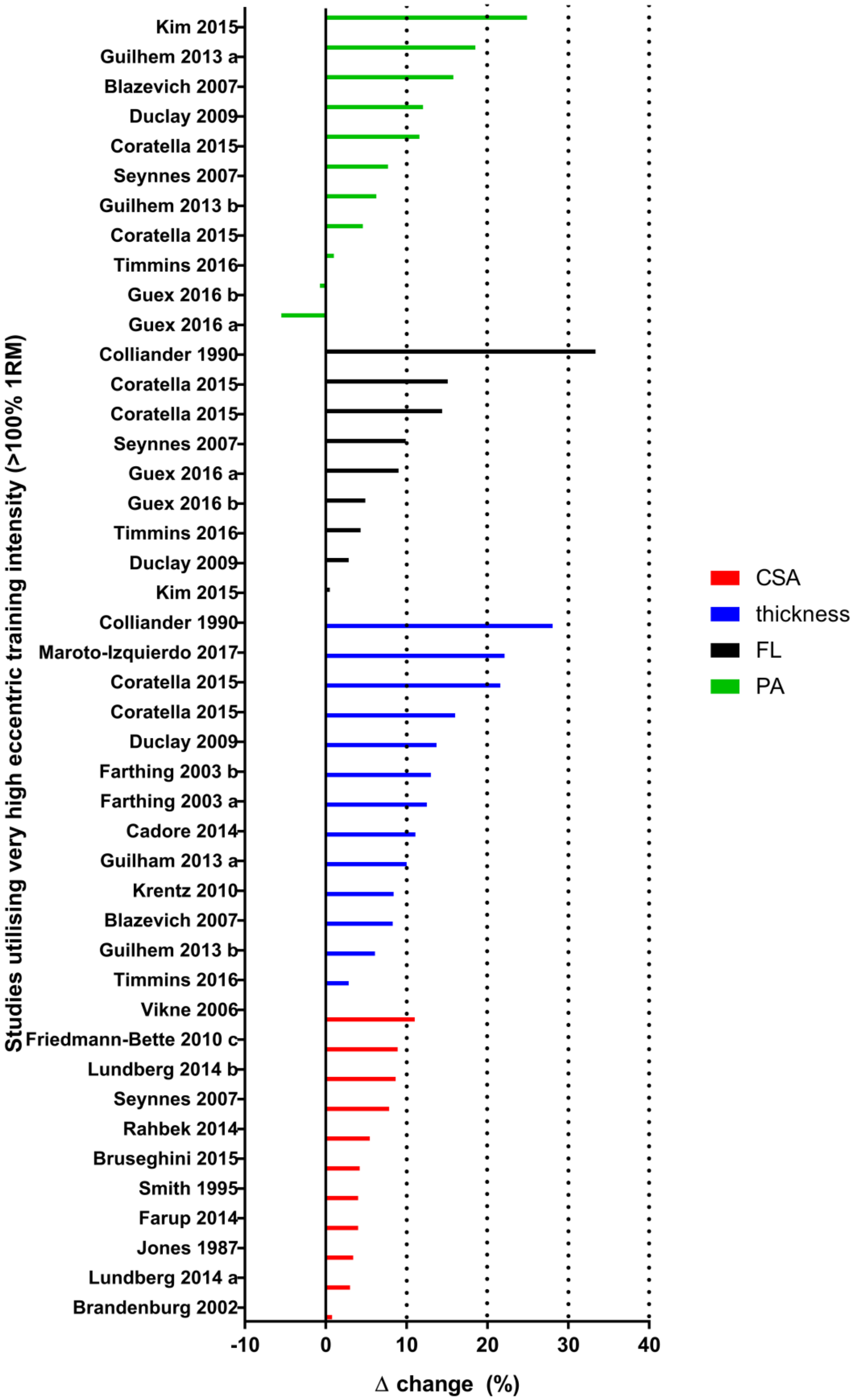

Figure 9: Average % change of muscle cross-sectional area (CSA, red bars), muscle thickness (CON, blue bars), fascicle length (FL, black bars) and pennation angle (PA, green bars) in studies utilising very high eccentric training intensity (≥100% concentric 1RM) (20,127,136,143,163,166,169,176,183,186,189,191,193,195,202–204,210,214,292–294)

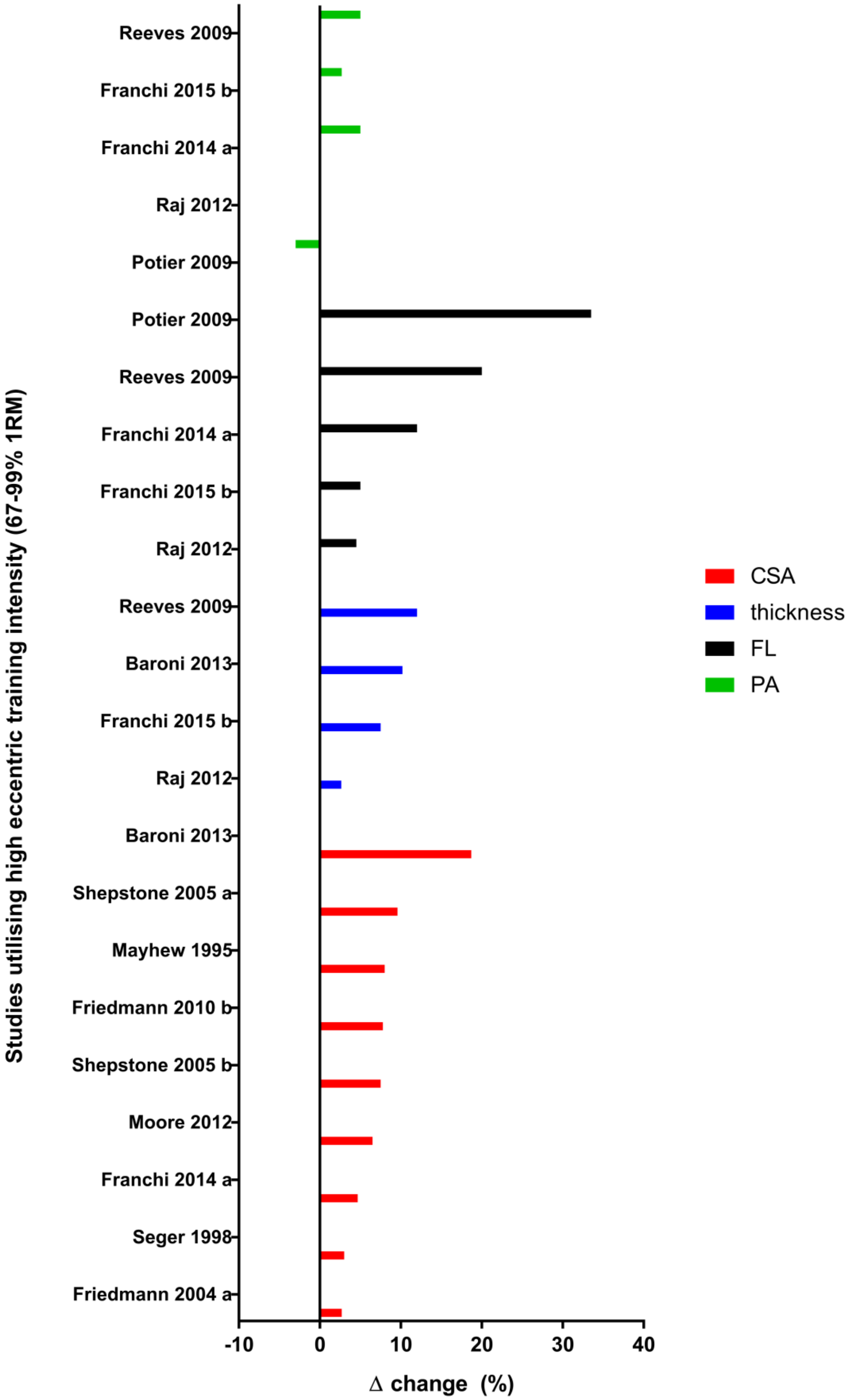

Figure 10: Average % change of muscle cross-sectional area (CSA, red bars), muscle thickness (CON, blue bars), fascicle length (FL, black bars) and pennation angle (PA, green bars) in studies utilising high eccentric training intensity (67-99% concentric 1RM) (202,218,222,229,235,237,240,241,243,252,260,262)

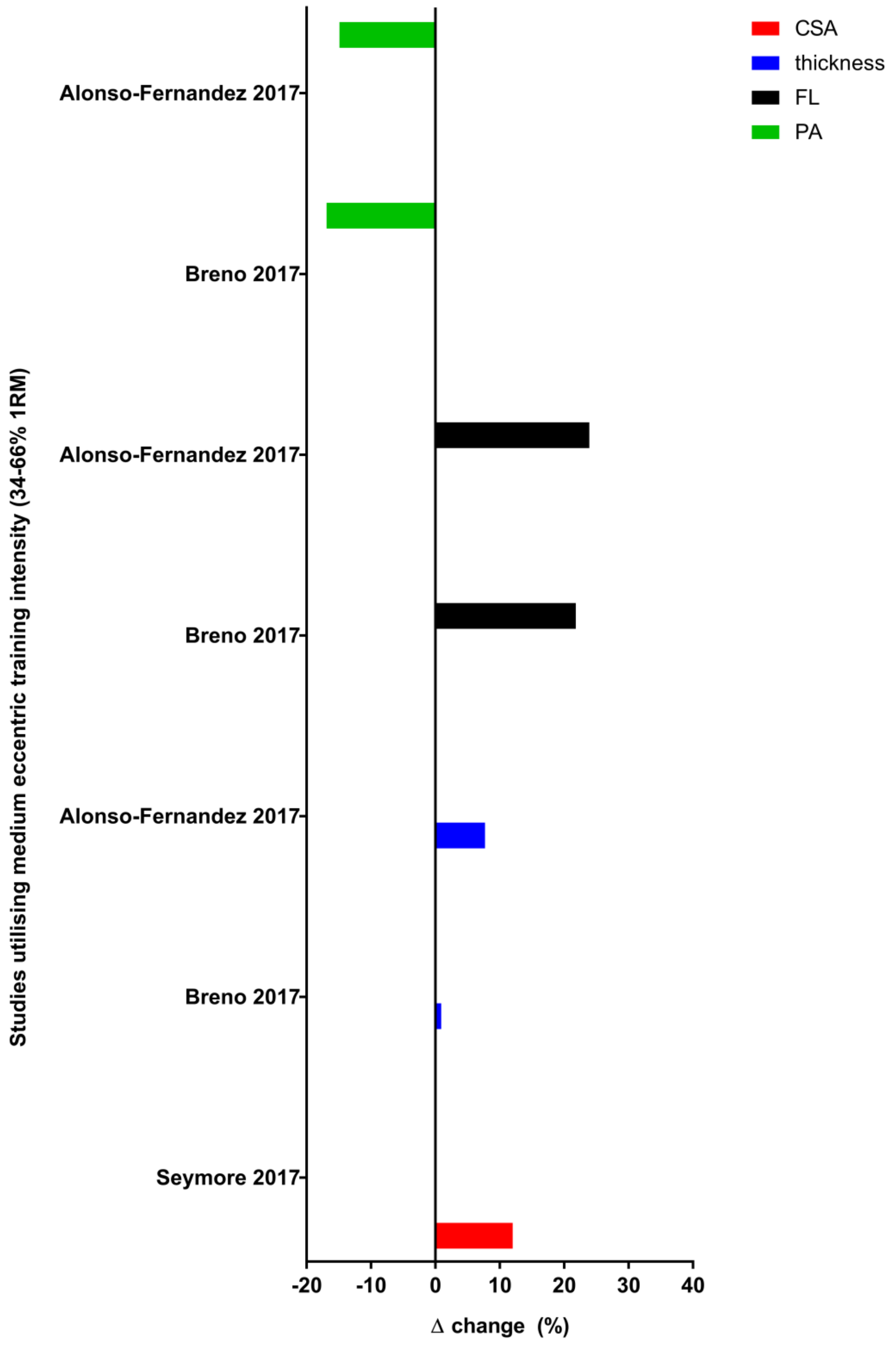

Figure 11: Average % change of muscle cross-sectional area (CSA, red bars), muscle thickness (CON, blue bars), fascicle length (FL, black bars) and pennation angle (PA, green bars) in studies utilising medium eccentric training intensity (34-66% concentric 1RM) (270,271,295)

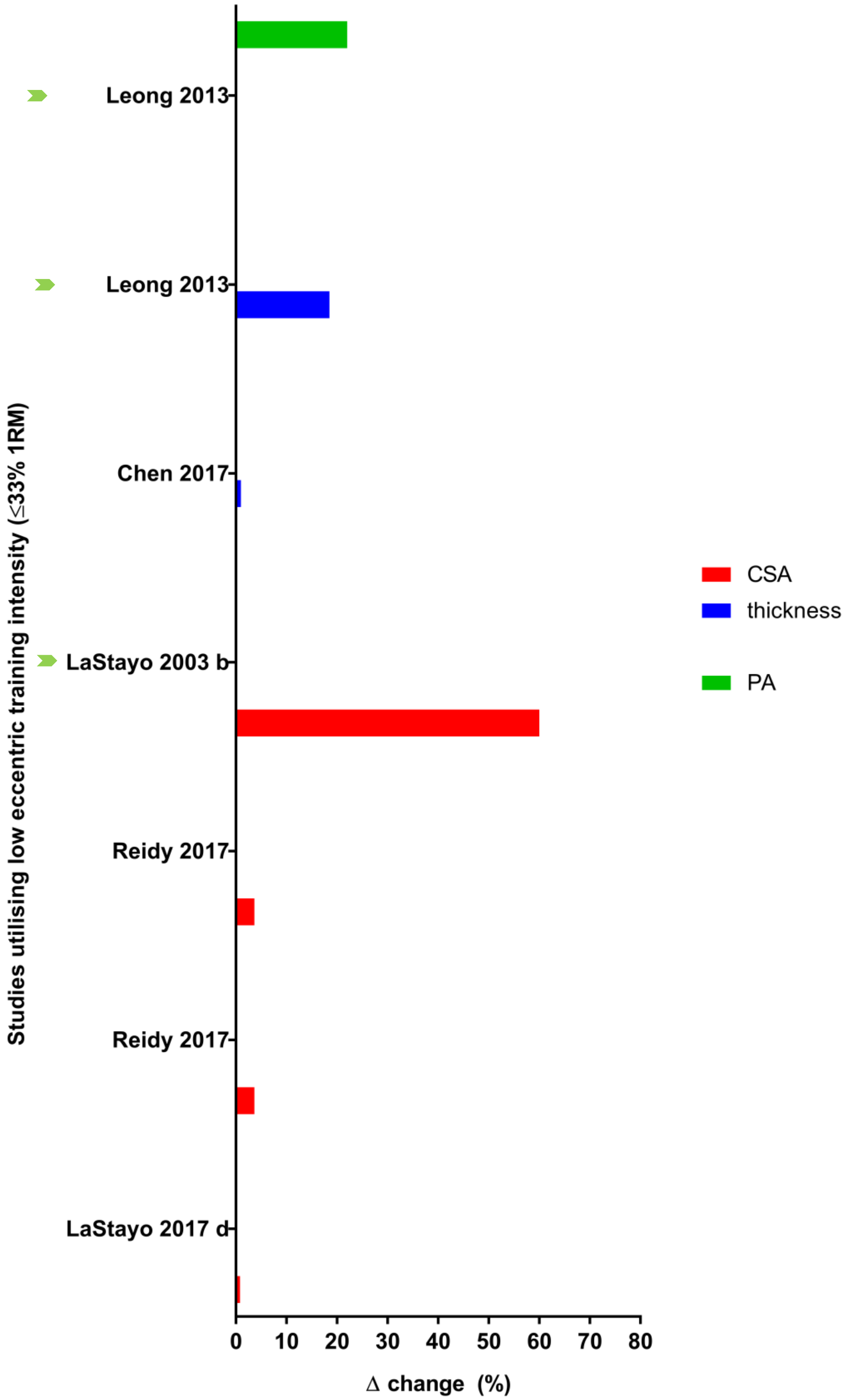

Figure 12: Average % change in muscle cross-sectional area (CSA, red bars), muscle thickness (CON, blue bars), and pennation angle (PA, green bars) in studies utilising low eccentric training intensity (≤33% concentric 1RM). Green arrow indicates eccentric cycling studies. (22,26,141,296–298)

3.5.1 Muscle cross-sectional area

Out of 78 studies that investigated changes in muscle architecture, 25 studies measured CSA. For the low-intensity category, 4 studies measured CSA, 1 study using medium intensity, 9 studies using high intensity and 11 studies using very high intensity. The CSA improved on average by 17.04 ± 24.83% (0.8 to 60%) after low intensity, 12% after medium intensity, 7.61 ± 4.5% (2.7 to 18.7%) after high intensity, and by 5.57 ± 2.96% (0.8 to 11%) after very high intensity. There were no significant differences between intensity categories (P = 0.7298) (Figure 12).

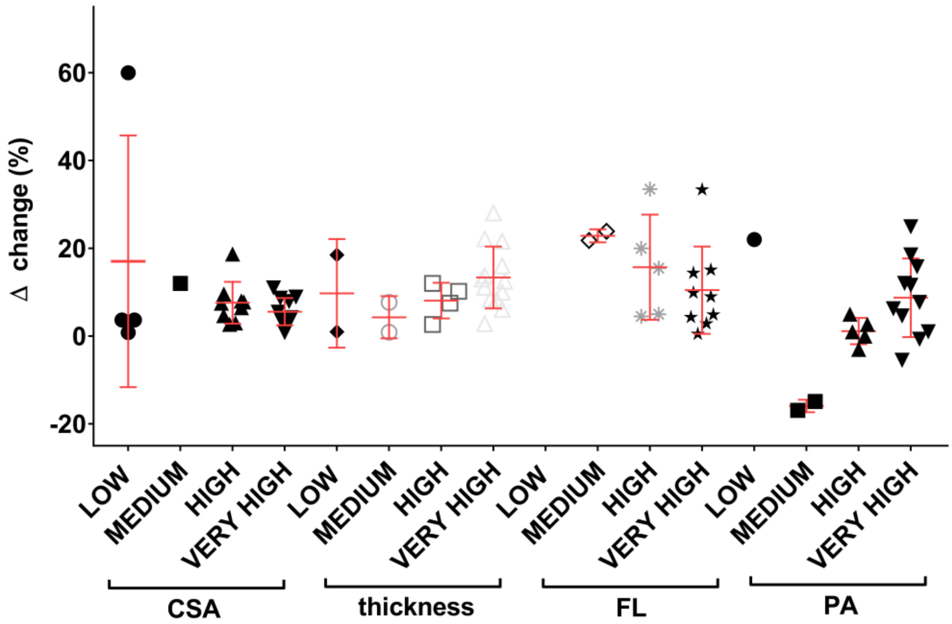

Figure 13: Average % change in muscle cross-sectional area (CSA), muscle thickness (thickness), fascicle length (FL), and pennation angle (PA) between low (≤33% concentric 1RM), medium (34-66 % concentric 1RM), high (67-99 % concentric 1RM) and very high (≥100% concentric 1RM) eccentric training intensity. There were no significant differences

3.5.2 Muscle thickness

Across the 78 studies that have investigated changes in muscle architecture, there was a total of 21 studies that measured changes in muscle thickness. There were 2 studies using low intensity, 2 medium intensity, 4 high intensity and 13 very high intensity that have measured changes in muscle thickness. On average muscle thickness increased by 9.75 ± 8.75% (1 to 18.5%) after low intensity, 4.3 ± 3.4% (0.9 to 7.7%) after medium intensity, 8.09 ± 3.52% (2.66 to 12%) after high intensity, and 13.36% ± 6.79% (2.85 to 28.06%) after very high intensity training. There was no significant differences between intensity categories (P = 0.7298) (Figure 12).

3.5.3 Fascicle length

Across the total 78 studies measuring changes in muscle architecture, there were 16 studies investigating changes in fascicle length. In low intensity there was no study, in medium intensity, there were 2 studies, in high intensity 5 studies, and in very high intensity there were 9 studies that measured fascicle length. The results showed an average increase in fascicle length of 22.85 ± 1.05% (21.8 to 23.9%) after medium intensity, 15.7 ± 10.73% (4.5 to 33.5%) after high-intensity training and 10.48 ± 9.37% (0.5 to 33.37%) after very high-intensity training. There were no significant differences between intensity categories (P = 0.7298) (Figure 12).

3.5.4 Pennation angle

A total of 19 studies investigated changes in the pennation angle of fascicles. One study utilised low-intensity exercise, 2 studies medium intensity, 5 studies high intensity, and 11 studies very high intensity. The low-intensity study increased pennation angle by 22%, the two studies with medium intensity decreased pennation angle by 15.9 ± 1% (-16.9 to -14.9%), high intensity increased pennation angle by 1.14 ± 2.68% (-3 to 5%), and very high intensity increased pennation angle by 8.74 ± 8.54% (-5.5 to 24.9%). There were no significant differences between intensity categories (P = 0.7298) (Figure 12).

3.5.5 Summary muscle morphology

Similar to the findings about strength, there were no differences in the outcomes measures of muscle morphology between training intensities. Previous studies have concluded that eccentric training is specifically beneficial for increases in muscle mass and size when performed at very high intensities (17,117). It is plausible to assume that there might be a threshold in overload that has to either be reached by training intensity or volume. Eccentric cycling showed in one study an increase in CSA of 60% (22), and in another study an increase of 18.5% in muscle thickness and 22% in pennation angle (26). The latter increase in pennation angle is different from previously mainly reported increases in fascicle length, while pennation angle was concluded to be increased greater after concentric strength training (16). Furthermore, there was an increases of 1.8-6.5% in lean leg mass after eccentric cycling (49,50,288,291,299). As eccentric cycling in these studies was performed for 5-20 minutes at a cadence of 60 rpm, it is possible that the high volume of 300-1200 eccentric muscle actions has contributed to the increases in muscle morphology. As previously stated in chapter 2, such conclusions have been recently also made for hypertrophy after concentric strength training (117).

3.6 Performance parameters

A total of 78 studies out of all 220 eccentric training studies have investigated changes in countermovement jump height, squat jump height, improvements in sprint running performance, functional parameters like the 6 minute walk test, timed up and go test, number of repetitions until failure or stair ascend and descend time, as well as improvements in concentric peak power. Generally, there were 31 studies at very high intensity (Figure 13), 26 at high intensity (Figure 14), 7 at medium intensity (Figure 15), and 14 studies at low intensity (Figure 16).

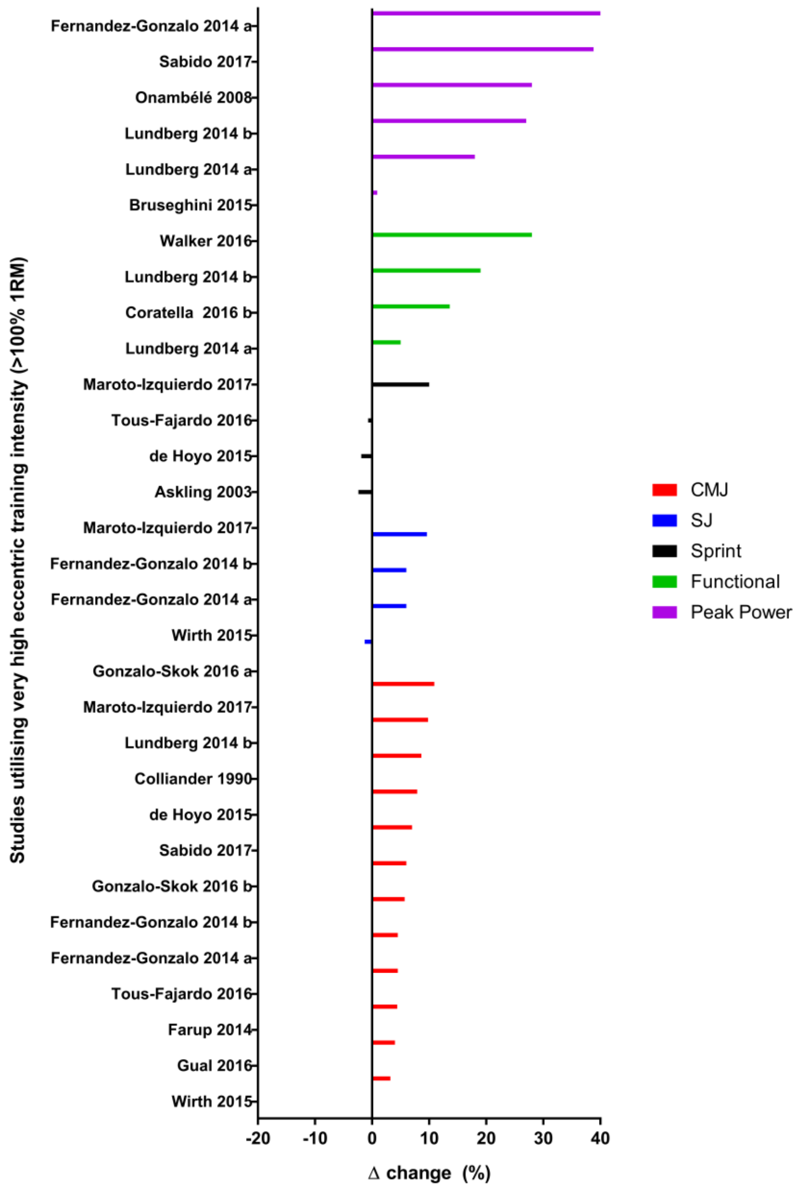

Figure 14: Average % change in countermovement jump height (CMJ, red bars), squat jump height (SJ, blue bars), sprinting time (Sprint, black bars), functional measures (Functional, green bars) and concentric peak power output (Peak power, purple bars) in studies utilising very high eccentric training intensity (≥100% concentric 1RM) (20,166,173,181,186,190,193,201,206,212,253,294,300–303)

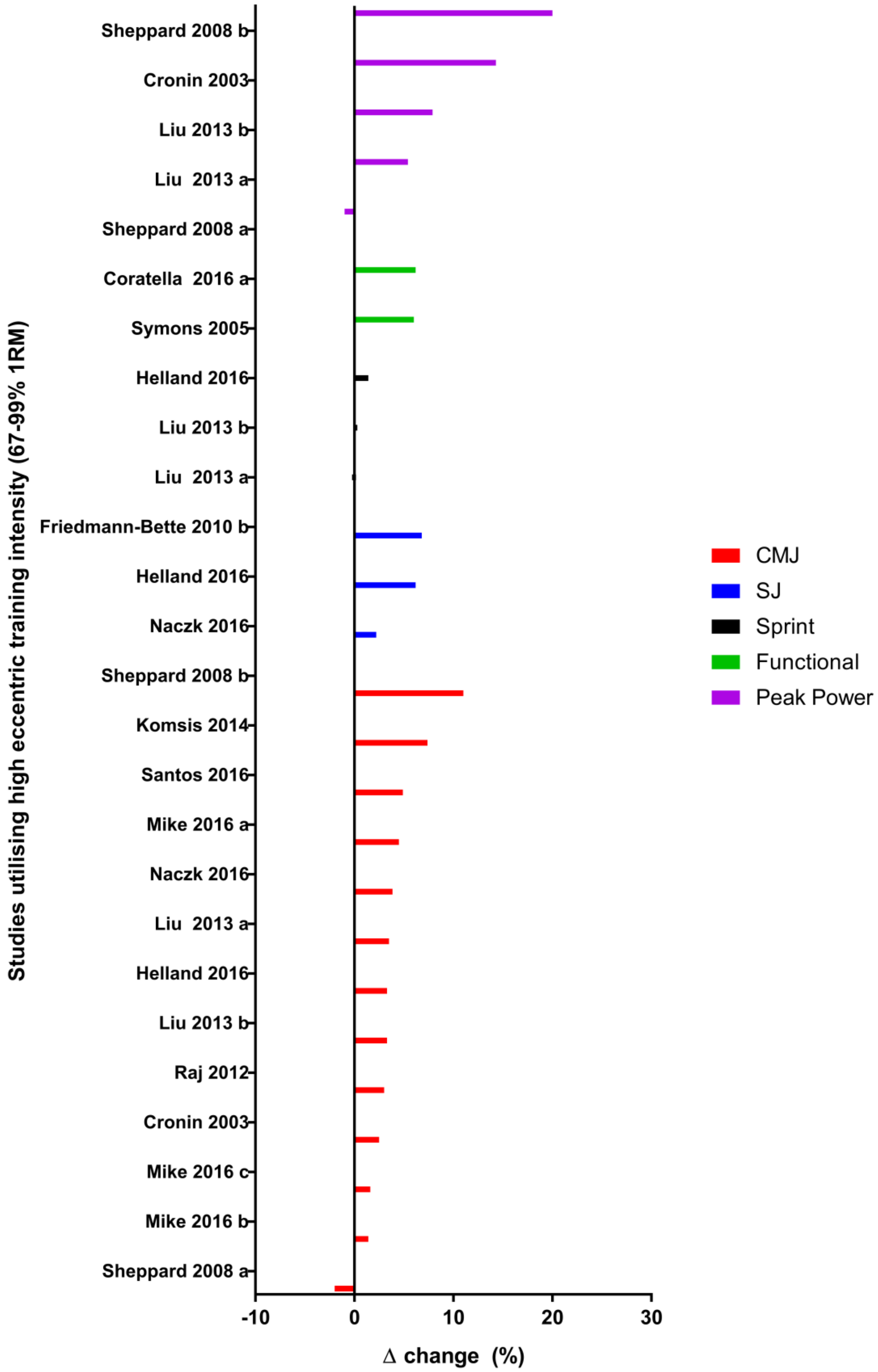

Figure 15: Average % change in countermovement jump height (CMJ, red bars), squat jump height (SJ, blue bars), sprinting time (Sprint, black bars), functional measures (Functional, green bars) and concentric peak power output (Peak power, purple bars) in studies utilising high eccentric training intensity (67-99% concentric 1RM) (202,224,232,233,243,246–248,253,254,304,305)

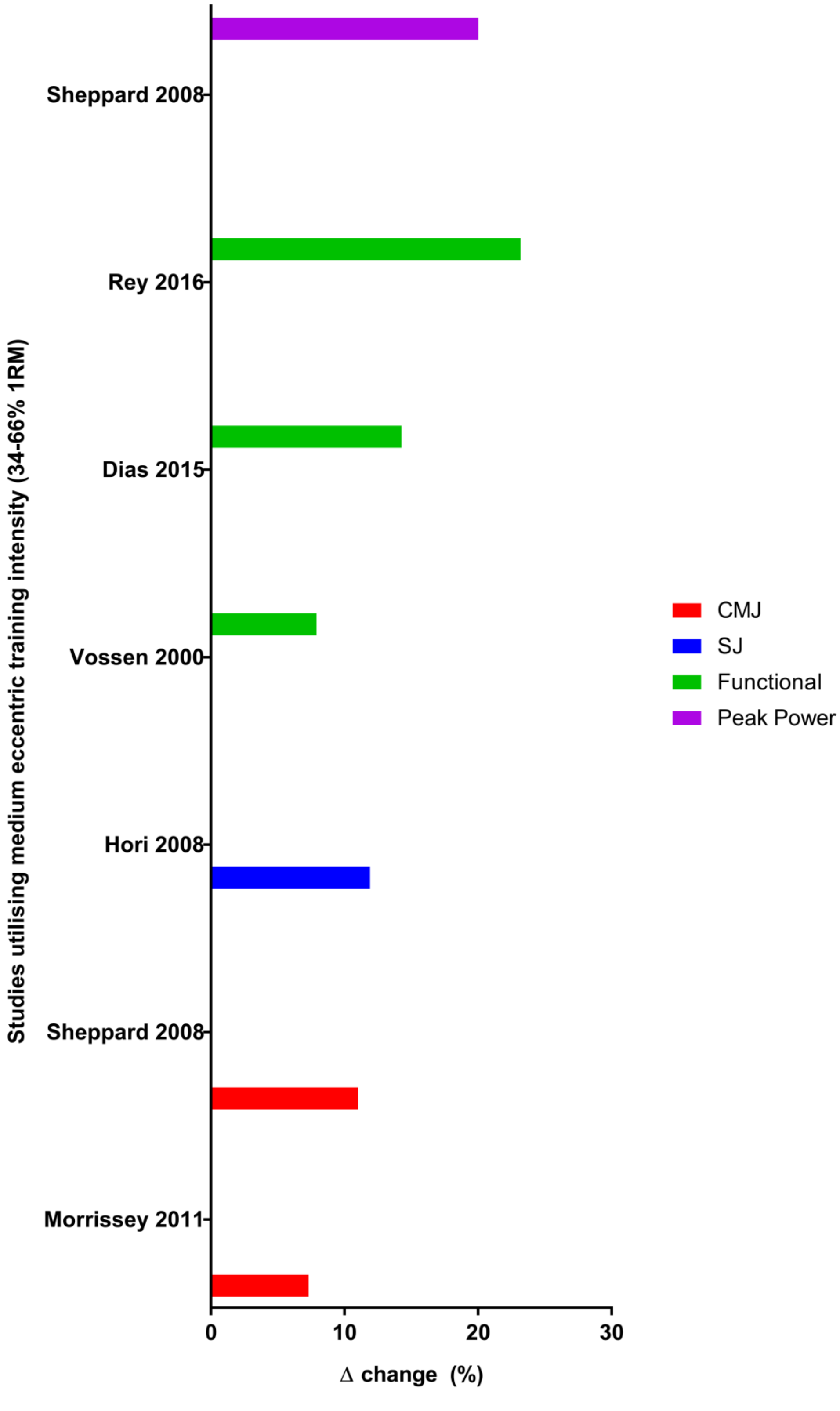

Figure 16: Average % change in countermovement jump height (CMJ, red bars), squat jump height (SJ, blue bars), sprinting time (Sprint, black bars), functional measures (Functional, green bars) and concentric peak power output (Peak power, purple bars) in studies utilising medium eccentric training intensity (34-66% concentric 1RM) (254,254,277,278,282,306,307)

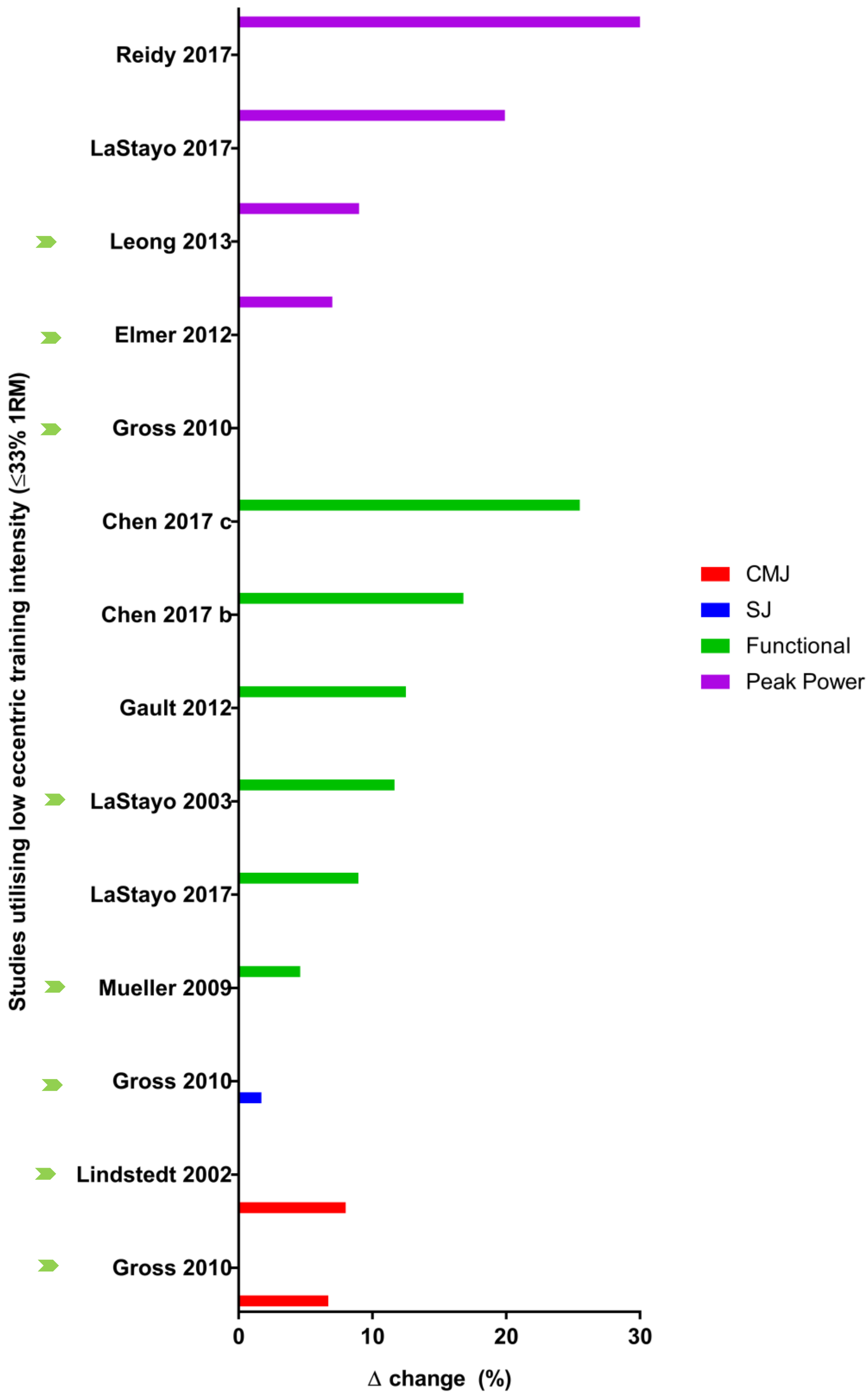

Figure 17: Average % change in countermovement jump height (CMJ, red bars), squat jump height (SJ, blue bars), sprinting time (Sprint, black bars), functional measures (Functional, green bars) and concentric peak power output (Peak power, purple bars) in studies utilising low eccentric training intensity (≤33% concentric 1RM). Green arrow indicates eccentric cycling studies. (10,22,25,26,41,50,141,287,291,296,298)

3.6.1 Countermovement jump

Out of 73 studies that measured performance parameters 30 studies measured countermovement jump height before and after eccentric training. After low-intensity eccentric training countermovement jump height was measured in 2 studies, after medium intensity in 2 studies, after high intensity in 13 studies, as well as in 13 studies after very high intensity. The average change in countermovement jump height was 7.4 ± 0.7% (6.7 to 8%) after low intensity, 9.2 ± 1.9% (7.3 to 11%) after medium intensity, 3.7 ± 3% (-2 to 11%) after high intensity, and 5.9 ± 2.8% (0 to 10.9%) after very high intensity. There were no significant differences between intensity categories (P > 0.9999) (Figure 17).

