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Authors: James Mckendry, Leigh Breen, Brandon J. Shad, Carolyn Greig



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Muscle Morphology and Performance in Master Athletes: A Systematic Review and Meta-analyses

Running Title: Exercise and Health in Older Age

James Mckendry ^a, Leigh Breen ^{a, b}, Brandon J. Shad ^a, Carolyn Greig ^{a, b}

^a School of Sport, Exercise and Rehabilitation Sciences and ^b MRC-Arthritis Research UK
Centre for Musculoskeletal Ageing Research, University of Birmingham, Birmingham B15
2TT, UK

*Corresponding author: James McKendry, M.Res.

School of Sport, Exercise and Rehabilitation Sciences and MRC-Arthritis Research UK
Centre for Musculoskeletal Ageing Research, University of Birmingham, Edgbaston, B15
2TT.

Phone: (+44) 7879332731

Email: jxm965@student.bham.ac.uk

Highlights

- Ageing athletes are a unique population, who maintain excellent health in older age.
- This is the first systematic review and meta-analyses of data from master athletes.
- Age-associated decrements in physical function are offset in master athletes.
- Unfavourable fat mass gain is mitigated in master athletes.

Abstract

Introduction: The extent to which chronic exercise training preserves age-related decrements in physical function, muscle strength, mass and morphology is unclear. Our aim was to conduct a systematic review of the literature to determine to what extent chronically trained master athletes (strength/power and endurance) preserve levels of physical function, muscle strength, muscle mass and morphology in older age, compared with older and younger controls and young trained individuals.

Methods: The systematic data search included Medline, EMBASE, SPORTDiscus, CINAHL and Web of Science databases. **Inclusion criteria:** i) master athletes mean exercise training duration ≥ 20 years ii) master athletes mean age of cohort > 59 years iii) at least one measurement of muscle mass/volume/fibre-type morphology and/or strength/physical function.

Results: Fifty-five eligible studies were identified. Meta-analyses were carried out on maximal aerobic capacity, maximal voluntary contraction and body composition. Master endurance athletes ($42.0 \pm 6.6 \text{ ml.kg}^{-1}.\text{min}^{-1}$) exhibited $\text{VO}_{2\text{max}}$ values comparable with young healthy controls ($43.1 \pm 6.8 \text{ ml.kg}^{-1}.\text{min}^{-1}$, $P=0.84$), greater than older controls ($27.1 \pm 4.3 \text{ ml.kg}^{-1}.\text{min}^{-1}$, $P<0.01$) and master strength/power athletes ($26.5 \pm 2.3 \text{ ml.kg}^{-1}.\text{min}^{-1}$, $P<0.01$), and lower than young endurance trained individuals ($60.0 \pm 5.4 \text{ ml.kg}^{-1}.\text{min}^{-1}$, $P<0.01$). Master strength/power athletes (0.60 (0.28 to 0.93) $P<0.01$) and young controls (0.71 (0.06 to 1.36) $P<0.05$) were significantly stronger compared with the other groups. Body fat % was greater in master endurance athletes than young endurance trained (-4.44 % (-8.44 to -0.43) $P<0.05$) but lower compared with older controls (7.11 % (5.70 to 8.52) $P<0.01$).

Conclusion: Despite advancing age, this review suggests that chronic exercise training preserves physical function, muscular strength and body fat levels similar to that of young, healthy individuals in an exercise mode-specific manner.

Keywords: Sarcopenia, Lifelong exercise, Muscle mass, Muscle strength, Endurance Capacity.

1. Introduction

The UK population is projected to increase by ~25% between 2013 and 2060, from 64.1 to 80.1 million (Mitchell et al., 2012) which heralds a demographic shift towards an ageing society. This changing demographic presents a significant and overwhelming challenge to healthcare provision in the UK (Holloszy, 2000). Indeed, although individuals are living longer (i.e., lifespan), many endure a large portion of their later years with a number of age-related comorbidities (Seals et al., 2015). Extending the length of time individuals remain healthy and disease-free (i.e. health-span) with an emphasis on compressing morbidity is therefore an important focus (Seals et al., 2015). Physical function (e.g., aerobic capacity and muscular strength) typically declines with advancing age and this is often highlighted as a principal risk factor for the development of a number of degenerative chronic health conditions (Niccoli and Partridge, 2012). However, it has been suggested that exercise throughout the lifespan (i.e., ‘chronic’ exercise training) can attenuate or even prevent age-related declines in physical function. Understanding whether, and to what extent, chronic exercise training preserves physical function, muscle strength, mass and morphology is of great importance in the pursuit of appropriate countermeasures to age-related health deterioration.

Reductions of aerobic capacity (VO_{2max}) and muscular strength are major risk factors for all-cause mortality in older age (Lee et al., 2011; Ortega et al., 2012; Ruiz et al., 2008). VO_{2max} and muscular strength are often considered robust measures of physical function and health as they require successful integration of the cardiovascular, respiratory and neuromuscular systems (Harridge and Lazarus, 2017). The gradual decline of these bodily systems with ageing ultimately reduces the ability of older individuals to carry out activities of daily living (ADL); forcing many into a state of reduced physical independence and a poorer quality of life (Sonn, 1996). Delineating the relative contribution of primary ageing and environmental influences (or secondary ageing) to the age-related decline in physical function, muscle strength, mass and morphology is problematic. One aspect of secondary aging that is considered to be particularly influential is habitual physical activity. The majority of older adults reduce habitual physical activity with advancing age (Blair, 2009), and this is often accompanied by the presence of at least one chronic disease (Hung et al., 2011). However, a small sub-set of the population, referred to as master athletes, are unique in that they have chronically undertaken and continue to maintain high levels of physical activity, including structured exercise training. Indeed, Zampieri and colleagues (Zampieri et al., 2015) demonstrated that senior sportsmen from varied training backgrounds exhibited muscular strength, performance, myofibre properties and function comparable with young, healthy individuals. These findings suggest that chronic exercise training can preserve physical function and skeletal muscle properties in older age. As such, the study of Master athletes may allow us the opportunity to distinguish the contribution of primary and secondary ageing to the age-related decline in health, function and performance (Harridge and Lazarus, 2017; Lazarus and Harridge, 2007). However, Mackey and colleagues observed no difference in type I or type II fibre size between young and old regardless of training status, despite differences in VO_{2max} ; making it challenging to draw firm conclusions regarding the impact

ageing and/or chronic endurance exercise elicits on fibre area (Mackey et al., 2014). To further complicate the variable findings in these unique individuals, Piasecki and colleagues demonstrated that the loss of muscle size, strength and motor units in the *Tibialis anterior* was similar between master endurance athletes and age-matched untrained controls (Piasecki et al., 2016a). The inconsistent findings highlighted advocate the need for a quantitative summary of the existing literature surrounding the effect of chronic exercise training on indices of performance and skeletal muscle properties.

Earlier comparisons between young and older individuals and master athletes have typically included master athletes younger than 60 y (Gent and Norton, 2013; Kusy and Zielinski, 2014; Maffulli et al., 1994). Specifically, this systematic review will focus on master athletes 60 y or older as these individuals would typically have begun to experience age-related decrements in physical function, muscle strength, mass and morphology (Doherty, 2003; Janssen et al., 2000). Additionally, most systematic review comparisons between young and older individuals and master athletes have focused on single outcome measures, specifically body composition (Ballor and Keeseey, 1991), aerobic capacity (Fitzgerald et al., 1997; Wilson and Tanaka, 2000), muscular strength (Peterson et al., 2010) adaptations to training (Daskalopoulou et al., 2017) and protein supplementation (Doering et al., 2015). Therefore, the primary aim of this systematic review was to establish whether older individuals who have undertaken chronic exercise training, preserve physical function, muscular strength, mass and fibre properties (i.e. size and relative distribution) compared with untrained age-matched individuals, as well as younger trained and untrained individuals. A secondary aim was to determine the influence of exercise modality (i.e., strength/power vs. endurance) on the included parameters.

2. Methods

2.1. Information sources and literature search

A systematic literature search of online databases was conducted in November 2017 using selected key words, free text terms, indexed terms, and Boolean operators. The search strategies were applied to Medline, EMBASE, SPORTDiscus, CINAHL and Web of Science databases. Recursive searching of the bibliographies of eligible studies and relevant reviews was performed to identify additional articles. The systematic review was conducted in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) report (Moher et al., 2009).

2.2. Study Selection Criteria

2.2.1. Inclusion Criteria

Studies were included in the review if they met the following inclusion criteria: 1) Exercise training for a minimum of 20 years in the master athletes group, explicitly stated within the study. 2) Mean age of older cohorts older than 59 years. 3) Inclusion of at least one measurement of muscle mass/volume/fibre type morphology (fibre type, size, area) and/or a measurement of strength/physical function. 4) Muscle mass measurement using magnetic resonance imaging (MRI), computed tomography (CT), dual x-ray absorptiometry (DXA), air displacement plethysmography (BodPod), hydrostatic weighing, bioelectrical impedance analysis (BIA) or B-Mode ultrasonography. Physical function/strength/performance measurements to include one, or more, of: handgrip strength, isometric/isotonic strength/power/torque or aerobic capacity (VO_{2max}). 5) Freedom from any neurological, neuromuscular, cardiovascular and metabolic disease. 6) Studies published only in English with no date restrictions.

2.2.2. Exclusion Criteria

Studies were excluded from the review if: 1) The authors did not explicitly state the length of time that master athletes had been continuously training, or if that time was less than 20 years. 2) No inclusion of relevant measures of muscle mass/morphology or physical function. 3) Relevant data could not be obtained directly from potentially eligible articles or via contact with the study authors.

2.3. Participant criteria

Sedentary older control groups were required to be of a similar age to master athlete groups (mean group >59 years) and have undertaken little, to no, structured exercise training. Older control groups did not have to be completely sedentary compared with master athlete groups. Young controls were required to be younger than 40 years, and have undertaken little to no structured exercise training. Young controls did not have to be completely sedentary compared with young trained individuals, who were required to be younger than 40 years and undertaking either structured endurance or strength/power-based exercise training.

2.4. Study Selection

Titles and abstracts were screened for relevance by 2 reviewers (J.M. and B.J.S). Irrelevant titles were removed. Full-text articles were obtained for potentially relevant studies via a combination of online databases, hardcopy sourcing and direct contact with the authors, and these were further evaluated to determine whether they met the inclusion criteria. Studies deemed eligible were included in the systematic review. Two reviewers (J.M and B.J.S.) independently assessed full-texts for eligibility; any disagreements between the two reviewers were settled by consensus. All records were managed using the reference software EndNote (Thomson Reuters, v.X7)

2.5. Data Extraction

Predetermined variables were extracted from each of the included studies using a customised data extraction form (J.M and B.J.S). Measures of interest included participant characteristics (number, age, and anthropometrics), training type and duration, measurements of muscle mass, physical function (strength, aerobic capacity) and fibre-type characteristics along with various aspects of study design/assessment (measurement tool or analytical method). In situations where the necessary data could not be obtained, either directly from the article or by contacting the corresponding authors of the paper, the study (or particular outcome measure) was excluded from review and/or meta-analysis. Where BMI was not reported, it was calculated manually from the reported mean height and weight of the study groups.

2.6. Data Syntheses & Statistical Analyses

Statistical analyses were dependent upon the number of studies obtained and the associated outcomes measures in the relevant studies. If sufficient studies incorporating an eligible analytical protocol were identified for a single outcome measure (e.g., VO_{2max}), a meta-analysis was conducted. In cases where insufficient data were available from eligible studies to conduct a meta-analysis for a single outcome measure (e.g., muscle mass), findings were presented narratively/qualitatively.

Meta-analyses were performed on studies (and variables) which included direct comparisons (within study) between master athletes (power/endurance) and a non-exercising older controls (older control) or young trained/non-trained groups. Meta-analyses were carried out with a random effects model using RevMan software (Review Manager (RevMan) V.5.3. Copenhagen, The Nordic Cochrane Centre, The Cochrane Collaboration, 2014). Data in meta-analyses were presented as mean differences (MD)/standardised mean differences (SMD) \pm 95% confidence interval (CI). Standardised mean differences were presented only for outcomes reported using non-comparable scales (i.e. muscular strength). All data were

presented as mean \pm SD, along with the number of studies/study groups reporting that particular variable and the number of participants included in that comparison.