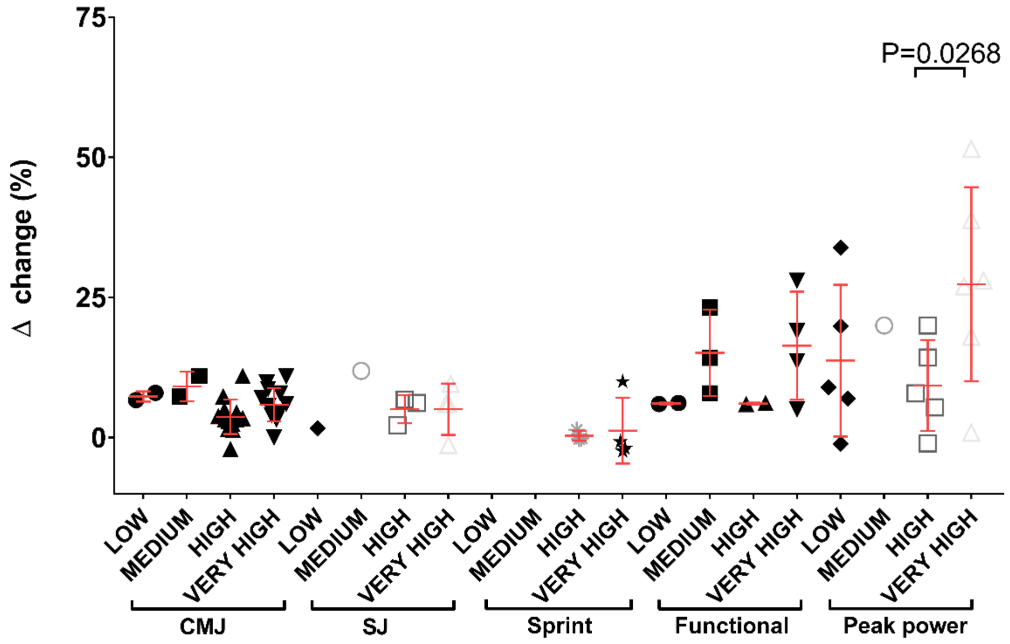

Figure 18: Average % change in countermovement jump height (CMJ), squat jump height (SJ), sprint time (Sprint), functional measures (Functional), and concentric peak power output (Peak power) between low (≤33% concentric 1RM), medium (34-66 % concentric 1RM), high (67-99 % concentric 1RM) and very high (≥100% concentric 1RM) eccentric training intensity

3.6.2 Squat jump

Squat jump height (SJ) was measured in 9 out of 73 studies that investigated performance parameters before and after eccentric training. There was 1 study that used low intensity, and 1 study that used medium intensity, the high intensity was used in 3 studies and very high intensity in 4 studies. For low-intensity SJ changed by 1.7%, for medium intensity it was 11.9%, for high intensity it was 5.1 ± 2% (2.2 to 6.8%) and for very high intensity it was 5.1 ± 4% (-1.3 to 9.6%). There were no significant differences between intensity categories (P > 0.9999) (Figure 17).

3.6.3 Sprint

Out of all 73 studies that investigated changes to performance parameters after eccentric training, 7 studies measured changes in sprint running. No study used low or medium intensity. There were 3 studies in the high-intensity category and 4 studies in the maximal intensity category. The average change in sprint running after high-intensity eccentric training was 0.4 ± 0.7% (-0.2 to 1.4%), and after maximal intensity training, it was 1.25 ± 5.1% (-2.4 to 10%). There were no significant differences between intensity categories ($P > 0.9999$) (Figure 17).

3.6.4 Functional measures

There were 15 studies out of 73 that used some functional measure. These measures include the maximal amount of repetitions until failure for a chosen exercise, 6-min walking distance, timed up-and-go test, balance tests, as well as stair, descends and ascends. For the low intensity category there were 6 studies, for medium intensity 3 studies, for high intensity 2 studies, and for the very high intensity category, there were 4 studies that measured one or several functional parameters. The studies in the low intensity showed an average change of 13.3 ± 6.6% (4.6 to 25.5%), the medium intensity showed a change of 15.1 ± 6.3% (7.9 to 23.2%), the high intensity showed a change of 6.1 ± 0.1% (6 to 6.2%), and for very high intensity it was 16.4 ± 8.4% (5 to 28%). There were no significant differences between intensity categories ($P \geq 0.9975$) (Figure 17).

3.6.5 Concentric peak power output

Out of all 73 studies investigating changes in performance parameters, 17 studies measured concentric peak power output. This concentric peak power output has been measured during various forms of concentric exercise (e.g. cycling sprints, jumps, squats). It was assumed that increases in concentric peak power output measured for one concentric exercise would be similar to the others. Thus, all types of concentric peak power output were analysed together. There were 5 studies that used low intensity, 1 study using medium intensity, 5 studies using high intensity, and 6 studies using very high intensity. The studies using low intensity showed a change in concentric peak power by 13.3 ± 12.1% (-1.1 to 33.9%), while the one study in the medium intensity category showed an increase by 20%. For high intensity, there was an average increase of 9.3 ± 7.3% (-1 to 20%), and for very high intensity it was 27.4 ± 15.8% (0.9 to 51.5%). The very high-intensity category showed a greater increase in peak power output than high-intensity category ($P = 0.0268$), while there were no other significant differences ($P \geq 0.2695$) (Figure 17).

3.6.6 Summary performance parameters

While there were no other significant differences ($P \geq 0.2695$), concentric peak power output between the very high-intensity category and high-intensity category was significantly greater ($P = 0.0268$). In comparison to the strength and morphology measures, the analysis of the performance parameters has to be viewed with more caution. There were many methodological variations in the assessment of all performance parameters.

Still, eccentric cycling has been shown to increase CMJ in two studies by 8 and 6.7% (10,50), and functional measures by 11.6% (22). It is not clear how eccentric cycling improved performance during jumps. There is an indication of increased stiffness as measured by increases in hopping frequency (10) and vertical spring stiffness of the whole body (308) after eccentric cycling training. It is possible though that the uninterrupted fashion of eccentric cycling combined with the medium velocity (180 degrees per second at 60 rpm) can improve utilisation of the stretch-shortening cycle. Additionally, as outlined in chapter 1, most functional measures have been shown to increase significantly in clinical populations (54,57,58,62,63,66). Thus, it is possible that to measure increases in functional performance with healthy populations after eccentric cycling, other parameters have to be considered. Such measures might have to be more related to high power production, such as shown with jump heights, or alternative parameters (e.g. sprint time or peak power output).

3.7 Conclusions

The current literature review showed that there was no significant difference between eccentric training intensities in the magnitude of change for muscle strength, morphology, and performance parameters. Although contraction velocity was reported in less than expected studies, it was shown that it hat no significant impact in the increases of isometric, concentric and eccentric muscle strength. Furthermore, studies utilising eccentric cycling, despite its very low training intensity relative to the majority of studies, were able to show a similar magnitude of change for all parameters, and the highest improvements for some changes. Considering that there is a large range of power output that can be performed during eccentric cycling, the utilised training intensities were very low in comparison to the existent capacity. The existent capacity was shown by the average increase of 547%.power output or workload during training. Thus, there is a large potential for improvements, and application of greater loads throughout the training programmes, such as modifying training through various interval methods.

CHAPTER FOUR

STUDY ONE

Cardiopulmonary responses to incremental eccentric and concentric cycling tests to task failure

4.1 Abstract

This study compared cardio-pulmonary responses between incremental concentric and eccentric cycling tests and examined factors affecting the maximal eccentric cycling capacity. On separate days, nine men and two women (32.6 ± 9.4 y) performed an upright seated concentric (CON-T) and an eccentric (ECC-T) cycling test, which started at 75 W and increased 25 $W{\cdot}min^{-1}$ until task failure. Gas exchange, heart rate (HR) and power output were continuously recorded during the tests. Participants also performed maximal voluntary contractions of the quadriceps (MVC), squat and countermovement jumps. Peak power output was 53% greater ($P<0.001$, $g=1.77$) for ECC-T (449 ± 115 W) than CON (294 ± 61 W), but peak oxygen consumption was 43% lower ($P<0.001$, $g=2.18$) for ECC (30.6 ± 5.6 $ml{\cdot}kg{\cdot}min^{-1}$) than CON (43.9 ± 6.9 $ml{\cdot}kg{\cdot}min^{-1}$). Maximal HR was not different between ECC-T (175 ± 20 bpm) and CON-T (182 ± 13 bpm), but the increase in HR relative to oxygen consumption was 33% greater ($P=0.01$) during ECC-T than CON-T. Moderate to strong correlations ($P<0.05$) were observed between ECC-T peak power output and CON-T peak power ($r=0.84$), peak oxygen consumption ($r=0.54$) and MVC ($r=0.53$), while no significant relationships were observed between ECC peak power output and squat as well as countermovement jump heights. Unexpectedly, maximal HR was similar between CON and ECC. Although ECC power output can be predicted from CON peak power output, an incremental eccentric cycling test performed after 3-6 familiarisation sessions may be useful in programming ECC training with healthy and accustomed individuals.

4.2 Introduction

Eccentric cycling was first introduced in a scientific journal in 1952 and repetitively confirmed that the metabolic load is lower during eccentric than concentric cycling at the same power output (8,36,309). Several studies have since shown the potent effects of eccentric cycling training on muscle function and strength (23,24,26). With several review papers highlighting the importance of low-intensity, high volume eccentric exercise (28,29,34), and more eccentric cycling and stepping ergometers available on the market, it is probable that eccentric cycling training will become more popular. Thus, it is necessary to establish a protocol to determine eccentric cycling capacity and to safely and effectively prescribe eccentric cycling to different populations.

Several studies have examined cardiopulmonary responses to continuous eccentric cycling, and shown greater increases in cardiac output (310) and heart rate (311,312) for any oxygen consumption when compared with concentric cycling at low intensities. Furthermore, two studies have examined physiological responses during an incremental eccentric cycling protocol (309,313). In both studies, power output during eccentric cycling was increased until participants reached the maximal power output achieved during concentric cycling. As a result, participants achieved only 256 to 330 Watts at a heart rate of 106.5 to 117 bpm during eccentric cycling. The latter indicates that volitional exhaustion and maximal eccentric cycling performance were not achieved, thus not providing any information about unique characteristics of maximal eccentric cycling capacity. To the best of our knowledge, no previous research has examined the potentially unique physiological responses to eccentric cycling until exhaustion, and as such little is known with regards to the factors that limit maximal eccentric cycling capacity.

Previous studies that examined the effectiveness of eccentric cycling exercise training set the intensity based on maximal heart rate or age-predicted heart rate (23,25), peak power output (26,67) or rating of perceived exertion (RPE) (288,314) measured during an incremental concentric cycling test to task failure. Despite the uniquely low metabolic load of eccentric cycling at submaximal intensities, all previous studies have prescribed eccentric cycling training based on the information from a concentric cycling test. It may be that an incremental eccentric cycling test to task failure provides more information on the factors limiting eccentric cycling capacity and that peak power output obtained from an eccentric cycling test is more specific for eccentric cycling prescription. For a comprehensive understanding of the performance during an eccentric cycling test, factors that determine peak power output should

also be considered. However, we are not aware of any studies that have examined factors limiting eccentric cycling performance.

Conversely, possible factors limiting exercise capacity during maximal concentric cycling have been well documented. Maximal aerobic capacity and peak power output during incremental concentric cycling are typically limited by oxygen delivery and oxygen utilisation (82,315). Based on these factors, several submaximal tests have been designed to estimate maximal exercise capacity during concentric cycling and other exercise modes (316,317). Given the low metabolic cost and greater work achievable during eccentric cycling, it is plausible that peak power output during an eccentric cycling test is more closely associated with neuromuscular rather than cardiovascular function. Neuromuscular function and fatigue have been assessed before and after eccentric exercises by measuring maximal voluntary isometric contraction (MVC) strength (23,240) or squat and countermovement jumps (318,319). Since these measurements have been shown to improve following eccentric exercise training (254,301), they may correlate better with peak power output during incremental eccentric cycling.

Therefore, the present study compared physiological responses (oxygen consumption, minute ventilation, tidal volume, breathing frequency, and heart rate) in relation to power output between an incremental eccentric versus concentric cycling test. Relationships between peak power during eccentric cycling and peak oxygen consumption and peak power output during concentric cycling, MVC torque of the knee extensors, countermovement and squat jump height and their ratio were investigated. The first hypothesis tested was that peak oxygen consumption, minute ventilation, tidal volume, breathing frequency, and peak heart rate at task failure of an incremental cycling test would be greater during concentric than eccentric cycling, while peak power output would be greater during eccentric cycling. The second hypothesis tested was that MVC torque of the knee extensors, countermovement jump height and the countermovement to squat jump ratio would be strong predictors of peak power during eccentric cycling.

4.3 Methods

4.3.1 Participants

The institutional human research ethics committee approved this study before commencing the research. Eleven healthy men (n=9) and women (n=2) were recruited for the study, and their average ± standard deviation (SD) age, height and body mass were 33 ± 9 y, 181.4 ± 8.2 cm, and 81.1 ± 17.1 kg, respectively. They were physically active and/or training recreationally in cycling, cricket or volleyball, but had not performed any specific eccentric

exercise beyond those in normal daily activities (i.e., downstairs/downhill walking, sitting down) in the 6 months prior to the study. Participants were not taking any medication and did not have any history of lower limb musculoskeletal injuries. They refrained from exercise, alcohol and caffeine in the 48 h prior to each testing session. They were fully informed of the requirements and risks associated with the study and provided written informed consent before participation. The sample size was estimated using the heart rate data from a previous study (36) in which heart rate was compared between eccentric and concentric cycling at submaximal intensities. It was assumed that the difference in heart rate at task failure would be smaller than at submaximal intensities. Thus, based on G*Power (Version 3.0.10, 2008, Kiel, Germany), the effect size was estimated to be 0.9, with an α level of 0.05 and a power of 0.8 ($1-\beta$), it was found that 10 participants would suffice.

4.3.2 Study design

For this study participants visited the laboratory on five separate occasions (Figure 18). During the first visit, participants performed a concentric cycling test. On the following three visits, participants performed 5, 8 and 10 minutes of practice continuous eccentric cycling at 30, 30 and 40% of their concentric peak power output (PPO), respectively. During the three practice (familiarisation) sessions, cadence was set at 60 rpm and the bike operated in isokinetic mode. These sessions were specifically designed and performed to provide a repeated bout effect without major increases in indirect markers of muscle damage and soreness (36). Measurements of MVC knee extension torque and squat and countermovement jump heights were taken before each eccentric cycling session. Before the final session for this study, participants participated in five further separate sessions of interval and continuous eccentric cycling. These sessions included two continuous eccentric cycling protocols: 20 minutes at 60% of concentric PPO and 13.2 minutes at 60% of concentric PPO, with the former performed at 60 rpm, and the latter at 90 rpm. There were also three different interval eccentric cycling protocols: 4 x 4 min at 75% of concentric PPO with a 2-min rest between bouts, 12 x 1 min at 100% of concentric PPO with a 1-min rest between bouts, and 10 x 1 min at 150% of concentric PPO with a 1-min rest between bouts. As no previous study has investigated maximal eccentric cycling performance, these additional eccentric cycling sessions guaranteed that the participants were well familiarised and could reach a “true” maximal eccentric cycling performance. During the last visit to the laboratory, participants performed the incremental eccentric cycling test to task failure.

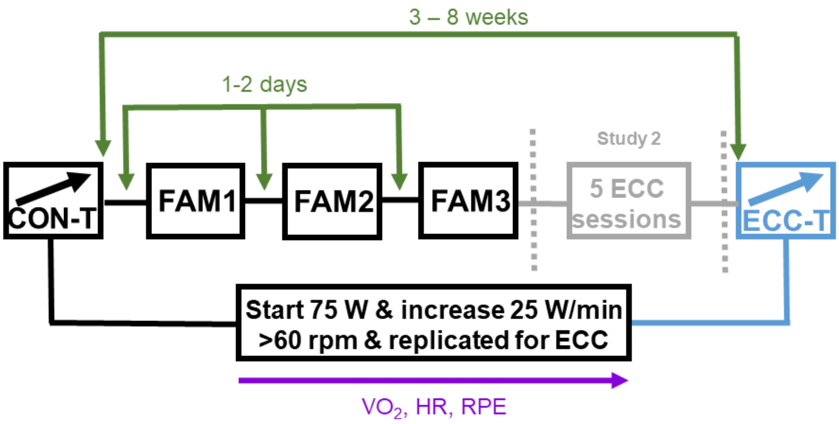

Figure 19: The design of study 1, with the concentric (CON-T) and eccentric (ECC-T; blue) incremental test, and the three familiarisations (FAM1-3). Sessions part of study 2 are indicated in grey. The time between sessions is shown in green. The measurements of oxygen consumption (VO_2), heart rate (HR), and rating of perceived exertion (RPE) are shown in purple

4.3.4 Incremental concentric and eccentric cycling tests

The concentric and eccentric cycling tests were performed in an upright position, and the seat height of the ergometers described below was adjusted to the comfort of each participant (a slight bend of the knee joint at knee extension). Before the incremental concentric and eccentric cycling tests, participants completed a 3-min warm-up, in the relevant cycling mode, between 50 W and 120 W at 60 rpm. Both concentric and eccentric protocols begun at 75 W and increased by 25 W every minute until the participants could no longer cycle at a target power output. The concentric cycling test was performed on an electromagnetically braked cycling ergometer (Velotron, RacerMate, Inc., Seattle, Washington USA) and the eccentric cycling test was performed on an eccentric cycling ergometer (Cyclus2 Eccentric Trainer, RBM Elektronik-Automation GmbH, Leipzig, Germany).

The ergometers automatically controlled power output during the concentric and eccentric cycling tests with the electromagnetic brake during the concentric test (320) and the motor during the eccentric test. The resistance was adjusted based on the cadence of participants. Participants were able to self-select their cadence during the concentric cycling test, with the average cadence during this trial being a target cadence for the eccentric cycling test. The concentric cycling test was terminated when the cadence dropped below 60 rpm for more than 30 s. Given the participants are required to resist against the motor during eccentric cycling, the test was terminated when increased 10 rpm above the target for more than 30 s. During both incremental cycling tests, participants were provided with visual feedback on their power output, cadence and elapsed time. Verbal encouragement was provided during the final stages of both incremental tests.

Expired gases were measured each breath by a TrueOne 2400 metabolic cart (ParvoMedics, Sandy, Utah, USA) and averaged every 15 s. Peak oxygen consumption (VO_{2peak}) was taken as the highest value in any 15 s interval. The gas analyser and ventilometer were calibrated before each test using gases of known concentrations and a 3-L syringe (5530 series, Hans Rudolph, Inc., Shawnee, Kansas, U.S.A.). Minute ventilation (V_E), tidal volume (V_t) and breathing frequency (B_f) at the task failure were analysed as the average values of one minute of each protocol. Heart rate was recorded during cycling and measured every 5 s (S610, Polar, Finland). Due to the expected greater power output during eccentric cycling in comparison to concentric cycling, it was assumed that the eccentric protocol would last significantly longer. To avoid the influence of the greater exercise time on the cardiopulmonary parameters, the analysis of heart rate (HR) relative to oxygen consumption (VO_2) was normalised for stages completed. Thus, an average heart rate was calculated for every 10% of exercise time for each condition. To compare between conditions a linear regression that was based on the 10 averages was computed and the difference in the slope of both regressions was determined using the provided function in the GraphPad statistical package (Prism version 7.02, GraphPad Software, La Jolla, California, USA). The slope of the linear regressions was also compared between conditions for the relationship of HR and VO_2 to power output. This comparison was averaged for each stage during the incremental test, not for 10% of exercise time like for HR over VO_2. Furthermore, the relationship for HR and VO_2 over power output for each stage was only computed until the average peak power output achieved during each condition. Selected participants were able to achieve much higher peak power output at task failure.

4.3.5 MVC knee extension torque

Maximal voluntary isometric contractions of the right knee extensors at 70° knee angle were performed on a custom made chair with a load cell (Xtran S1W, Applied Measurements, Melbourne, Australia) to measure knee extensor muscle strength as previously reported (321). Participants performed a 5 min warm-up on a cycling ergometer (Monark 828E, Monark Exercise AB, Vansbro, Sweden) at 15% of their concentric peak power output at 60 rpm before the measure. Participants then performed three submaximal isometric knee extensions for 3 s at 50%, 50% and 80% of a maximal effort, separated by a 1-min passive rest. A total of three 3 s maximal isometric knee extensions were performed, separated by a 1-min passive rest. Participants were advised to contract as fast and as hard as possible. Trials with any countermovement were disregarded and repeated. The torque output was shown on a computer

screen, and torque data was sampled at a frequency of 1000 Hz, and a digital zero-phase lag finite impulse response low-pass filter with a cut-off frequency of 14 Hz was applied. The trial with the greatest peak torque value was used for further analysis. Verbal encouragement was provided during the measurements.

4.3.6 Squat and counter movement jump

Jump height was measured via a digital vertical jump meter (Vertical Jump Meter T.K.K. 5406, JUMP-MD, Takei Scientific Instruments Co. Ltd., Japan). Participants performed all jumps with hands placed on their hips and a self-chosen squat depth. For the squat jumps (SJ), participants were asked to squat down to the depth of their choice, remain in the squat position for 3 s and then jump without any countermovement. For the countermovement jump (CMJ) participants were asked to jump as high as possible from an upright standing position on a count of three. Verbal encouragement was provided before and during both jumps.

4.3.7 Statistical analyses

Data is reported as mean ± SD. Peak values (pulmonary parameters and power output) were compared between concentric and eccentric cycling using paired t-tests. The effect size for the difference in the dependent variables between concentric and eccentric cycling was calculated by Hedges' g (322). The slope of the linear regression calculated for the relationships between HR and VO2, VO2 and peak power output, and HR and peak power output was used to compare differences in these relationships between conditions. Pearson's correlations were used to assess the relationship between peak power output during eccentric cycling and VO_{2peak} and peak power output during concentric cycling, MVC torque of the knee extensors, countermovement and squat jump heights. Significance was set at $P < 0.05$ and all statistical analyses were performed using GraphPad statistical package (Prism version 7.02, GraphPad Software, La Jolla, California, USA).

4.4 Results

4.4.1 Heart rate, oxygen consumption and power output during incremental tests

Figure 19 shows changes in heart rate and oxygen consumption during the concentric and eccentric incremental cycling test. The slope of the linear regression for heart rate over power output was not different (P=0.276) between the eccentric (0.26 ± 0.03) and concentric (0.23 ± 0.01) tests. In contrast, the slope of the linear regression of oxygen consumption over power output was greater (P<0.0001) for the concentric (0.13 ± 0.004) than the eccentric test (0.047 ±

0.002). As shown in Figure 20, heart rate relative to oxygen consumption was greater during eccentric than concentric cycling, and the linear regression line was steeper (P=0.01) for eccentric (3.99 ± 0.30) than concentric cycling (2.99 ± 0.19).

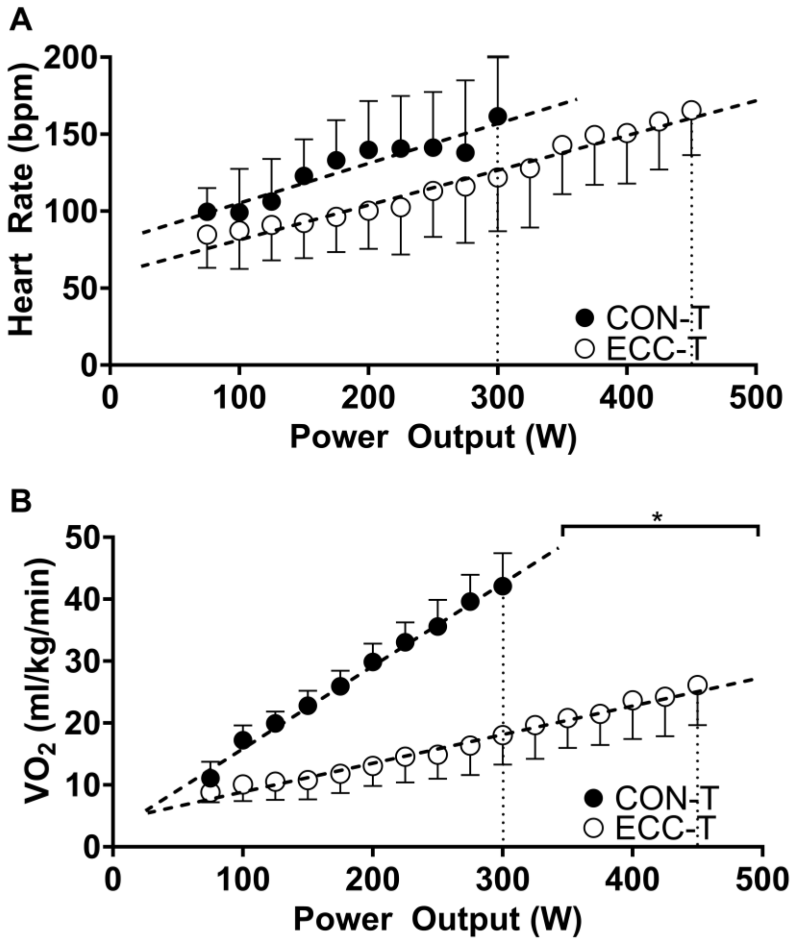

Figure 20: Comparison between concentric (CON-T) and eccentric cycling (ECC-T) for changes in heart rate (a) and oxygen consumption (b) over incremental power output stages from 75 W to the average peak power output among participants (CON: 300 W, ECC: 450 W). It should be noted that some participants were able to achieve much higher peak power output at task failure. Thus the heart rate and oxygen consumption values shown in the figures are not peak values. *: significant (P < 0.01) difference between the slope of the linear regression for ECC-T and CON-T

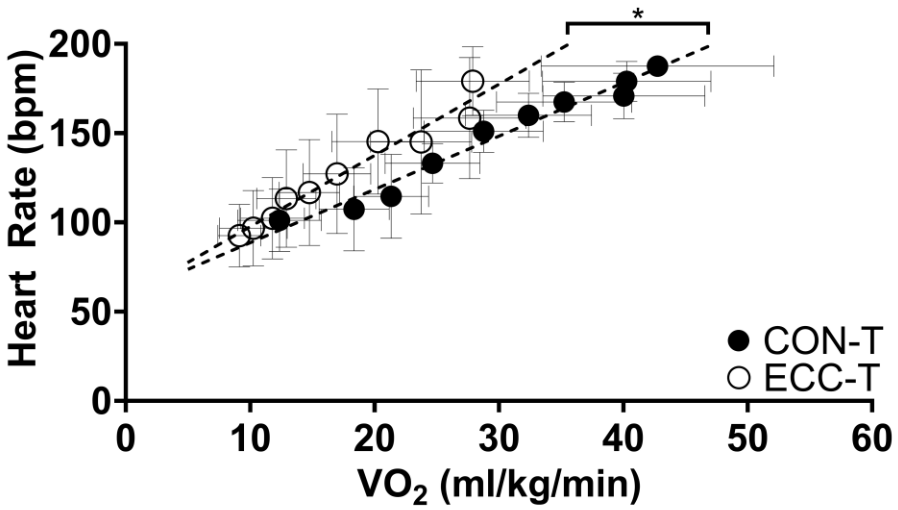

Figure 21: Comparison between concentric (CON-T) and eccentric cycling (ECC-T) for the relationship between heart rate and oxygen consumption normalised by total exercise time in steps of 10%. The vertical bar for the SD of the last data point of ECC is not visible as its size is smaller than the chosen symbol size. *: significant (P < 0.01) difference between the slope of the linear regression for ECC-T and CON-T

4.4.2 Comparison of peak values at task failure

Peak power output was greater ($P<0.001$; $g=1.77$) during eccentric cycling (449 ± 115 W) compared with concentric cycling (294 ± 61 W) (Figure 21a). The peak power output was 53% greater for eccentric than concentric cycling in average, but the power difference between eccentric and concentric cycling varies among the participants (Figure 21b). As shown in Figure 21c & d, maximal heart rate was not different ($P=0.21$; $g=0.43$) between concentric (182 ± 13 bpm) and eccentric cycling (175 ± 20 bpm). Peak oxygen consumption was lower ($P<0.001$; $g=2.18$) for eccentric (30.6 ± 5.6 $ml \cdot kg^{-1} \cdot min^{-1}$) than concentric cycling (43.9 ± 6.9 $ml \cdot kg^{-1} \cdot min^{-1}$) (Figure 21e). The average peak oxygen consumption was 43% lower during eccentric than concentric cycling, yet a large variability in the magnitude of difference among participants was evident (Figure 21f).

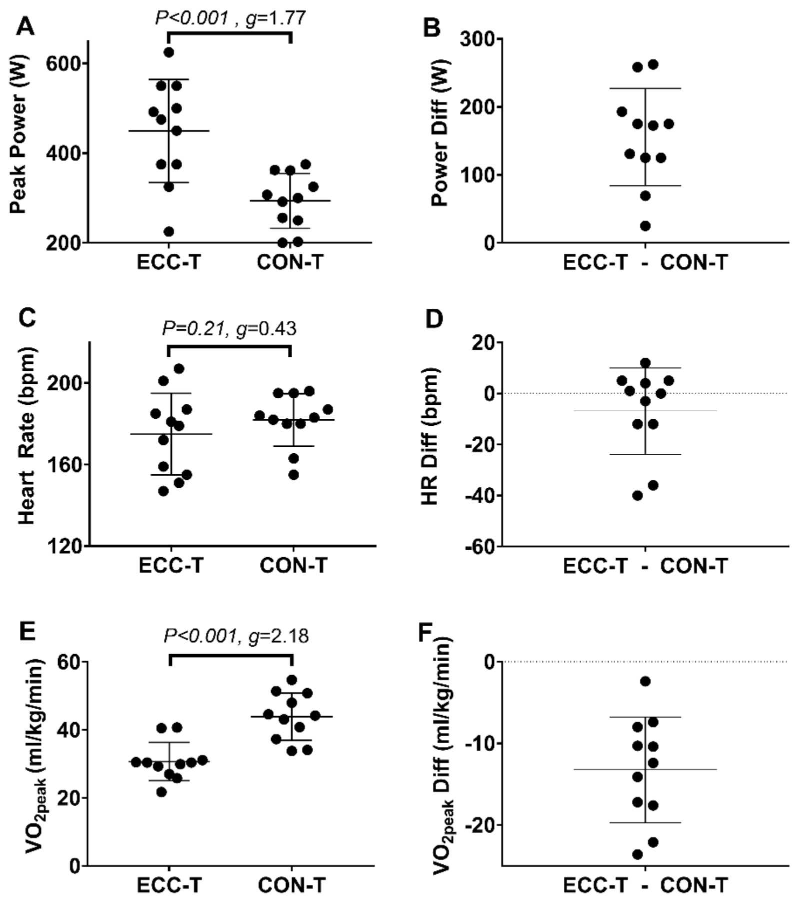

Figure 22: Comparison between eccentric (ECC-T) and concentric (CON-T) cycling for peak power output (a), maximal heart rate (c) and peak oxygen consumption (e) in the incremental tests and the difference between ECC-T and CON-T for each variable is shown in b, d, and f, respectively. For each figure, individual data, and the average (long line) and ± 1SD (short lines) of 11 participants are shown. P values based on t-test and effect size (g) for the comparison between ECC-T and CON-T are shown

V_E (P=0.0008, *g*=1.89; Figure 22a) and V_t (P<0.0001, *g*=2.53; Figure 22c) at task failure were lower for eccentric cycling (65 ± 22 L·min^{-1}; 1.8 ± 0.4 L) than concentric cycling (110 ± 28 L·min^{-1}; 2.8 ± 0.4 l). On average, V_E was 41% lower (Figure 22b), and V_t was 37% lower (Figure 22d) for eccentric than concentric cycling. However, B_f was not different (P=0.07, *g*=0.74) between eccentric and concentric cycling. The comparison of pulmonary parameters at 50% peak power output during each condition (221 ± 51 W during eccentric cycling vs 149 ± 30 W during concentric cycling) showed that V_E and V_t were lower (P<0.01) during eccentric than concentric cycling, but breathing frequency was not different between conditions (P=0.393).

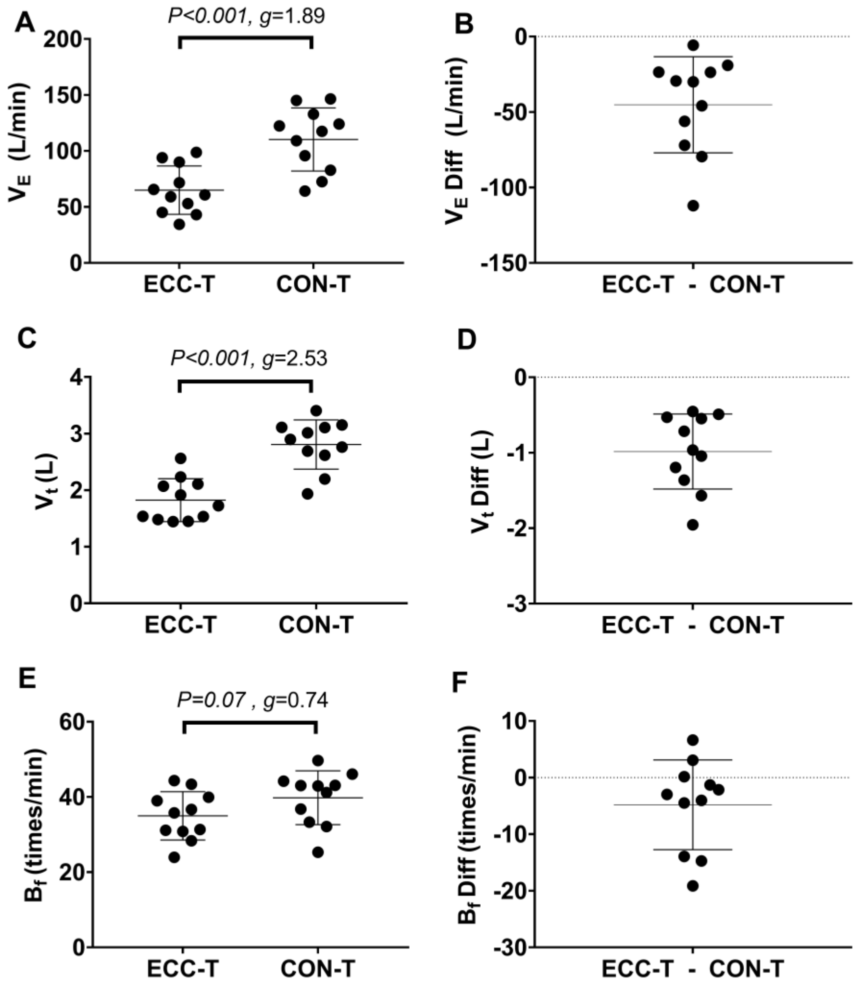

Figure 23: Comparison between eccentric (ECC-T) and concentric (CON-T) cycling for minute ventilation (A), tidal volume (C) and breathing frequency (E) in the incremental tests, and the difference between ECC-T and CON-T for each variable is shown in B, D, and F, respectively. For each figure, individual data, and the average (long line) and ± 1SD (short lines) of 11 participants are shown. P values based on t-test and effect size (g) for the comparison between ECC-T and CON-T are shown

4.4.3 Correlation between peak eccentric cycling power and other variables

Figure 23 shows correlations between eccentric cycling peak power and other variables. Eccentric peak power was significantly correlated with peak oxygen consumption and peak power during concentric cycling and isometric peak force of the knee extensors. Peak oxygen consumption explained 30% (P= 0.0839, r=0.54, R^2=0.295, Figure 5a), peak power output during concentric cycling explained 71% (P= 0.0011, r=0.84, R^2=0.71, Figure 5b) and isometric peak force of the knee extensor explained 28% (P= 0.0929, r=0.53, R^2=0.28, Figure 5c) of the variance of peak power output during eccentric cycling. However, countermovement jump height (P= 0.9281, r=0.03, R^2=0.001, Figure 5d), squat jump height (P= 0.8566, r=0.06, R^2=0.004, Figure 5e) and the ratio between the two (P= 0.8343, r= 0.06, R^2=0.003, Figure 5f) did not explain the variance for peak power output during eccentric cycling.