3. Results

3.1. Study Selection

A total of 14,572 studies were identified by the extensive literature search and a further 1 study was identified by manual searching of reference lists. Following removal of duplicates, 393 study titles and abstracts were screened resulting in 143 articles being excluded from the review; leaving 250 full texts to be independently screened (J.M and B.J.S). Figure 1 highlights the study identification, screening process and reasons for study exclusion.

3.2. Study Characteristics

The 55 included studies demonstrated substantial heterogeneity regarding the outcome measures and methodology (Table 1). Further, the participant characteristics displayed substantial incongruity, specifically the mode and level of exercise training, and the number of years training experience (Table 2). Twenty-one studies included young untrained control groups, 43 studies included 44 older control groups, 2 studies each included a young strength/power trained group, 11 studies included 12 endurance trained young groups and all studies included at least one master endurance and/or strength/power training group.

3.3. Participant Characteristics

The 55 eligible studies included 2449 participants (2181 were Male and 268 Female). In short, included groups were master endurance athletes (67.3 ± 5.1 years, 1.73 ± 0.04 m, 71.6 ± 5.2 kg, 56 study groups, $n=958$) and master power athletes (71.7 ± 4.8 years, 1.73 ± 0.03 m, 76.2 ± 8.0 kg, 15 study groups, $n=218$), older controls (67.9 ± 4.5 years, 1.73 ± 0.03 m, 78.2 ± 6.2 kg, 44 study groups, $n=746$), young endurance trained (25.4 ± 3.1 years, 1.79 ± 0.03 m, 70.1 ± 5.0 kg, 13 study groups, $n=143$), young power trained (26.0 ± 1.6 years, 1.80 ± 0.02

m, 77.0 ± 0.4 kg, 3 study groups, n=47) and young controls (26.6 ± 3.9 years, 1.79 ± 0.03 m, 75.9 ± 5.0 kg, 23 study groups, n=337). The participant characteristics and anthropometrics of the sub-groups included in the review are outlined in detail in Table 2.

3.4. Training characteristics

Experience – Master athletes had been training for 31.1 ± 9.3 (56 study groups, n=958) and 35.6 ± 9.6 (15 study groups, n=218) years for endurance and strength/power groups, respectively. Young athletes had been training for 6.1 ± 2.6 (13 study groups, n=143) and 11.2 ± 5.5 (3 study groups, n=47) years for endurance and strength/power groups, respectively.

Frequency - The included groups reported similar training frequency 4.6 ± 1.4 , 3.6 ± 1.1 , 5.0 ± 0.8 and 4.1 ± 2.5 times per week, for master endurance (21 study groups, n=339), master strength/power (7 study groups, n=111), young endurance (4 study groups, n=66) and young strength/power trained groups (2 study groups, n=35), respectively.

Duration – The included groups reported a similar number of training hours per week; master endurance 6.8 ± 3.0 h (19 study groups, n=298), master strength/power 6.3 ± 0.7 h (8 study groups, n=164) young endurance 7.7 ± 3.6 h (6 study groups, n=45) and young strength/power 10.0 ± 2.1 h (2 study groups, n=42), respectively.

Distance - Seventeen study groups of master endurance (44.5 ± 10.8 km, n=302) and 3 study groups of young endurance trained athletes (44.7 ± 2.9 km, n=30) completed similar weekly cycling distances.

3.5. Fat-Free Mass

A total of 12 studies (Carrick-Ranson et al., 2014a; Dub   et al., 2016; Hawkins et al., 2001; Hayes et al., 2015; Marcell et al., 2003; Marcell et al., 2014; Pollock et al., 2015; Proctor and Joyner, 1997; Sanada et al., 2009; Tarpenning et al., 2004b; Trappe et al., 2013; Yataco et al.,

1997) reported indices of whole body fat-free mass (FFM) using DXA, hydrostatic weighing or bioelectrical impedance. Nineteen study groups included master endurance athletes (55.2 ± 6.1 kg FFM, $n=366$), 5 study groups included older controls (54.5 ± 7.7 kg FFM, $n=122$), 1 study group included young controls (53.8 ± 5.7 kg FFM, $n=23$) and 4 study groups included young endurance trained individuals (54.8 ± 7.3 kg FFM, $n=56$).

3.6. Fat Mass

Only three studies (Dub   et al., 2016; Schmidt et al., 2015; Yataco et al., 1997) reported measures of whole-body fat mass (FM) measured using DXA or hydrostatic weighing. Three study groups included master endurance athletes (14.1 ± 3.6 kg FM, $n=91$), 2 study groups included older untrained individuals (20.1 ± 6.3 kg FM, $n=65$) and 1 study group included young endurance trained individuals (12.0 ± 4.2 kg FM, $n=14$).

3.7. Body Fat Percentage

A meta-analysis was conducted for body fat % for studies that made direct comparisons with master endurance athletes (Figure 2); this allowed for the greatest number of within-study comparisons to be incorporated into the statistical analysis. Twenty-nine studies (Aagaard et al., 2007; Arbab-Zadeh et al., 2004; Ari et al., 2004; Bjork et al., 2012; Buford et al., 2010; Buyukyazi, 2004; Carrick-Ranson et al., 2014b; Cristea et al., 2008; Dub   et al., 2016; Hawkins et al., 2001; Hayes et al., 2015; Katzel et al., 1998; Korhonen et al., 2006; Korhonen et al., 2012; Marcell et al., 2003; Marcell et al., 2014; Matelot et al., 2016; Mortensen et al., 2012; Nyberg et al., 2012; Ojanen et al., 2007; Pollock et al., 2015; Proctor and Joyner, 1997; Sallinen et al., 2008; Sanada et al., 2009; Schmidt et al., 2015; Tarpenning et al., 2004a; Trappe et al., 2013; Witkowski et al., 2010; Yataco et al., 1997) reported data for body fat percentage measured using bioelectrical impedance, DXA, hydrostatic weighing or multiple-

site skinfold. Thirty study groups included master endurance athletes (19.7 ± 3.8 %, $n=594$), 11 study groups included master strength/power athletes (16.4 ± 4.4 %, $n=136$), 19 study groups older control (24.5 ± 4.6 %, $n=361$), 5 study groups included young endurance trained (15.4 ± 5.2 %, $n=63$), 2 study groups included young strength/power trained individuals (14.1 ± 3.5 %, $n=42$) and 8 study groups included young controls (17.4 ± 3.0 %, $n=126$).

Master endurance athletes had a significantly lower body fat % than older control individuals ($P<0.01$), and a significantly greater body fat % than young endurance trained ($P<0.05$). No significant differences were observed in the body fat % between master endurance athletes when compared with young controls and master strength/power athletes. Young strength/power trained individuals were not included in the meta-analyses as no eligible studies made direct within-study comparisons with the other included groups.

3.8. Maximal Oxygen Consumption (VO_{2max})

A meta-analysis was conducted for VO_{2max} for studies that made direct comparisons with master endurance athletes (Figure 3); this allowed for the greatest number of within-study comparisons to be incorporated into the statistical analysis. VO_{2max} was measured in 43 studies (Aagaard et al., 2007; Anselme et al., 1994; Arbab-Zadeh et al., 2004; Ari et al., 2004; Bhella et al., 2014; Bjork et al., 2012; Buford et al., 2010; Buyukyazi, 2004; Carrick-Ranson et al., 2014b; Dub   et al., 2016; Franzoni et al., 2005; Galetta et al., 2005; Galetta et al., 2006; Hawkins et al., 2001; Hayes et al., 2015; Katzel et al., 1998; Katzel et al., 2001; Mackey et al., 2014; Marcell et al., 2003; Marcell et al., 2014; Matelot et al., 2016; Mikkelsen et al., 2013; Molmen et al., 2012; Mortensen et al., 2012; Mucci et al., 1999; Nyberg et al., 2012; Ojanen et al., 2007; Pollock et al., 2015; Prasad et al., 2007; Prefaut et al., 1994; Proctor and Joyner, 1997; Rivier et al., 1994; Sanada et al., 2009; Schmidt et al., 2015; Shibata and Levine, 2012; Sundstrup et al., 2010; Suominen and Rahkila, 1991;

Tarpenning et al., 2004a; Thomas et al., 2013; Trappe et al., 2013; Witkowski et al., 2010; Yataco et al., 1997) using treadmill or cycle/rowing ergometer protocols. All studies reported the data relative to bodyweight ($\text{ml.kg}^{-1}.\text{min}^{-1}$). Forty-nine study groups included master endurance athletes ($42.0 \pm 6.6 \text{ ml.kg}^{-1}.\text{min}^{-1}$, $n=889$), 3 study groups included master power athletes ($26.5 \pm 2.3 \text{ ml.kg}^{-1}.\text{min}^{-1}$, $n=37$), 32 study groups included older controls ($27.1 \pm 4.3 \text{ ml.kg}^{-1}.\text{min}^{-1}$, $n=602$), 13 study groups included young endurance trained individuals ($60.0 \pm 5.4 \text{ ml.kg}^{-1}.\text{min}^{-1}$, $n=143$) and 16 study groups included young controls ($43.1 \pm 6.8 \text{ ml.kg}^{-1}.\text{min}^{-1}$, $n=221$). $\text{VO}_{2\text{max}}$ was higher in master endurance athletes than older controls ($P<0.0001$) and master power athletes ($P=0.0005$). $\text{VO}_{2\text{max}}$ was higher in endurance trained young than all other groups ($P < 0.01$). $\text{VO}_{2\text{max}}$ was higher in young controls than older controls ($P<0.01$) and master strength/power athletes ($P<0.01$). No significant differences were observed between young controls and master endurance athletes or between older controls and master strength/power athletes. Young strength/power trained individuals were not included in the meta-analyses as no eligible studies made direct within-study comparisons with the other included groups.

3.9. Strength

Maximal voluntary contraction (MVC) was measured in 16 studies (Aagaard et al., 2007; Coupe et al., 2014; Korhonen et al., 2006; Korhonen et al., 2012; Marcell et al., 2014; Mikkelsen et al., 2013; Mosole et al., 2014; Pollock et al., 2015; Power et al., 2012; Power et al., 2010b; Sanada et al., 2009; Sipila and Suominen, 1991; Stenroth et al., 2016; Sundstrup et al., 2010; Suominen and Rahkila, 1991; Tarpenning et al., 2004a; Zampieri et al., 2015); 9 studies with 22 study groups were included in a meta-analysis. A meta-analysis was conducted for studies that made direct comparisons with master endurance athletes (Figure 4); to allow for the greatest number of within-study comparisons to be incorporated into the

statistical analysis. Due to the diversity of measurement scales/methods of assessment (i.e. knee extension, plantar flexion, elbow flexion and handgrip dynamometry) data are presented as SMD \pm 95% CI in figure 4. MVC was significantly greater in master strength/power athletes (0.60 (0.28, 0.93)) and young healthy controls (0.71 (0.06, 1.36)) than master endurance athletes $P < 0.01$ and $P < 0.05$, respectively. No significant differences were observed in MVC between master endurance athletes when compared with older controls and young endurance trained individuals. Young strength/power trained individuals were not included in the meta-analyses as no eligible studies made direct within-study comparisons with the other included groups.

3.10. Muscle Architecture

Three studies reported muscle architecture outcomes (Korhonen et al., 2006; Ojanen et al., 2007; Sipila and Suominen, 1991); included in those studies were measurements of muscle thickness (3 studies) and fascicle length (1 study). Of the studies that measured muscle thickness, one study (Korhonen et al., 2006) used the midpoint of the *vastus lateralis* in young controls 18-33 y (2.61 ± 0.08 cm, $n=16$) and master sprinters of 60-69 (2.1 ± 0.09 cm, $n=21$) and 70-84 y (1.96 ± 0.08 cm, $n=20$). Another study (Ojanen et al., 2007) summed muscle thickness measurements of the *vastus lateralis* and *vastus intermedius* in master throwers of 65 (3.9 ± 0.7 cm, $n=12$) and 70 (3.7 ± 0.7 cm, $n=9$) years compared with older controls, 60 (3.8 ± 0.4 cm, $n=10$) and 75 (3.1 ± 0.2 cm, $n=5$), with no differences between the groups. The final study (Sipila and Suominen, 1991) measured muscle thickness of the *rectus femoris*, finding no difference between master strength/power athletes (2.73 ± 0.37 cm, $n=7$), master endurance athletes (2.77 ± 0.39 cm, $n=14$) and older controls (2.8 ± 0.56 cm, $n=11$). One study (Korhonen et al., 2006) included measurements of *vastus lateralis* fascicle length which identified no significant differences between the groups of 18-33 year olds

(7.91 ± 0.49 cm, $n=16$), 60-69 (7.99 ± 0.27 cm, $n=21$) and 70-84 (7.38 ± 0.27 cm, $n=20$) year old sprint athletes.