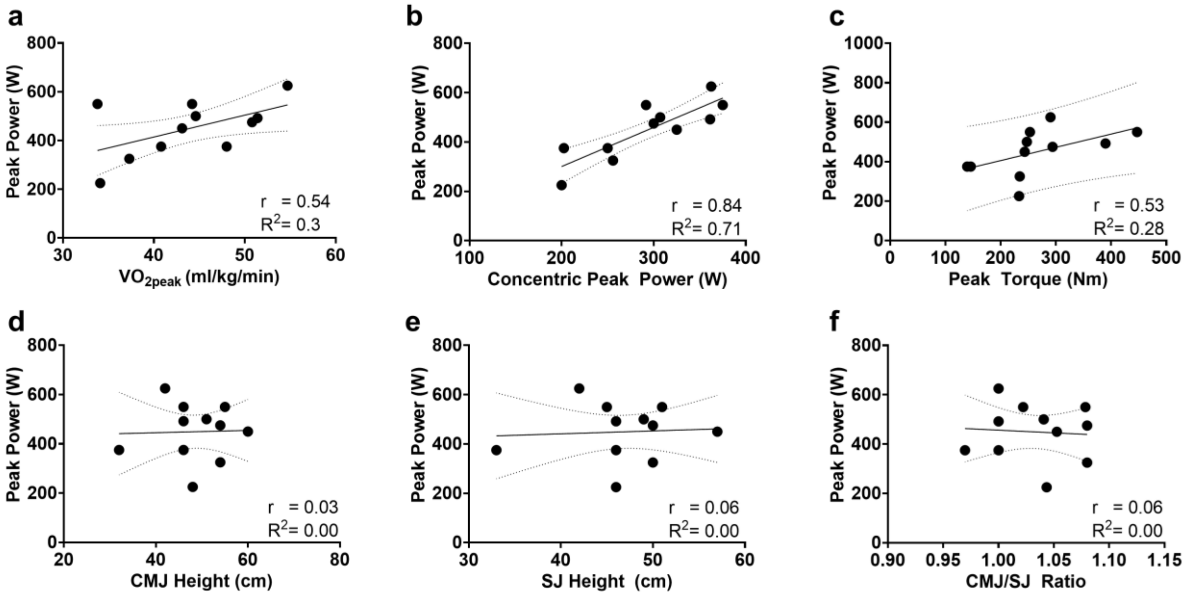

Figure 24: Correlations between peak power output during eccentric cycling and peak oxygen consumption during concentric cycling (A), concentric peak power output (B), MVC torque of the knee extensors (C), countermovement jump height (D), squat jump height (E), and countermovement to squat jump height ratio (F). The dotted lines represent the 90% confidence intervals

4.5 Discussion

The present study compared heart rate, pulmonary parameters and power output between incremental eccentric and concentric cycling tests to task failure. As expected, oxygen consumption during the eccentric test was lower than that of the concentric test for all stages, and heart rate was lower during submaximal stages for eccentric than concentric cycling (Figure 19). However, peak heart rate was the same between eccentric and concentric cycling tests, and the slope of the linear regression calculated from the relationship between heart rate and oxygen consumption was 25% greater during eccentric than concentric cycling (Figure 20). Peak oxygen consumption was 43% smaller, while peak power output was 53% greater for the eccentric than concentric test (Figure 21). Minute ventilation and tidal volumes were 41% and 36% lower during eccentric cycling than concentric cycling at task failure, but breathing frequency showed no difference between modalities (Figure 22). Interestingly, eccentric peak power output was strongly correlated with concentric peak power, while correlations with concentric VO_{2peak} and MVC strength were moderate (Figure 23). In contrast to the hypothesis, no significant relationships were observed between eccentric peak power output and countermovement or squat jump heights.

Previous research on a similar cohort of participants and using similar incremental concentric cycling tests to that of the present study have shown comparable values of peak

power output, peak heart rate and peak oxygen consumption to those of the present study (107,317). Thus, the values obtained in the incremental concentric cycling test of the present study appear to be typical. The average peak power output obtained in the incremental eccentric cycling test (450 W) was 1.5 times greater of that in the incremental concentric cycling test, and approximately half of the peak value (~1000 W) previously reported during eccentric sprint cycling (255). It should be noted that in the present study eccentric cycling was performed incrementally and with the ergometer set to an isopower mode. In the isopower mode, the cadence is variable, and the ergometer adjusts the velocity based on the participant's torque production to maintain the pre-set power output. Performing eccentric cycling at a constant cadence in isokinetic mode (255) appears to lead to a greater variation in the power output produced in comparison to the isopower mode. Interestingly, the mean power output (~500 W) achieved during the 6 s sprints at 60 rpm in the study by Brughelli and Van Leemputte (2013) was very similar to the average eccentric peak power obtained in the present study. Clearly, further research is needed in order to better understand the influence of both cadence and the exercise duration on peak eccentric power outputs.

The lower oxygen consumption and heart rate observed during eccentric cycling for the same power output as that of concentric cycling (Figure 19) is in line with the findings of previous studies (8,36,309). When the peak power was achieved in the eccentric test, oxygen consumption was 61 to 95 % of the peak values obtained in the concentric test, and minute ventilation and tidal volume were also 23 to 94 % of the peak values in the concentric cycling, but the heart rate was similar (Figures 21 & 22). The present study is the first to show that both exercise modes lead to similar maximal heart rates at task failure. Additionally, there was a 25% greater increase in heart rate relative to oxygen consumption during eccentric cycling than concentric cycling (Figure 20). Importantly, the relationship shown in Figure 20 is normalised for the time between conditions, so that every data point represents an average of 10% of exercise time. Therefore, the relationship shows that despite differences in exercise time resulting from the specific protocols used, greater increases in HR occur relative to VO_2 during eccentric than concentric cycling. Furthermore, these increases occurred over more stages during eccentric compared with concentric cycling, and thus the same heart rate and oxygen consumption were maintained over a greater range of power outputs. For example, 50% of the eccentric peak power output resulted in a heart rate of 116 ± 30 bpm, which is similar to 115 ± 23 bpm observed at only 30% of the concentric peak power output. At these heart rates, oxygen consumption was lower during eccentric cycling (14.7 ± 2.4 $ml \cdot kg^{-1} \cdot min^{-1}$), than concentric cycling (21.3 ± 3 $ml \cdot kg^{-1} \cdot min^{-1}$). Such differences in the relationship between HR and VO_2

during concentric and eccentric cycling has previously been reported during submaximal exercise (309,313). However, this is the first study to show that this difference increases with increasing intensity (Figure 20). Based on these findings, heart rate zones determined from an incremental concentric cycling test to task failure should not be used to prescribe training during eccentric cycling directly. Preferably, exercise intensity during eccentric cycling should be prescribed from the power outputs achieved specifically during an eccentric cycling test. Although the calculations in this study were successful at normalising for differences in total exercise time, future studies should consider comparing shorter incremental eccentric tests where participants start at a greater intensity to decrease potential influences of exercise time and accumulated fatigue on cardiopulmonary parameters.

The similar maximal heart rate between the concentric and eccentric incremental cycling tests may be explained by a combination of several factors including differences in thermogenesis, body position, breathing frequency and recruited muscle mass. It is plausible that greater heat production during eccentric muscle actions (323) as a result of the high mechanical load required to achieve the high power outputs, may have increased thermal strain leading to an increase in heart rate within the present study. But this difference was found utilising a modification of the Krogh bicycle ergometer (69) that consisted of a recumbent seat. The current study used upright seated cycling that required the use of the upper body muscles to work against the bike and remain on the seat in comparison to the recumbent position. Although the differences between upright seated and recumbent eccentric cycling have not been previously investigated, it can be assumed that the back of the seat during the recumbent position will increase stability and generated reaction forces that will decrease the required eccentric force production of the agonist's muscles. In that case, the performance during upright seated eccentric cycling is a more precise reflection of the true eccentric strength and maximal eccentric cycling capacity as it does not benefit from the additional support. Moreover, breathing frequency was the only pulmonary parameter that was not significantly different between concentric and eccentric cycling at both 50% of peak power output and task failure (Figure 22). Lechauve et al., (114) have previously reported a greater breathing frequency during eccentric recumbent cycling than concentric cycling at the same oxygen consumption (2 $L \cdot min^{-1}$), and stated that this could be due to limited increases in the end-inspiratory lung volume because of the required trunk stabilisation. It is also possible that the higher heart rate during eccentric compared with concentric cycling was associated with an increased input from peripheral mechanical (joints and muscles) and chemical receptors (metaboreceptors) (324), as it has been also shown that the heart rate is greater during eccentric than concentric cycling

when performed at the same VO_2 (47). Further studies are necessary to investigate the mechanisms underpinning the similar maximal heart rate despite large differences in oxygen consumption and peak power output between the concentric and eccentric cycling tests.

It is interesting to note that 71% of the variance of the eccentric peak power output was explained by peak power output during concentric cycling (Figure 22B). VO_{2peak} during concentric cycling (Figure 4a) and MVC torque of the knee extensors (Figure 22D) were only moderately correlated to the eccentric peak power. In contrast to the hypothesis, countermovement and squat jump heights and their ratio had no significant correlation with eccentric peak power output (Figure 23E-F). Eccentric cycling in this study was performed at a constant and uninterrupted cadence of at least 60 rpm, resulting in an angular velocity of approximately $180°{\cdot}s^{-1}$ at the knee. As the knee joint can reach a peak angular velocity of $860°{\cdot}s^{-1}$ during a countermovement jump (130), the countermovement to squat jump ratio (eccentric utilisation ratio) may not be able to characterise eccentric peak power output accordingly. Furthermore, this underlines the questionable assumption that the eccentric utilisation ratio is a valid representation of eccentric "ability", "skill", "capacity" or even eccentric strength. Performance during specific skills like jumps or changes of direction is affected by many different factors. Although eccentric strength or coordination could be a factor influencing performance during jumping, one should be careful when generalising relationships between various forms of exercises that include eccentric muscle actions.

Individuals with a greater concentric strength are able to produce more torque with decreasing concentric velocities and increasing eccentric velocities (325). For concentrically stronger participants it might have been easier for them to resist an increase in speed of the pedals during the latter stages of the eccentric test. Indeed, with fatigue, it would have become more difficult for the participants to resist the motor of the eccentric ergometer that increased the cadence to match the target power output, despite participants attempting to maintain the target cadence. Failure to generate large torque to maintain the target cadence at maximal intensities may also be related to an initial suboptimal cadence choice. It is plausible that optimal and freely chosen cadence may differ between eccentric and concentric cycling. Emanuele et al. (132) reported that a freely chosen cadence during concentric cycling differed up to 20 rpm among individuals, and this depended on intensity and duration of the exercise. Additionally, the freely chosen cadence may be different from the energetically optimal cadence (327). Further research is needed to understand the influence of cadence on eccentric cycling capacity better. The moderate correlation between the MVC torque of the knee extensors and eccentric peak power output could be explained by the involvement of other

muscles such as iliopsoas, gluteus, gastrocnemius and soleus during eccentric cycling (45). It should be noted that electromyographic activity of the vastus lateralis was reduced after familiarisation to eccentric cycling (328), but the present study had several familiarisation sessions before the incremental eccentric cycling test. Furthermore, there were 3 to 8 weeks between the concentric and eccentric incremental tests, where participants performed a total of 8 eccentric cycling sessions. It is possible that the total of 8 eccentric cycling sessions had induced a training effect on the participant's strength or cardiovascular characteristics. Future studies may control for such effects if the concentric cycling test is repeated a couple of days after the last eccentric session and before the eccentric cycling test.

As presented by the high power outputs achieved by the participants in the present study, the incremental maximal eccentric cycling test appears feasible and safe within this healthy population. However, when this test cannot be performed, other options to determine or estimate eccentric peak power output should be considered. This is especially important for the application of eccentric cycling to older adults and clinical populations. For instance, training intensity of eccentric cycling could be determined based on concentric peak power output, since the concentric peak power correlated reasonably well with the eccentric peak power output (Figure 22B). Secondly, the efficacy of using submaximal HR, VO_2 and power output to predict maximal eccentric cycling performance needs to be established, as has been done in concentric tasks (316). Such submaximal protocols would be suitable for a wide range of populations and would make it easier to set up eccentric cycling protocols. Lastly, due to the novelty of the eccentric cycling in comparison to concentric cycling, which is learned from a young age, could increase the inter-individual differences. It is plausible to assume that participants with a greater history of eccentric loading could perform better during eccentric cycling. For example, one participant had a 21 % (40 bpm) lower HR and 43% (29 ml/kg/min) lower oxygen consumption (Figure 21D & 21E) during eccentric cycling, but reached only 36 % greater power output (492 W) than during concentric cycling, which is clearly lower than the average increase of 53%. During concentric cycling, he achieved 361 W with a VO_{2peak} of 51 ml/kg/min (Figure 21A & 21B), both above the average of the group. As his aerobic capacity was not limiting performance, other factors might: suboptimal eccentric coordination to apply his high isometric strength of 389.84 Nm (Figure 23C) or a potentially lower stiffness in the muscle-tendon unit as indicated by a countermovement to squat jump height ratio of 1 (Figure 23F). Specific prior eccentric loading and coordination (67) was not determined in this study but should be considered as a potential influence on performance outcomes during eccentric cycling in future studies.

4.6 Conclusions

In conclusion, this is the first study to present the cardio-pulmonary differences during eccentric and concentric cycling until volitional exhaustion. Although the differences in maximal power output and peak oxygen consumption have been previously reported for submaximal intensities, it is crucial to point out that none of the previous studies (309,313) has investigated these differences during maximal intensities with accumulated fatigue until exhaustion. Especially the similar maximal heart rate was not expected based on findings from these previous studies investigating differences in submaximal intensities. It is known that such “all-out” intensities result in drastically different cardiopulmonary responses during concentric exercise in comparison to submaximal intensities. Therefore, the effects of protocols conducted till exhaustion have to be studied during continuous eccentric cycling to understand potential maximal eccentric cycling capacity truly. Thus, the unique findings of the present study indicate that especially the relationship between heart rate and oxygen consumption per power output differ between incremental eccentric and concentric cycling tests till exhaustion. Furthermore, concentric peak power output was the best correlate with eccentric peak power output, but the individual variability in the magnitude of difference in peak parameters between eccentric and concentric cycling has to be considered. Thus, when prescribing eccentric cycle training, after an adequate amount of familiarisation sessions (3-6), an assessment of eccentric peak power from an incremental eccentric cycling test is recommended. The use of heart rate for eccentric cycling prescription requires some caution. Future research should investigate other incremental eccentric cycling test protocols including the effect of cadence on eccentric cycling performance, and set up a standardised protocol to determine eccentric cycling intensity for exercise prescription.

CHAPTER FIVE

STUDY TWO

Oxygen consumption, rate of perceived exertion and enjoyment in high-intensity interval eccentric cycling

5.1 Abstract

To compare oxygen consumption (VO_2) and perceptual responses between continuous and interval eccentric cycling protocols in order to test the hypothesis that metabolic demand and enjoyment would be greater for interval than continuous eccentric cycling protocols. Eleven recreationally active men (n=9) and women (32.6 ± 9.4 y) performed a concentric cycling test to determine peak power output (PPO) followed by five eccentric cycling protocols on separate occasions; continuous eccentric cycling at 60% of PPO for 20 min at 60 rpm ($CONT_{20@60\%}$) and 13.2 min at 90 rpm ($CONT_{13@60\%}$), 4 x 4 min at 75% of PPO with 2 min rest ($INT_{4x4@75\%}$), 12 x 1 min at 100% of PPO with 1 min rest ($INT_{1x12@100\%}$) and 10 x 1 min at 150% of PPO with 1 min rest ($INT_{1x10@150\%}$). Gas exchange and power output were recorded continuously, and rate of perceived exertion (RPE) and enjoyment were assessed after each exercise. Total VO_2 including the rest periods was the greatest ($p<0.0001$) during $INT_{1x10@150\%}$ (382 ± 73 $ml \cdot kg^{-1}$) and lowest ($p<0.0001$) during $CONT_{13@60\%}$ (146 ± 27 $ml \cdot kg^{-1}$). Total VO_2 during $INT_{1x12@100\%}$ (312 ± 59 $ml \cdot kg^{-1}$) was greater ($p<0.0001$) than $CONT_{20@60\%}$ (246 ± 63 $ml \cdot kg^{-1}$) and $INT_{4x4@75\%}$ (257 ± 42 $ml \cdot kg^{-1}$). RPE was greater ($p<0.0001$) after $INT_{1x10@150\%}$ (17 ± 2) than other conditions, but perceived enjoyment was not significantly different between protocols. It was concluded that the interval protocols increased metabolic demand without increasing RPE and enjoyment. It appears that high-intensity interval protocols can be used in eccentric cycling prescription.

5.2 Introduction

It has been well documented that oxygen consumption (VO_2) during eccentric cycling is 40-80% lower when compared with concentric cycling at the same workload (8,36,309). As a result, much greater power outputs can be achieved during eccentric than concentric cycling for the same VO_2 (8). The lower metabolic demand in eccentric cycling is an advantage since improvements in muscle strength and muscle volume can be achieved with reduced metabolic cost (23,288). Conversely, it seems difficult to improve aerobic capacity by eccentric cycling, as reported by previous studies showing that maximal oxygen consumption was unchanged (329), slightly reduced (23,24) or in one case increased (70) following eccentric cycle training. It should be noted that all of these studies used continuous eccentric cycling at relatively low intensities (197-309 W). Eccentric cycling sprints can potentially be performed at power outputs up to 1700 W (255). However, it is not known what intensities can be performed over durations longer than that used for a short (e.g., 6 s) eccentric cycling sprint.

Many studies have reported that high-intensity interval training (HIT) is effective in rapidly improving maximal oxygen consumption (82,103). The improvement in maximal oxygen consumption after HIT is achieved despite a lower total work, a reduced total exercise time, or the same total VO_2 when compared with continuous exercise (103,330–332). Furthermore, HIT has been shown to be more enjoyable than continuous exercise (333–335), but it appears that such perceptual differences are affected by the protocols. For example, Foster et al. (336) reported that HIT protocols with a large work to rest ratio (2:1) were less enjoyable than continuous protocols, and Martinez et al. (337) showed that this was also the case for longer intervals than 60 s. Rating of perceived exertion (RPE) has been reported to be similar between HIT and continuous conventional cycling exercise (338). RPE was used in several training studies in which continuous eccentric cycling protocols were used (23,27), but RPE in interval eccentric cycling protocols has not been reported. It is plausible that HIT eccentric cycling provides a unique exercise modality that could simultaneously induce significant neuromuscular and cardiovascular adaptations at a relatively low RPE. However, to the best of our knowledge, no previous study has examined the physiological and perceptual responses to interval eccentric cycling.

Therefore, the present study compared two continuous eccentric cycling protocols and three interval eccentric cycling protocols for VO_2, rating of perceived exertion and enjoyment. It was hypothesised that interval eccentric cycling would require greater total VO_2 and result in greater perceived exertion and enjoyment when compared with continuous eccentric cycling.

5.3 Methods

5.3.1 Participants

Eleven healthy participants (9 men and 2 women) volunteered for this study. Their mean (±SD) age, height, body mass, maximal oxygen consumption (VO_{2peak}) and concentric cycling peak power output (PPO) were 33 ± 9 y, 181.4 ± 8.2 cm, 81.1 ± 17.1 kg, 44 ± 7 $ml \cdot kg^{-1} \cdot min^{-1}$ and 294 ± 61 W, respectively. Participants were training recreationally in cycling, cricket or volleyball, but had not been involved in any structured eccentric exercise. Participants were excluded if they performed any sport on a regional level or above, or they had performed structured strength and/or endurance training in the last 6 months. Participants were instructed to refrain from caffeine, alcohol, and exercise for 48 h before each visit to the laboratory. The effect size was estimated to be 0.93 for a possible difference in VO_2 between interval and continuous eccentric cycling, based on a concentric cycling study that compared interval and continuous protocols (339). Using a G*Power (Version 3.0.10, 2008, Kiel, Germany), it was found that 9 participants would suffice, with an α level of 0.05 and a power of 0.8 (1-β). They were informed of the requirements and risks associated with the study and provided written consent in accordance with the Institutional Human Research Ethics Committee.

5.3.2 Study design

Participants visited the laboratory on nine separate occasions (Figure 24). The following order was chosen as familiarisation to eccentric cycling and to minimise muscle damage (36). During the first visit, participants performed a concentric incremental cycling test. During the next three visits, participants were familiarised with eccentric cycling while performing 5, 8 and 10 minutes at 30, 30 and 40% of their concentric PPO, respectively. During the subsequent five visits, participants performed two continuous and three intermittent cycling protocols described below in a semi-randomised fashion. The familiarisation sessions were separated by 1 to 2 day, and the five eccentric cycling protocols by 2 to 14 days.

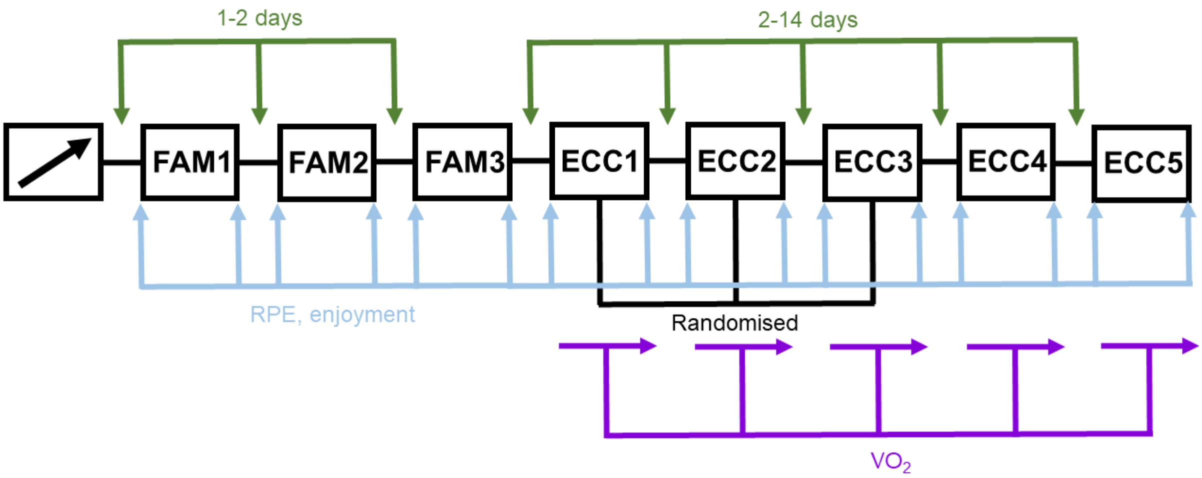

Figure 25: The design of study 2, with the incremental test (diagonal arrow), the three familiarisations (FAM1-3), and five experimental sessions (ECC1-5). The time between sessions is shown in green. The measurements of the rating of perceived exertion (RPE) and enjoyment before and after each session are shown in light blue. The measurements of oxygen consumption (VO_2) during experimental sessions are shown in purple.

5.3.3 Incremental concentric test till task failure

Participants completed a 3-minute concentric cycling warm-up at 50 W and 60 rpm before commencing an incremental protocol on a Velotron cycle ergometer (RacerMate, Inc., Seattle, Washington USA). The test started at 75 W and increased by 25 W every minute until exhaustion. Cadence was self-selected, but the test was terminated when cadence decreased below 60 rpm for more than 30 s. Participants were provided with visual feedback of power output, cadence and elapsed time, and verbal encouragement during the final stages. The PPO was calculated based on the last completed stage and used to determine intensity in subsequent sessions. Throughout the trial, expired gas was measured with each breath and averaged over every 15 s using a metabolic cart (TrueOne 2400, ParvoMedics, Sandy, USA). The ventilometer and gas analyser was calibrated before each test using a 3-L syringe (5530 series, Hans Rudolph, Inc., Shawnee, Kansas, U.S.A.) and gas of known O_2 and CO_2 concentrations. Peak oxygen consumption (VO_{2peak}) was taken as the highest 15 s mean.

5.3.4 Continuous and interval eccentric cycling protocols

Five different eccentric cycling protocols were performed on an eccentric cycling ergometer (Cyclus2 Eccentric Trainer, RBM Elektronik-Automation GmbH, Leipzig, Germany) (Table 1). There were two continuous eccentric cycling protocols: 20 minutes at 60% of concentric PPO ($CONT_{20@60\%}$) and 13.2 minutes at 60% of concentric PPO ($CONT_{13@60\%}$), with the former performed at 60 rpm, and the latter at 90 rpm. Interval eccentric cycling was performed in three different protocols: 4 x 4 min at 75% of concentric PPO with a 2-min rest

between bouts ($INT_{4x4@75\%}$), 12 x 1 min at 100% of concentric PPO with a 1-min rest between bouts ($INT_{1x12@100\%}$), and 10 x 1 min at 150% of concentric PPO with a 1-min rest between bouts ($INT_{1x10@150\%}$). The interval designs of 10 x 1 min (98,106) and 4 x 4 min (340) are often used to study interval concentric cycling. The 10 x 1 min were adapted to 12 intervals to match the total workload with $INT_{4x4@75\%}$ and $CONT_{20@60\%}$. The intensity of 150% of PPO in $INT_{1x10@150\%}$ was chosen as it was close to the mean power output achievable during a 6 s eccentric cycling sprint (255), and the total workload for this protocol was greater than others.

The eccentric ergometer was set to isokinetic mode at 60 rpm for all protocols except $CONT_{13@60\%}$, which was performed in the isokinetic mode as well, but at 90 rpm. As with 90 rpm more contractions, and therefore more work was performed during each exercise minute, to account for the same total workload as 3 of the other session the duration during $CONT_{13@60\%}$ was adjusted to 13.2 minutes. Due to the constant cadence, it was not possible to produce an entirely constant power output. To ensure participants maintain the target power output, they were provided live visual feedback (2 Hz) on their power output as both a line and a number on a computer screen. A target power output was also displayed on the screen. To analyse the success of reaching the target power output the ratio between the actual and target power output was calculated. Actual power output was measured at 2 Hz and was calculated for $CONT_{20@60\%}$ and $CONT_{13@60\%}$ as the mean for the whole protocol, while for the interval protocols the average power output during each interval was calculated first before taking the mean of all intervals.

5.3.5 Dependant variables

Throughout the trials, VO_2 was measured using the metabolic cart. Average relative VO_2 was compared between the first and last minute for each interval protocol, and between the second and last minute for the continuous protocols. The $VO_{2(total)}$ was defined as the area under the curve (AUC) of the VO_2 throughout each entire protocol (including the rest periods). Additionally, $VO_{2(cycling)}$ during cycling only was calculated as $VO_{2(total)}$ divided by exercise time excluding rest time. While it may be possible to determine the total energy cost, this was not done since the substrate oxidation during eccentric cycling is controversial (80,341). It is currently unclear if the greater respiratory exchange ratio observed during eccentric than concentric cycling (313) is due to substrate utilisation. Immediately following exercise,

participants rated their perceived exertion (RPE) using the 6 to 20 Borg's scale and completed the validated 8-item Physical Activity Enjoyment Scale (PACES) (333). In the familiarisation sessions, participants were familiarised with the assessment of the rate of perceived exertion (RPE) using the 6 to 20 Borg's scale (342), and the 8-item physical activity enjoyment scale (PACES) (333). Participants were informed that RPE was in reference to the degree of difficulty experienced during the exercise. Participants were asked directly after cessation of exercise; "rate your current level of whole-body exertion on the scale from 6 to 20." For the enjoyment, participants were asked immediately after the exercise; "rate how you feel at the moment about the physical activity you have just completed." It was explained that a scale of 4 represented "neutral." Rating of perceived enjoyment was calculated as the average of 8 items on the PACES scale.

5.3.6 Statistical analysis

A one-way repeated measures ANOVA was used to compare relative VO_2, $VO_{2(total)}$, $VO_{2(cycling)}$, RPE and enjoyment, followed by a Tukey´s post hoc test for multiple comparisons. An unpaired t-test was used to compare actual and target power outputs. The effect size for total and exercise VO_2 were determined using Hedges' *g*. The significance level was set at $P < 0.05$. All statistical analyses were performed using statistical software (GraphPad Prism version 7.02, GraphPad Software, La Jolla California, USA).

5.4 Results

5.4.1 Power output

The actual power output was not significantly ($p \geq 0.1264$) different from the target for all protocols (Table 1). The average power output for each interval during the three interval eccentric cycling sessions is shown in Table 2.

Table 1: Intensity, cadence, cycling time, rest time, the total exercise time, total workload, target power, and actual power (range, mean ± SD of 11 participants) during continuous cycling protocols; 20 minutes at 60 rpm (CONT20@60%) or for 13.2 minutes at 90 rpm at 60% of peak power output (CONT13@60%), and interval eccentric cycling protocols; 4 x 4 min at 75% of peak power output with 2 min rest (INT4x4@75%), 12 x 1 min at 100% of peak power output with 1 min rest (INT1x12@100%) and 10 x 1 minute at 150% of peak power output with 1 min rest (INT1x10@150%).

	$CONT_{20@60\%}$	$INT_{4x4@75\%}$	$INT_{1x12@100\%}$	$INT_{1x10@150\%}$	$CONT_{13@60\%}$
Intensity (% PPO)	60	75	100	150	60
Cadence (rpm)	60	60	60	60	90
Cycling Time (min)	20	16	12	10	13.2
Rest time (min)	0	6	11	9	0
Exercise Time (min)	20	22	23	19	13.2
Total Workload (kJ)	149 – 268 218 ± 39	152 – 284 225 ± 40	146 – 260 205 ± 37	196 – 335 232 ± 42	166 – 340 235 ± 54
Target Power (W)	121 – 227 182 ± 32	154 – 284 233 ± 41	202 – 375 304 ± 56	304 – 563 456 ± 92	121 – 227 184 ± 35
Actual Power (W)	124 – 224 183 ± 32	158 – 296 235 ± 39	202 – 361 285 ± 85	272 – 462 387 ± 129	139 – 283 198 ± 40

Table 2: Average power in W (range, mean ± SD of 11 participants) during each interval for the interval eccentric cycling sessions: 4 x 4 min at 75% of peak power output with 2 min rest ($INT_{4x4@75\%}$), 12 x 1 min at 100% of peak power output with 1 min rest ($INT_{1x12@100\%}$) and 10 x 1 minute at 150% of peak power output with 1 min rest ($INT_{1x10@150\%}$).

Interval	$INT_{1x12@100\%}$	$INT_{4x4@75\%}$	$INT_{1x10@150\%}$
1	298 ± 64	227 ± 42	400 ± 91
2	251 ± 122	235 ± 39	350 ± 173
3	303 ± 52	238 ± 36	425 ± 78
4	307 ± 52	225 ± 35	416 ± 83
5	301 ± 52		406 ± 83
6	303 ± 52		411 ± 78
7	310 ± 49		419 ± 77
8	311 ± 41		426 ± 62
9	304 ± 48		414 ± 69
10	306 ± 54		413 ± 72
11	292 ± 38		
12	291 ± 49		

5.4.2 Oxygen consumption

Changes in VO_2 over time for the five protocols are shown in Figure 25. During $CONT_{20@60\%}$ VO_2 showed no difference (p = 0.0722) between the second and last minute, but during $CONT_{13@60\%}$ VO_2 increased for this time period (P = 0.0017). VO_2 gradually increased with repetitions such that the VO_2 in the last bout was higher than the first bout during interval protocols ($p \leq 0.001$).

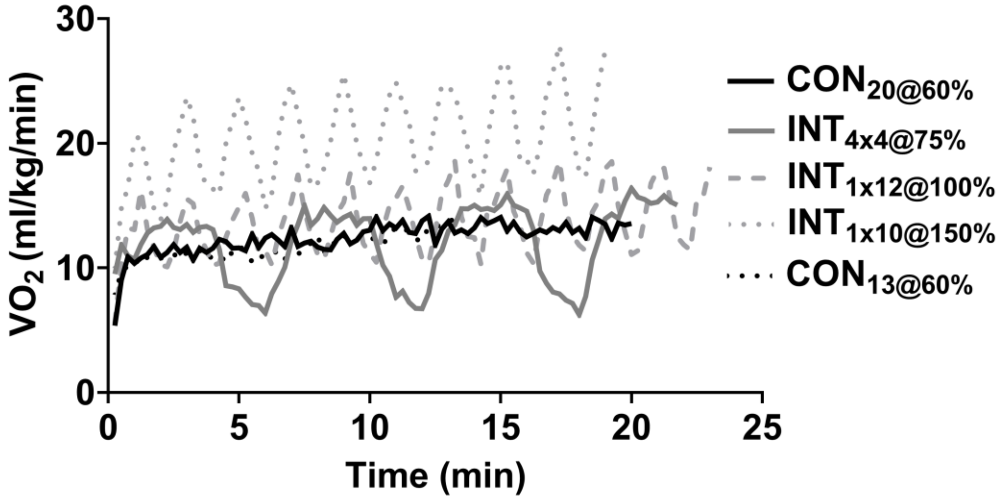

Figure 26: Changes in oxygen consumption during eccentric exercise including resting time in continuous cycling for 20 minutes at 60 rpm (CONT20@60%) or for 13.2 minutes at 90 rpm at 60% of peak power output (CONT13@60%), interval eccentric cycling for 4 x 4 min at 75% of peak power output with 2 min of passive rest (INT4x4@75%), 12 x 1 min at 100% of peak power output with 1 min rest (INT1x12@100%) and 10 x 1 minute at 150% of peak power output with 1 minute rest (INT1x10@150%).

$VO_{2(total)}$ was 246 ± 63 $ml{\cdot}kg^{-1}$ for $CONT_{20@60\%}$, 257 ± 42 $ml{\cdot}kg^{-1}$ for $INT_{4x4@75\%}$, 312 ± 59 $ml{\cdot}kg^{-1}$ for $INT_{1x12@100\%}$, 382 ± 73 $ml{\cdot}kg^{-1}$ for $INT_{1x10@150\%}$ and 146 ± 27 $ml{\cdot}kg^{-1}$ for $CONT_{13@60\%}$ (Figure 26A). $VO_{2(total)}$ was the lowest during $CONT_{13@60\%}$ ($p < 0.0001$, $g = 2.13$) and the highest during $INT_{1x10@150\%}$ ($p < 0.0001$, $g = 1.10$) among all protocols. $VO_{2(total)}$ during $INT_{1x12@100\%}$ was greater than $CONT_{20@60\%}$ ($p < 0.0001$, $g = 1.13$) and $INT_{4x4@75\%}$. ($p = 0.0006$, $g = 1.11$).

$VO_{2(cycling)}$ (the $VO_{2(total)}$ – the rest VO_2) was 12.3 ± 3.2 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$ for $CONT_{20@60\%}$, 16.1 ± 2.6 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$ for $INT_{4x4@75\%}$, 26.0 ± 4.9 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$ for $INT_{1x12@100\%}$, 38.2 ± 7.3 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$ for $INT_{1x10@150\%}$ and 11.1 ± 2.0 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$ for $CONT_{13@60\%}$ (Figure 26B). $VO_{2(cycling)}$ was lower during $CONT_{13@60\%}$ than that of the three interval protocols ($p \leq 0.001$, $g \geq 2.22$). $VO_{2(cycling)}$ during $INT_{1x10@150\%}$ was the largest among the protocols ($p < 0.0001$, $g \geq 2.05$), and VO_2 during $INT_{1x12@100\%}$ was greater than that of $CONT_{20@60\%}$ ($p < 0.0001$, $g = 3.46$)

and $INT_{4x4@75\%}$ ($p = 0.0006$, $g = 2.62$). Additionally, $VO_{2(cycling)}$ during $INT_{4x4@75\%}$ was greater than $CONT_{20@60\%}$ ($p = 0.0171$, $g = 1.37$).

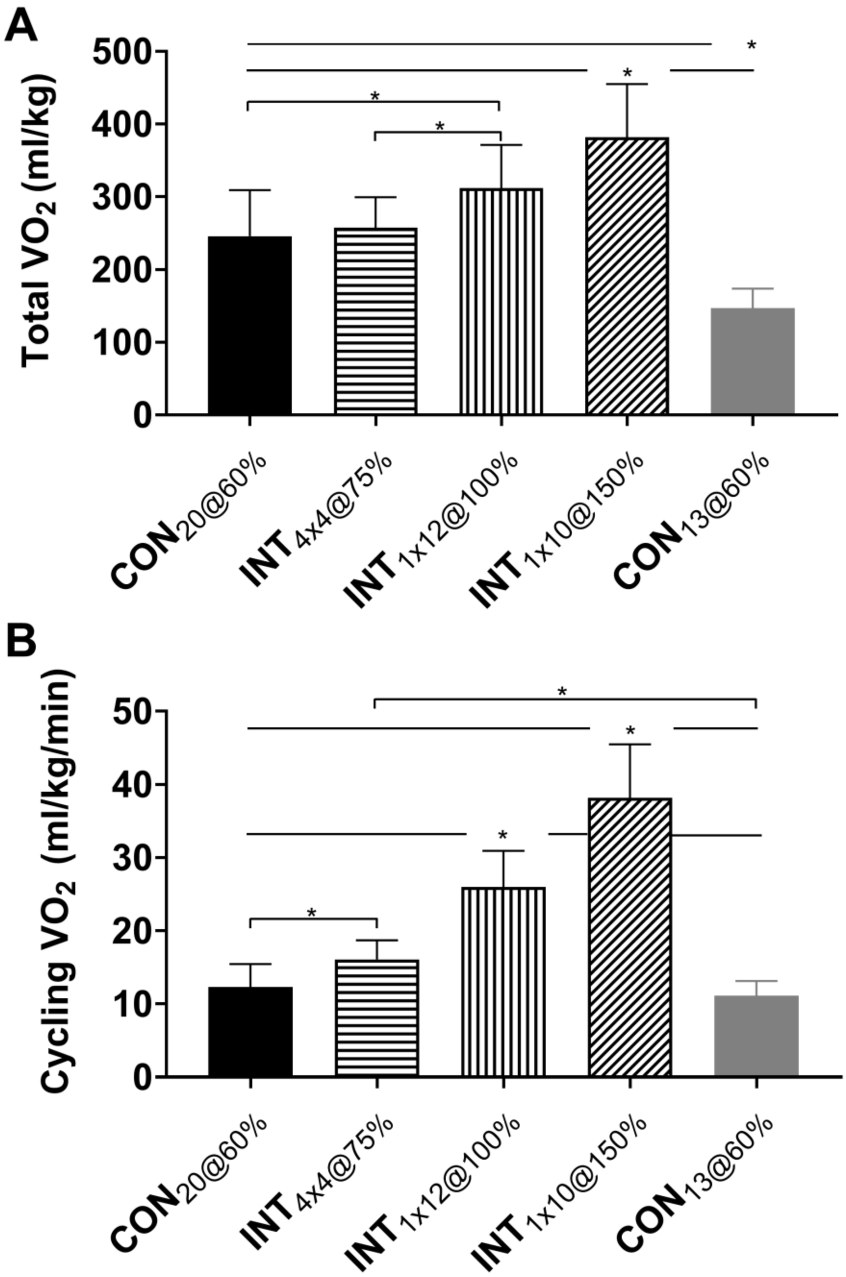

Figure 27: Comparison of total oxygen consumption during the whole exercise (A) and cycling VO2 representing oxygen consumption per minute of cycling time only (B) between continuous cycling for 20 minutes at 60 rpm (CONT20@60%) or for 13.2 minutes at 90 rpm at 60% of peak power output (CONT13@60%), interval eccentric cycling for 4 x 4 min at 75% of peak power output with 2 min of passive rest (INT4x4@75%), 12 x 1 min at 100% of peak power output with 1 min rest (INT1x12@100%) and 10 x 1 minute at 150% of peak power output with 1 minute rest (INT1x10@150%). *: significant difference between conditions (P < 0.05)

5.4.3 Rating of perceived exertion and enjoyment

RPE was 12 ± 2 after $CONT_{20@60\%}$, 13 ± 2 after $INT_{4x4@75\%}$, 13 ± 2 after $INT_{1x12@100\%}$, 17 ± 2 after $INT_{1x10@150\%}$ and 13 ± 2 after $CONT_{13@60\%}$. RPE was greater during $INT_{1x10@150\%}$

(17 ± 2) when compared with other conditions ($p < 0.0001$). No significant differences in RPE were evident among $CONT_{20@60\%}$ (12 ± 2), $INT_{4x4@75\%}$ (13 ± 2), $INT_{1x10@150\%}$ (13 ± 2), and $CONT_{13@60\%}$ (13 ± 2). There were no differences in perceived enjoyment between $CONT_{20@60\%}$ (41 ± 10), $INT_{4x4@75\%}$ (41 ± 10), $INT_{1x12@100\%}$ (44 ± 8), $INT_{1x10@150\%}$ (41 ± 8), and $CONT_{13@60\%}$ (41 ± 10).