3.11. Muscle Cross-Sectional Area

Four studies (Couppe et al., 2014; Mikkelsen et al., 2013; Rantalainen et al., 2014; Sipila and Suominen, 1991) reported muscle CSA; two of which used MRI at the mid-thigh level, another used mid-thigh CSA with B-mode ultrasonography and another study used p-QCT to measure mid-tibia muscle CSA. Mid-thigh muscle CSA was reported in two studies, which highlighted muscle size being greater in younger individuals compared with older individuals and also greater in trained individuals compared with untrained controls; young endurance trained (7859 ± 636 mm², $n=10$), young controls (6792 ± 696 mm², $n=12$), master endurance trained (6481 ± 775 mm², $n=15$) and older controls (5504 ± 727 mm², $n=12$) (Couppe et al., 2014; Mikkelsen et al., 2013). Muscle CSA measured using ultrasonography in another study did not identify any differences between master power athletes (5250 ± 1080 mm², $n=7$), master endurance athletes (5270 ± 880 mm², $n=14$) or older controls (4840 ± 1110 mm², $n=11$) (Sipila and Suominen, 1991). CSA of the mid-tibia region indicated that exercising individuals have a larger muscle CSA than non-exercising individuals and young individuals have a larger mid-tibia muscle CSA than older controls with no age-group interaction observed (Rantalainen et al., 2014); young power athletes (7140 ± 820 mm², $n=26$), young control (7040 ± 1310 mm², $n=41$), master power athletes (6270 ± 910 mm², $n=35$), older controls (5890 ± 890 mm², $n=24$).

3.12. Muscle Fibre Area

In total 9 studies (Aagaard et al., 2007; Cristea et al., 2008; Korhonen et al., 2006; Larsson et al., 1997; Mackey et al., 2014; Mosole et al., 2014; Sundstrup et al., 2010; Tarpenning et al.,

2004a; Zampieri et al., 2015) measured muscle fibre morphology (type/distribution), including measures of type I, type II, type IIa, type IIx, type IIax and denervated fibres; using a variety of analytical techniques (Table 1). Type 1 fibre area was reported in 5 groups of master endurance athletes ($5367 \pm 588 \mu\text{m}^2$, $n=74$), 4 groups of master power athletes ($4750 \pm 1273 \mu\text{m}^2$, $n=34$), 3 groups of older controls ($5488 \pm 459 \mu\text{m}^2$, $n=28$), 2 groups of young controls ($4282 \pm 26 \mu\text{m}^2$, $n=28$) and 1 group of young endurance athletes ($5550 \pm 1337 \mu\text{m}^2$, $n=10$).

Type 2 fibre area was reported in 3 groups of master endurance athletes ($4478 \pm 347 \mu\text{m}^2$, $n=55$), 1 group of older controls ($4149 \pm 903 \mu\text{m}^2$, $n=12$) 1 group of young controls ($4783 \pm 872 \mu\text{m}^2$, $n=12$) and 1 group of young endurance trained ($5498 \pm 1559 \mu\text{m}^2$, $n=10$).

Type 2a fibre area was reported in 2 groups of master endurance athletes ($5043 \pm 41 \mu\text{m}^2$, $n=19$), 4 groups of master strength/power athletes ($4755 \pm 1404 \mu\text{m}^2$, $n=34$), 2 groups of older controls ($5411 \pm 484 \mu\text{m}^2$, $n=16$) and 1 young control group ($4700 \pm 560 \mu\text{m}^2$, $n=16$).

Type 2x fibre area was reported in 2 groups of master endurance athletes ($3955 \pm 88 \mu\text{m}^2$, $n=19$), 4 groups of master strength/power athletes ($4019 \pm 990 \mu\text{m}^2$, $n=34$), 2 groups of older controls ($3794 \pm 0 \mu\text{m}^2$, $n=16$) and 1 young control group ($3200 \pm 2720 \mu\text{m}^2$, $n=16$).

Type 2ax fibre area was reported in 1 young control group ($3700 \pm 760 \mu\text{m}^2$, $n=16$) and 3 groups of master strength/power athletes ($4120 \pm 495 \mu\text{m}^2$, $n=27$).

3.13. Muscle Fibre Distribution

Type 1 fibre distribution was reported in 7 groups of master endurance athletes (60.8 ± 10.7 %, $n=96$), 5 groups of master strength/power athletes (48.0 ± 8.0 %, $n=59$), 6 groups of older controls (49.8 ± 4.2 %, $n=45$), 4 young control groups (43.5 ± 4.5 %, $n=37$), and 2 young endurance trained groups (51.5 ± 13.4 %, $n=15$).

Type 2 fibre distribution was reported in 5 groups of master endurance athletes (38.4 ± 11.3 %, $n=77$), 3 groups of older controls (50.3 ± 4.0 %, $n=27$), 2 young control groups (53.5 ± 5.0 %, $n=17$) and 2 young endurance trained groups (48.6 ± 13.5 %, $n=15$).

Type 2a fibre distribution was reported in 2 groups of master endurance athletes (32.6 ± 10.7 %, $n=19$), 5 groups of master strength/power athletes (31.8 ± 3.8 %, $n=59$), 2 groups of older controls (23.5 ± 0 %, $n=16$) and 1 young control group (35 ± 12 %, $n=16$).

Type 2x fibre distribution was reported in 3 groups of master endurance athletes (10.3 ± 2.7 %, $n=21$), 5 groups of master strength/power athletes trained individuals (10.7 ± 4.1 %, $n=59$) 3 groups of older controls (22.2 ± 13.1 %, $n=18$) and 2 young control groups (7.5 ± 6.4 %, $n=20$).

Type 2ax fibre distribution was reported in 2 groups of master endurance athletes (6.3 ± 8.1 %, $n=9$), 4 groups of master strength/power athletes (11.6 ± 2.6 %, $n=52$), 2 groups of older controls (5.9 ± 5.8 %, $n=8$), 2 young control groups (12.0 ± 00 %, $n=20$) and 1 groups of young endurance trained individuals (0.5 ± 0.6 %, $n=5$).

The percentage of denervated fibres, defined as fibre size smaller than $30\mu\text{m}$, was reported in 2 groups of master endurance athletes (1.9 ± 0.1 %, $n=22$), 2 groups of older controls (5.3 ± 1.8 %, $n=15$) 1 young control group (0.3 ± 0.0 %, $n=5$) and 1 young endurance trained group (0.4 ± 0.5 %, $n=5$).

4. Discussion

To our knowledge, this is the first systematic review and meta-analyses to focus on the effect of long-term exercise (i.e., endurance or strength/power) on physical function, muscular strength, muscle mass and morphology, to understand whether chronic exercise training preserves these parameters compared with age-matched untrained individuals, as well as younger trained and untrained individuals. There has been considerable debate about the relative contribution of primary and secondary ageing to the deterioration in performance and skeletal muscle parameters and whether or not this deterioration is inevitable in ageing. Our principal findings demonstrate that master endurance athletes are able to completely prevent the decline in $\text{VO}_{2\text{max}}$ found in age-matched untrained individuals; to values similar to those observed in young untrained individuals. In addition, we demonstrate that master strength/power athletes possess greater strength compared with age-matched master endurance athletes and untrained individuals; comparable with young untrained individuals. Further, all master athletes maintained a similar body fat percentage to untrained young controls, whereas untrained older individuals had a higher body fat percentage than endurance trained young. In the absence of structured exercise training, many older individuals displaying impairments in exercise performance and functional capacity (Tanaka and Seals, 2008), increased fat and reduced lean mass (Evans and Campbell, 1993) and changes to muscle fibre morphology (i.e. fibre atrophy and shifts in fibre sub-type) (Zampieri et al., 2015). Nevertheless, our findings, as well as those of others, demonstrate that older individuals maintain the capacity to adapt to exercise stimuli (Malbut et al., 2002; Newton et al., 2002). The results from this review highlight that regardless of the exercise modality (i.e., endurance or strength/power), chronic exercise training delays the canonical age-related deterioration in physical function and body composition. The maintenance/continuation of

structured exercise training into older age may therefore be seen as the cornerstone to optimal ageing and extension of the health-span in our ageing population.

4.1. $\text{VO}_{2\text{max}}$

The reductions in function of multiple bodily systems observed with ageing leads to a decline of $\text{VO}_{2\text{max}}$ at a rate of equivalent to ~10-12% per decade (or ~1% per annum) (Rogers et al., 1990). Cardiorespiratory fitness is independently associated with all-cause mortality regardless of age, smoking status, body composition, and other risk factors (Lee et al., 2010; Lee et al., 2011) and thus a high $\text{VO}_{2\text{max}}$ may be protective against premature mortality. Meta-analysis comparisons revealed a 57% ($15.4 \text{ ml.kg}^{-1}.\text{min}^{-1}$) greater $\text{VO}_{2\text{max}}$ in master endurance athletes compared with age-matched untrained individuals. Furthermore, master endurance athletes exhibited a greater $\text{VO}_{2\text{max}}$ ($7.8 \text{ ml.kg}^{-1}.\text{min}^{-1}$) than master strength/power athletes. Collectively, these findings highlight that age-related declines in $\text{VO}_{2\text{max}}$ can be prevented by chronic exercise in an exercise mode-specific manner.

The reductions in $\text{VO}_{2\text{max}}$ reported in master athletes appear to begin at the same age and decline at a similar (Faulkner et al., 2008; Wilson and Tanaka, 2000), if not greater ((Eskurza et al., 2002; Fitzgerald et al., 1997; Tanaka et al., 1997)), rate compared with age-matched untrained individuals; providing evidence that despite continuous endurance exercise training there is an unavoidable decline of aerobic capacity. It is proposed that as age progresses, master athletes undergo a greater alteration to their activity status (e.g. training intensity and volume) (Eskurza et al., 2002; Fitzgerald et al., 1997), which may underpin the accelerated rate of decline in $\text{VO}_{2\text{max}}$ observed (Eskurza et al., 2002; Tanaka et al., 1997). However, the studies included in the current review highlighted no observable difference in training frequency (Aagaard et al., 2007; Bhella et al., 2014; Buyukyazi, 2004; Carrick-Ranson et al.,

2014b; Coupe et al., 2014; Dub   et al., 2016; Franzoni et al., 2005; Galetta et al., 2005; Galetta et al., 2006; Korhonen et al., 2006; Korhonen et al., 2012; Larsson et al., 1997; Marcell et al., 2003; Marcell et al., 2014; Molmen et al., 2012; Ojanen et al., 2007; Power et al., 2010b; Sallinen et al., 2008; Sanada et al., 2009; Sipila and Suominen, 1991; Sundstrup et al., 2010; Witkowski et al., 2010; Yataco et al., 1997; Zampieri et al., 2015), distance (Arbab-Zadeh et al., 2004; Coupe et al., 2014; Hawkins et al., 2001; Mackey et al., 2014; Marcell et al., 2003; Marcell et al., 2014; Mikkelsen et al., 2013; Power et al., 2010b; Shibata and Levine, 2012; Stenroth et al., 2016; Suominen and Rahkila, 1991; Tarpenning et al., 2004a; Thomas et al., 2013; Witkowski et al., 2010) and session duration (Ari et al., 2004; Bjork et al., 2012; Buford et al., 2010; Buyukyazi, 2004; Carrick-Ranson et al., 2014b; Coupe et al., 2014; Korhonen et al., 2006; Korhonen et al., 2012; Matelot et al., 2016; Mortensen et al., 2012; Mosole et al., 2014; Mucci et al., 1999; Nyberg et al., 2012; Proctor and Joyner, 1997; Rantalainen et al., 2014; Rivier et al., 1994; Sanada et al., 2009; Schmidt et al., 2015; Stenroth et al., 2016; Suominen and Rahkila, 1991; Trappe et al., 2013; Zampieri et al., 2015) between younger and older endurance athletes; although alterations to training intensity cannot be excluded as none were reported. $\text{VO}_{2\text{max}}$ values included in this meta-analysis were ~32% lower in master endurance athletes ($42 \pm 6.6 \text{ ml.kg}^{-1}.\text{min}^{-1}$) than young endurance trained individuals ($62.0 \pm 5.4 \text{ ml.kg}^{-1}.\text{min}^{-1}$), which is supported by recent research demonstrating an inescapable reduction in $\text{VO}_{2\text{max}}$ in master endurance athletes, despite continuous levels of endurance exercise training (Everman et al., 2018). It is beyond the scope of this review to identify the relative rate of decline in $\text{VO}_{2\text{max}}$ as no longitudinal studies were incorporated. Regardless of the rate at which $\text{VO}_{2\text{max}}$ declines with age, the maintenance of endurance-type exercise and thus cardiorespiratory fitness are paramount to offset age-associated health decrements. The greater $\text{VO}_{2\text{peak}}$ in these highly trained master