5.5 Discussion

The main findings were that: i) oxygen consumption was greater during interval eccentric cycling protocols when compared with continuous eccentric cycling protocols, despite similar total workloads, ii) the oxygen consumption of continuous eccentric cycling was not significantly different between 60 and 90 rpm.

The higher VO_2 observed during interval compared with continuous eccentric cycling observed in this study is likely due to the greater power outputs. Indeed, power output was 111% greater during $INT_{1x10@150\%}$ than $CONT_{20@60\%}$. Interestingly, these differences were at least twofold greater than the differences (20-60%) in power output or running velocity between interval and continuous protocols in concentric exercise (339,343,344), and highlight the high power that can be achieved during eccentric cycling. But despite the greater exercise intensity during $INT_{1x10@150\%}$ and $INT_{1x12@100\%}$ participants achieved on average 85% and 94% of the target power output, respectively. The up to 15% lower actual power output indicates that interval eccentric cycling at greater intensity could be more difficult to perform than continuous forms of eccentric cycling. Additionally, although there were significant differences in oxygen consumption between continuous and interval protocols, these differences might be underestimated, as participants were not able to achieve the programmed power output. It is possible that after a longer introduction to eccentric cycling, after several more training session and with a more specific training design, participants would be able to successfully achieve the target power output and increase oxygen consumption even more. Furthermore, even when examining VO_2 over the entire trial ($VO_{2(total)}$), it was greater during interval compared with continuous eccentric cycling. The greater VO_2 may be due to differences in metabolism, interval design, or other factors, including recruitment of synergistic muscles or lack of specific eccentric coordination.

The greater VO_2 might be influenced by an increased demand for aerobic metabolism to drive the eccentric muscle actions. It is possible that due to the greater maximal eccentric than concentric strength (8), the threshold for mainly aerobic substrate utilisation is also greater during eccentric muscle actions. In such a case the greater intensity of the interval protocols

would not be high enough to require a shift towards an anaerobic metabolism. Eccentric cycling has the potential to require greater fat oxidation than concentric cycling at the same power output during exercise(80). When compared at the same VO_2 and therefore a 2.5 times greater power output during eccentric than concentric cycling, there was no difference in substrate utilisation (341). Despite a greater heart rate and blood pressure during continuous eccentric in comparison to continuous concentric cycling at the same VO_2, there were no differences in local muscle oxygenation (345). In light of possible differences in RER between eccentric and concentric cycling (313), the greater fat oxidation during eccentric cycling is questionable, and it is not clear if the calculations used to determine substrate utilisation are valid for eccentric muscle actions. Thus, it is not known whether any difference in the metabolism exists between interval eccentric and continuous eccentric cycling.

The relationship between intensity, work to rest ratio and interval duration might affect VO_2 during eccentric cycling differently than during concentric cycling. Due to the greater power output during interval eccentric, the rest periods might have been not long enough to equalise VO_2 in comparison to the continuous protocols. As the work to rest ratio in $INT_{1x12@100\%}$ and $INT_{1x10@150\%}$ was 1:1, and their total oxygen consumption was greater than that of $INT_{4x4@75\%}$ with the work to rest ratio of 2:1 (Figure 26), it is possible that the 25 to 75% difference in intensity was more relevant to increasing VO_2 than a high work to rest ratio. A greater work to rest ratio than 1 in concentric exercise sustains VO_2 closer to VO_{2peak} for a longer time, which is important to increase cardiovascular adaptations (99). Additionally, the longer interval duration of $INT_{4x4@75\%}$ in this study did not lead to a greater total oxygen consumption than $CONT_{20@60\%}$. The results of the current study suggest that for interval eccentric cycling a work to rest ratio of 1:1 at or above 100% PPO is enough to increase total oxygen consumption significantly. It may be that an interval protocol with the intensity of ≥ 100% PPO and the work to rest ratio of > 1 (e.g., 2 min work, 1 min rest) increases VO_2 further. In studies on level running or concentric cycling, it has been reported that total oxygen consumption was similar between continuous and interval protocols (331,333) when the work to rest ratio was 1:1 or smaller. Average and peak VO_2 was only greater in an interval design with a work to rest ratio of 3:1 (343). Therefore, in contrast to concentric exercise, a 1:1 work to rest ratio, was enough to significantly increase total and cycling oxygen consumption.

Coordination in eccentric cycling could have contributed to the differences in VO_2 between interval and continuous protocols. It is interesting that when the cadence was increased from 60 rpm to 90 rpm, the total oxygen consumption was significantly different between $CONT_{20@60\%}$ and $CONT_{13@60\%}$ (Figure 26), but cycling only oxygen consumption was not

different (Figure 26B). These results differ to concentric cycling where greater cadences above ~60 rpm are typically found to be less economical (i.e. higher VO_2) (346). The reason for such differences between eccentric and concentric cycling is not clear. However, these results indicate that individuals may utilise higher cadences during eccentric cycling if they are unable to maintain a required torque, without influencing aerobic demands. The choice of a higher cadence could be beneficial for individuals who are not able to generate the required torque to meet a target power output at a lower cadence for continuous eccentric cycling protocols. The absorption of force during daily physical activities could be considered a specific skill that may transfer between modalities. An individual that has a well-developed eccentric skill on the eccentric cycling bike may perform better during other physical activities dominated by eccentric muscle actions, such as downhill running or skiing. Greater intensities during these eccentric modalities require greater energy expenditure. Thus it is possible that high-intensity interval cycling similarly increases VO_2.

Furthermore, other factors such as recruitment of other muscles could have increased the total oxygen consumption observed during interval compared with continuous eccentric cycling. Agonist muscles used during eccentric cycling, such as ankle flexors, hip flexors and extensors (347) could require greater muscle activation during the interval protocols. Moreover, since during upright eccentric cycling upper body muscles were used to remain seated, it may have contributed to the greater VO_2 during interval than continuous protocols.

Several studies reported that interval protocols were more enjoyable than continuous protocols (333,335), but this was not found in another study (338). HIT protocols with a 2:1 work to rest ratio (336) and reported that HIT protocols with a large work to rest ratio (2:1) or with a longer interval than 60 s (337) were shown to be less enjoyable than continuous protocols. The present study found no significant difference in the perceived enjoyment between the protocols. The three familiarisation sessions were sufficient to avoid muscle damage, but it is possible that the exercise was still perceived as novel. It should be noted that eccentric cycling is a unique form of locomotion that requires many sessions to develop a skill to cycle naturally. Thus the novelty of the eccentric cycling may have affected the enjoyment. RPE was high (17 ± 2) in $INT_{1x10@150\%}$, but other protocols showed a similar RPE (~ 15). It is possible that the novelty of the exercise influenced the perceptual responses during eccentric

cycling at higher intensities. RPE relates to increases in heart rate, ventilation and oxygen consumption (348), but does not reflect increases in intensity during continuous eccentric cycling (349). A large variability in the use of RPE exists among studies in terms of the interpretation of the scale (350). Future studies should design and implement psychophysiological measurements specifically for eccentric exercise.

One limitation of the study was that rating of perceived effort (349) or fatigue (351) were not assessed in the study. Since the sample size estimation did not include RPE and enjoyment, it is possible that the sample size was not adequate to detect differences between protocols. However, the differences do not appear to be practically significant, even if a statistical significance was found by increasing the sample size. In the present study, heart rate was not focused, but it would have been better to compare the protocols for heart rate responses. It is possible that other cardiovascular parameters such as blood pressure, stroke volume or muscle oxygenation present significant differences between interval and continuous eccentric cycling.

5.6 Conclusion

The current study found that the interval eccentric cycling protocols required a higher VO_2 than the continuous eccentric cycling protocols, but RPE was similar between the protocols. Even for the interval protocol in which the highest VO_2 was achieved, VO_2 was still under 60% of VO_{2peak}. No significant difference in perceived enjoyment was evident between the protocols. These results suggest that interval protocols should be considered for prescription of eccentric cycling. Further studies should investigate the effects of interval eccentric cycling training on cardiovascular and neuromuscular adaptations.

CHAPTER SIX

STUDY THREE

Effects of high-intensity interval eccentric versus concentric cycling training

6.1 Abstract

This study compared the training effects of high-intensity interval eccentric (EC) versus concentric cycling (CC). Healthy men (19-56 y) performed EC (n=9) or CC (n=8) twice a week for 8 weeks on an isokinetic cycling ergometer. Training intensity was matched for perceived effort and started at 30% and 45%, and increased to 36% and 70% of concentric peak power output (PPO) for CC and EC, respectively. Both groups started with 5 x 2 min with a 1-min rest and progressively increased to 7 x 2 min with a 30-s rest between repetitions. The dependent variables included peak oxygen consumption (VO_{2peak}), PPO in an incremental concentric cycling test (PPO_{inc}), 6-min walking distance (6MW), 10 s concentric peak power output (PPO_{10s}), maximal isometric strength of the knee extensors (MVC), countermovement (CMJ) and squat jump heights (SJ), quadriceps cross-sectional area (CSA), and fascicle length and pennation angle of vastus lateralis. Changes in the variables from before and after training were compared between EC and CC by a two-way ANOVA, t-test and Hedges' *g* effect size. Greater increases were evident for EC than CC for PPO_{10s} (EC: 26.9 ± 10.5% vs. CC: 8.9 ± 8.0%, P=0.0013, *g*=2.03), CMJ (3.9 ± 1.8% vs. -3.3 ± 7.4%, P=0.0131, *g*=1.46) and SJ (7.4 ± 4.7% vs. -2.3 ± 4.4%, P=0.0005; *g*=2.26) and CSA (6.1 ± 4.7% vs. 0.1 ± 3.8%, P=0.0116; *g*=1.48), but not for VO_{2peak} (P=0.3052; *g*=-0.55), PPO_{inc} (P=0.8323; *g*=-0.11), 6MW (P=0.0647; *g*=-1.03) and MVC (P=0.2712; *g*=0.59). It was concluded that EC was more effective than CC for improving both muscle function and endurance.

6.2 Introduction

In eccentric cycling, knee extensor muscles perform repeated eccentric muscle actions when resisting to backward rotations of the crank (308). It has been reported that oxygen consumption during eccentric cycling is 40-60% lower than that during concentric cycling at the same power output (8,36). Previous studies (23,24,67,299) used eccentric cycling protocols consisting of 10 to 30 minutes of continuous cycling started training at approximately 60% of maximal heart rate or 20-60% of concentric peak power output. In such protocols, the relative intensity to maximal eccentric cycling capability at the start of training is low (e.g. 100-200 W), considering the highest power output during eccentric cycling could reach 1700 W during a sprint (255).

Several studies reported that low-intensity eccentric cycling performed for 10-30 min per session for over 25 sessions in 6-11 weeks improved muscle strength (24), muscle size (23), and jumping and stair walking ability (10,22). Although Meyer et al. (71) have shown that eccentric cycling training improves maximal oxygen consumption in a clinical population, the effect of such training on cardiovascular parameters in healthy populations is equivocal (23,70). It appears that the less metabolic demand nature of eccentric cycling is a disadvantage for improving aerobic capacity.

Performing high-intensity interval training (HIT) has been shown to be effective in improving maximal oxygen consumption and exercise performance (103), insulin sensitivity (95), and an array of markers associated with enhanced mitochondrial biogenesis and function (90), but not for increasing muscle strength and muscle size (352). HIT is an efficient mode of exercise that requires a short exercise time, which is important since the time taken for exercise is a factor affecting the compliance to exercise (353). Thus, an exercise protocol that requires less time but produce greater effects on health and fitness parameters is warranted.

It may be that a combination of a HIT protocol with eccentric cycling provides a greater stimulus to not only muscle function but also aerobic capacity when compared with low-intensity continuous eccentric cycling. However, to date, eccentric cycling research has predominately used continuous protocols performed at low intensities. To the best of the authors' knowledge, no previous study has investigated the effects of HIT eccentric cycling training on aerobic performance, muscle morphology and function. It is possible that HIT eccentric cycling training produces greater adaptations in these parameters when compared with HIT concentric cycling training.

Therefore, the present study compared the effects of HIT eccentric versus concentric cycling training on aerobic performance, muscle morphology and muscle function. It was

hypothesized that changes in muscle morphology and function would be greater after 8 weeks of HIT eccentric cycling, while changes in VO_{2peak} would be greater after of HIT concentric cycling, but changes in aerobic performance such as 6-min walking distance and incremental peak power would be similar between training groups.

6.3 Methods

6.3.1 Participants

Seventeen men who were physically active (performing exercise or sports at least once a week) volunteered to participate in the study. None of the participants had performed any specific eccentric exercise, beyond those performed in daily activities, in the 6 months prior to the study. Participants reported that they were not under any medication or had any history of lower limb musculoskeletal injuries. Participants were also instructed to refrain from exercise, alcohol and caffeine in the 48 h prior to each testing session. Participants were fully informed of the requirements and risks associated with the study and provided written informed consent before participation in accordance with the institutional Human Research Ethics Committee that approved this study. Their mean ± SD age, body mass and height were 37.0 ± 10.5 years, 83.9 ± 13.5 kg, and 178.3 ± 7.2 cm, respectively. The participants were randomly placed in a group performing eccentric cycling training (n=9) or a group performing concentric cycling training (n=8). No significant difference in the average age, body mass and height were found between the groups.

6.3.2 Study design

All participants performed either interval concentric (CC) or eccentric cycling (EC) training twice a week for 8 weeks (Figure 27). Baseline measurements were taken 3 to 7 days before the first training session, and all measurements were repeated 2 to 5 days following the last training session. The outcome measures included 6-minute walking distance (6MW), countermovement jump height (CMJ), squat jump height (SJ), maximal voluntary isometric contraction strength of the knee extensors (MVC), peak oxygen consumption (VO_{2peak}), incremental peak power output (PPO_{inc}), quadriceps cross-sectional area (CSA), fascicle length (FL), pennation angle (PA), and concentric sprint peak power output (PPO_{10s}) in the measurement order.

The first day of the testing included 6MW, CMJ, SJ, MVC and an incremental cycling test to exhaustion, and CSA, FL and PA of the quadriceps were measured on the second day.

All participants were familiarized with cycling over two sessions to practice eccentric cycling (EC group) or experience concentric cycling (CC group), on an isokinetic cycling ergometer. A 10-s maximal concentric cycling sprint was performed to measure PPO_{10s} by all participants. The first familiarization session for the EC group consisted of 8 min eccentric cycling at 30% of PPO_{10s}, and 3 repetitions of 1 min concentric cycling at 30% of PPO_{10s} with 30-s rest between repetitions for CC group. The second familiarization session consisted of 10 min eccentric cycling at 35% of PPO_{10s} for EC and 2 repetitions of 2 min concentric cycling at 30% of PPO_{10s} with 1-min rest between repetitions for CC. The familiarisation sessions were completed 1 to 3 days before the first training session. All participants had 16 training sessions (twice a week for 8 weeks) detailed below. Changes in the outcome measures from baseline to post-training were compared between EC and CC groups.

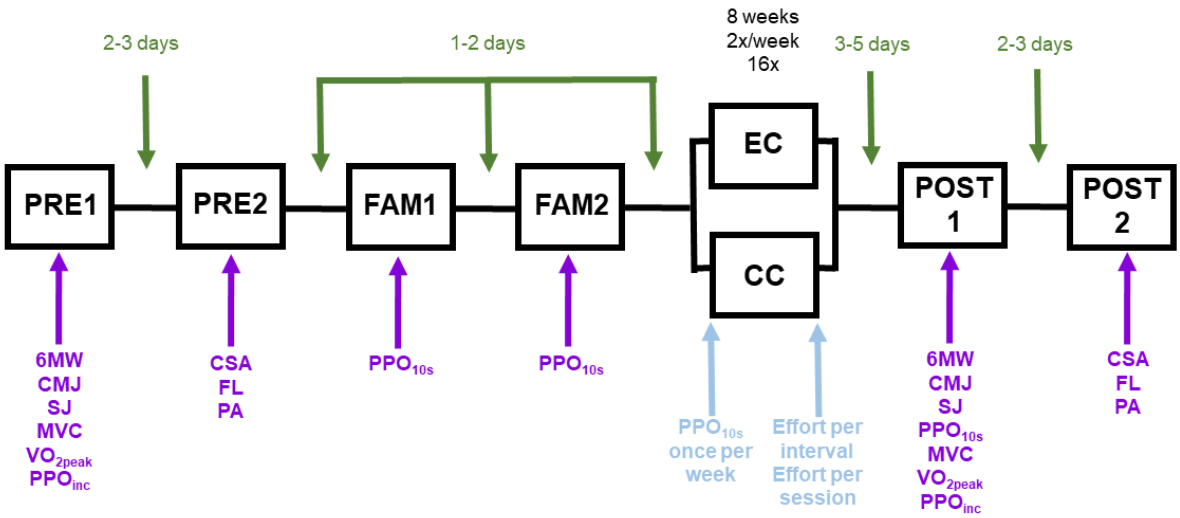

Figure 28: The design of study 3, with pre (PRE1-2) and post (POST 1-2) measurement days, the two familiarisations (FAM1-2), and eccentric (EC) and concentric (CC) cycling training groups. The time between sessions is shown in green. The measurements of peak oxygen consumption (VO_{2peak}), PPO in an incremental concentric cycling test (PPO_{inc}), 6-min walking distance (6MW), 10 s concentric peak power output (PPO_{10s}), maximal isometric strength of the knee extensors (MVC), countermovement (CMJ) and squat jump heights (SJ), quadriceps cross-sectional area (CSA), and fascicle length and pennation angle of vastus lateralis before after training are shown in purple. The measurements of the PPO_{10s} and rating of perceived effort (Effort) and during the training period are shown in light blue.

6.3.3 Training protocols

Both training groups performed all sessions on the same isokinetic cycling ergometer (Grucox Isokinetic Ergometer, South Africa) at a constant cadence of 60 revolutions per minute (RPM). All training sessions were performed in intervals, and the training intensity and volume were periodised. The duration of cycling was always 2 min, but during the rest periods, the target wattage and effort were manipulated for each session (Figure 28A). Due to the different physiological characteristics between EC and CC (8,36), both groups were matched only for

training time and perceived effort. Exercise intensity was adjusted for each session based on the individual's rating of perceived effort (scale from 0 to 10, with 0.5 increments), which was recorded after each repetition. Participants were also asked to rate their perceived effort for the training 1 min after each training session. The training sessions were periodised to have double peaks of intensity and volume in week 5 and week 7, with a decrease in the intensity and volume in week 8 (Figure 28A). The intensity of the training was set to the rating of perceived effort to be between 7 and 9 in the first to the second last sessions, and 6 in the last training session (Figure 28D). The target power output was increased from 45% to 70% of PPO_{10s} for EC, and from 30% to 36% of PPO_{10s} for CC. When the reported rating of perceived effort was above or below the target, the target power output was adjusted for the following repetitions. Both groups performed 5 repetitions of 2-min cycling with 1-min rest in the first session, and it increased to a maximum of 7 repetitions of 2-min with 30-s rest (Figure 28A).

6.3.4 Outcome measures

6.3.4.1 Muscle morphology

CSA, FL and PA were assessed via extended-field-of-view B-mode ultrasonography (10 MHz linear-array: Aloka SSD-alpha10, Aloka Co., Ltd., Tokyo Japan). For all three measurements, the images were obtained with the participant lying in a supine position rested for at least 10 min (354). At a distance of 33 (distal), 50 (mid) and 66% (proximal) from the middle point between the lateral centre of the knee joint and the top of the greater trochanter of the femur, three axial perpendicular lines were marked. Images were taken while applying consistent pressure to the probe over a transmission gel and muscle compression was avoided. On the marked lines, the probe was moved transversely over the thigh while taking a single continuous view. Three images were taken for each site and were analysed with a digitising software (ImageJ 1.41, Wayne Rusband, National Institutes of Health, USA) for cross-sectional area of all compartments of the quadriceps femoris at the distal, mid and proximal sites. All cross-sectional area measures were analysed in triplicate. Total CSA for each site was calculated by taking the sum of CSA for all quadriceps compartments at the relevant site (354).

Scans for FL and PA were taken from the vastus lateralis (VL) at a distance of 50% between the lateral centre of the knee joint and the top of the greater trochanter of the femur. Each point was marked with a 4-mm wide double-sided adhesive tape to provide a shadow in the ultrasound image. FA and PA were analysed using digitising software (ImageJ 1.41, Wayne Rusband, National Institutes of Health, USA). For vastus lateralis the fascicle at 50% of the distance from the deep aponeurosis to the superficial aponeurosis marked by the shadow

produced by the adhesive tape was analyzed for length. Pennation angle for vastus lateralis was analysed based on an additional line that was drawn from 3 mm above the starting point of the line drawn for the fascicle length at the deep aponeurosis to the shadow at 50% of the fascicle length. The FL and PA measures were analysed in triplicate, and the average of the three measures was used for further analysis.

6.3.4.2 Aerobic performance

The incremental test was performed to establish PPO_{inc} and VO_{2peak} on a Velotron cycling ergometer (RacerMate, Inc., Seattle, Washington USA). Prior to the incremental test, participants completed a 3 min concentric warm-up at 50 W and 60 rpm. The incremental protocol began at 75 W and increased by 25 W every minute until volitional exhaustion, and verbal encouragement was provided during the final stages of the test. Participants were able to self-select their cadence during the concentric cycling test, and the test was terminated when the cadence dropped below 60 rpm for more than 30 s. The PPO_{inc} was calculated based on the last stage completed and pro rata of any uncompleted stages (i.e. 25 W / 60 s x time completed in the last stage). Expired gases were measured breath-by-breath and averaged every 15 s using a metabolic cart (TrueOne 2400 metabolic cart, ParvoMedics, Sandy, USA). The metabolic cart was calibrated before each test using gases of known concentrations and a 3-L syringe (5530 series, Hans Rudolph,Inc., Shawnee, Kansas, U.S.A.). The VO_{2peak} was the highest value in any 15 s interval. Heart rate was recorded using (S610, Polar, Finland), and maximal heart rate was noted as the highest heart rate observed in the test.

A six-minute walk test (6MW) was performed indoors between two cones placed 20 m apart with a mark every 5 m. Participants were instructed to start at the first cone, walk to the second cone 20 m away, turn around and repeat it for 6 minutes. For the turn participants were required to place any foot on the line drawn on the floor beside the cone. Any technique for the change of direction was allowed as long as one foot touched the line. Participants were strictly instructed to walk and not run. Participants were provided with verbal encouragement, and the time was indicated at 4, 3, and 1 min remaining. The total walking distance achieved was recorded. The CV for this test was 4.9%.

6.3.4.3 Muscle function

As shown in above, participants performed a 10 s seated cycling sprint at 60 rpm on the isokinetic cycling ergometer after a warm-up for 2 min and 30 s at 60 W. Verbal encouragement was provided during all sprints. PPO_{10s} was the highest power output reached in the 10 s.

Maximal voluntary isometric contraction torque of the knee extensors (MVC) was measured using a custom-made chair with a load cell (Xtran S1W, Applied Measurements, Melbourne, Australia) (321). The measurement was taken at 70° knee flexion from the right leg. Prior to the measurements participants performed a 5 min warm-up on a cycling ergometer (Monark 828E, Monark Exercise AB, Vansbro, Sweden) at 15% of their PPO_{inc} and 60 rpm. The warm-up was followed by three submaximal isometric knee extensions for 3 s at 50%, 50% and 80% of a maximal effort, each with a 1-min passive rest in between. Then, three 3-s maximal isometric knee extensions were performed, separated by a 1-min passive rest. Participants were advised to contract as fast and as hard as possible, and trials with any countermovement were disregarded and repeated. The torque data was sampled at a frequency of 1000 Hz, and a digital zero-phase lag finite impulse response low-pass filter with a cut-off frequency of 14 Hz was applied. The attempt with the greatest peak torque value was used for further analysis. Verbal encouragement was provided during all measurements.

Countermovement and squat jumps were performed on a force plate (9290AD; Kistler Instruments, Winterthur, Switzerland). Participants performed all jumps at a self-chosen squat depth but with less than 90° knee flexion while hands were placed on their hips. For the countermovement jump (CMJ), participants were asked to jump as high as possible from an upright standing position on a count of three. During the squat jump (SJ), participants were asked to squat down, remain in the squat position for 3 s and then jump without any countermovement. Vocal encouragement was provided during both jumps. First, participants performed 3 countermovement jumps followed by 3 squat jumps. Participants freely choose their rest, but no more than 2 minutes was allowed between jumps. Maximal jump heights were measured based on the flight time using computer software (MARS 2.1, Kistler Instruments, Winterthur, Switzerland), and the highest value was used for further analysis. The CV for PPO10s, MVC, CMJ and SJ was 4.4%, 3.2%, 1.9% and 1.8%, respectively.

6.3.4 Statistical analysis

A two-way repeated measures analysis of variance (ANOVA) was used to compare the changes in the outcome measures from before to after the 8 weeks of training between EC and CC groups. When a significant interaction or time effect was found, a Sidak´s post hoc was followed. An independent t-test was used to compare the percentage change of each measure between EC and CC groups. Hedges' *g* was used to calculate the effect size for the magnitude of the changes in each measure within a group, as well as to compare the magnitude of percentage change between groups for each measure. The significance was set at $P < 0.05$ for

all analyses and all statistical analyses were performed using GraphPad statistical package (Prism version 7.02, GraphPad Software, La Jolla, California, USA).

6.4 Results

6.4.1 Training

Heart rate, power output and rating of perceived effort for each training session are presented in Figure 28B-D. The power output during all training sessions was greater during EC than CC ($P < 0.0001$). Heart rate ($P \geq 0.53$) and sessional rating of perceived effort ($P \geq 0.06$) was not different between groups for all training sessions, but average heart rate across all training sessions was significantly greater ($P<0.0001$) for CC (151 ± 8 bpm) than EC (138 ± 22 bpm).

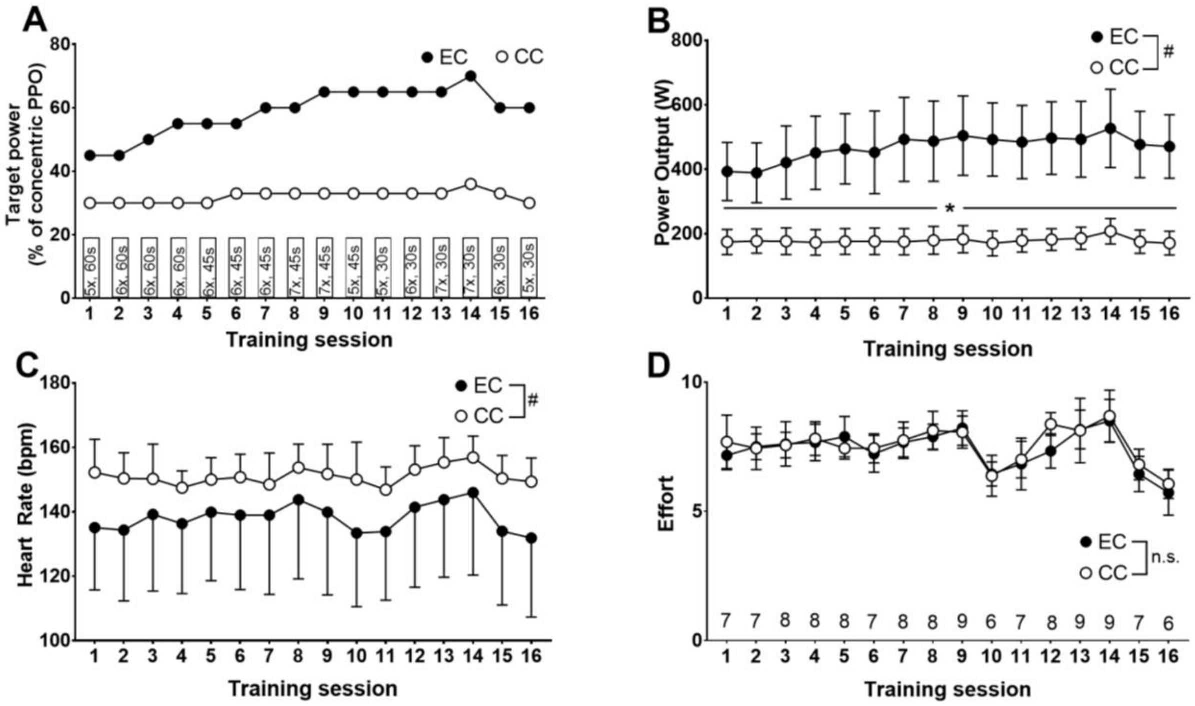

Figure 29: Training program based on concentric peak power output (PPO) (A), and actual average power output (B), heart rate (C), and rating of perceived effort (D) over 16 training sessions for eccentric (EC) and concentric (CC) cycling training groups. A: the target power output is shown as the percentage of the peak power output achieved during a concentric 10s sprint. The duration of cycling was always 2 min per repetition, while the rest between repetitions was initially 60 s, and progressed to 45 s then 30 s. For each training session, the number of repetitions and rest time for each session were indicated in the bar (e.g. 5 repetitions, 60 s interval: 5x, 60s). D: Target rating of perceived effort for each session is shown above the x-axis. #: significant ($P < 0.05$) group effect, *: significant ($P < 0.05$) difference between groups

6.4.2 Muscle morphology

Significant interaction effects were found for changes in CSA measured at distal, mid and proximal sites between groups. As shown in Figure 29A, CSA at the mid-section increased significantly from pre- to post-training ($P=0.0011$, $g=0.47$) for EC, but not for CC ($P=0.9623$,

g=0.02). This was also the case for the distal (EC: P<0.0001, g=0.82; CC: P=0.787, g=-0.06) and proximal (EC: P<0.0001, g=0.6; CC: P=0.8268, g=-0.04) sites. The percentage change in total CSA at the mid-section was significantly greater (P=0.0116, g=1.48) for EC (6.1 ± 4.7%) than CC (0.1 ± 3.8%) (Figure 29B). This was also found for the distal (P=0.0054, g=1.68; EC: 10.6 ± 7.7%; CC: 1.3 ± 2.6%) and proximal (P=0.0007, g=2.2; ECC: 9.8 ± 5.5%; CC: 1 ± 2%) sections.

The FL of VL did not change significantly ($F_{1,15}$ =1.158, P=0.2989) from pre- to post-training for EC and CC groups (Figure 29C), and no significant difference in the changes was evident between groups (P=0.4433, g=0.4) (Figure 29D). PA of VL also did not show significant ($F_{1,15}$ =0.3216, P=0.5790) changes (Figure 29E), and no significant difference between EC and CC groups was found (P=0.9169, g=0.06) (Figure 29F).

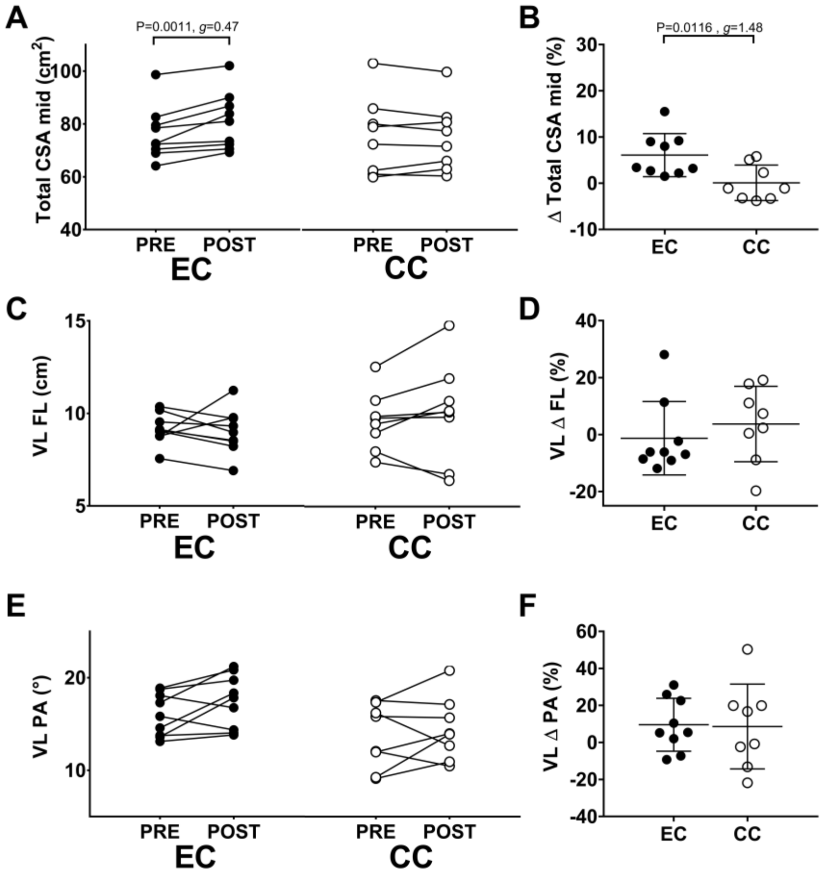

Figure 30: Comparison between eccentric (EC) and concentric (CC) cycling training groups for changes in quadriceps cross sectional area (CSA) (panel A, B), fascicle length of the vastus lateralis (FL) (panel C, D) and pennation angle of the vastus lateralis (PA) (panel E, F). For each figure, individual data are plotted for changes in the variable from before (pre) to after training (post) on the left side (A, C, E), and percentage changes from pre- to post-training, and the average (long line) and ± 1SD (short lines) on the right side (B, D, F). Effect size (g) for the difference between EC and CC groups is also shown.

6.4.3 Aerobic performance

Significant time effects were found for changes in VO_{2peak}, PPO_{inc}, and 6MW. As shown in Figure 30A, the increase in $VO2_{peak}$ from pre- to post-training did not reach significance for EC (P=0.0532, *g*=0.19), but was significant for CC (P=0.0133, *g*=0.24). However, the magnitude of the VO_{2peak} change was not significantly different (P=0.3052, *g*=-0.55) between EC (3.7 ± 3.9 %) and CC (6.6 ± 6.9 %) due to the large variability among participants (Figure 30B). PPO_{inc} increased significantly after training for both EC (P=0.0013; *g*=0.35), and CC (P=0.0019, *g*=0.33) (Figure 30C). The magnitude of increase in PPO_{inc} was similar (P=0.8323) between EC (6.0 ± 4.2 %) and CC (6.4 ± 4.6 %). The 6MW distance also increased after training for both EC (P=0.0119, *g*=0.66) and CC (P<0.0001, *g*=0.48) (Figure 3E), and the magnitude of the increase was similar (P=0.0647) between EC (4.5 ± 4.6 %) and CC (8.5 ± 3.5 %) (Figure 30F).

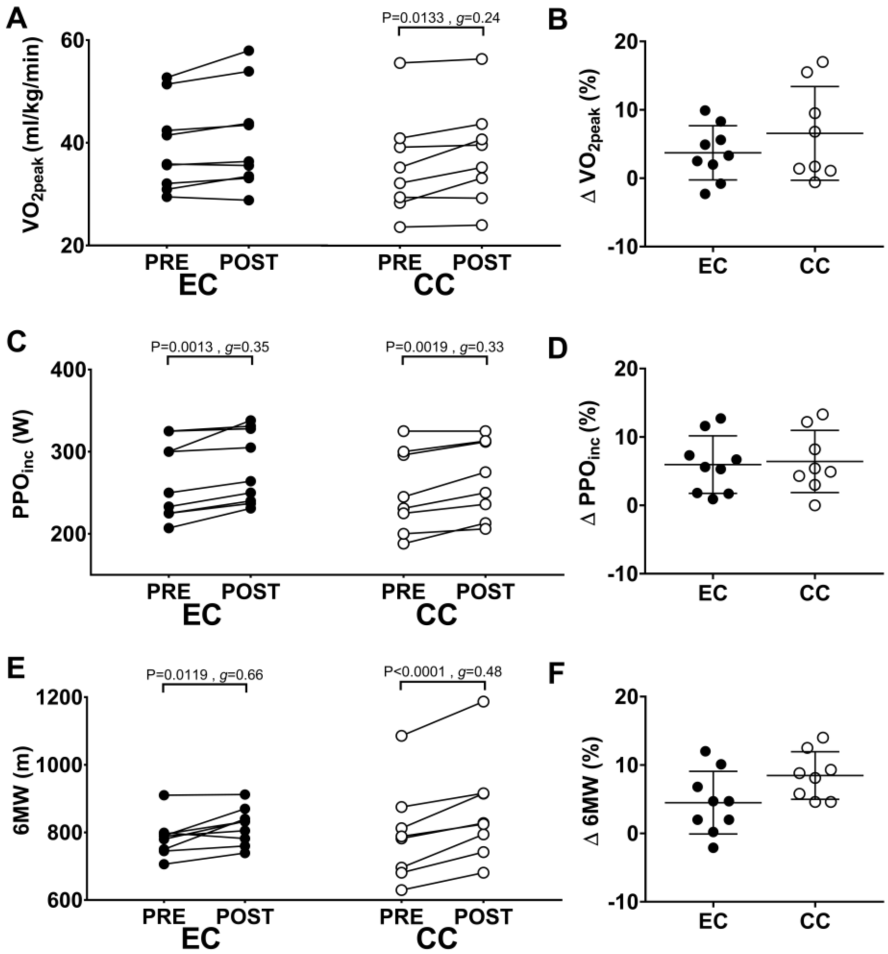

Figure 31: Comparison between eccentric (EC) and concentric (CC) cycling training groups for changes in peak oxygen consumption (VO2peak) (panel A, B), peak power output achieved in an incremental concentric cycling test (PPOinc) (panel C, D) and distance covered in a 6 minute walking test (6MW) (panel E, F). For each figure, individual data are plotted for changes in the variable from before (pre) to after training (post) on the left side (A, C, E), and percentage changes from pre- to post-training, and the average (long line) and ± 1SD (short lines) on the right side (B, D, F). Effect size (g) for the difference between EC and CC groups is also shown.