athletes may therefore allow larger reductions to occur before reduced physical capacity and functional independence is compromised, compared with age-matched untrained individuals.

Although not established in the current review, it is generally acknowledged that reduced physical activity is a key contributor towards the development of disease, disability and physical dysfunction (Booth et al., 2012). Continuation of exercise training may protect against the deterioration of health status and age-associated co-morbidities, by commencing the decline in bodily function from an elevated $\text{VO}_{2\text{peak}}$ the ageing process reflects inherent ageing uncompromised by inactivity (Harridge and Lazarus, 2017). From a mechanistic perspective, the parameters that determine $\text{VO}_{2\text{max}}$ (cardiac output and arterio-venous difference) are known to decrease with advancing age; inclusive of master athletes (Tanaka and Seals, 2008). The relative contribution of each parameter is unclear, though the reduction of $\text{VO}_{2\text{max}}$ observed in master endurance athletes may be due to maintenance of stroke volume and O_2 extraction, as they do not appear to decrease by the same magnitude as heart rate with age (Pollock et al., 1987). Consistent with this, maximal heart rate has been shown to decrease at approximately $0.7 \text{ beat} \cdot \text{min}^{-1} \cdot \text{year}^{-1}$, and this is similar regardless of sex or physical activity status (Rodeheffer et al., 1984). In addition, peripheral factors influencing the arterio-venous difference proposed to contribute to the differences in $\text{VO}_{2\text{max}}$ between older, young, trained and control groups, include the amount of fat-free and fat mass (Tanaka and Seals, 2008), which have been shown to decrease and increase, respectively, with advancing age (Janssen et al., 2000; Kuk et al., 2009). However, the results from the present review demonstrated no discernible differences between groups in the amount of fat-free mass for master endurance athletes, age-matched untrained individuals, young untrained individuals and young endurance trained individuals. Wroblewski and colleagues (2011) demonstrated that chronic endurance exercise is able to preserve thigh muscle CSA in master

athletes (Wroblewski et al., 2011). From our data, it is perhaps surprising that the older untrained individuals did not display a marked reduction in fat-free mass with advancing age. However, it has previously been shown that $\text{VO}_{2\text{max}}$ remains lower in older trained individuals compared with young trained individuals, despite corrections for muscle mass (Proctor and Joyner, 1997). Therefore, it is more likely that reductions in capillary density, mitochondrial function and enzyme activity (Coggan et al., 1990) are responsible for the lower $\text{VO}_{2\text{max}}$ values observed in master endurance athlete and older controls.

4.2. Strength

Muscle strength and power are ~40 and ~80 % lower in older vs. younger individuals (Thom et al., 2007). At the top level of competition, this is reflected by decreases in sprint times, jumping and throwing distances (Gava et al., 2015). In terms of the general population, the functional significance of this decline impacts individuals' ability to maintain ADL such as stair climbing, rising from a chair or opening a jar (Hairi et al., 2010). Moreover, low levels of muscular strength are strongly associated with an elevated risk of functional impairment (Cruz-Jentoft et al., 2010) and all-cause mortality (Ortega et al., 2012; Ruiz et al., 2008). The current meta-analyses (Figure 3) revealed that chronic endurance exercise does not prevent age-related declines in muscular strength. However, strength was preserved in master strength/power athletes to a level comparable with young untrained individuals, again suggesting that preservation of physical function into older age is specific to the mode of exercise performed.

It should be noted that assessment of strength within the studies included in the meta-analyses was achieved through a variety of methods; knee extension MVC, unilateral (Aagaard et al., 2007; Couppe et al., 2014; Korhonen et al., 2012; Marcell et al., 2014; Mikkelsen et al., 2013; Mosole et al., 2014; Pollock et al., 2015; Sipila and Suominen, 1991;

Sundstrup et al., 2010; Zampieri et al., 2015) and bilateral (Korhonen et al., 2006), plantar flexion MVC (Stenroth et al., 2016), dorsiflexion MVC (Power et al., 2010b), elbow flexion MVC (Power et al., 2012) and handgrip strength (Sanada et al., 2009; Suominen and Rahkila, 1991)). In addition, the present review lacked a young strength/power trained group for comparison, as no studies incorporating this population met the inclusion criteria for the review. Therefore, we cannot draw firm conclusions on whether master strength/power athletes were able to maintain strength similar to that of young strength/power trained athletes. However, it is generally accepted that, similar to VO_{2max} , there is an inevitable decline in muscle strength/power with ageing (Goodpaster et al., 2006; Rittweger et al., 2009), evidenced longitudinally in the performance decrements of master power vs. young power trained athletes (Gava et al., 2015). This suggests that the relative rate of decline in muscle strength is similar between trained individuals and age-matched controls. However, the higher absolute levels of strength provide strength-trained individuals with a much greater strength reserve, thus delaying the onset of impaired function and loss of independence.