6.4.4 Muscle function

Significant interaction effects were found for PPO_{10s}, MVC, CMJ, and SJ. As shown in Figure 31A, PPO_{10s} increased significantly from pre- to post-training (P<0.0001, *g*=1.71) after EC as well as CC (P=0.0348, *g*=0.56). The magnitude of increase in PPO_{10s} was significantly (P=0.0013; *g*=2.03) greater for EC (26.9 ± 10.5%) than CC (8.9 ± 8 %) (Figure 31B). Compared to the baseline, MVC increased significantly for EC (P=0.0072, *g*=0.69) but not for CC (P=0.3029, *g*=0.47) (Figure 31C). However, no significant difference (P=0.2712, *g*=0.59) in the magnitude of change in MVC was found between EC (12.5 ± 13.3%) and CC (6.2 ± 8.3 %) due to the large variability among participants (Figure 31D). Neither EC (P=0. 0.0955, *g*=0.26) nor CC (P=0.1976; g=0.19) showed significant increases in CMJ after training (Figure 31E), but SJ increased after EC (P=0.0005, *g*=0.52) but not after CC (P= 0.3055; *g*=0.19) (Figure 31G). The magnitude of increase in CMJ (P=0.0131, *g*=1.46; EC: 3.9 ± 1.8%; CC: -3.2 ± 7.4 %) and SJ (P=0.0005, *g*=2.26; EC: 7.4 ± 4.7 CC: -2.3 ± 4.4 %) were greater for EC than CC (Figure 31H).

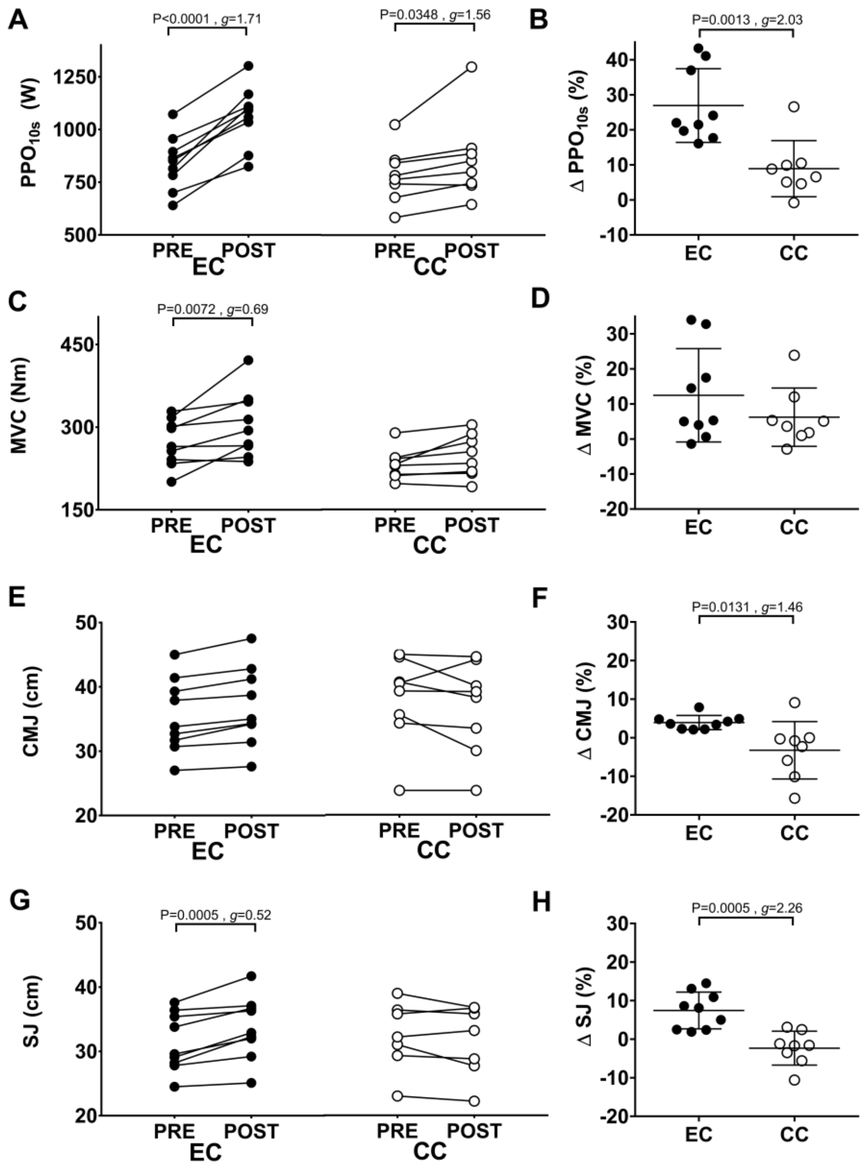

Figure 32: Comparison between eccentric (EC) and concentric (CC) cycling training groups for peak power output achieved during a 10 s sprint (PPO10s) (panel A, B), maximal voluntary isometric strength of the knee extensors (MVC) (panel C, D), countermovement jump height (panel E, F) and squat jump height (G, H). For each figure, individual data are plotted for changes in the variable from before (pre) to after training (post) on the left side (A, C, E, G), and percentage changes from pre- to post-training, and the average (long line) and ± 1SD (short lines) on the right side (B, D, F, H). Effect size (g) for the difference between EC and CC groups is also shown.

6.5. Discussion

The present study tested the hypothesis that HIT eccentric cycling training (EC) would induce greater changes in muscle morphological (CSA, FL, PA) and functional parameters (MVC, PPO_{10s}, SJ, CMJ), as well as aerobic parameters except for VO_2peak (PPO_{inc}, 6MW) when compared with HIT concentric cycling training (CC). The results showed that EC induced significant increases in CSA, PPO_{inc}, 6MW, PPO_{10s}, MVC and SJ, but significant increases after CC were limited to PPO_{10s}, VO_{2peak}, PPO_{inc} and 6MW. The magnitude of changes in CSA,

PPO_{10s}, CMJ and SJ was significantly greater after EC than CC. These partially supported the hypothesis, but EC did not affect FL and PA, and interestingly the magnitude of changes in aerobic parameters was similar between EC and CC.

The matching of the training intensity between groups by the rating of perceived effort was successful (Figure 28D). Across all sessions, target effort was achieved in both EC (97 ± 5%) and CC (98 ± 8%) (details are shown in Appendix B). The average power output during training increased from 392 ± 85 W to 530 ± 114 W for EC (35%), and from 175 ± 39 W to 208 ± 39 W for CC (19%). The 35% increase in the power output over EC training sessions was smaller than the magnitude of increase in power after continuous eccentric cycling training reported in previous studies showing 3-4 fold increase (22–24,26,51). It should be noted that these previous studies started with a low power output (~100W) to avoid muscle damage and soreness. However, in the present study, the participants were familiarised with eccentric cycling before the commencement of the training, thus started from higher power output to maximise exercise intensity from the begging of the training. Although the training was programmed to begin at 45% of PPO_{10s} and progress to 70% for the hardest session (Figure 28A), the progressive increase in training wattage ranged from 7 to 32% of PPO_{10s} among participants in EC. These differences are reflected by the large individual difference in training heart rate in the EC group (Figure 28C). It should be noted that heart rate during EC was more than 160 bpm for participants, but less than 130 bpm for others. This difference seems to be due to variable ability to produce high eccentric force continuously during eccentric cycling. This individual difference might have contributed to the large variability in the changes in the outcome measures among participants (Figures 29-31). Although heart rate for each session was not significantly different between EC and CC (Figure 29C), the average heart rate across all sessions was significantly greater for CC (151 ± 8 bpm) than EC (138 ± 22 bpm). It appears that the cardiovascular load indicated by the heart rate was high enough to induce aerobic adaptations (355) for both CC and EC. It is possible that the differences in the power output and heart rate during the training sessions between EC and CC groups influenced the changes in outcome measures after training.

The greater increases in muscle CSA for EC than CC were expected since previous studies also found greater increases in lean leg mass after eccentric than concentric cycling training (49,50). It is possible that the greater power output during EC than CC (Figure 28B) contributed to the greater increases in quadriceps muscle CSA after EC. As shown in Figure 29B, large variability in the magnitude of CSA increase after EC was observed among participants. It should be noted that the four participants who showed larger increases in CSA

than others had greater power output in EC training. Leong et al. (26) reported that eccentric cycling in a recumbent position performed for 10 minutes continuously at 20 to 55% of peak power output achieved during a 6 s sprint, induced 13% increase in VL muscle thickness and 24% increase in rectus femoris muscle thickness. Other studies using continuous eccentric cycling in a recumbent position also showed increases in muscle fibre CSA of VL by 40 to 60% (22,23,51). The current study utilised upright seated eccentric cycling that requires greater use of the hip flexors. Unlike during eccentric recumbent cycling, participants were required to use core and upper body muscles to stabilise the body to remain seated, and generate force to push against the pedals. Even during recumbent eccentric cycling, 58% of power is produced at the knee joint, and the rest at the ankle and the hip joint (45). It is possible that other muscles involved in upright eccentric cycling also showed an increase in CSA, but in the present study, only the CSA for the quadriceps muscles was measured.

Franchi et al. (16) in their review article have stated that FL increases after eccentric training and PA increases after concentric training, but none of the included studies in the review utilised eccentric cycling. For example, Reeves et al. (218) reported 20% increase in FL after eccentric resistance training, and 35% increase in PA after concentric training, in which consisted of 14 weeks (three times per week) of isotonic knee extensions and leg press (2 x 10 repetitions) at 80% of eccentric 5 repetition maximum (RM) for the eccentric, and at 80% of concentric 5RM for concentric training. Franchi et al. (240,260) also showed that FL increased 5% or 12% after 4 weeks or 10 weeks of isotonic leg press training performed twice a week (4 x 8-10 repetitions per session) at 80% of eccentric 1RM, and PA increased 7% or 30% after 4 weeks or 10 weeks of the leg press training at 80% of concentric 1RM. In contrast, Leong et al. (26) reported that continuous eccentric cycling performed in a recumbent position for 5-10 min at 20 to 55% of peak power output during a 6-s concentric sprint performed twice per week for 8 weeks increased PA of the VL by 24%. Although no significant changes in FL and PA were observed after EC as a group, it is interesting that many participants in the EC group showed decreases in FL and increases in PA, and some participants in the CC group showed increases in FL and decreases in PA (Figure 29). It seems possible that effects of eccentric cycling on FL and PA were very different from those of resistance exercise training in which a heavier load and a smaller number of contractions are used. Indeed, Reeves et al. (218) and Franchi et al. (16) stated that greater external loads, especially during eccentric muscle actions were necessary to induce architectural changes. Additionally, the contraction velocity in the previous studies was approximately 30°/s, which is much slower than the velocity in the cycling (180°/s

at 60 rpm). This might contribute to the different adaptations in FL and PA between eccentric resistance exercise versus eccentric cycling training.

There was no significant difference in the magnitude of change in PPO_{inc}, VO_{2peak} and 6MW after training between groups, and both groups showed significant increases in the variables (Figure 30). The VO_{2peak} after CC increased by 6.6 ± 6.9 %, which seems to be smaller when compared with a previous study in which HIT concentric cycling was used, which showed 13 ± 7% increase in $VO2_{peak}$ (356). It should be noted that in the study, HIT concentric cycling was performed on average for 81 ± 79 s at 99 ± 22 rpm with a work to rest ratio of 0.1 – 2. In the present study, the cadence was lower, and the rest to work ratio was 2-4. This might have attenuated the increase in VO_{2peak} after CC training. The magnitude of the increase in VO_{2peak} was not significantly different between EC and CC groups, although a couple of participants in the CC group showed large increases (Figure 30B). Previous studies in which continuous eccentric cycling training was performed for several weeks (23,357) showed little or no increases in VO_{2peak}. Thus, it is likely that the high-intensity interval protocol implemented in the present study worked to increase VO_{2peak}. As stated previously, the average heart rate across all sessions was greater during CC than EC, but when compared for each session there was no significant difference (Figure 28). Interestingly, some participants in the EC group had an average heart rate of over 150 during training, which showed 2.6% increase in VO_{2peak}. Additionally, it has been reported that resistance training increases parameters associated with aerobic performance (358), and individuals with lower levels of aerobic capacity at baseline could specifically benefit from increases in lower limb strength and power production (359). It seems likely that the increases in PPO_{inc}, VO_{2peak} and 6MW after the cycling training were at least partially due to the increases in muscle function (Figure 31).

Despite a significant increase in MVC from pre- to post-training for EC but not for CC (Figure 31C), there was no significant difference in the magnitude of the change between groups (Figure 31D). This was due to a large variability among participants for their responses to EC or CC training. In contrast to the previous studies reporting an increase in MVC of 13-60% after continuous eccentric cycling (22–24,27), HIT eccentric cycling in the present study increased MVC by 12.5 ± 13.3% (-1.4 to 34%). As discussed previously for CSA, a difference in the power output in the EC training may be a factor for the variability. In the present study, it was shown that parameters associated with power production (PPO_{10s}, CMJ, and SJ) showed greater increases after EC than CC. The increases in jump height confirm previous findings of 8% and 6.5% increase in CMJ height after 6 weeks of eccentric cycling training of basketball players and skiers, respectively (10,50). It may be that HIT eccentric cycling improved force

transfer and usage of the stretch-shortening cycle during jumps, which may have contributed to the larger increase (27%) in PPO_{10s} after EC when compared with CC (9%) (Figure 31B). It is important to note that PPO_{10s} was measured in concentric cycling. The larger increase in PPO_{10s} suggests that specificity of muscle contraction mode is secondary for improving muscle function. It may be that cyclists can benefit from including HIT eccentric cycling training in their training routine to improve their performance.

6.6 Conclusions

In summary, HIT eccentric cycling training performed twice a week for 8 weeks induced greater increases in quadriceps muscle CSA, PPO_{10s}, CMJ and SJ when compared with HIT concentric cycling training, and the increases in aerobic performance were similar between the two training modalities. HIT eccentric cycling appears to be effective training for improving muscle strength and VO_{2peak} simultaneously. Future studies should investigate the different effects between eccentric cycling and various other forms of eccentric exercise on strength and endurance parameters, as well as consider the potential effects of several individual differences.

CHAPTER SEVEN

INTEGRATED DISCUSSION AND

FUTURE RESERCH DIRECTION

7.1 Overview

The main purpose of this PhD thesis projects was to investigate whether the metabolic load during eccentric cycling would increase by application of high-intensity interval protocols and whether the high-intensity interval eccentric cycling could increase strength and endurance simultaneously. The present thesis included three studies by which acute and chronic effects of interval eccentric cycling were investigated. To the best of my knowledge, this research project was the first to investigate "high-intensity interval eccentric cycling." In the three studies, incremental concentric and eccentric cycling test until exhaustion were compared for the relationship between power output and physiological parameters <Study1>; interval and continuous eccentric cycling protocols were compared for oxygen consumption, perceived exertion and enjoyment <Study 2>; and changes in aerobic performance, muscle morphology and function after 8-week interval eccentric versus concentric cycling training were investigated <Study 3>. The previous chapters showed the results of each study and discussed the results, so in this chapter, the more integrated discussion will be made on eccentric cycling prescription and its potential.

The peak power output in Study 1 was 53% greater during the incremental eccentric cycling test (449 ± 115 W) than the incremental concentric cycling test (294 ± 61 W). The power output during the eccentric interval protocols in Study 2 was up to 111% (387 ± 129 W) greater than that during the continuous protocol (183 ± 32W). In Study 3, the highest power output of the eccentric cycling group (530 ± 114 W) was 365% greater than that of the concentric cycling group (114 ± 39 W). The greater power output during eccentric than concentric is likely due to the greater force production in eccentric than concentric contractions (4,6). When comparing the maximal force production at the angular velocity of 180°/s, which is seen in cycling, between eccentric and concentric contractions of the knee extensors, the eccentric force is approximately 1.5-fold of the concentric fore (4). Especially during eccentric cycling, peak power output during sprints can reach 1700 W (255). Thus, the range of possible power outputs is larger during eccentric than concentric cycling and can be achieved for the significantly smaller metabolic cost.

At the task failure, peak oxygen consumption in Study 1 was 43% lower during the eccentric than concentric cycling test. Although it was possible in Study 2 to increase the oxygen consumption of eccentric cycling with the usage of higher intensities, the relative oxygen consumption never surpassed 60% of VO_{2peak}. Despite such a medium oxygen consumption, participants performed the interval protocols up to an average of 387 ± 129 W (Table 1). Similarly, the participants in Study 3 progressed from an average of 392 ± 85 W to

530 ± 114 W as mentioned above. Using the interval format, it is possible to start eccentric cycling training at greater intensities and increase the training load to a higher level. Importantly, as shown in Study 2, there are many possible interval protocols which give a wide range of choices. Thus, high-intensity eccentric cycling can increase a variety of eccentric cycling training.

The application of one of such protocols in Study 3 showed that high-intensity interval eccentric cycling training could improve both muscle function and aerobic ability. In conjunction with the results on the maximal heart rate in Study 1, and the oxygen consumption during the interval protocols in Study 2, the interval design of Study 3 was determined. The interval duration was increased to 2 minutes and started with a 1-minute rest, as Study 2 showed that even when performed at up to 150% of PPOinc and a work to rest ratio of 1 to 1, 60% of VO2peak was not surpassed. To further increase the metabolic load, the sets were increased from 5 to 7 and the rest periods were decreased from 1 minute to 45 s, and then to 30 s over the period of the training intervention. In the present research project, no comparison between a high-intensity interval eccentric cycling and continuous eccentric cycling training effects was made. However, when comparing to the previous studies in which continuous eccentric cycling was used, some adaptations appears to be greater after the interval than continuous protocol. The 6% increase in CSA after the high-intensity interval eccentric training was smaller than the average increase (approximately 10%) reported in several studies in which continuous eccentric cycling training was performed (16,17,117). The increases in jump height of 4% for the CMJ and 7% for the SJ were similar to those of previous studies (10,50). The large increase in PPO_{10s} (27%) found in Study 3 after eccentric cycling training was greater than expected. In comparison to the previous study showing 5-9% increase in peak power output achieved during a 6 concentric cycling sprint after continuous eccentric cycling (26), the magnitude of PPO_{10s} increase after the eccentric cycling in Study 3 was greater. It is plausible to assume that high-intensity eccentric cycling can be more efficient as a training method when compared with continuous eccentric cycling.

In Study 1, maximal heart rate between the eccentric (175 ± 20 bpm) and concentric test (182 ± 13 bpm) was not significantly different, and in Study 3 there was no significant difference in the heart rate during training between the eccentric and concentric cycling group in each training session. It appears that despite a lower metabolic load during eccentric cycling, as shown by the 43% lower VO_{2peak} during the eccentric test in Study 1, the 53% greater power output during the eccentric test and the 365% greater power output during Study 3 suggest that eccentric cycling increases cardiovascular function. Previously it was reported that continuous

eccentric cycling at 2.5 times greater power output than concentric cycling but the same oxygen consumption (341,345) resulted in significantly greater heart rate already 5 minutes into the exercise. Other aspects of the cardiovascular system, like blood pressure and stroke volume (309,345), have been shown to be greater during eccentric than concentric cycling, while the peripheral factors such as muscle oxygenation were the same between the two (345,360). If muscle oxygenation is not reduced, but the central function of the cardiovascular system is increased during continuous eccentric cycling, high-intensity interval eccentric cycling could attenuate such characteristics even more. Although the mechanisms underpinning the increase in aerobic performance after high-intensity interval eccentric cycling are not clear, it is possible that the increases in heart rate, blood pressure and stroke volume induced during high-intensity interval eccentric cycling contributed to the adaptations.

The greater increases in CSA, strength and muscle function after EC in Study 3, could have also contributed to the similar increases in aerobic parameters to CC. Improvements in knee extension strength (361,362), muscle mass (363), and strength (358,364) are all related to increases in aerobic performance. Sedentary and unfit individuals with a VO_{2peak} of under 40 $ml \cdot kg \cdot min^{-1}$ seem more sensitive to increases in VO_{2peak} after strength training than fitter individuals (359), while for athletes with a VO_{2peak} greater than 60 $ml \cdot kg \cdot min^{-1}$, performance measures and time trails are influenced more than VO_{2peak} (365,366). In Study 3, 7 out of 9 participants in the EC group had a VO_{2peak} of less than 42 $ml \cdot kg \cdot min^{-1}$ before training. As it was shown in Study 2 that relative oxygen consumption never surpassed 60% of VO_{2peak}, aerobic requirements during high-intensity interval eccentric cycling are still low to moderate. Although the training protocol in Study 3 was performed with longer intervals and greater work to rest ratio than those in Study 2, it can be assumed that the relative oxygen consumption did not reach high levels. It seems likely that increases in muscle strength and function were more relevant contributors to the increases in aerobic performance after the eccentric cycling training.

Individual differences and responses to the high-intensity interval eccentric cycling have to be considered. Although the results of Study 1 showed that eccentric peak power output was significantly correlated with concentric peak power output (r=0.84), there were several participants who either under- or overperformed on the eccentric test, resulting in a greater or smaller eccentric peak power than the correlation of concentric peak power would explain. Likewise, in Study 3 one individual began at 48% of PPO_{10s} and peaked at 54%, while another one began at 36% and reached 68%. Indeed, the latter participant who progressed by 32%, increased CSA by 18%, VO_{2peak} by 3.3%, PPO_{inc} by 7.3%, 6MW by 10.1%, PPO_{10s} by 22%, MVC by 32.8%, CMJ by 4.9% and SJ by 8.1%. Another participant that progressed during

training by 20% increased CSA by 25.7%, PPO_{inc} by 6.7%, 6MW by 2%, PPO_{10s} by 43.3%, MVC by 5.3%, CMJ by 3.6% and SJ by 14.5%. In contrast, one participant increased only by 8% during training, who showed a decrease in MVC by -1.4%, but increased CSA by 2.2%, VO_{2peak} by 5.6%, PPO_{inc} by 12.6%, 6MW by 2%, PPO_{10s} by 19.7%, CMJ by 3.4% and SJ by 1.9%. The individuals who were unaccustomed to eccentric cycling showed a large variance in the precision of reaching a target power output continuously. This "eccentric coordination" has been shown to improve significantly over time (50,67). It is possible that this unique ability is not only specific to producing high eccentric peak power output but also falls under the "eccentric skill". As neural characteristics have been extensively shown to be different between concentric and eccentric muscle actions (115,116), it is possible to assume that the motor control during eccentric cycling can be better in some individuals. Recently, it has been shown that muscles contain a "memory" for certain genes that contribute to muscle hypertrophy, even over a short period of time like 22 weeks (367). Other types of memory could exist in muscle, connective, and neural tissues that could contribute to the eccentric skill.

7.2 Significance and practical implications

This project was able to extend the body of knowledge about eccentric training. It has provided insights into eccentric cycling until task failure, which is a popular method in concentric cycling but has not been previously used during eccentric cycling. The findings are significant for future research and application of eccentric cycling, as parameters for exercise prescription have been discussed. As such, despite its popularity, based on current knowledge it is not recommended to use heart rate to prescribe and monitor eccentric cycling training. In practice, prescription of training based on concentric peak power may be better. Furthermore, the metabolic increases highlighted for interval protocols may have contributed to the increases in outcome measures after the eccentric cycling training. The selected adaptations in muscle strength, and endurance after high-intensity eccentric cycling training showcased that such protocols were valid, and potentially a time-saving alternative to continuous eccentric cycling. Furthermore, as the relative metabolic load during interval protocols was still low to moderate, a wide range of population could benefit from HIT eccentric cycling training. For practical application, interval protocols should be considered for already familiarised individuals to increase the benefits of eccentric cycling training potentially. For the general populations, such protocols could be utilised in conjunction with continuous eccentric cycling to prevent boredom and provide a challenge. In athletic populations, especially in sports with low or now impact forces like cycling, rowing and swimming, it could be used as an alternative to strength training.

7.3 Future research directions

Further investigations about eccentric exercise are required. In the development of eccentric cycling tests, other protocols for establishing maximal performance during eccentric cycling should be considered. Especially new protocols specifically designed around the known characteristics of uninterrupted eccentric exercise should be examined. The association and correlation of eccentric peak power output and other parameters than those presented in Study 1 should be investigated further. Such parameters could be related to other types of strength measures at variable velocities to establish the association of eccentric peak power output with different parts of the force-velocity relationship. Furthermore, other parameters such as concentric sprint peak power, change of direction performance, reactive strength index or leg stiffness measured via hopping frequency could provide further insights. A special focus should be put on understanding the difference in the progressive increase of heart rate during incremental eccentric cycling protocols, and its relationship to other physiological parameters. The current data suggest that the known models for increases in physiological parameters like oxygen consumption, or heart rate during concentric cycling are not applicable to eccentric cycling. Furthermore, these relationships should be investigated for the difference between different populations (e.g. sedentary, clinical & athletic populations), as well as between different predispositions within each population (e.g. strength vs endurance athletes).

Similarly, other types of interval eccentric cycling protocols than the one presented in Study 2 should be investigated for cardiovascular, neural, mechanical and psycho-perceptual responses. Due to the current popularity and the time-saving aspects of high-intensity interval training, it is necessary to understand the details of various protocols applied to eccentric cycling. As stated previously, unique protocols of eccentric cycling should be designed based on the known characteristics of eccentric muscle actions and further investigated for acute and chronic effects. Based on the still-moderate metabolic load of the high-intensity interval protocols in Study 2, there seems to be untapped potential for greater adaptations for eccentric cycling. It is important to understand if such training intensities and protocols are beneficial to elderly, clinical and frail populations over low-intensity continuous eccentric cycling protocols. One important aspect of future research should be the investigation of similar characteristics and effects of eccentric cycling in male and female individuals. Due to the potential differences in muscle strength and muscle-tendon unit stiffness, it is possible that there are specific effects in female participants, which were not indicated in the present studies. As the continuous eccentric cycling protocols have already been shown to increase outcome measures with these populations greatly, high-intensity interval eccentric cycling may show much greater benefits

or at least as a good alternative. Application of such protocols, resultant adaptations, as well as the feasibility, enjoyment and compliance with such training should be investigated in long-term intervention studies.

7.4 Conclusions

This project has provided further evidence that eccentric exercise and training are unique. Furthermore, the various forms of eccentric exercise and training, have different characteristics and could lead to unique adaptations. Although currently, these specific details about the various characteristics and effects are unknown, this project has shown how interval eccentric cycling is different from continuous eccentric cycling, and interval concentric cycling. Based on the present project, and the currently available knowledge about heart rate behaviour during eccentric cycling, prescribing eccentric cycling training based on heart rate is not recommended. The present research also showed that oxygen consumption increased through interval protocols in comparison to continuous protocols during eccentric cycling. The application of interval eccentric training over 8 weeks showed similar improvements in aerobic performance to interval concentric training while leading to greater adaptations of muscle cross-sectional area and parameters of physical performance. Thus, this project has identified acute characteristics and chronic effects of high-intensity interval eccentric cycling, as well as showcased its potential as a concurrent training method for strength and endurance. High-intensity interval eccentric could be the next exercise trend if the availability of eccentric cycling ergometers to the general population increases.

REFERENCES

1. Ito M, Kawakami Y, Ichinose Y, Fukashiro S, Fukunaga T. Nonisometric behavior of fascicles during isometric contractions of a human muscle. J Appl Physiol. 1998 Oct 1;85(4):1230–5.

2. Hodges P w., Pengel L h. m., Herbert R d., Gandevia S c. Measurement of muscle contraction with ultrasound imaging. Muscle Nerve. 2003 Jun 1;27(6):682–92.

3. Muramatsu T, Muraoka T, Takeshita D, Kawakami Y, Hirano Y, Fukunaga T. Mechanical properties of tendon and aponeurosis of human gastrocnemius muscle in vivo. J Appl Physiol. 2001 May 1;90(5):1671–8.

4. Rutherford OM, Purcell C, Newham DJ. The human force:velocity relationship; activity in the knee flexor and extensor muscles before and after eccentric practice. Eur J Appl Physiol. 2001 Feb 1;84(1–2):133–40.

5. Cress NM, Peters KS, Chandler JM. Eccentric and concentric force-velocity relationships of the quadriceps feimoris muscle. J Orthop Sports Phys Ther. 1992;16(2):82–6.

6. HILL AV. Production and absorption of work by muscle. Science. 1960 Mar 25;131(3404):897–903.

7. Hill AV. The Mechanics of Active Muscle. Proc R Soc Lond Ser B - Biol Sci. 1953 Mar 11;141(902):104–17.

8. Abbott BC, Bigland B, Ritchie JM. The physiological cost of negative work. J Physiol. 1952 Jul 28;117(3):380–90.

9. Jindrich D L, Besier T F, Loyd, D G. A hypothesis for the function of braking forces during running turns. J Biomech. 2006;39:1611–20.

10. Lindstedt SL, Reich TE, Keim P, LaStayo PC. Do muscles function as adaptable locomotor springs? J Exp Biol. 2002 Aug;205(Pt 15):2211–6.

11. Jamurtas AZ, Theocharis V, Tofas T, Tsiokanos A, Yfanti C, Paschalis V, et al. Comparison between leg and arm eccentric exercises of the same relative intensity on indices of muscle damage. Eur J Appl Physiol. 2005 Oct;95(2–3):179–85.

12. Beaven CM, Willis SJ, Cook CJ, Holmberg H-C. Physiological Comparison of Concentric and Eccentric Arm Cycling in Males and Females. PLoS ONE. 2014 Nov 5;9(11):e112079.

13. Gault ML, Willems MET. Aging, functional capacity and eccentric exercise training. Aging Dis. 2013 Sep 25;4(6):351–63.

14. Schoenfeld B, Grgic J. Eccentric Overload Training: A Viable Strategy to Enhance Muscle Hypertrophy?. Strength Cond J [Internet]. 2017 Nov 20 [cited 2017 Nov 26];Publish Ahead of Print. Available from: http://journals.lww.com/nsca-scj/Abstract/publishahead/Eccentric_Overload_Training___A_Viable_Strategy_to.99465.aspx

15. Schoenfeld BJ, Ogborn DI, Vigotsky AD, Franchi MV, Krieger JW. Hypertrophic Effects of Concentric vs. Eccentric Muscle Actions: A Systematic Review and Meta-analysis. J Strength Cond Res. 2017 Sep;31(9):2599.

16. Franchi MV, Reeves ND, Narici MV. Skeletal muscle remodelling in response to eccentric vs. concentric loading: morphological, molecular and metabolic adaptations. Front Physiol [Internet]. 2017 [cited 2017 Jun 22];8. Available from: http://journal.frontiersin.org/article/10.3389/fphys.2017.00447/abstract

17. Roig M, O'Brien K, Kirk G, Murray R, McKinnon P, Shadgan B, et al. The effects of eccentric versus concentric resistance training on muscle strength and mass in healthy adults: a systematic review with meta-analysis. Br J Sports Med. 2009 Aug;43(8):556–68.

18. Guilhem G, Cornu C, Guével A. Neuromuscular and muscle-tendon system adaptations to isotonic and isokinetic eccentric exercise. Ann Phys Rehabil Med. 2010 Jun;53(5):319–41.

19. Maeo S, Yamamoto M, Kanehisa H. Downhill walking training with and without exercise-induced muscle damage similarly increase knee extensor strength. J Sports Sci. 2016 Nov;34(21):2018–26.

20. Maroto-Izquierdo S, García-López D, Fernandez-Gonzalo R, Moreira OC, González-Gallego J, Paz JA de. Skeletal muscle functional and structural adaptations after eccentric overload flywheel resistance training: a systematic review and meta-analysis. J Sci Med Sport [Internet]. 2017 Mar 21 [cited 2017 Mar 28];0(0). Available from: http://www.jsams.org/article/S1440-2440(17)30333-X/abstract

21. Tesch PA, Fernandez-Gonzalo R, Lundberg TR. Clinical Applications of Iso-Inertial, Eccentric-Overload (YoYo™) Resistance Exercise. Front Physiol [Internet]. 2017 [cited 2017 Apr 28];8. Available from: http://journal.frontiersin.org/article/10.3389/fphys.2017.00241/full

22. LaStayo PC, Ewy GA, Pierotti DD, Johns RK, Lindstedt S. The positive effects of negative work: increased muscle strength and decreased fall risk in a frail elderly population. J Gerontol A Biol Sci Med Sci. 2003 May;58(5):M419-424.

23. LaStayo PC, Pierotti DJ, Pifer J, Hoppeler H, Lindstedt SL. Eccentric ergometry: increases in locomotor muscle size and strength at low training intensities. Am J Physiol Regul Integr Comp Physiol. 2000 May;278(5):R1282-1288.

24. Lastayo PC, Reich TE, Urquhart M, Hoppeler H, Lindstedt SL. Chronic eccentric exercise: improvements in muscle strength can occur with little demand for oxygen. Am J Physiol. 1999 Feb;276(2 Pt 2):R611-615.

25. Elmer S, Hahn S, McAllister P, Leong C, Martin J. Improvements in multi-joint leg function following chronic eccentric exercise. Scand J Med Sci Sports. 2012 Oct;22(5):653–61.

26. Leong CH, McDermott WJ, Elmer SJ, Martin JC. Chronic Eccentric Cycling Improves Quadriceps Muscle Structure and Maximum Cycling Power. Int J Sports Med. 2013 Nov 14;

27. Lewis M. The feasibility of eccentric cycling as a training modality for increasing quadriceps strength at low cardiovascular cost [Internet] [Master's thesis]. University of Wollongong; 2012. Available from: http://ro.uow.edu.au/theses/3938

28. LaStayo P, Marcus RL, Dibble L, Frajacomo F, Lindstedt SL. Eccentric Exercise in Rehabilitation: Safety, Feasibility and Application. J Appl Physiol [Internet]. 2013 Jul 3 [cited 2014 May 14]; Available from: http://jap.physiology.org/content/early/2013/07/02/japplphysiol.00008.2013

29. Hoppeler HH, Herzog W. Eccentric Exercise: Many Questions Unanswered. J Appl Physiol [Internet]. 2014 Apr 17 [cited 2014 May 28]; Available from: http://jap.physiology.org/content/early/2014/04/07/japplphysiol.00239.2014

30. Isner-Horobeti M-E, Dufour SP, Vautravers P, Geny B, Coudeyre E, Richard R. Eccentric Exercise Training: Modalities, Applications and Perspectives. Sports Med. 2013 May 9; 43(6):483-512.

31. Bridgeman L, Gill N, McGuigan M. Eccentric exercise as a training modality: a brief review. Available from: https://www.researchgate.net/publication/281103262_Eccentric_exercise_as_a_training_modality_A_brief_review , 2015 Nov 2;23(5):52–65.

32. Butterfield TA, Lepley LK. Eccentric Contractions: They Are Not So "Odd" Anymore. J Sport Rehabil. 2017 Mar 1;26(2):117–9.

33. Lastayo PC. Eccentric Muscle Contractions: Their Contribution to Injury, Prevention, Rehabilitation, and Sport. J Orthop Sports Phys Ther. 2003 Oct 1;33(10):557–71.

34. Hoppeler H. Moderate load eccentric exercise; a distinct novel training modality. Exerc Physiol. 2016;7:483.

35. American College of Sports Medicine. American College of Sports Medicine position stand. Progression models in resistance training for healthy adults. Med Sci Sports Exerc. 2009 Mar;41(3):687–708.

36. Peñailillo L, Blazevich A, Numazawa H, Nosaka K. Metabolic and Muscle Damage Profiles of Concentric versus Repeated Eccentric Cycling. Med Sci Sports Exerc. 2013 Mar 7; 45(9):1773-81.

37. Clarkson PM, Nosaka K, Braun B. Muscle function after exercise-induced muscle damage and rapid adaptation. Med Sci Sports Exerc. 1992 May;24(5):512–20.

38. Paulsen G, Vissing K, Kalhovde JM, Ugelstad I, Bayer ML, Kadi F, et al. Maximal eccentric exercise induces a rapid accumulation of small heat shock proteins on myofibrils and a delayed HSP70 response in humans. Am J Physiol - Regul Integr Comp Physiol. 2007 Aug 1;293(2):R844–53.

39. Lauritzen F, Paulsen G, Raastad T, Bergersen LH, Owe SG. Gross ultrastructural changes and necrotic fiber segments in elbow flexor muscles after maximal voluntary eccentric action in humans. J Appl Physiol. 2009 Oct 1;107(6):1923–34.

40. Chen TC, Hsieh C-C, Tseng K-W, Ho C-C, Nosaka K. Effects of Descending Stair Walking on Health and Fitness of Elderly Obese Women. Med Sci Sports Exerc. 2017 Mar 13;

41. Chen TC-C, Tseng W-C, Huang G-L, Chen H-L, Tseng K-W, Nosaka K. Superior Effects of Eccentric to Concentric Knee Extensor Resistance Training on Physical Fitness, Insulin Sensitivity and Lipid Profiles of Elderly Men. Front Physiol [Internet]. 2017 Apr 10;8. Available from: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC5385383/

42. Maeo S, Ochi Y, Yamamoto M, Kanehisa H, Nosaka K. Effect of a prior bout of preconditioning exercise on muscle damage from downhill walking. Appl Physiol Nutr Metab. 2014 Nov 19;40(3):274–9.

43. Lin M-J, Chen TC-C, Chen H-L, Wu B-H, Nosaka K. Low-intensity eccentric contractions of the knee extensors and flexors protect against muscle damage. Appl Physiol Nutr Metab Physiol Appl Nutr Metab. 2015 Oct;40(10):1004–11.

44. Hyldahl RD, Chen TC, Nosaka K. Mechanisms and Mediators of the Skeletal Muscle Repeated Bout Effect. Exerc Sport Sci Rev. 2016 Oct 25;

45. Elmer SJ, Madigan ML, LaStayo PC, Martin JC. Joint-specific power absorption during eccentric cycling. Clin Biomech Bristol Avon. 2010 Feb;25(2):154–8.

46. Elmer SJ, Danvind J, Holmberg H-C. Development of a novel eccentric arm cycle ergometer for training the upper body. Med Sci Sports Exerc. 2013 Jan;45(1):206–11.

47. Perrey S, Betik A, Candau R, Rouillon JD, Hughson RL. Comparison of oxygen uptake kinetics during concentric and eccentric cycle exercise. J Appl Physiol. 2001 Nov;91(5):2135–42.

48. Dufour SP, Doutreleau S, Lonsdorfer-Wolf E, Lampert E, Hirth C, Piquard F, et al. Deciphering the metabolic and mechanical contributions to the exercise-induced circulatory response: insights from eccentric cycling. Am J Physiol Regul Integr Comp Physiol. 2007 Apr;292(4):R1641-1648.

49. LaStayo PP, McDonagh P, Lipovic D, Napoles PM, Bartholomew A, Esser K, et al. Elderly Patients and High Force Resistance Exercise-A Descriptive Report: Can an Anabolic, Muscle Growth Response Occur Without Muscle Damage or Inflammation? J Geriatr Phys Ther Dec 2007. 2007;30(3):128–34.

50. Gross M, Lüthy F, Kroell J, Müller E, Hoppeler H, Vogt M. Effects of eccentric cycle ergometry in alpine skiers. Int J Sports Med. 2010 Aug;31(8):572–6.

51. Fridén J, Seger J, Sjöström M, Ekblom B. Adaptive response in human skeletal muscle subjected to prolonged eccentric training. Int J Sports Med. 1983 Aug;4(3):177–83.

52. Rooyackers JM, Berkeljon DA, Folgering HTM. Eccentric exercise training in patients with chronic obstructive pulmonary disease. Int J Rehabil Res Int Z Für Rehabil Rev Int Rech Réadapt. 2003 Mar;26(1):47–9.

53. MacMillan NJ, Kapchinksy S, Konokhova Y, Gouspillou G, de Sousa Sena R, Jagoe RT, et al. Eccentric ergometer training promotes locomotor muscle strength but not mitochondrial adaptation in patients with severe Chronic Obstructive Pulmonary Disease. Front Physiol [Internet]. 2017 [cited 2017 Feb 25];8. Available from: http://journal.frontiersin.org/article/10.3389/fphys.2017.00114/full

54. Marcus RL, Lastayo PC, Dibble LE, Hill L, McClain DA. Increased strength and physical performance with eccentric training in women with impaired glucose tolerance: a pilot study. J Womens Health 2002. 2009 Feb;18(2):253–60.

55. Gremeaux V, Duclay J, Deley G, Philipp JL, Laroche D, Pousson M, et al. Does eccentric endurance training improve walking capacity in patients with coronary artery disease? A randomized controlled pilot study. Clin Rehabil. 2010 Jul;24(7):590–9.

56. Casillas JM, Besson D, Hannequin A, Gremeaux V, Morisset C, Tordi N, et al. Effects of an eccentric training personalized by a low rate of perceived exertion on the maximal capacities in chronic heart failure: a randomized controlled trial. Eur J Phys Rehabil Med. 2016 Apr;52(2):159–68.

57. Hayes HA, Gappmaier E, LaStayo PC. Effects of High-Intensity Resistance Training on Strength, Mobility, Balance, and Fatigue in Individuals With Multiple Sclerosis: A Randomized Controlled Trial. J Neurol Phys Ther. 2011 Mar;35(1):2–10.

58. Dibble LE, Hale TF, Marcus RL, Gerber JP, LaStayo PC. High intensity eccentric resistance training decreases bradykinesia and improves Quality Of Life in persons with Parkinson's disease: a preliminary study. Parkinsonism Relat Disord. 2009 Dec;15(10):752–7.

59. Harris-Love MO. Safety and efficacy of submaximal eccentric strength training for a subject with polymyositis. Arthritis Rheum. 2005 Jun 15;53(3):471–4.

60. Lastayo PC, Larsen S, Smith S, Dibble L, Marcus R. The feasibility and efficacy of eccentric exercise with older cancer survivors: a preliminary study. J Geriatr Phys Ther 2001. 2010 Sep;33(3):135–40.

61. Steiner R, Meyer K, Lippuner K, Schmid J-P, Saner H, Hoppeler H. Eccentric endurance training in subjects with coronary artery disease: a novel exercise paradigm in cardiac rehabilitation? Eur J Appl Physiol. 2004 May;91(5–6):572–8.

62. Hansen PA, Dechet CB, Porucznik CA, LaStayo PC. Comparing Eccentric Resistance Exercise in Prostate Cancer Survivors On and Off Hormone Therapy: A Pilot Study. PM&R. 2009 Nov;1(11):1019–24.

63. LaStayo PC, Marcus RL, Dibble LE, Smith SB, Beck SL. Eccentric exercise versus Usual-care with older cancer survivors: The impact on muscle and mobility- an exploratory pilot study. BMC Geriatr. 2011 Jan 27;11(1):5.

64. Marcus RL, Smith S, Morrell G, Addison O, Dibble LE, Wahoff-Stice D, et al. Comparison of combined aerobic and high-force eccentric resistance exercise with aerobic exercise only for people with type 2 diabetes mellitus. Phys Ther. 2008 Nov;88(11):1345–54.

65. Dibble LE, Hale TF, Marcus RL, Droge J, Gerber JP, LaStayo PC. High-intensity resistance training amplifies muscle hypertrophy and functional gains in persons with Parkinson's disease. Mov Disord Off J Mov Disord Soc. 2006 Sep;21(9):1444–52.

66. LaStayo PC, Meier W, Marcus RL, Mizner R, Dibble L, Peters C. Reversing Muscle and Mobility Deficits 1 to 4 Years after TKA: A Pilot Study. Clin Orthop. 2009 Jun;467(6):1493–500.

67. Mueller M, Breil FA, Vogt M, Steiner R, Lippuner K, Popp A, et al. Different response to eccentric and concentric training in older men and women. Eur J Appl Physiol. 2009 Sep;107(2):145–53.

68. Knuttgen HG, Nadel ER, Pandolf KB, Patton JF. Effects of training with eccentric muscle contractions on exercise performance, energy expenditure, and body temperature. Int J Sports Med. 1982 Feb;3(1):13–7.

69. Bonde-Petersen F, Henriksson J, Knuttgen HG. Effect of training with eccentric muscle contractions on skeletal muscle metabolites. Acta Physiol Scand. 1973 Aug;88(4):564–70.

70. Knuttgen HG, Klausen K. Oxygen debt in short-term exercise with concentric and eccentric muscle contractions. J Appl Physiol. 1971 May;30(5):632–5.

71. Meyer K, Steiner R, Lastayo P, Lippuner K, Allemann Y, Eberli F, et al. Eccentric exercise in coronary patients: central hemodynamic and metabolic responses. Med Sci Sports Exerc. 2003 Jul;35(7):1076–82.

72. Besson D, Joussain C, Gremeaux V, Morisset C, Laurent Y, Casillas J-M, et al. Eccentric training in chronic heart failure: feasibility and functional effects. Results of a comparative study. Ann Phys Rehabil Med. 2013 Feb;56(1):30–40.

73. O'Reilly KP, Warhol MJ, Fielding RA, Frontera WR, Meredith CN, Evans WJ. Eccentric exercise-induced muscle damage impairs muscle glycogen repletion. J Appl Physiol. 1987 Jul 1;63(1):252–6.

74. Asp S, Daugaard JR, Richter EA. Eccentric exercise decreases glucose transporter GLUT4 protein in human skeletal muscle. J Physiol. 1995 Feb 1;482(Pt 3):705–12.

75. Asp S, Daugaard JR, Kristiansen S, Kiens B, Richter EA. Eccentric exercise decreases maximal insulin action in humans: muscle and systemic effects. J Physiol. 1996 Aug 1;494(Pt 3):891–8.

76. Del Aguila LF, Krishnan RK, Ulbrecht JS, Farrell PA, Correll PH, Lang CH, et al. Muscle damage impairs insulin stimulation of IRS-1, PI 3-kinase, and Akt-kinase in human skeletal muscle. Am J Physiol Endocrinol Metab. 2000 Jul;279(1):E206-212.

77. Kirwan JP, Hickner RC, Yarasheski KE, Kohrt WM, Wiethop BV, Holloszy JO. Eccentric exercise induces transient insulin resistance in healthy individuals. J Appl Physiol . 1985. 1992 Jun;72(6):2197–202.

78. Paschalis V, Nikolaidis MG, Theodorou AA, Panayiotou G, Fatouros IG, Koutedakis Y, et al. A weekly bout of eccentric exercise is sufficient to induce health-promoting effects. Med Sci Sports Exerc. 2011 Jan;43(1):64–73.

79. Paschalis V, Nikolaidis MG, Giakas G, Theodorou AA, Sakellariou GK, Fatouros IG, et al. Beneficial changes in energy expenditure and lipid profile after eccentric exercise in overweight and lean women. Scand J Med Sci Sports. 2010 Feb 1;20(1):e103–11.

80. Peñailillo L, Blazevich A, Nosaka K. Energy expenditure and substrate oxidation during and after eccentric cycling. Eur J Appl Physiol. 2014 Jan 5;

81. Metcalfe RS, Babraj JA, Fawkner SG, Vollaard NBJ. Towards the minimal amount of exercise for improving metabolic health: beneficial effects of reduced-exertion high-intensity interval training. Eur J Appl Physiol. 2012 Jul;112(7):2767–75.

82. Wisløff U, Støylen A, Loennechen JP, Bruvold M, Rognmo Ø, Haram PM, et al. Superior Cardiovascular Effect of Aerobic Interval Training Versus Moderate Continuous Training in Heart Failure Patients A Randomized Study. Circulation. 2007 Jun 19;115(24):3086–94.

83. Tjønna AE, Stølen TO, Bye A, Volden M, Slørdahl SA, Ødegård R, et al. Aerobic interval training reduces cardiovascular risk factors more than a multitreatment approach in overweight adolescents. Clin Sci. 2009 Feb 1;116(4):317.

84. Hwang C-L, Wu Y-T, Chou C-H. Effect of Aerobic Interval Training on Exercise Capacity and Metabolic Risk Factors in People With Cardiometabolic Disorders: A META-ANALYSIS. J Cardiopulm Rehabil Prev. 2011;31(6):378–85.

85. Little JP, Safdar A, Wilkin GP, Tarnopolsky MA, Gibala MJ. A practical model of low-volume high-intensity interval training induces mitochondrial biogenesis in human skeletal muscle: potential mechanisms. J Physiol. 2010 Mar 15;588(Pt 6):1011–22.

86. Gibala MJ, Little JP, van Essen M, Wilkin GP, Burgomaster KA, Safdar A, et al. Short-term sprint interval versus traditional endurance training: similar initial adaptations in human skeletal muscle and exercise performance. J Physiol. 2006 Sep 15;575(Pt 3):901–11.

87. Weston KS, Wisløff U, Coombes JS. High-intensity interval training in patients with lifestyle-induced cardiometabolic disease: a systematic review and meta-analysis. Br J Sports Med. 2014 Aug;48(16):1227–34.

88. Henriksson J, Reitman JS. Quantitative measures of enzyme activities in type I and type II muscle fibres of man after training. Acta Physiol Scand. 1976 Jul;97(3):392–7.

89. Saltin B, Nazar K, Costill DL, Stein E, Jansson E, Essén B, et al. The nature of the training response; peripheral and central adaptations of one-legged exercise. Acta Physiol Scand. 1976 Mar;96(3):289–305.

90. Burgomaster KA, Hughes SC, Heigenhauser GJF, Bradwell SN, Gibala MJ. Six sessions of sprint interval training increases muscle oxidative potential and cycle endurance capacity in humans. J Appl Physiol . 1985. 2005 Jun;98(6):1985–90.

91. Hood MS, Little JP, Tarnopolsky MA, Myslik F, Gibala MJ. Low-Volume Interval Training Improves Muscle Oxidative Capacity in Sedentary Adults: Med Sci Sports Exerc. 2011 Oct;43(10):1849–56.

92. Burgomaster KA, Howarth KR, Phillips SM, Rakobowchuk M, MacDonald MJ, McGee SL, et al. Similar metabolic adaptations during exercise after low volume sprint interval and traditional endurance training in humans. J Physiol. 2008 Jan 1;586(Pt 1):151–60.

93. Gibala M. Molecular responses to high-intensity interval exercise. Appl Physiol Nutr Metab Physiol Appliquée Nutr Métabolisme. 2009 Jun;34(3):428–32.

94. Burgomaster KA, Cermak NM, Phillips SM, Benton CR, Bonen A, Gibala MJ. Divergent response of metabolite transport proteins in human skeletal muscle after sprint interval training and detraining. Am J Physiol Regul Integr Comp Physiol. 2007 May;292(5):R1970-1976.

95. Babraj JA, Vollaard NB, Keast C, Guppy FM, Cottrell G, Timmons JA. Extremely short duration high intensity interval training substantially improves insulin action in young healthy males. BMC Endocr Disord. 2009 Jan 28;9(1):3.

96. Whyte LJ, Gill JMR, Cathcart AJ. Effect of 2 weeks of sprint interval training on health-related outcomes in sedentary overweight/obese men. Metabolism. 2010 Oct;59(10):1421–8.

97. Richards JC, Johnson TK, Kuzma JN, Lonac MC, Schweder MM, Voyles WF, et al. Short-term sprint interval training increases insulin sensitivity in healthy adults but does not affect the thermogenic response to beta-adrenergic stimulation. J Physiol. 2010 Aug 1;588(Pt 15):2961–72.

98. Guiraud T, Nigam A, Gremeaux V, Meyer P, Juneau M, Bosquet L. High-intensity interval training in cardiac rehabilitation. Sports Med . 2012 Jul 1;42(7):587–605.

99. Buchheit M, Laursen PB. High-Intensity Interval Training, Solutions to the Programming Puzzle. Sports Med. 2013 May 1;43(5):313–38.

100. Laursen PB, Jenkins DG. The scientific basis for high-intensity interval training: optimising training programmes and maximising performance in highly trained endurance athletes. Sports Med . 2002;32(1):53–73.

101. Midgley AW, Mc Naughton LR. Time at or near VO2max during continuous and intermittent running. A review with special reference to considerations for the optimisation of training protocols to elicit the longest time at or near VO2max. J Sports Med Phys Fitness. 2006 Mar;46(1):1–14.

102. Midgley AW, McNaughton LR, Wilkinson M. Is there an optimal training intensity for enhancing the maximal oxygen uptake of distance runners?: empirical research findings, current opinions, physiological rationale and practical recommendations. Sports Med . 2006;36(2):117–32.

103. Gibala MJ, Little JP, Macdonald MJ, Hawley JA. Physiological adaptations to low-volume, high-intensity interval training in health and disease. J Physiol. 2012 Mar 1;590(Pt 5):1077–84.

104. Jacobs RA, Flück D, Bonne TC, Bürgi S, Christensen PM, Toigo M, et al. Improvements in exercise performance with high-intensity interval training coincide with an increase in skeletal muscle mitochondrial content and function. J Appl Physiol. 2013 Sep 15;115(6):785–93.

105. Gosselin LE, Kozlowski KF, DeVinney-Boymel L, Hambridge C. Metabolic response of different high-intensity aerobic interval exercise protocols. J Strength Cond Res. 2012 Oct;26(10):2866–71.

106. Abbiss CR, Karagounis LG, Laursen PB, Peiffer JJ, Martin DT, Hawley JA, et al. Single-leg cycle training is superior to double-leg cycling in improving the oxidative potential and metabolic profile of trained skeletal muscle. J Appl Physiol. 2011 May 1;110(5):1248–55.

107. Pfeiffer JJ, Quintana R, Parker DL. The influence of graded exercise test selection on Pmax and a subsequent single interval bout. J Exerc Physio. 2005 Jan 1;8(5):10–7.

108. Ferrari Bravo D, Impellizzeri FM, Rampinini E, Castagna C, Bishop D, Wisloff U. Sprint vs. interval training in football. Int J Sports Med. 2008 Aug;29(8):668–74.

109. Helgerud J, Engen LC, Wisloff U, Hoff J. Aerobic endurance training improves soccer performance. Med Sci Sports Exerc. 2001 Nov;33(11):1925–31.

110. Hoff J, Wisløff U, Engen LC, Kemi OJ, Helgerud J. Soccer specific aerobic endurance training. Br J Sports Med. 2002 Jun 1;36(3):218–21.

111. Iaia FM, Rampinini E, Bangsbo J. High-intensity training in football. Int J Sports Physiol Perform. 2009 Sep;4(3):291–306.

112. Impellizzeri FM, Marcora SM, Castagna C, Reilly T, Sassi A, Iaia FM, et al. Physiological and performance effects of generic versus specific aerobic training in soccer players. Int J Sports Med. 2006 Jun;27(6):483–92.

113. McMillan K, Helgerud J, Macdonald R, Hoff J. Physiological adaptations to soccer specific endurance training in professional youth soccer players. Br J Sports Med. 2005 May;39(5):273–7.

114. Sporis G, Ruzic L, Leko G. Effects of a new experimental training program on V.O2max and running performance. J Sports Med Phys Fitness. 2008 Jun;48(2):158–65.

115. Duchateau J, Baudry S. Insights into the neural control of eccentric contractions. J Appl Physiol [Internet]. 2013 Feb 21 [cited 2014 May 14]; Available from: http://jap.physiology.org/content/early/2013/02/19/japplphysiol.00002.2013

116. Duchateau J, Enoka RM. Neural control of lengthening contractions. J Exp Biol. 2016 Jan;219(Pt 2):197–204.

117. Schoenfeld BJ, Ogborn D, Vigotsky AD, Franchi M, Krieger JW. Hypertrophic effects of concentric versus eccentric muscle actions: A systematic review and meta-analysis. J Strength Cond Res. 2017 May 5;

118. Lepley LK, Butterfield TA. Shifting the Current Clinical Perspective: Isolated Eccentric Exercise as an Effective Intervention to Promote the Recovery of Muscle After Injury. J Sport Rehabil. 2017 Mar 1;26(2):122–30.

119. Lepley LK, Lepley AS, Onate JA, Grooms DR. Eccentric Exercise to Enhance Neuromuscular Control. Sports Health. 2017 Jun 1;1941738117710913.

120. Lovering RM, Brooks SV. Eccentric exercise in aging and diseased skeletal muscle: good or bad? J Appl Physiol [Internet]. 2013 Mar 7 [cited 2014 May 14]; Available from: http://jap.physiology.org/content/early/2013/03/04/japplphysiol.00174.2013

121. Mitchell WK, Taivassalo T, Narici MV, Franchi MV. Eccentric Exercise and the Critically Ill Patient. Front Physiol [Internet]. 2017 [cited 2017 Sep 12];8. Available from: http://journal.frontiersin.org/article/10.3389/fphys.2017.00120/full

122. Hortobágyi T. The Positives of Negatives: Clinical Implications of Eccentric Resistance Exercise in Old Adults. J Gerontol A Biol Sci Med Sci. 2003 May 1;58(5):M417–8.

123. Buchheit M, Laursen PB. High-intensity interval training, solutions to the programming puzzle. Part II: anaerobic energy, neuromuscular load and practical applications. Sports Med . 2013 Oct;43(10):927–54.

124. Toigo M, Boutellier U. New fundamental resistance exercise determinants of molecular and cellular muscle adaptations. Eur J Appl Physiol. 2006 Jul 15;97(6):643–63.

125. Fatouros IG, Jamurtas AZ, Leontsini D, Taxildaris K, Aggelousis N, Kostopoulos N, et al. Evaluation of Plyometric Exercise Training, Weight Training, and Their Combination on Vertical Jumping Performance and Leg Strength. J Strength Cond Res. 2000 Nov;14(4):470.

126. Vogt M, Hoppeler HH. Eccentric exercise - mechanisms and effects when used as training regime or training adjunct. J Appl Physiol . 1985. 2014 Feb 6;

127. Farthing JP, Chilibeck PD. The effects of eccentric and concentric training at different velocities on muscle hypertrophy. Eur J Appl Physiol. 2003 Aug;89(6):578–86.

128. Paddon-Jones D, Abernethy PJ. Acute adaptation to low volume eccentric exercise. Med Sci Sports Exerc. 2001 Jul;33(7):1213–9.

129. Tinwala F, Cronin J, Haemmerle E, Ross A. Eccentric Strength Training: A Review of the Available Technology. Strength Cond J. 2017 Feb;39(1):32–47.

130. Bobbert MF, Mackay M, Schinkelshoek D, Huijing PA, Schenau GJ van I. Biomechanical analysis of drop and countermovement jumps. Eur J Appl Physiol. 1986 Feb 1;54(6):566–73.

131. Nedergaard NJ, Kersting U, Lake M. Using accelerometry to quantify deceleration during a high-intensity soccer turning manoeuvre. J Sports Sci. 2014 Dec 14;32(20):1897–905.

132. Kamandulis S, Skurvydas A, Snieckus A, Masiulis N, Aagaard P, Dargeviciute G, et al. Monitoring markers of muscle damage during a 3 week periodized drop-jump exercise programme. J Sports Sci. 2011 Feb 15;29(4):345–53.

133. Child RB, Saxton JM, Donnelly AE. Comparison of eccentric knee extensor muscle actions at two muscle lengths on indices of damage and anglespecific force production in humans. J Sports Sci. 1998 Jan 1;16(4):301–8.

134. Newham DJ, Jones DA, Ghosh G, Aurora P. Muscle fatigue and pain after eccentric contractions at long and short length. Clin Sci Lond Engl 1979. 1988 May;74(5):553–7.

135. Nosaka K, Newton M, Sacco P, Chapman D, Lavender A. Partial Protection against Muscle Damage by Eccentric Actions at Short Muscle Lengths: Med Sci Sports Exerc. 2005 May;37(5):746–53.

136. Guex K, Degache F, Morisod C, Sailly M, Millet GP. Hamstring Architectural and Functional Adaptations Following Long vs. Short Muscle Length Eccentric Training. Front Physiol. 2016;7:340.

137. Armstrong BW, Hh H, Workman JM. Downhill walking as a possible form of negative work. Am J Physiol -- Leg Content. 1966 Nov 1;211(5):1264–8.

138. Chen TC, Nosaka K, Lin M-J, Chen H-L, Wu C-J. Changes in running economy at different intensities following downhill running. J Sports Sci. 2009 Sep;27(11):1137–44.

139. Erfani A, Moezy A, Mazaherinezhad A, Mousavi SAJ. Does Downhill Walking on Treadmill Improve Physical Status and Quality of Life of A Patient With COPD? Asian J Sports Med. 2015 Dec;6(4):e25821.

140. Maeo S, Yamamoto M, Kanehisa H. Muscular adaptations to short-term low-frequency downhill walking training. Int J Sports Med. 2015 Feb;36(2):150–6.

141. Chen TC, Hsieh C-C, Tseng K-W, Ho C-C, Nosaka K. Effects of Descending Stair Walking on Health and Fitness of Elderly Obese Women. Med Sci Sports Exerc. 2017 Mar 13;

142. Purtsi J, Vihko V, Kankaanpää A, Havas E. The motor-learning process of older adults in eccentric bicycle ergometer training. J Aging Phys Act. 2012 Jul;20(3):345–62.

143. Guilhem G, Cornu C, Maffiuletti NA, Guével A. Neuromuscular adaptations to isoload versus isokinetic eccentric resistance training. Med Sci Sports Exerc. 2013 Feb;45(2):326–35.

144. Elmer SJ, Anderson DJ, Wakeham TR, Kilgas MA, Durocher JJ, Lindstedt SL, et al. Chronic eccentric arm cycling improves maximum upper-body strength and power. Eur J Appl Physiol. 2017 May 17;1–11.

145. Gerber JP, Marcus RL, Dibble LE, Greis PE, Burks RT, LaStayo PC. Effects of early progressive eccentric exercise on muscle structure after anterior cruciate ligament reconstruction. J Bone Joint Surg Am. 2007 Mar;89(3):559–70.

146. Schoenfeld BJ. Does exercise-induced muscle damage play a role in skeletal muscle hypertrophy? J Strength Cond Res. 2012 May;26(5):1441–53.

147. Hyldahl RD, Chen TC, Nosaka K. Mechanisms and Mediators of the Skeletal Muscle Repeated Bout Effect. Exerc Sport Sci Rev. 2017 Jan;45(1):24-33.

148. McHugh MP. Recent advances in the understanding of the repeated bout effect: the protective effect against muscle damage from a single bout of eccentric exercise. Scand J Med Sci Sports. 2003 Apr;13(2):88–97.

149. Nosaka K, Clarkson PM. Muscle damage following repeated bouts of high force eccentric exercise. Med Sci Sports Exerc. 1995 Sep;27(9):1263–9.

150. Camillo CA, Burtin C, Hornikx M, Demeyer H, De Bent K, van Remoortel H, et al. Physiological responses during downhill walking: A new exercise modality for subjects with chronic obstructive pulmonary disease? Chron Respir Dis. 2015 May;12(2):155–64.

151. Schoenfeld BJ, Grgic J, Ogborn D, Krieger JW. Strength and Hypertrophy Adaptations Between Low- vs. High-Load Resistance Training: A Systematic Review and Meta-analysis. J Strength Cond Res. 2017 Dec;31(12):3508.

152. Douglas J, Pearson S, Ross A, McGuigan M. Chronic Adaptations to Eccentric Training: A Systematic Review. Sports Med. 2017 May;47(5):917-941.

153. Hyldahl RD, Hubal MJ. Lengthening our perspective: Morphological, cellular, and molecular responses to eccentric exercise. Muscle Nerve. 2014 Feb 1;49(2):155–70.

154. Hyldahl RD, Nelson B, Xin L, Welling T, Groscost L, Hubal MJ, et al. Extracellular matrix remodeling and its contribution to protective adaptation following lengthening contractions in human muscle. FASEB J Off Publ Fed Am Soc Exp Biol. 2015 Jul;29(7):2894–904.

155. Hessel AL, Lindstedt SL, Nishikawa KC. Physiological Mechanisms of Eccentric Contraction and Its Applications: A Role for the Giant Titin Protein. Front Physiol [Internet]. 2017 [cited 2017 Feb 9];8. Available from: http://journal.frontiersin.org/article/10.3389/fphys.2017.00070/abstract

156. Herzog W. Mechanisms of enhanced force production in lengthening (eccentric) muscle contractions. J Appl Physiol [Internet]. 2013 Feb 21 [cited 2014 May 14]; Available from: http://jap.physiology.org/content/early/2013/02/19/japplphysiol.00069.2013

157. Herzog W. The role of titin in eccentric muscle contraction. J Exp Biol. 2014 Aug 15;217(Pt 16):2825–33.

158. Brzycki M. Strength Testing—Predicting a One-Rep Max from Reps-to-Fatigue. J Phys Educ Recreat Dance. 1993 Jan 1;64(1):88–90.

159. Hortobágyi T, DeVita P. Favorable neuromuscular and cardiovascular responses to 7 days of exercise with an eccentric overload in elderly women. J Gerontol A Biol Sci Med Sci. 2000 Aug;55(8):B401-410.

160. Hortobágyi T, Barrier J, Beard D, Braspennincx J, Koens P, Devita P, et al. Greater initial adaptations to submaximal muscle lengthening than maximal shortening. J Appl Physiol . 1985. 1996 Oct;81(4):1677–82.

161. Kidgell DJ, Frazer AK, Daly RM, Rantalainen T, Ruotsalainen I, Ahtiainen J, et al. Increased cross-education of muscle strength and reduced corticospinal inhibition following eccentric strength training. Neuroscience. 2015 Aug 6;300:566–75.

162. Laycoe RR, Marteniuk RG. Learning and tension as factors in static strength gains produced by static and eccentric training. Res Q. 1971 Oct;42(3):299–306.

163. Blazevich AJ, Cannavan D, Coleman DR, Horne S. Influence of concentric and eccentric resistance training on architectural adaptation in human quadriceps muscles. J Appl Physiol . 1985. 2007 Nov;103(5):1565–75.

164. Hawkins SA, Schroeder ET, Wiswell RA, Jaque SV, Marcell TJ, Costa K. Eccentric muscle action increases site-specific osteogenic response. Med Sci Sports Exerc. 1999 Sep;31(9):1287–92.

165. Housh TJ, Housh DJ, Weir JP, Weir LL. Effects of eccentric-only resistance training and detraining. Int J Sports Med. 1996 Feb;17(2):145–8.

166. Colliander EB, Tesch PA. Effects of eccentric and concentric muscle actions in resistance training. Acta Physiol Scand. 1990 Sep 1;140(1):31–9.

167. Amiridis IG, Cometti G, Morlon B, Van Hoecke J. Concentric and/or eccentric training-induced alterations in shoulder flexor and extensor strength. J Orthop Sports Phys Ther. 1997 Jan;25(1):26–33.

168. Miller LE, Pierson LM, Nickols-Richardson SM, Wootten DF, Selmon SE, Ramp WK, et al. Knee extensor and flexor torque development with concentric and eccentric isokinetic training. Res Q Exerc Sport. 2006 Mar;77(1):58–63.

169. Coratella G, Milanese C, Schena F. Unilateral eccentric resistance training: A direct comparison between isokinetic and dynamic constant external resistance modalities. Eur J Sport Sci. 2015;15(8):720–6.

170. Colliander EB, Tesch PA. Effects of detraining following short term resistance training on eccentric and concentric muscle strength. Acta Physiol Scand. 1992 Jan;144(1):23–9.

171. Duclay J, Martin A, Robbe A, Pousson M. Spinal reflex plasticity during maximal dynamic contractions after eccentric training. Med Sci Sports Exerc. 2008 Apr;40(4):722–34.

172. Kaminski TW, Wabbersen CV, Murphy RM. Concentric versus enhanced eccentric hamstring strength training: clinical implications. J Athl Train. 1998 Jul;33(3):216–21.

173. Wirth K, Keiner M, Szilvas E, Hartmann H, Sander A. Effects of Eccentric Strength Training on Different Maximal Strength and Speed-Strength Parameters of the Lower Extremity. J Strength Cond Res. 2015 Jul;29(7):1837–45.

174. Hortobágyi T, Devita P, Money J, Barrier J. Effects of standard and eccentric overload strength training in young women. Med Sci Sports Exerc. 2001 Jul;33(7):1206–12.

175. Hortobágyi T, Dempsey L, Fraser D, Zheng D, Hamilton G, Lambert J, et al. Changes in muscle strength, muscle fibre size and myofibrillar gene expression after immobilization and retraining in humans. J Physiol. 2000 Apr 1;524 Pt 1:293–304.

176. Cadore EL, González-Izal M, Pallarés JG, Rodriguez-Falces J, Häkkinen K, Kraemer WJ, et al. Muscle conduction velocity, strength, neural activity, and morphological

changes after eccentric and concentric training. Scand J Med Sci Sports. 2014 Oct;24(5):e343-352.

177. Weir JP, Housh DJ, Housh TJ, Weir LL. The effect of unilateral eccentric weight training and detraining on joint angle specificity, cross-training, and the bilateral deficit. J Orthop Sports Phys Ther. 1995 Nov;22(5):207–15.

178. Oliveira BRR, Slama FA, Deslandes AC, Furtado ES, Santos TM. Continuous and High-Intensity Interval Training: Which Promotes Higher Pleasure? PLOS ONE. 2013 Nov 26;8(11):e79965.

179. Keles SB, Sekir U, Gur H, Akova B. Eccentric/concentric training of ankle evertor and dorsiflexors in recreational athletes: muscle latency and strength. Scand J Med Sci Sports. 2014 Feb;24(1):e29-38.

180. Connelly DM, Carnahan H, Vandervoort AA. Motor skill learning of concentric and eccentric isokinetic movements in older adults. Exp Aging Res. 2000 Sep;26(3):209–28.

181. Askling C, Karlsson J, Thorstensson A. Hamstring injury occurrence in elite soccer players after preseason strength training with eccentric overload. Scand J Med Sci Sports. 2003 Aug;13(4):244–50.

182. Colson S, Pousson M, Martin A, Van Hoecke J. Isokinetic elbow flexion and coactivation following eccentric training. J Electromyogr Kinesiol Off J Int Soc Electrophysiol Kinesiol. 1999 Feb;9(1):13–20.

183. Timmins RG, Ruddy JD, Presland J, Maniar N, Shield AJ, Williams MD, et al. Architectural Changes of the Biceps Femoris Long Head after Concentric or Eccentric Training. Med Sci Sports Exerc. 2016 Mar;48(3):499–508.

184. Pensini M, Martin A, Maffiuletti NA. Central versus peripheral adaptations following eccentric resistance training. Int J Sports Med. 2002 Nov;23(8):567–74.

185. Nickols-Richardson SM, Miller LE, Wootten DF, Ramp WK, Herbert WG. Concentric and eccentric isokinetic resistance training similarly increases muscular strength, fat-free soft tissue mass, and specific bone mineral measurements in young women. Osteoporos Int J Establ Result Coop Eur Found Osteoporos Natl Osteoporos Found USA. 2007 Jun;18(6):789–96.

186. Lundberg TR, Fernandez-Gonzalo R, Tesch PA. Exercise-induced AMPK activation does not interfere with muscle hypertrophy in response to resistance training in men. J Appl Physiol . 1985. 2014 Mar 15;116(6):611–20.

187. Coratella G, Milanese C, Schena F. Cross-education effect after unilateral eccentric-only isokinetic vs dynamic constant external resistance training. Sport Sci Health. 2015 Dec 1;11(3):329–35.

188. Tesch PA, Ekberg A, Lindquist DM, Trieschmann JT. Muscle hypertrophy following 5-week resistance training using a non-gravity-dependent exercise system. Acta Physiol Scand. 2004 Jan;180(1):89–98.

189. Kim SY, Ko JB, Farthing JP, Butcher SJ. Investigation of supraspinatus muscle architecture following concentric and eccentric training. J Sci Med Sport. 2015 Jul;18(4):378–82.

190. Walker S, Blazevich AJ, Haff GG, Tufano JJ, Newton RU, Häkkinen K. Greater Strength Gains after Training with Accentuated Eccentric than Traditional Isoinertial Loads in Already Strength-Trained Men. Front Physiol [Internet]. 2016 Apr 27 [cited 2017 Apr 25];7. Available from: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC4847223/

191. Vikne H, Refsnes PE, Ekmark M, Medbø JI, Gundersen V, Gundersen K. Muscular performance after concentric and eccentric exercise in trained men. Med Sci Sports Exerc. 2006 Oct;38(10):1770–81.

192. Porter MM, Vandervoort AA. Standing strength training of the ankle plantar and dorsiflexors in older women, using concentric and eccentric contractions. Eur J Appl Physiol. 1997;76(1):62–8.

193. Bruseghini P, Calabria E, Tam E, Milanese C, Oliboni E, Pezzato A, et al. Effects of eight weeks of aerobic interval training and of isoinertial resistance training on risk factors of cardiometabolic diseases and exercise capacity in healthy elderly subjects. Oncotarget. 2015 Jul 10;6(19):16998–7015.

194. Paddon-Jones D, Leveritt M, Lonergan A, Abernethy P. Adaptation to chronic eccentric exercise in humans: the influence of contraction velocity. Eur J Appl Physiol. 2001 Sep 1;85(5):466–71.

195. Krentz JR, Farthing JP. Neural and morphological changes in response to a 20-day intense eccentric training protocol. Eur J Appl Physiol. 2010 Sep;110(2):333–40.

196. Hortobágyi T, Hill JP, Houmard JA, Fraser DD, Lambert NJ, Israel RG. Adaptive responses to muscle lengthening and shortening in humans. J Appl Physiol . 1985. 1996 Mar;80(3):765–72.

197. Okamoto T, Masuhara M, Ikuta K. Effects of eccentric and concentric resistance training on arterial stiffness. J Hum Hypertens. 2006 May;20(5):348–54.

198. Dudley GA, Tesch PA, Miller BJ, Buchanan P. Importance of eccentric actions in performance adaptations to resistance training. Aviat Space Environ Med. 1991 Jun;62(6):543–50.

199. Schroeder ET, Hawkins SA, Jaque SV. Musculoskeletal adaptations to 16 weeks of eccentric progressive resistance training in young women. J Strength Cond Res. 2004 May;18(2):227–35.

200. Bem-Sira D, Ayalon A, Tavi M. The Effect of Different Types of Strength Training on Concentric Strength in Women. J Strength Cond Res. 1995 Aug 1;9.

201. Fernandez-Gonzalo R, Lundberg TR, Alvarez-Alvarez L, de Paz JA. Muscle damage responses and adaptations to eccentric-overload resistance exercise in men and women. Eur J Appl Physiol. 2014 May;114(5):1075–84.

202. Friedmann-Bette B, Bauer T, Kinscherf R, Vorwald S, Klute K, Bischoff D, et al. Effects of strength training with eccentric overload on muscle adaptation in male athletes. Eur J Appl Physiol. 2010 Mar;108(4):821–36.

203. Brandenburg JP, Docherty D. The effects of accentuated eccentric loading on strength, muscle hypertrophy, and neural adaptations in trained individuals. J Strength Cond Res. 2002 Feb;16(1):25–32.

204. Smith RC, Rutherford OM. The role of metabolites in strength training. I. A comparison of eccentric and concentric contractions. Eur J Appl Physiol. 1995;71(4):332–6.

205. English KL, Loehr JA, Lee SMC, Smith SM. Early-phase musculoskeletal adaptations to different levels of eccentric resistance after 8 weeks of lower body training. Eur J Appl Physiol. 2014 Nov;114(11):2263–80.

206. Sabido R, Hernández-Davó JL, Botella J, Navarro A, Tous-Fajardo J. Effects of adding a weekly eccentric-overload training session on strength and athletic performance in team-handball players. Eur J Sport Sci. 2017 Jun;17(5):530–8.

207. Yarrow JF, Borsa PA, Borst SE, Sitren HS, Stevens BR, White LJ. Early-phase neuroendocrine responses and strength adaptations following eccentric-enhanced resistance training. J Strength Cond Res. 2008 Jul;22(4):1205–14.

208. Martin A, Martin L, Morlon B. Changes induced by eccentric training on force-velocity relationships of the elbow flexor muscles. Eur J Appl Physiol. 1995;72(1–2):183–5.

209. Bishop KN, Duurant E, Allsen PE, Merrill G. The effect of eccentric strength training at various speeds on concentric strength of the quadriceps and hamstring muscles. J Orthop Sports Phys Ther. 1991;13(5):226–30.

210. Seynnes OR, de Boer M, Narici MV. Early skeletal muscle hypertrophy and architectural changes in response to high-intensity resistance training. J Appl Physiol . 1985. 2007 Jan;102(1):368–73.

211. Norrbrand L, Fluckey JD, Pozzo M, Tesch PA. Resistance training using eccentric overload induces early adaptations in skeletal muscle size. Eur J Appl Physiol. 2008 Feb;102(3):271–81.

212. Onambélé GL, Maganaris CN, Mian OS, Tam E, Rejc E, McEwan IM, et al. Neuromuscular and balance responses to flywheel inertial versus weight training in older persons. J Biomech. 2008 Nov 14;41(15):3133–8.

213. Lundberg TR, Fernandez-Gonzalo R, Gustafsson T, Tesch PA. Aerobic exercise does not compromise muscle hypertrophy response to short-term resistance training. J Appl Physiol . 1985. 2013 Jan 1;114(1):81–9.

214. Jones DA, Rutherford OM. Human muscle strength training: the effects of three different regimens and the nature of the resultant changes. J Physiol. 1987 Oct;391:1–11.

215. Blazevich AJ, Horne S, Cannavan D, Coleman DR, Aagaard P. Effect of contraction mode of slow-speed resistance training on the maximum rate of force development in the human quadriceps. Muscle Nerve. 2008 Sep;38(3):1133–46.

216. Lepley LK, Palmieri-Smith RM. Cross-education strength and activation after eccentric exercise. J Athl Train. 2014 Oct;49(5):582–9.

217. Papadopoulos C, Theodosiou K, Bogdanis GC, Gkantiraga E, Gissis I, Sambanis M, et al. Multiarticular isokinetic high-load eccentric training induces large increases in eccentric and concentric strength and jumping performance. J Strength Cond Res. 2014 Sep;28(9):2680–8.

218. Reeves ND, Maganaris CN, Longo S, Narici MV. Differential adaptations to eccentric versus conventional resistance training in older humans. Exp Physiol. 2009 Jul;94(7):825–33.

219. Higbie EJ, Cureton KJ, Warren GL, Prior BM. Effects of concentric and eccentric training on muscle strength, cross-sectional area, and neural activation. J Appl Physiol . 1996 Nov;81(5):2173–81.

220. Duncan PW, Chandler JM, Cavanaugh DK, Johnson KR, Buehler AG. Mode and speed specificity of eccentric and concentric exercise training. J Orthop Sports Phys Ther. 1989;11(2):70–5.

221. Seger JY, Thorstensson A. Effects of eccentric versus concentric training on thigh muscle strength and EMG. Int J Sports Med. 2005 Feb;26(1):45–52.

222. Baroni BM, Rodrigues R, Franke RA, Geremia JM, Rassier DE, Vaz MA. Time course of neuromuscular adaptations to knee extensor eccentric training. Int J Sports Med. 2013 Oct;34(10):904–11.

223. Spurway NC, Watson H, McMillan K, Connolly G. The effect of strength training on the apparent inhibition of eccentric force production in voluntarily activated human quadriceps. Eur J Appl Physiol. 2000 Aug;82(5–6):374–80.

224. Symons TB, Vandervoort AA, Rice CL, Overend TJ, Marsh GD. Effects of maximal isometric and isokinetic resistance training on strength and functional mobility in older adults. J Gerontol A Biol Sci Med Sci. 2005 Jun;60(6):777–81.

225. Hilliard-Robertson PC, Schneider SM, Bishop SL, Guilliams ME. Strength gains following different combined concentric and eccentric exercise regimens. Aviat Space Environ Med. 2003 Apr;74(4):342–7.

226. Tomberlin JP, Basford JR, Schwen EE, Orte PA, Scott SC, Laughman RK, et al. Comparative study of isokinetic eccentric and concentric quadriceps training. J Orthop Sports Phys Ther. 1991;14(1):31–6.

227. Tallent J, Goodall S, Gibbon KC, Hortobágyi T, Howatson G. Enhanced Corticospinal Excitability and Volitional Drive in Response to Shortening and Lengthening Strength Training and Changes Following Detraining. Front Physiol. 2017;8:57.

228. Barrué-Belou S, Amarantini D, Marque P, Duclay J. Neural adaptations to submaximal isokinetic eccentric strength training. Eur J Appl Physiol. 2016 May;116(5):1021–30.

229. Seger JY, Arvidsson B, Thorstensson A. Specific effects of eccentric and concentric training on muscle strength and morphology in humans. Eur J Appl Physiol. 1998 Dec;79(1):49–57.

230. Takahashi ACM, Melo RC, Quitério RJ, Silva E, Catai AM. The effect of eccentric strength training on heart rate and on its variability during isometric exercise in healthy older men. Eur J Appl Physiol. 2009 Jan;105(2):315–23.

231. Komi PV, Buskirk ER. Effect of eccentric and concentric muscle conditioning on tension and electrical activity of human muscle. Ergonomics. 1972 Jul;15(4):417–34.

232. Komsis S, Komsis G, Gissis I, Papadopoulos C, Patikas D, Mademli L, et al. The Effects of Eccentric Training on Electromyographic Activity and Performance in Soccer Players. Am J Sports Sci. 2014 Jan 1;2(2):23.

233. Santos HH, Avila MA, Hanashiro DN, Camargo PR, Salvini TF. The effects of knee extensor eccentric training on functional tests in healthy subjects. Rev Bras Fisioter Sao Carlos Sao Paulo Braz. 2010 Aug;14(4):276–83.

234. Mont MA, Cohen DB, Campbell KR, Gravare K, Mathur SK. Isokinetic concentric versus eccentric training of shoulder rotators with functional evaluation of performance enhancement in elite tennis players. Am J Sports Med. 1994 Aug;22(4):513–7.

235. Shepstone TN, Tang JE, Dallaire S, Schuenke MD, Staron RS, Phillips SM. Short-term high- vs. low-velocity isokinetic lengthening training results in greater hypertrophy of the elbow flexors in young men. J Appl Physiol. 2005 May 1;98(5):1768–76.

236. Carvalho A, Caserotti P, Carvalho C, Abade E, Sampaio J. Effect of a short time concentric versus eccentric training program on electromyography activity and peak torque of quadriceps. J Hum Kinet. 2014 Jun 28;41:5–13.

237. Moore DR, Young M, Phillips SM. Similar increases in muscle size and strength in young men after training with maximal shortening or lengthening contractions when matched for total work. Eur J Appl Physiol. 2012 Apr;112(4):1587–92.

238. Barstow IK, Bishop MD, Kaminski TW. Is enhanced-eccentric resistance training superior to traditional training for increasing elbow flexor strength? J Sports Sci Med. 2003 Jun;2(2):62–9.

239. Malliaras P, Kamal B, Nowell A, Farley T, Dhamu H, Simpson V, et al. Patellar tendon adaptation in relation to load-intensity and contraction type. J Biomech. 2013 Jul 26;46(11):1893–9.

240. Franchi MV, Atherton PJ, Reeves ND, Flück M, Williams J, Mitchell WK, et al. Architectural, functional and molecular responses to concentric and eccentric loading in human skeletal muscle. Acta Physiol Oxf Engl. 2014 Mar;210(3):642–54.

241. Potier TG, Alexander CM, Seynnes OR. Effects of eccentric strength training on biceps femoris muscle architecture and knee joint range of movement. Eur J Appl Physiol. 2009 Apr;105(6):939–44.

242. Roth SM, Martel GF, Ivey FM, Lemmer JT, Metter EJ, Hurley BF, et al. High-volume, heavy-resistance strength training and muscle damage in young and older women. J Appl Physiol . 1985. 2000 Mar;88(3):1112–8.

243. Raj IS, Bird SR, Westfold BA, Shield AJ. Effects of eccentrically biased versus conventional weight training in older adults. Med Sci Sports Exerc. 2012 Jun;44(6):1167–76.

244. Roth SM, Martel GF, Ivey FM, Lemmer JT, Tracy BL, Hurlbut DE, et al. Ultrastructural muscle damage in young vs. older men after high-volume, heavy-resistance strength training. J Appl Physiol . 1985. 1999 Jun;86(6):1833–40.

245. Naczk M, Naczk A, Brzenczek-Owczarzak W, Arlet J, Adach Z. Impact of Inertial Training on Strength and Power Performance in Young Active Men. J Strength Cond Res. 2016 Aug;30(8):2107–2113.

246. Naczk M, Naczk A, Brzenczek-Owczarzak W, Arlet J, Adach Z. Efficacy of inertial training in elbow joint muscles: influence of different movement velocities. J Sports Med Phys Fitness. 2016 Mar;56(3):223–31.

247. Liu C, Chen C-S, Ho W-H, Füle RJ, Chung P-H, Shiang T-Y. The effects of passive leg press training on jumping performance, speed, and muscle power. J Strength Cond Res. 2013 Jun;27(6):1479–86.

248. Cronin J, McNair PJ, Marshall RN. The effects of bungy weight training on muscle function and functional performance. J Sports Sci. 2003 Jan;21(1):59–71.

249. Melo RC, Quitério RJ, Takahashi ACM, Silva E, Martins LEB, Catai AM. High eccentric strength training reduces heart rate variability in healthy older men. Br J Sports Med. 2008 Jan;42(1):59–63.

250. Alves T, Guarnier FA, Campoy FAS, Gois MO, Albuquerque MC, Seraphim PM, et al. Strength gain through eccentric isotonic training without changes in clinical signs or blood markers. BMC Musculoskelet Disord. 2013 Nov 21;14:328.

251. Raue U, Terpstra B, Williamson DL, Gallagher PM, Trappe SW. Effects of short-term concentric vs. eccentric resistance training on single muscle fiber MHC distribution in humans. Int J Sports Med. 2005 Jun;26(5):339–43.

252. Friedmann B, Kinscherf R, Vorwald S, Müller H, Kucera K, Borisch S, et al. Muscular adaptations to computer-guided strength training with eccentric overload. Acta Physiol Scand. 2004 Sep;182(1):77–88.

253. Coratella G, Schena F. Eccentric resistance training increases and retains maximal strength, muscle endurance, and hypertrophy in trained men. Appl Physiol Nutr Metab Physiol Appl Nutr Metab. 2016 Nov;41(11):1184–9.

254. Sheppard J, Hobson S, Barker M, Taylor K, Chapman D, McGuigan M, et al. The Effect of Training with Accentuated Eccentric Load Counter-Movement Jumps on Strength and Power Characteristics of High-Performance Volleyball Players. Int J Sports Sci Coach. 2008 Sep 1;3(3):355–63.

255. Brughelli M, Van Leemputte M. Reliability of power output during eccentric sprint cycling. J Strength Cond Res Natl Strength Cond Assoc. 2013 Jan;27(1):76–82.

256. Kay AD, Richmond D, Talbot C, Mina M, Baross AW, Blazevich AJ. Stretching of Active Muscle Elicits Chronic Changes in Multiple Strain Risk Factors. Med Sci Sports Exerc. 2016 Jul;48(7):1388–96.

257. Vangsgaard S, Taylor JL, Hansen EA, Madeleine P. Changes in H reflex and neuromechanical properties of the trapezius muscle after 5 weeks of eccentric training: a randomized controlled trial. J Appl Physiol. 2014 Jun 15;116(12):1623–31.

258. Margaritelis NV, Theodorou AA, Baltzopoulos V, Maganaris CN, Paschalis V, Kyparos A, et al. Muscle damage and inflammation after eccentric exercise: can the repeated bout effect be removed? Physiol Rep. 2015 Dec;3(12).

259. Ruas CV, Brown LE, Lima CD, Costa PB, Pinto RS. Effect of three different muscle action training protocols on knee strength ratios and performance. J Strength Cond Res. 2017 Jul 12;

260. Franchi MV, Wilkinson DJ, Quinlan JI, Mitchell WK, Lund JN, Williams JP, et al. Early structural remodeling and deuterium oxide-derived protein metabolic responses to eccentric and concentric loading in human skeletal muscle. Physiol Rep. 2015 Nov;3(11).

261. Sorichter S, Mair J, Koller A, Secnik P, Parrak V, Haid C, et al. Muscular adaptation and strength during the early phase of eccentric training: influence of the training frequency. Med Sci Sports Exerc. 1997 Dec;29(12):1646–52.

262. Mayhew TP, Rothstein JM, Finucane SD, Lamb RL. Muscular adaptation to concentric and eccentric exercise at equal power levels. Med Sci Sports Exerc. 1995 Jun;27(6):868–73.

263. Chen TC, Hsieh SS. Effects of a 7-day eccentric training period on muscle damage and inflammation. Med Sci Sports Exerc. 2001 Oct;33(10):1732–8.

264. Jensen J, Hölmich P, Bandholm T, Zebis MK, Andersen LL, Thorborg K. Eccentric strengthening effect of hip-adductor training with elastic bands in soccer players: a randomised controlled trial. Br J Sports Med. 2014 Feb;48(4):332–8.

265. Lacerte M, deLateur BJ, Alquist AD, Questad KA. Concentric versus combined concentric-eccentric isokinetic training programs: effect on peak torque of human quadriceps femoris muscle. Arch Phys Med Rehabil. 1992 Nov;73(11):1059–62.

266. Albert MS, Hillegass E, Spiegel P. Muscle torque changes caused by inertial exercise training. J Orthop Sports Phys Ther. 1994 Nov;20(5):254–61.

267. Iga J, Fruer CS, Deighan M, Croix MDS, James DVB. 'Nordic' hamstrings exercise - engagement characteristics and training responses. Int J Sports Med. 2012 Dec;33(12):1000–4.

268. Delahunt E, McGroarty M, De Vito G, Ditroilo M. Nordic hamstring exercise training alters knee joint kinematics and hamstring activation patterns in young men. Eur J Appl Physiol. 2016 Apr;116(4):663–72.

269. Valour D, Rouji M, Pousson M. Effects of eccentric training on torque-angular velocity-power characteristics of elbow flexor muscles in older women. Exp Gerontol. 2004 Mar;39(3):359–68.

270. Breno de A R Alvares J, Marques VB, Vaz MA, Baroni BM. Four weeks of Nordic hamstring exercise reduce muscle injury risk factors in young adults. J Strength Cond Res. 2017 Apr 26;

271. Seymore KD, Domire ZJ, DeVita P, Rider PM, Kulas AS. The effect of Nordic hamstring strength training on muscle architecture, stiffness, and strength. Eur J Appl Physiol. 2017 May;117(5):943–53.

272. Mjølsnes R, Arnason A, Østhagen T, Raastad T, Bahr R. A 10-week randomized trial comparing eccentric vs. concentric hamstring strength training in well-trained soccer players. Scand J Med Sci Sports. 2004 Oct;14(5):311–7.

273. Deleu S. Effect of a concentric, isometric and eccentric exercise program on the external rotator strength of the shoulder, measured with a hand held dynamometer. 2014.

274. Uhl TL, Rice T, Papotto B, Butterfield TA. Effectiveness of a Home-Based Eccentric-Exercise Program on the Torque-Angle Relationship of the Shoulder External Rotators: A Pilot Study. J Sport Rehabil. 2017 Mar 1;26(2):141–50.

275. Brzenczek-Owczarzak W, Naczk M, Arlet J, Forjasz J, Jedrzejczak T, Adach Z. Estimation of the Efficacy of Inertial Training in Older Women. J Aging Phys Act. 2013 Oct 1;21(4):433–43.

276. Naczk M, Brzenczek-Owczarzak W, Arlet J, Naczk A, Adach Z. Training Effectiveness of the Inertial Training and Measurement System. J Hum Kinet. 2014;44(1):19–28.

277. Dias CP, Toscan R, de Camargo M, Pereira EP, Griebler N, Baroni BM, et al. Effects of eccentric-focused and conventional resistance training on strength and functional capacity of older adults. Age Dordr Neth. 2015 Oct;37(5):99.

278. Vossen FJ, Kramer EJ, Burke GD, Vossen PD. Comparison of Dynamic Push-Up Training and Plyometric Push-Up Training on Upper-Body Power and Strength. J Strength Cond Res. 2000 Aug 1;14.

279. Dolezal SM, Frese DL, Llewellyn TL. The Effects of Eccentric, Velocity-Based Training on Strength and Power in Collegiate Athletes. Int J Exerc Sci. 2016;9(5):657–66.

280. Fernandez-Gonzalo R, Paz JAD, Rodriguez-Miguelez P, Cuevas MJ, González-Gallego J. Effects of eccentric exercise on toll-like receptor 4 signaling pathway in peripheral blood mononuclear cells. J Appl Physiol. 2012 Jun 15;112(12):2011–8.

281. Nosaka K, Newton M. Concentric or eccentric training effect on eccentric exercise-induced muscle damage. Med Sci Sports Exerc. 2002 Jan;34(1):63–9.

282. Hori N, Newton RU, Kawamori N, McGuigan MR, Andrews WA, Chapman DW, et al. Comparison of weighted jump squat training with and without eccentric braking. J Strength Cond Res. 2008 Jan;22(1):54–65.

283. Pavone E, Moffat M. Isometric torque of the quadriceps femoris after concentric, eccentric and isometric training. Arch Phys Med Rehabil. 1985 Mar;66(3):168–70.

284. Naclerio F, Larumbe-Zabala E, Monajati A, Goss-Sampson M. Effects of two different injury prevention resistance exercise protocols on the hamstring torque-angle relationship: a randomized controlled trial. Res Sports Med Print. 2015;23(4):379–93.

285. Orishimo KF, McHugh MP. Effect of an eccentrically biased hamstring strengthening home program on knee flexor strength and the length-tension relationship. J Strength Cond Res. 2015 Mar;29(3):772–8.

286. Fernandez-Gonzalo R, Bresciani G, de Souza-Teixeira F, Hernandez-Murua JA, Jimenez-Jimenez R, Gonzalez-Gallego J, et al. Effects of a 4-week eccentric training program on the repeated bout effect in young active women. J Sports Sci Med. 2011;10(4):692–9.

287. Gault ML, Clements RE, Willems MET. Functional mobility of older adults after concentric and eccentric endurance exercise. Eur J Appl Physiol. 2012 Nov;112(11):3699–707.

288. Flann KL, LaStayo PC, McClain DA, Hazel M, Lindstedt SL. Muscle damage and muscle remodeling: no pain, no gain? J Exp Biol. 2011 Feb 15;214(4):674–9.

289. Rodio A, Fattorini L. Downhill walking to improve lower limb strength in healthy young adults. Eur J Sport Sci. 2014;14(8):806–12.

290. Tanner RE, Brunker LB, Agergaard J, Barrows KM, Briggs RA, Kwon OS, et al. Age-related differences in lean mass, protein synthesis and skeletal muscle markers of proteolysis after bed rest and exercise rehabilitation. J Physiol. 2015 Sep 15;593(18):4259–73.

291. Mueller M, Breil FA, Vogt M, Steiner R, Lippuner K, Popp A, et al. Different response to eccentric and concentric training in older men and women. Eur J Appl Physiol. 2009 Sep;107(2):145–53.

292. Duclay J, Martin A, Duclay A, Cometti G, Pousson M. Behavior of fascicles and the myotendinous junction of human medial gastrocnemius following eccentric strength training. Muscle Nerve. 2009 Jun;39(6):819–27.

293. Rahbek SK, Farup J, Møller AB, Vendelbo MH, Holm L, Jessen N, et al. Effects of divergent resistance exercise contraction mode and dietary supplementation type on anabolic signalling, muscle protein synthesis and muscle hypertrophy. Amino Acids. 2014 Oct;46(10):2377–92.

294. Farup J, Rahbek SK, Riis S, Vendelbo MH, Paoli F de, Vissing K. Influence of exercise contraction mode and protein supplementation on human skeletal muscle satellite cell content and muscle fiber growth. J Appl Physiol . 1985. 2014 Oct 15;117(8):898–909.

295. Alonso-Fernandez D, Docampo-Blanco P, Martinez-Fernandez J. Changes in muscle architecture of Biceps Femoris induced by eccentric strength training with Nordic Hamstring Exercise. Scand J Med Sci Sports. 2017 Mar 1;n/a-n/a.

296. Reidy PT, Borack MS, Markofski MM, Dickinson JM, Fry CS, Deer RR, et al. Post-absorptive muscle protein turnover affects resistance training hypertrophy. Eur J Appl Physiol. 2017 Mar 9;

297. Reidy PT, Fry CS, Dickinson JM, Drummond MJ, Rasmussen BB. Postexercise essential amino acid supplementation amplifies skeletal muscle satellite cell proliferation in older men 24 hours postexercise. Physiol Rep. 2017 Jun 1;5(11):e13269.

298. LaStayo P, Marcus R, Dibble L, Wong B, Pepper G. Eccentric versus traditional resistance exercise for older adult fallers in the community: a randomized trial within a multi-component fall reduction program. BMC Geriatr. 2017 Jul 17;17(1):149.

299. Mueller M, Breil FA, Lurman G, Klossner S, Flück M, Billeter R, et al. Different molecular and structural adaptations with eccentric and conventional strength training in elderly men and women. Gerontology. 2011;57(6):528–38.

300. Tous-Fajardo J, Gonzalo-Skok O, Arjol-Serrano JL, Tesch P. Enhancing Change-of-Direction Speed in Soccer Players by Functional Inertial Eccentric Overload and Vibration Training. Int J Sports Physiol Perform. 2016 Jan;11(1):66–73.

301. de Hoyo M, Pozzo M, Sañudo B, Carrasco L, Gonzalo-Skok O, Domínguez-Cobo S, et al. Effects of a 10-week in-season eccentric-overload training program on muscle-injury prevention and performance in junior elite soccer players. Int J Sports Physiol Perform. 2015 Jan;10(1):46–52.

302. Gonzalo-Skok O, Tous-Fajardo J, Valero-Campo C, Berzosa C, Bataller AV, Arjol-Serrano JL, et al. Eccentric Overload Training in Team-Sports Functional Performance: Constant Bilateral Vertical vs. Variable Unilateral Multidirectional Movements. Int J Sports Physiol Perform. 2016 Dec 14;1–23.

303. Gual G, Fort-Vanmeerhaeghe A, Romero-Rodríguez D, Tesch PA. Effects of In-Season Inertial Resistance Training With Eccentric Overload in a Sports Population at Risk for Patellar Tendinopathy. J Strength Cond Res. 2016 Jul;30(7):1834–42.

304. Helland C, Hole E, Iversen E, Olsson MC, Seynnes O, Solberg PA, et al. Training Strategies to Improve Muscle Power: Is Olympic-style Weightlifting Relevant? Med Sci Sports Exerc. 2016 Nov 3;

305. Mike J, Cole N, Herrera C, McLain T, Kravitz L, Kerksick C. The Effects of Eccentric Contraction Duration on Muscle Strength, Power Production, Vertical Jump and Soreness. J Strength Cond Res. 2016 Oct 20;

306. Rey E, Paz-Domínguez Á, Porcel-Almendral D, Paredes-Hernández V, Barcala-Furelos R, Abelairas-Gómez C. Effects of a 10-Week Nordic Hamstring Exercise and Russian

Belt Training on Posterior Lower Limb Muscle Strength in Elite Junior Soccer Players. J Strength Cond Res. 2016 Jul 26;

307. Morrissey D, Roskilly A, Twycross-Lewis R, Isinkaye T, Screen H, Woledge R, et al. The effect of eccentric and concentric calf muscle training on Achilles tendon stiffness. Clin Rehabil. 2011 Mar;25(3):238–47.

308. Elmer SJ, Martin JC. Construction of an Isokinetic Eccentric Cycle Ergometer for Research and Training. J Appl Biomech. 2012 Aug 22;

309. Dufour SP, Lampert E, Doutreleau S, Lonsdorfer-Wolf E, Billat VL, Piquard F, et al. Eccentric cycle exercise: training application of specific circulatory adjustments. Med Sci Sports Exerc. 2004 Nov;36(11):1900–6.

310. Thomson DA. Cardiac Output during Positive and Negative Work. Scand J Clin Lab Invest. 1971 Jan 1;27(3):193–200.

311. Knuttgen HG, Petersen FB, Klausen K. Oxygen uptake and heart rate responses to exercise performed with concentric and eccentric muscle contractions. Med Sci Sports. 1971;3(1):1–5.

312. Hesser CM, Linnarsson D, Bjurstedt H. Cardiorespiratory and metabolic responses to positive, negative and minimum-load dynamic leg exercise. Respir Physiol. 1977 Jun;30(1–2):51–67.

313. Lechauve JB, Perrault H, Aguilaniu B, Isner-Horobeti ME, Martin V, Coudeyre E, et al. Breathing patterns during eccentric exercise. Respir Physiol Neurobiol. 2014 Oct 1;202:53–8.

314. Laroche D, Joussain C, Espagnac C, Morisset C, Tordi N, Gremeaux V, et al. Is it possible to individualize intensity of eccentric cycling exercise from perceived exertion on concentric test? Arch Phys Med Rehabil. 2013 Aug;94(8):1621-1627.e1.

315. Gibala MJ, Jones AM. Physiological and performance adaptations to high-intensity interval training. Nestlé Nutr Inst Workshop Ser. 2013;76:51–60.

316. Coquart J, Tabben M, Farooq A, Tourny C, Eston R. Submaximal, Perceptually Regulated Exercise Testing Predicts Maximal Oxygen Uptake: A Meta-Analysis Study. Sports Med. 2016 Jan 20;46(6):885–97.

317. Cornelis N, Buys R. The effects of exercise modality on maximal and submaximal exercise parameters obtained by graded maximal exercise testing. Int J Cardiol. 2016 Jul 29;222:538–47.

318. Bridgeman LA, McGuigan MR, Gill ND, Dulson DK. Relationships Between Concentric and Eccentric Strength and Countermovement Jump Performance in Resistance Trained Men. J Strength Cond Res. 2016 Jul 18;

319. Cormie P, McGuigan MR, Newton RU. Changes in the eccentric phase contribute to improved stretch-shorten cycle performance after training. Med Sci Sports Exerc. 2010 Sep;42(9):1731–44.

320. Abbiss CR, Quod MJ, Levin G, Martin DT, Laursen PB. Accuracy of the Velotron ergometer and SRM power meter. Int J Sports Med. 2009 Feb;30(2):107–12.

321. Peñailillo L, Blazevich A, Numazawa H, Nosaka K. Rate of force development as a measure of muscle damage. Scand J Med Sci Sports. 2014 Jun 1;n/a-n/a.

322. Hedges LV. Distribution Theory for Glass's Estimator of Effect size and Related Estimators. J Educ Stat. 1981 Jun 1;6(2):107–28.

323. Nadel ER, Bergh U, Saltin B. Body temperatures during negative work exercise. J Appl Physiol. 1972 Nov;33(5):553–8.

324. Amann M, Blain GM, Proctor LT, Sebranek JJ, Pegelow DF, Dempsey JA. Group III and IV muscle afferents contribute to ventilatory and cardiovascular response to rhythmic exercise in humans. J Appl Physiol . 1985. 2010 Oct;109(4):966–76.

325. Hortobágyi T, Katch FI. Eccentric and concentric torque-velocity relationships during arm flexion and extension. Eur J Appl Physiol. 1990 Sep 1;60(5):395–401.

326. Emanuele U, Horn T, Denoth J. The Relationship between Freely Chosen Cadence and Optimal Cadence in Cycling. Int J Sports Physiol Perform. 2012 Dec 1;7(4):375–81.

327. Hansen EA, Smith G. Factors affecting cadence choice during submaximal cycling and cadence influence on performance. Int J Sports Physiol Perform. 2009 Mar;4(1):3–17.

328. LaStayo P, Pifer J, Pierotti D, Lindstedt S. Electromyographic adaptations elicited by submaximal exercise in those naive to and in those adapted to eccentric exercise: a descriptive report. J Strength Cond Res. 2008 May;22(3):833–8.

329. Fridén J, Sjöström M, Ekblom B. Myofibrillar damage following intense eccentric exercise in man. Int J Sports Med. 1983 Aug;4(3):170–6.

330. Weston M, Taylor KL, Batterham AM, Hopkins WG. Effects of low-volume high-intensity interval training (HIT) on fitness in adults: a meta-analysis of controlled and non-controlled trials. Sports Med . 2014 Jul;44(7):1005–17.

331. Drust B, Reilly T, Cable NT. Physiological responses to laboratory-based soccer-specific intermittent and continuous exercise. J Sports Sci. 2000 Jan 1;18(11):885–92.

332. Schaun GZ, Pinto SS, Silva MR, Dolinski DB, Alberton CL. Whole-Body High-Intensity Interval Training Induce Similar Cardiorespiratory Adaptations Compared With Traditional High-Intensity Interval Training and Moderate-Intensity Continuous Training in Healthy Men. J Strength Cond Res. 2018 May 7;

333. Bartlett JD, Close GL, MacLaren DPM, Gregson W, Drust B, Morton JP. High-intensity interval running is perceived to be more enjoyable than moderate-intensity continuous exercise: implications for exercise adherence. J Sports Sci. 2011 Mar;29(6):547–53.

334. Jung ME, Bourne JE, Little JP. Where Does HIT Fit? An Examination of the Affective Response to High-Intensity Intervals in Comparison to Continuous Moderate- and Continuous Vigorous-Intensity Exercise in the Exercise Intensity-Affect Continuum. PLOS ONE. 2014 Aug 12;9(12):e114541.

335. Heisz JJ, Tejada MGM, Paolucci EM, Muir C. Enjoyment for High-Intensity Interval Exercise Increases during the First Six Weeks of Training: Implications for Promoting Exercise Adherence in Sedentary Adults. PLOS ONE. 2016 Dec 14;11(12):e0168534.

336. Foster C, Farland CV, Guidotti F, Harbin M, Roberts B, Schuette J, et al. The Effects of High Intensity Interval Training vs Steady State Training on Aerobic and Anaerobic Capacity. J Sports Sci Med. 2015 Nov 24;14(4):747–55.

337. Martinez N, Kilpatrick MW, Salomon K, Jung ME, Little JP. Affective and Enjoyment Responses to High-Intensity Interval Training in Overweight-to-Obese and Insufficiently Active Adults. J Sport Exerc Psychol. 2015 Apr 1;37(2):138–49.

338. Kilpatrick MW, Greeley SJ, Collins LH. The Impact of Continuous and Interval Cycle Exercise on Affect and Enjoyment. Res Q Exerc Sport. 2015 Jul 3;86(3):244–51.

339. Zafeiridis A, Kounoupis A, Dipla K, Kyparos A, Nikolaidis MG, Smilios I, et al. Oxygen Delivery and Muscle Deoxygenation during Continuous, Long- and Short-Interval Exercise. Int J Sports Med. 2015 Nov;36(11):872–80.

340. Baar K. Training for endurance and strength: lessons from cell signaling. Med Sci Sports Exerc. 2006 Nov;38(11):1939–44.

341. Isacco L, Ritter O, Tordi N, Laroche D, Degano B, Bouhaddi M, et al. Similar substrate oxidation rates in concentric and eccentric cycling matched with aerobic power output. Appl Physiol Nutr Metab [Internet]. 2016 Aug 11 [cited 2016 Aug 18]; Available from: http://www.nrcresearchpress.com/doi/10.1139/apnm-2016-0107

342. Borg G. Perceived exertion as an indicator of somatic stress. Scand J Rehabil Med. 1970;2(2):92–8.

343. Gosselin LE, Kozlowski KF, DeVinney-Boymel L, Hambridge C. Metabolic Response of Different High-Intensity Aerobic Interval Exercise Protocols: J Strength Cond Res. 2012 Oct;26(10):2866–71.

344. Christmass MA, Dawson B, Passeretto P, Arthur PG. A comparison of skeletal muscle oxygenation and fuel use in sustained continuous and intermittent exercise. Eur J Appl Physiol. 1999 Oct;80(5):423–35.

345. Rakobowchuk M, Isacco L, Ritter O, Represas AG, Bouhaddi M, Degano B, et al. Muscle Oxygenation Responses to Low-intensity Steady Rate Concentric and Eccentric Cycling. Int J Sports Med. 2018 Jan 24;

346. Moore JL, Shaffrath JD, Casazza GA, Stebbins CL. Cardiovascular effects of cadence and workload. Int J Sports Med. 2008 Feb;29(2):116–9.

347. Elmer SJ, Martin JC. Joint-specific power loss after eccentric exercise. Med Sci Sports Exerc. 2010 Sep;42(9):1723–30.

348. Ekblom B, Goldbarg AN. The influence of physical training and other factors on the subjective rating of perceived exertion. Acta Physiol Scand. 1971 Nov;83(3):399–406.

349. Peñailillo L, Mackay K, Abbiss CR. RPE During Concentric and Eccentric Cycling: Are We Measuring Effort or Exertion? Int J Sports Physiol Perform. 2017 Oct 16;1–22.

350. Abbiss CR, Peiffer JJ, Meeusen R, Skorski S. Role of Ratings of Perceived Exertion during Self-Paced Exercise: What are We Actually Measuring? Sports Med . 2015 Sep;45(9):1235–43.

351. Micklewright D, Gibson ASC, Gladwell V, Salman AA. Development and Validity of the Rating-of-Fatigue Scale. Sports Med. 2017 Nov 1;47(11):2375–93.

352. Ross A, Leveritt M. Long-term metabolic and skeletal muscle adaptations to short-sprint training: implications for sprint training and tapering. Sports Med . 2001;31(15):1063–82.

353. Kimm SYS, Glynn NW, McMahon RP, Voorhees CC, Striegel-Moore RH, Daniels SR. Self-perceived barriers to activity participation among sedentary adolescent girls. Med Sci Sports Exerc. 2006 Mar;38(3):534–40.

354. Noorkoiv M, Nosaka K, Blazevich AJ. Assessment of quadriceps muscle cross-sectional area by ultrasound extended-field-of-view imaging. Eur J Appl Physiol. 2010 Jul 1;109(4):631–9.

355. Garber CE, Blissmer B, Deschenes MR, Franklin BA, Lamonte MJ, Lee I-M, et al. Quantity and Quality of Exercise for Developing and Maintaining Cardiorespiratory, Musculoskeletal, and Neuromotor Fitness in Apparently Healthy Adults: Guidance for Prescribing Exercise. Med Sci Sports Exerc. 2011 Jul;43(7):1334.

356. Milanović Z, Sporiš G, Weston M. Effectiveness of High-Intensity Interval Training (HIT) and Continuous Endurance Training for VO2max Improvements: A Systematic Review and Meta-Analysis of Controlled Trials. Sports Med. 2015 Oct 1;45(10):1469–81.

357. Knuttgen HG, Patton JF, Vogel JA. An ergometer for concentric and eccentric muscular exercise. J Appl Physiol. 1982 Sep;53(3):784–8.

358. Beattie K, Kenny IC, Lyons M, Carson BP. The effect of strength training on performance in endurance athletes. Sports Med . 2014 Jun;44(6):845–65.

359. Ozaki H, Loenneke JP, Thiebaud RS, Abe T. Resistance training induced increase in VO2max in young and older subjects. Eur Rev Aging Phys Act. 2013 Oct 1;10(2):107–16.

360. Walsh B, Tonkonogi M, Malm C, Ekblom B, Sahlin K. Effect of eccentric exercise on muscle oxidative metabolism in humans. Med Sci Sports Exerc. 2001 Mar;33(3):436–41.

361. Hickson RC, Dvorak BA, Gorostiaga EM, Kurowski TT, Foster C. Potential for strength and endurance training to amplify endurance performance. J Appl Physiol. 1988 Nov 1;65(5):2285–90.

362. Marcinik EJ, Potts J, Schlabach G, Will S, Dawson P, Hurley BF. Effects of strength training on lactate threshold and endurance performance. Med Sci Sports Exerc. 1991 Jun;23(6):739–43.

363. Sanada K, Kearns CF, Kojima K, Abe T. Peak oxygen uptake during running and arm cranking normalized to total and regional skeletal muscle mass measured by magnetic resonance imaging. Eur J Appl Physiol. 2005 Mar;93(5–6):687–93.

364. Østerås H, Helgerud J, Hoff J. Maximal strength-training effects on force-velocity and force-power relationships explain increases in aerobic performance in humans. Eur J Appl Physiol. 2002 Dec 1;88(3):255–63.

365. Yamamoto LM, Lopez RM, Klau JF, Casa DJ, Kraemer WJ, Maresh CM. The effects of resistance training on endurance distance running performance among highly trained runners: a systematic review. J Strength Cond Res. 2008 Nov;22(6):2036–44.

366. Mikkola J, Vesterinen V, Taipale R, Capostagno B, Häkkinen K, Nummela A. Effect of resistance training regimens on treadmill running and neuromuscular performance in recreational endurance runners. J Sports Sci. 2011 Oct 1;29(13):1359–71.

367. Seaborne RA, Strauss J, Cocks M, Shepherd S, O'Brien TD, Someren KA, et al. Human Skeletal Muscle Possesses an Epigenetic Memory of Hypertrophy. Sci Rep. 2018 Jan 30;8(1):1898.

APPENDICES

A - Characteristics of eccentric exercise, their categories, explanations and examples

Characteristic	Categories	Examples

Intensity or load	Very high
	> 100% of 1RM
	
	High:
	67-99% of 1RM
	
	Moderate:
	34-66% of 1RM
	
	Low:
	0-33% of 1RM
		Very high:
		• Any exercise that can be performed at a load above concentric 1RM
		• Including all type of classic "overload" eccentric exercise
		    o e.g. squats, bench press, maximal isokinetic, isotonic and isoinertial exercises
		• Usually prescribed for a certain amount of sets with as many repetitions as possible until failure
		
		High:
		• Any exercise that can be performed at close to maximal concentric intensities
		• Including all exercises from the maximal category
		• Usually prescribed for a certain amount of sets and pre-determined % of 1RM, but also often until failure
		
		Moderate:
		• Either internally controlled and interrupted exercise
		    o e.g. squats, bench press, drops jumps, Nordic hamstring exercise, any isotonic or isoinertial exercise
		    o Prescribed at predetermined intensities, set and rep schemes, failure never reached
		• Or externally controlled and uninterrupted exercise
		    o e.g. eccentric cycling, eccentric stepping, eccentric arm cranking, fast downhill running
		    o Prescribed at high power outputs or movement velocities, preferably designed in interval protocols
		
		Any exercise that is interrupted and internally controlled, rarely externally controlled

		Low:
		• Mainly uninterrupted and externally controlled
		    ○ e.g. eccentric cycling, eccentric stepping, eccentric arm cranking, downhill walking
		• Usually prescribed in a continuous design (e.g. 20 min eccentric cycling)
		• Rarely interrupted and internally controlled
		    ○ e.g. isotonic knee extensions,
		• Prescribed with large volume of repetitions without concentric phase and failure
		    ○ e.g. 10x10 knee extensions, 100 drop jumps without concentric jump, 3x30 eccentric heel raises and concentric phase done by knee and hip extensors without involving agonist muscle

Control	Internally controlled:
	The movement and velocity is controlled by the individual
	
	Externally controlled:
	The movement and velocity is controlled by external devices like dynamometers and ergometers
		Internally:
		• Any gravity-based interrupted exercise
		    ○ e.g. squats, bench press, lunges, drop jumps
		• Uninterrupted exercises without use of external devices or devices with variable cadence
		    ○ e.g. downhill running, walking, downstairs walking, eccentric stepping and cycling in iso power mode with variable cadence, downhill walking and running on non-motorised treadmill
		• All isoinertial exercises performed controlled and at low to medium intensity
		    ○ e.g. Yo-Yo squats, lunges, rows
		
		Externally:
		• Any exercises controlled by an external device
		    ○ e.g. isokinetic knee extension and flexions, eccentric stepping and cycling in isokinetic mode with fixed cadence, downhill running and walking on motorised treadmill

Velocity	Slow:
	0 – 90 deg/s at main joint
	
	Moderate:
	91-180 deg/s at main joint
	
	Fast:
	>180 deg/s at main joint
		Slow:
		• All interrupted and externally controlled exercise with pre-set velocities
		    ○ e.g. isokinetic knee extensions and flexions, elbow extension and flexion
		• All interrupted and internally controlled exercises with a practiced range of motion and standardised velocity via metronome
		    ○ e.g. isotonic squats, knee extensions and flexions
		• All uninterrupted and externally controlled exercise with pre-set cadence
		    ○ e.g. eccentric cycling up to 30 rpm
		
		Moderate:
		• All interrupted and externally controlled exercise with pre-set velocities
		    ○ e.g. isokinetic knee extensions and flexions, elbow extension and flexion
		• All interrupted and internally controlled exercises with a practiced range of motion and standardised velocity via metronome
		    ○ e.g. isotonic squats, knee extensions and flexions
		• All uninterrupted and externally controlled exercise with pre-set cadence
		    ○ e.g. eccentric cycling up to 31 to 60 rpm
		
		Fast:
		• All interrupted and externally controlled exercise with pre-set velocities and participants that practiced fast velocities
		    ○ e.g. isokinetic knee extensions and flexions, elbow extension and flexion
		• All interrupted and internally controlled exercises with a practiced range of motion and standardised velocity via metronome and participants that practiced fast velocities

		○ e.g. isotonic squats, knee extensions and flexions, countermovement jumps, drop jumps, changes of direction in agility training • All uninterrupted and externally controlled exercise with pre-set cadence ○ e.g. eccentric cycling > 60 rpm
Muscle length & range of motion	Long: 67-100% of total joint range of motion Medium: 34-66% of total joint range of motion Short: < 33% of total joint range of motion	*Long:* • Any interrupted exercise with restricted range of motion to almost full flexion of joints ○ e.g. isotonic squats, bench press, lunges performed all at only limited range of motion at the turnaround point of each movement • Uninterrupted exercise with restricted range of motion ○ e.g. eccentric cycling closer to the pedals via lower seat or closer seat during recumbent eccentric stepping *Medium:* • Interrupted exercise with restricted range of motion to exclude minimum and maximum; ○ e.g. isotonic squats, bench press, lunges performed with partial range of motion as “constant tension training” • Uninterrupted exercise performed with bodyweight at high velocities ○ e.g. steep downhill running, eccentric cycling with a specifically chosen seat height *Short:* • Interrupted exercise with restricted range of motion to almost full extension of joints

		○ e.g. e.g. isotonic squats, bench press, lunges performed all at only limited range of motion at the starting point of each movement - Uninterrupted exercise ○ e.g. downhill running and walking, downstairs walking, eccentric cycling with high seat and eccentric stepping with far way seat
Muscle mass & joints	Whole-body: 1 or more joints for upper & lower body Multi-joint: 1 or more joints for upper or lower body Isolated: 1 joint	*Whole-body:* - Interrupted and internally controlled exercises ○ e.g. squats, lunges, drop jumps with usage of arms or external weight, multi-dimensional isoinertial exercises - Uninterrupted and externally controlled exercises ○ e.g. eccentric stepping and cycling at medium to high intensities as bracing of upper body is required, *Multi-joint:* - Interrupted exercise ○ e.g. isokinetic leg extension, isoinertial exercise with lower or upper body focus, isotonic squats, lunges, bench press - Uninterrupted exercise ○ e.g. downhill running and walking, downstairs walking, eccentric cycling and stepping at low intensities and in continuous design *Isolated:* - Interrupted exercise ○ e.g. isokinetic knee extensions or flexions, isotonic knee extensions or flexions, elbow extensions or flexions, ankle dorsi- or plantarflexions

Feedback	Live:
	Feedback provided directly during exercise without any delays
	
	Delayed:
	Feedback provided with a slower refresh rate or after completion of a set or repetition
	
	AND
	
	Graphic:
	Lines, bars, circles or dynamic graphics for live feedback during exercise. Maze like feedback to support coordination and precision of torque and power output during uninterrupted exercise (e.g. eccentric stepping and cycling) or interrupted exercise (e.g. isokinetic knee extensions)
	
	Numbers:
	Raw, smoothed or averaged feedback about target parameters during all modes
	
	AND
	
	Refresh rate:
	How often the given feedback is refreshed, reported in Hz
		Live:
		• Constant feedback during uninterrupted exercise
		  ○ e.g. actual power output or torque feedback during eccentric cycling or stepping, velocity feedback during downhill running or walking
		• Constant feedback during interrupted exercise
		  ○ e.g. meters per second during isotonic squats, lunges, drop jumps without jump, power output during isoinertial exercise, torque feedback during isokinetic knee extensions or flexions
		
		Delayed:
		• Delayed feedback during uninterrupted exercise
		  ○ e.g. smoothed power output or torque that gets refreshed every couple of seconds during eccentric stepping and cycling
		• Delayed feedback during interrupted exercise
		  ○ e.g. velocity for every repetition or average values after every set of interrupted exercises

Continuity	Interrupted: If any other muscle modes of muscle contractions are performed by the agonist muscle between eccentric muscle actions	*Interrupted:* • Squats, bench press, isokinetic knee extension and flexion, drop jumps *Continuous:*

	Uninterrupted:
	If no other muscle modes of muscle contractions are performed by the agonist muscle between eccentric muscle actions
	
	AND
	
	Bodyweight:
	If bodyweight is part of the load during exercise or not
	
	Impact:
	If an impact is part of the load during exercise or not
	
	AND
	
	Interval design:
	Specific work and rest periods and ratios
	
	Continuous design:
	No rest periods
		• Downhill walking and running, downstairs walking, eccentric stepping and cycling, eccentric muscle actions via electrical stimulation against passive motion
		
		Bodyweight yes:
		• Uninterrupted exercises with whole-body or multi-joint involvement
		    ○ e.g. eccentric cycling in a standing position to assist with bodyweight against the movement of the pedals
		• Interrupted and internally controlled exercises with whole-body or multi-joint involvement
		    ○ e.g. isotonic squats, bench press, lunges
		
		Bodyweight no:
		• Uninterrupted exercises
		    ○ e.g. eccentric cycling and stepping, downhill walking and running could be performed with reduced bodyweight via an antigravity treadmill
		• Interrupted exercises with single joint involvement
		    ○ e.g. isokinetic or isotonic knee extensions and flexions, elbow extensions and flexions

B – Details of training during Study 3 - Including: Average power output (P_{EC} & P_{CC}), power output range (P_{EC} range & P_{CC} range), target power output (EC target & CC target), achieved % of target power ouput (% target P_{EC} & % target P_{CC}) heart rate (HR), average heart rate (HR_{EC} & HR_{CC}), heart rate range (HR_{EC} range & HR_{CC} range), average session rating of perceived effort (Eff_{EC} & Eff_{CC}), range of effort (Eff_{EC} range & Eff_{CC} range), target effort (Eff target), and achieved % of target effort (% target Eff_{EC} & % target Eff_{CC}) for each session between the eccentric (EC) and concentric (CC) cycling training groups.

	Training sessions															
Parameters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
P_{EC} (W)	392 ± 85	390 ± 87	423 ± 107	454 ± 107	467 ± 103	454 ± 121	494 ± 122	486 ± 117	508 ± 116	493 ± 107	488 ± 107	502 ± 107	500 ± 113	530 ± 114	483 ± 99	475 ± 94
P_{EC} range (W)	271 - 585	241 - 576	251 - 654	257 - 674	262 - 673	241 - 706	269 - 715	282 - 711	276 - 727	300 - 676	305 - 723	319 - 703	339 - 719	359 - 715	350 - 646	339 - 642
P_{CC} (W)	85 ± 38	87 ± 37	107 ± 41	107 ± 39	103 ± 39	121 ± 40	122 ± 40	117 ± 43	116 ± 41	107 ± 38	107 ± 35	107 ± 33	113 ± 34	114 ± 39	99 ± 36	94 ± 36
P_{CC} range (W)	126 - 234	129 - 239	125 - 241	121 - 239	124 - 248	118 - 238	121 - 251	119 - 242	121 - 254	108 - 220	124 - 244	135 - 243	140 - 261	141 - 271	125 - 241	128 - 238
EC target (W)	380 ± 85	380 ± 87	422 ± 107	464 ± 107	464 ± 103	464 ± 121	506 ± 122	506 ± 117	548 ± 116	548 ± 107	548 ± 107	548 ± 107	548 ± 113	591 ± 114	506 ± 99	506 ± 94
% target P_{EC}	103%	102%	99%	97%	100%	97%	96%	95%	92%	89%	88%	91%	90%	89%	95%	94%
CC target (W)	233 ± 38	233 ± 37	233 ± 41	233 ± 39	233 ± 39	233 ± 40	257 ± 40	257 ± 43	257 ± 41	257 ± 38	257 ± 35	257 ± 33	257 ± 34	280 ± 39	257 ± 36	233 ± 36
% target P_{CC}	76%	77%	77%	75%	77%	77%	70%	71%	73%	68%	71%	72%	74%	75%	69%	74%
HR_{EC} (bpm)	131 ± 22	130 ± 23	135 ± 26	133 ± 22	136 ± 23	135 ± 24	135 ± 26	139 ± 27	135 ± 27	129 ± 24	130 ± 23	137 ± 26	139 ± 26	141 ± 28	130 ± 24	128 ± 25
HR_{EC} range (bpm)	95 - 159	95 - 162	98 - 171	98 - 168	98 - 166	97 - 165	97 - 165	97 - 170	96 - 167	96 - 166	94 - 164	93 - 170	91 - 175	89 - 174	89 - 163	95 - 162

HR_{CC} (bpm)	152 ± 10	150 ± 8	150 ± 10	147 ± 5	151 ± 5	152 ± 6	148 ± 9	155 ± 5	151 ± 9	149 ± 11	146 ± 7	153 ± 7	157 ± 5	158 ± 5	152 ± 5	149 ± 7
HR_{CC} range (bpm)	140 - 172	136 - 160	130 - 160	139 - 155	144 - 157	146 - 165	137 - 166	147 - 165	141 - 163	130 - 168	137 - 160	140 - 162	149 - 163	150 - 165	147 - 163	137 - 159
Eff_{EC}	7.1 ± 0.5	7.3 ± 0.3	7.5 ± 0.9	7.6 ± 0.7	7.8 ± 0.8	7.2 ± 0.7	7.8 ± 0.3	7.8 ± 0.5	8.1 ± 0.6	6.3 ± 0.4	6.6 ± 0.9	7.5 ± 0.4	8 ± 0.7	8.3 ± 0.6	6.5 ± 0.7	5.6 ± 0.9
Eff_{EC} range	6 - 8	7 - 8	6 - 8.5	6 - 8.5	6 - 8.5	6 - 8	7.5 - 8.5	7 - 8.5	7 - 9	6 - 7	6 - 9	7 - 8	7 - 9	7.5 - 9	5 - 7	4 - 7
Eff_{CC}	7.6 ± 1	7.4 ± 0.8	7.5 ± 0.4	7.8 ± 0.6	7.4 ± 0.4	7.4 ± 0.6	7.7 ± 0.7	8.1 ± 0.7	8 ± 0.6	6.3 ± 0.7	7 ± 0.7	8.3 ± 0.4	8.1 ± 1.2	8.8 ± 1.2	6.8 ± 0.5	6.2 ± 0.3
Eff_{CC} range	7 - 10	6 - 8.5	7 - 8	7 - 9	7 - 8	6.5 - 8	7 - 8.5	7 - 9	7 - 9	5 - 7.5	6 - 8	8 - 9	6 - 10	7 - 11	5.5 - 7.5	6 - 7
Eff target	7	7	8	8	8	7	8	8	9	6	7	8	9	9	7	6
% target Eff_{EC}	102%	105%	95%	95%	98%	104%	98%	98%	90%	106%	96%	94%	90%	92%	93%	95%
% target Eff_{CC}	110%	106%	95%	98%	93%	93%	97%	102%	90%	106%	100%	105%	90%	98%	97%	91%

C – Document of consent for Study 1 & 2

Edith Cowan University
School of Exercise and Health Science

CONSENT TO PARTICIPATE IN RESEARCH

Acute and chronic physiological effects of interval eccentric cycling
Study 1: Differences in the physiological demands of interval eccentric cycling in comparison to continuous eccentric cycling

I, ____ hereby agree to volunteer in a scientific investigation performed at Edith Cowan University.

The investigation and my part in the investigation have been outlined and explained to me in detail and I understand the explanation. I received a copy of the procedures and a description of any risks and discomforts has been provided to me and discussed in detail with me.

I, as a volunteer in this study,

- Have read and understood the information sheet about this research project and the testing protocols have been explained to me.
- Have been given an opportunity to ask any questions and all such questions and inquiries have been answered to my satisfaction.
- Understand that I am free to ask any questions and that they will be answered to my satisfaction at any time.
- Understand that as part of the testing I will be required to undergo maximal voluntary contractions, have my skin prepared for measurement of muscle activity, have my heart rate recorded, have gas exchange and local blood flow measured, have my movement recorded on video, as well as perform eccentric cycling exercises.
- Understand that the maximal strength measurement and eccentric cycling exercises may lead to muscle soreness if I am unaccustomed to the technique and exercise type.
- Understand that I am free to withdraw my consent and to discontinue participation in the project or activity at any time and without any reason or explanation required from me.
- Understand that my data will remain confidential with regard to my identity.
- Certify that to the best of my knowledge and belief, I have no physical condition that would increase the risk to me participating in this investigation.
- Agree that the research data obtained from this study may be published, provided I am not identifiable in any way.

Participant ________________________________ **Date** ______________________

I, the investigator, was present when the study was explained to the participant in detail and to the best of my knowledge and belief it was understood.

Investigator _______________________________ **Date** ______________________

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D – Medical questionnaire for Study 1 & 2

Edith Cowan University
School of Exercise and Health Science

AUSTRALIA ECU EDITH COWAN UNIVERSITY

PRE-EXERICSE MEDICAL QUESTIONAIRE

Acute and chronic physiological effects of interval eccentric cycling
Study 1: Differences in the physiological demands of interval eccentric cycling in comparison to continuous eccentric cycling

The following questionnaire establishes your medical history, and identifies any injury and/ or illness that may influence your testing and performance.
Please answer all questions as accurately as possible, and if you are unsure about anything please ask for clarification. All information provided is strictly confidential.

Personal Details

Participants ID:	________________________________
Age:	_____years
Weight:	_____kg
Height:	_____cm

Medical Information

Briefly describe the type and amount of exercise you have done in the past 6 months:

Type:

____

____

____

Amount:

____

____

____

Please tick yes or no and explain further details where necessary:

Part A

Have you ever been diagnosed with or did you ever had:

Being overweight (BMI >30 kg/m^2)? YES NO

Details: ______

High blood pressure (>140/90 mmHg)? YES NO

Details: ______

High cholesterol (>5.2 mm/L or >200 mg/dL)? YES NO

Details: ______

Diabetes? YES NO

Details: ______

Heart abnormalities? YES NO

Details: ______

Asthma? YES NO

Details: ______

Asthma attack during exercise? YES NO

Details: ______

Epilepsy? YES NO

Details: ______

An epileptic seizure? YES NO

Details: ______

Rheumatic fever? YES NO

Details: ______

Infectious disease? YES NO

Details: ______

Details: ______

Moderate or severe allergies? YES NO

Details: ____

Recurring back pain? YES NO

Details: ____

Any neurological disorders? YES NO

Details: ____

Recurring muscle or joint injuries? YES NO

Details: ____

Burning or cramping sensation in your limbs? YES NO

Details: ____

Chest discomfort, unreasonable breathlessness, dizziness, fainting or blackouts? YES NO

____

Part B

Do you smoke? YES NO

Have you smoked in the past? YES NO

Details: ____

Do you drink alcohol? YES NO

Details: ____

Are you currently taking any prescribed or non-prescribed medications? YES NO

Details: ____

Did you ever feel dizzy or disoriented during or after exercise? YES NO

Details: ____

Part C

Did you have the flu in the last week? YES NO

Details: ____

Do you currently have an injury or any discomfort that might affected by the exercise? YES NO

Details: ____

Part D

Have you ever been told by a medical practitioner, or do you think it is likely, that you have a blood clotting disorder?	YES NO

Details: ____

Are you currently taking any supplements (e.g. aspiring, fish oil) or blood thinning drugs that might affect blood clotting?	YES NO

Details: ____

Have you ever had a complication (including fainting or dizziness, uncontrolled bleeding or post-procedure bruising) from a medical blood test?	YES NO

Details: ____

Is there any other condition not previously mentioned that may affect your ability to participate in this study?

YES NO

Details: ____

Declaration

(to be signed in the presence of the researcher)

I, the participant, acknowledge that the information provided in this form, is to the best of my knowledge, a true and accurate indication of my current state of health.

Participant _________________________________ **Date** _______________________

I, the investigator, was present when the participant completed this questionnaire and provided my best help and knowledge, and belief that the participant completed it truthfully.

Investigator ________________________________ Date ________________________

E – Document of consent for Study 3

Edith Cowan University
School of Medical and Health Sciences

CONSENT TO PARTICIPATE IN RESEARCH

Acute and chronic physiological effects of interval eccentric cycling

Study 3: The long-term effects of interval eccentric cycling in comparison to continuous eccentric cycling on changes in proteins for endurance and strength adaptations, as well as on cardiovascular, metabolic, performance, muscle structure and everyday life parameters

I, ____ hereby agree to volunteer in a scientific investigation performed at Edith Cowan University.

The investigation and my part in the investigation have been outlined and explained to me in detail and I understand the explanation. I received a copy of the procedures and a description of any risks and discomforts has been provided to me and discussed in detail with me.

I, as a volunteer in this study,

- Have read and understood the information sheet about this research project and the testing protocols have been explained to me.
- Have been given an opportunity to ask any questions and all such questions and inquiries have been answered to my satisfaction.
- Understand that I am free to ask any questions and that they will be answered to my satisfaction at any time.
- Understand that as part of the testing I will be required to undergo
    - Measurement of body composition and bone mass density using dual-energy x-ray absorptiometry (DXA)
    - Non-invasive measurement of arterial stiffness
    - Maximal voluntary contractions
    - Jump height measurements
    - Measurements simulating everyday life activities

    - Incremental cycling performance with measurements of my heart rate and gas exchange
    - Perform eccentric cycling exercise for 8 weeks
    - Measurement of muscle cross sectional area using ultrasonography
    - A total of 3 venous blood samples
    - A total 3 muscle biopsies, 2 of that during the first training session
- Understand that the maximal strength, jump height, incremental cycling performance measurement and eccentric cycling training may lead to muscle soreness and discomfort if I am unaccustomed to the technique and exercise type.
- Understand that during and after the venous blood and muscle biopsy samples I may encounter extensive bleeding, bruises (hematoma), soreness, pain, discomfort and tissue damage
- Understand that I am free to withdraw my consent and to discontinue participation in the project or activity at any time and without any reason or explanation required from me.
- Understand that my data will remain confidential with regard to my identity.
- Certify that to the best of my knowledge and belief, I have no physical condition that would increase the risk to me participating in this investigation.
- Agree that the research data obtained from this study may be published, provided I am not identifiable in any way.

Participant ________________________________ **Date** ______________________

I, the investigator, was present when the study was explained to the participant in detail and to the best of my knowledge and belief it was understood.

Investigator _______________________________ **Date** ______________________

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F – Medical questionnaire for Study 3

Edith Cowan University
School of Medical and Health Sciences

PRE-EXERICSE MEDICAL QUESTIONAIRE

Acute and chronic physiological effects of interval eccentric cycling

Study 3: The long-term effects of interval eccentric cycling in comparison to continuous eccentric cycling on changes in proteins for endurance and strength adaptations, as well as on cardiovascular, metabolic, performance, muscle structure and everyday life parameters

The following questionnaire establishes your medical history, and identifies any injury and/ or illness that may influence your testing and performance.

Please answer all questions as accurately as possible, and if you are unsure about anything please ask for clarification. All information provided is strictly confidential.

Personal Details

Participants ID: ________________________________

Age: _____years

Weight: _____kg

Height: _____cm

Medical Information

Briefly describe the type and amount of exercise you have done in the past 6 months:

Type:

____

____

____

Amount:

____

____

Please tick yes or no and explain further details where necessary:

Part A

Have you ever been diagnosed with or did you ever had:

Being overweight (BMI >30 kg/m²)? YES NO

Details: ______________________________

High blood pressure (>140/90 mmHg)? YES NO

Details: ______________________________

High cholesterol (>5.2 mm/L or >200 mg/dL)? YES NO

Details: ______________________________

Diabetes? YES NO

Details: ______________________________

Heart abnormalities? YES NO

Details: ______________________________

Asthma? YES NO

Details: ______________________________

Asthma attack during exercise? YES NO

Details: ______________________________

Epilepsy? YES NO

Details: ______________________________

An epileptic seizure? YES NO

Details: ______________________________

Rheumatic fever? YES NO

Details: ______________________________

Infectious disease? YES NO

Details: ______________________________

Moderate or severe allergies?	YES	NO
Details: ______________________________		
Recurring back pain?	YES	NO
Details: ______________________________		
Any neurological disorders?	YES	NO
Details: ______________________________		
Recurring muscle or joint injuries?	YES	NO
Details: ______________________________		
Burning or cramping sensation in your limbs?	YES	NO
Details: ______________________________		
Chest discomfort, unreasonable breathlessness, dizziness, fainting or blackouts?	YES	NO
Details: ______________________________		

Part B

Do you smoke?	YES	NO
Have you smoked in the past?	YES	NO
Details: ______________________________		
Do you drink alcohol?	YES	NO
Details: ______________________________		
Are you currently taking any prescribed or non-prescribed medications?	YES	NO
Details: ______________________________		
Did you ever feel dizzy or disoriented during or after exercise?	YES	NO
Details: ______________________________		

Part C

Did you have the flu in the last week?	YES	NO
Details: ______________________________		

Do you currently have an injury or any discomfort that might affected by the exercise? YES NO

Details: ____

Part D

Have you ever been told by a medical practitioner, or do you think it is likely, that you have a blood clotting disorder? YES NO

Details: ____

Are you currently taking any supplements (e.g. aspiring, fish oil) or blood thinning drugs that might affect blood clotting? YES NO

Details: ____

Is there any other condition not previously mentioned that may affect your ability to participate in this study?

YES NO

Details:

____

____

____

Emergency contact information:

Name:

____

Contact number:____

Declaration

(to be signed in the presence of the researcher)

I, the participant, acknowledge that the information provided in this form, is to the best of my knowledge, a true and accurate indication of my current state of health.

Participant ________________________________ **Date** ______________________

I, the investigator, was present when the participant completed this questionnaire and provided my best help and knowledg, and belief that the participant completed it truthfully.

Investigator ______________________________ **Date** ______________________

G – Copy of presentation from Chapter 4 (Study 1; slide 1)

ECSS 2016 - Vienna

Eccentric versus Concentric Incremental Maximal Cycling Test

Marcin Lipski, Chris Abbiss, Ken Nosaka

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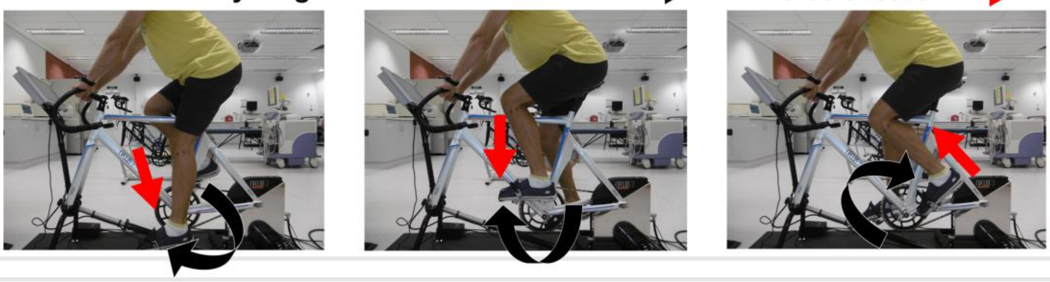
H – Copy of presentation from Chapter 5 (Study 2)

Metabolic Demand of Interval versus Continuous Eccentric Cycling Exercise

Marcin Lipski, Chris Abbiss, Ken Nosaka

Centre for Exercise and Sport Science Research, Edith Cowan University

What is Eccentric Cycling? Pedal movement ➡ Force direction ➡



Characteristics during continuous cycling at the same power output

(Dufour et al., 2007 AJP RIC; Penailillo et al., 2013 MSSE)

- Oxygen consumption (VO_2), Rate of perceived exertion (RPE)
  Eccentric cycling < Concentric (conventional) cycling

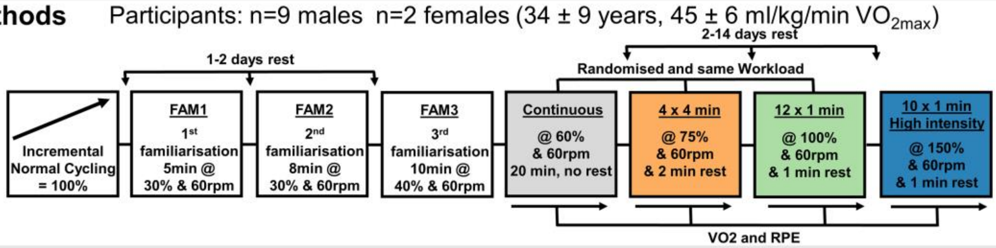
Adaptations after cycling training (LaStayo et al., 2000 AJP RIC; Leong et al., 2014 IJSM)

- Power output, Strength, Muscle mass, Functional physical fitness
  Eccentric cycling training > Concentric cycling training
- Maximal oxygen consumption (VO_{2max})
  Eccentric cycling training < Concentric cycling training

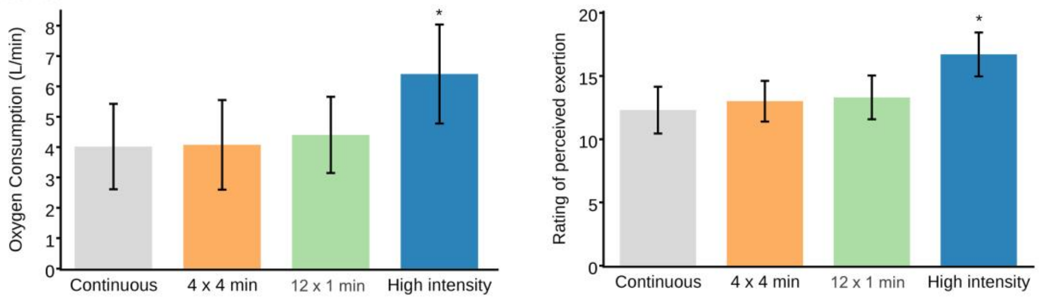
Research question: Can interval eccentric cycling increase VO_2 and RPE?

Hypothesis: VO_2 and RPE are greater in interval than continuous eccentric cycling

Methods Participants: n=9 males n=2 females (34 ± 9 years, 45 ± 6 ml/kg/min VO_{2max})



Results



Discussion & Conclusion

- **No difference in VO_2 and RPE between continuous and interval eccentric cycling when workload was matched, but VO_2 and RPE were greater in high intensity (150%) protocol**

⇒ **Interval eccentric cycling does not increase exercise intensity compared with continuous one**

⇒ **Supramaximal intensity interval eccentric cycling is an option to increase metabolic demand**

I– Copy of presentation from Chapter 6 (Study 3; slide 1)

HIGH-INTENSITY INTERVAL ECCENTRIC CYCLING TRAINING IMPROVES MUSCLE FUNCTION AND AEROBIC CAPACITY

M. Lipski, C. Abbiss, K. Nosaka (Edith Cowan University, Australia)

Eccentric training (e.g., eccentric cycling, descending stair walking):

Muscle strength, physical function, muscle mass

Metabolic parameters (e.g., insulin sensitivity, blood lipid profiles)

(LaStayo et al., 1999; 2000; 2001; 2011; Marcus et al., 2002; 2008; Dibble et al., 2006; Paschalis et al., 2011; Leong et al., 2013; Eidsheim et al., 2016; Chen et al., 2017a; 2017b)

No previous study has used
high-intensity interval eccentric cycling training (HIT-EC)

PURPOSE: To compare the 8-week training effects between HIT-EC and high-intensity interval concentric cycling training (HIT-CC)

J – Copy of publication from Chapter 4 (Study 1; page 1)

European Journal of Applied Physiology
https://doi.org/10.1007/s00421-018-3826-y

ORIGINAL ARTICLE

Cardio-pulmonary responses to incremental eccentric and concentric cycling tests to task failure

Marcin Lipski[1] · Chris R. Abbiss[1] · Kazunori Nosaka[1]

Received: 31 October 2017 / Accepted: 12 February 2018

Abstract

Purpose This study compared cardio-pulmonary responses between incremental concentric and eccentric cycling tests, and examined factors affecting the maximal eccentric cycling capacity.

Methods On separate days, nine men and two women (32.6 ± 9.4 years) performed an upright seated concentric (CON) and an eccentric (ECC) cycling test, which started at 75 W and increased 25 W min^{-1} until task failure. Gas exchange, heart rate (HR) and power output were continuously recorded during the tests. Participants also performed maximal voluntary contractions of the quadriceps (MVC), squat and countermovement jumps.

Results Peak power output was 53% greater ($P < 0.001$, $g = 1.77$) for ECC (449 ± 115 W) than CON (294 ± 61 W), but peak oxygen consumption was 43% lower ($P < 0.001$, $g = 2.18$) for ECC (30.6 ± 5.6 ml kg min^{-1}) than CON (43.9 ± 6.9 ml kg min^{-1}). Maximal HR was not different between ECC (175 ± 20 bpm) and CON (182 ± 13 bpm), but the increase in HR relative to oxygen consumption was 33% greater ($P = 0.01$) during ECC than CON. Moderate to strong correlations ($P < 0.05$) were observed between ECC peak power output and CON peak power ($r = 0.84$), peak oxygen consumption ($r = 0.54$) and MVC ($r = 0.53$), while no significant relationships were observed between ECC peak power output and squat as well as countermovement jump heights.

Conclusion Unexpectedly, maximal HR was similar between CON and ECC. Although ECC power output can be predicted from CON peak power output, an incremental eccentric cycling test performed after 3–6 familiarisation sessions may be useful in programming ECC training with healthy and accustomed individuals.

Keywords Lengthening contraction · Oxygen consumption · Heart rate · Peak power output · Maximal voluntary contraction · Graded exercise test

Abbreviations

B_f	Breathing frequency
CMJ	Countermovement jump
CON	Incremental concentric cycling test
ECC	Incremental eccentric cycling test
g	Hedges' *g*
HR	Heart rate
MVC	Maximal voluntary isometric contraction
RPE	Rating of perceived exertion
SD	Standard deviation
SJ	Squat jump
VO_2	Oxygen consumption
VO_{2peak}	Peak oxygen consumption
V_E	Minute ventilation
V_t	Tidal volume
VO_2	Oxygen consumption

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Introduction

Eccentric cycling was first introduced in a scientific journal in 1952 and repetitively confirmed that the metabolic load is lower during eccentric than concentric cycling at the same power output (Abbott et al. 1952; Dufour et al. 2004; Peñailillo et al. 2013). Several studies have since shown the potent effects of eccentric cycling training on muscle function and strength (Lastayo et al. 1999; LaStayo et al. 2000; Leong et al. 2013). With several review papers

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K – Copy of publication in review from Chapter 5 (Study 2; page 1 & 2)

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ORIGINAL ARTICLE

Oxygen consumption, rate of perceived exertion and enjoyment in high-intensity interval eccentric cycling

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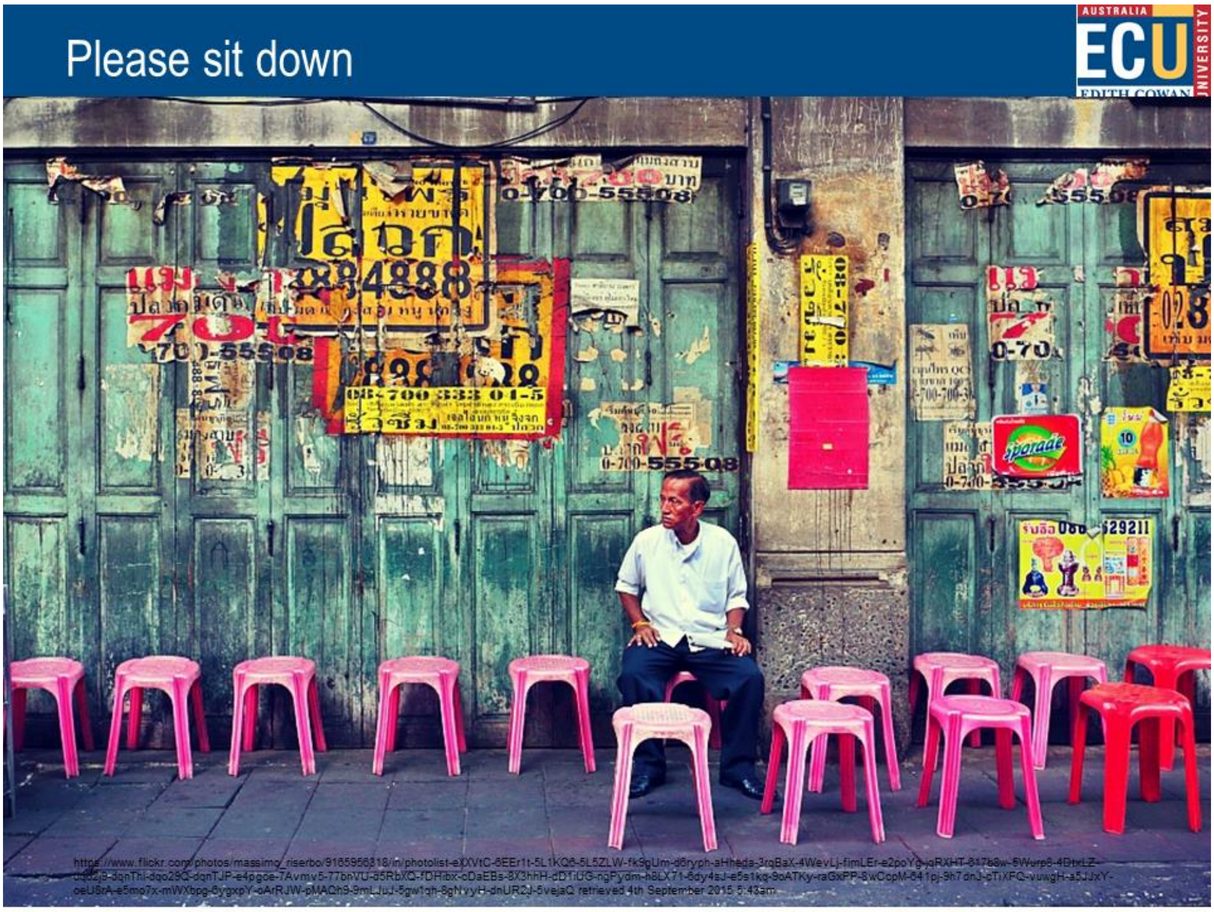
Abstract

Objectives: To compare oxygen consumption (VO_2) and perceptual responses between continuous and interval eccentric cycling protocols in order to test the hypothesis that metabolic demand and enjoyment would be greater for interval than continuous eccentric cycling protocols. **Methods:** Eleven recreationally active men (n=9) and women (32.6 ± 9.4 y) performed a concentric cycling test to determine peak power output (PPO) followed by five eccentric cycling protocols on separate occasions; continuous eccentric cycling at 60% of PPO for 20 min at 60 rpm ($CONT_{20@60\%}$) and 13.2 min at 90 rpm ($CONT_{13@60\%}$), 4 x 4 min at 75% of PPO with 2 min rest ($INT_{4x4@75\%}$), 12 x 1 min at 100% of PPO with 1 min rest ($INT_{1x12@100\%}$) and 10 x 1 min at 150% of PPO with 1 min rest ($INT_{1x10@150\%}$). Gas exchange and power output were recorded continuously, and rate of perceived exertion (RPE) and enjoyment were assessed after each exercise. **Results:** Total VO_2 including the rest periods was the greatest ($p<0.0001$) during $INT_{1x10@150\%}$ (382 ± 73 $ml \cdot kg^{-1}$) and lowest ($p<0.0001$) during $CONT_{13@60\%}$ (146 ± 27 $ml \cdot kg^{-1}$). Total VO_2 during $INT_{1x12@100\%}$ (312 ± 59 $ml \cdot kg^{-1}$) was greater ($p<0.0001$) than $CONT_{20@60\%}$ (246 ± 63 $ml \cdot kg^{-1}$) and $INT_{4x4@75\%}$ (257 ± 42 $ml \cdot kg^{-1}$). RPE was greater ($p<0.0001$) after $INT_{1x10@150\%}$ (17 ± 2) than other conditions, but perceived enjoyment was not significantly different between protocols. **Conclusions:** Greater metabolic cost in the interval than continuous eccentric cycling suggests that interval eccentric cycling is an effective training modality to simultaneously improve leg strength and cardio-pulmonary fitness.

Key words: gas exchange; VO2; rate of perceived exertion; power output; continuous cycling; lengthening contractions

L – 3MT 2014 slide

M – 3MT 2015 slide



N – 3MT 2016 slide