4.3. Muscle Mass and Morphology

One mechanism responsible for age-related strength loss is the decline in muscle mass (sarcopenia) (Narici and Maffulli, 2010). In young healthy individuals, muscle mass is generally maintained until the 5th decade of life, after which loss of mass progresses at a rate of ~0.5-1% per year (Mitchell et al., 2012); and is exacerbated by protracted disuse events (Alkner and Tesch, 2004). Thus, by the age of 80 years an individual may have lost ~30-40% of peak muscle mass (Janssen et al., 2000). Due to the central role of skeletal muscle in physical function, basal metabolism and nutrient deposition, muscle loss can have significant health implications. The results from the current review suggest no age or training-related differences in muscle mass between groups (master endurance, older untrained, young

untrained and young endurance trained individuals). This may be due to a paucity of studies that incorporated muscle mass assessment, or that most of the included studies used techniques (BIA, DXA, hydrostatic weighing) with lower precision and sensitivity in cross-sectional comparisons (MacDonald et al., 2011). The absence of any difference in muscle mass between groups is perhaps surprising given that the older individuals included in the current review were over 60 years and, therefore, beyond the age-range where sarcopenia or pre-sarcopenia (loss of muscle mass prior to any functional decline (Pereira et al., 2015)) may begin to manifest. The lack of consistency between studies highlights that further investigation into age and training-related differences in muscle mass is warranted.

It has been shown muscle mass/volume is associated with muscular strength in young and older men and women (Strasser et al., 2013; Young et al., 1984), however there is a clear dissociation in the rate at which each declines, with strength loss progressing at a greater rate than muscle loss (Delmonico et al., 2009; Frontera et al., 2000).

Concomitant with the changes in muscle mass, alterations to the neuromuscular system may also influence muscle force generating capacity, including reductions in the number of motor units, increased size and stimulation thresholds of existing motor units as a result of cyclical denervation and re-innervation, and increased instability of transmission at the neuromuscular junction (Piasecki et al., 2016b; Piasecki et al., 2015). Two studies (Mosole et al., 2014; Zampieri et al., 2015) identified the presence of greater numbers of denervated fibres in the muscles of the older controls, when compared with young and older untrained individuals. This lends credence to the notion that chronic exercise training, both endurance and resistance, is able to preserve the neural component of muscular contraction. There is evidence to suggest that the muscle quality (i.e., the force per unit of muscle) is more important than muscle mass per se and more closely associated with mortality (Newman et

al., 2006). Muscle quality diminishes with age due to changes in architecture (Strasser et al., 2013), fibre type morphology (Lexell, 1995) fat and non-contractile tissue infiltration (Kent-Braun et al., 2000), satellite cells and myonuclei (Kadi et al., 2004). Although it was not possible to draw firm conclusions on the impact of chronic exercise training on muscle mass and quality, it is clear that chronic strength/power exercise can prevent age-associated strength decrements.

Ageing is accompanied by a reduction in the total number of muscle fibres, but more critically the cross-sectional area and proportion of Type II fibres (Lexell, 1995). However, due to the paucity of studies reporting muscle cross sectional area (Couppe et al., 2014; Mikkelsen et al., 2013; Rantalainen et al., 2014; Sipila and Suominen, 1991), muscle architecture (Korhonen et al., 2006; Ojanen et al., 2007; Sipila and Suominen, 1991) and fibre morphology (Aagaard et al., 2007; Cristea et al., 2008; Korhonen et al., 2006; Larsson et al., 1997; Mackey et al., 2014; Mosole et al., 2014; Sundstrup et al., 2010; Tarpenning et al., 2004a; Zampieri et al., 2015), it is challenging to elucidate their relative contribution to the observed loss or preservation of muscle mass and strength between master athletes and age-matched untrained individuals. Nevertheless, previous studies have highlighted an association between muscle architecture and performance (Kumagai et al., 2000), and that muscle architecture may differ across sporting disciplines (Abe et al., 2000). Upon further investigation, differences in muscle CSA, thickness and morphology may be an artefact of differing analytical methods (i.e. MRI, CT, ultrasound) at divergent anatomical sites (i.e. thigh vs. mid-tibia). Though not statistically analysed in the current review, individual studies have shown that master strength/power athletes maintain greater fibre cross-sectional area compared with untrained older individuals (Aagaard et al., 2007; Korhonen et al., 2006). In addition to fibre atrophy, ageing increases the intramuscular infiltration of fat and connective

tissue (Taaffe et al., 2009), impairing contractile properties (Lexell, 1995). Studies have revealed conflicting findings with respect to muscle fibre distribution between young and older endurance trained individuals (Mackey et al., 2014; Mosole et al., 2014; Sundstrup et al., 2010; Zampieri et al., 2015), which are likely underpinned by differences in the specific mode of exercise training and analytical methods used (Summary data for studies that measured these outcomes demonstrate large heterogeneity; presented in Table 3).

4.4. Body Fat Mass

Age-related alterations in body composition, specifically the increase in adiposity, likely contributes to impairments in muscle strength and physical function, increases dependence on support services and the likelihood of institutionalised care (Guralnik et al., 1996) and ultimately presents a significant risk factor for mortality (Kuk et al., 2006). The current meta-analyses (Figure 2) illustrated that master endurance athletes had a significantly lower body fat percentage compared with age-matched controls. Body fat percentage was similar between master endurance, master strength/power and untrained young individuals, whereas young endurance trained individuals had a significantly lower body fat percentage than master endurance trained individuals. These data indicate that chronic exercise, endurance or strength/power oriented, can attenuate the increase in body fat with ageing. It has been shown that higher levels of physical activity are preventative for body fat mass gain (Ekelund et al., 2011). Further, the reduction in physical activity that occurs during ageing (from retirement, family commitments, and a lack of other preoccupations) is a critical driver of increasing body fat mass (Booth et al., 2012). Unfortunately, few studies included in this review provided data for absolute values of fat and fat-free mass, making it difficult to draw conclusions about effect that chronic exercise training has on these parameters. Interestingly, it has previously been shown that obese individuals possess higher levels of fat-free mass

compared with healthy older individuals (Murton et al., 2015), suggesting a minor protective role of obesity against sarcopenia. Nevertheless, we posit that muscle quality, and not quantity *per se*, plays a more important role in the maintenance of whole-body metabolic health (Smeuninx et al., 2017).

4.5. Conclusions and Practical applications

The aim of this systematic review and meta-analyses was to determine whether, and to what extent, chronic exercise preserves some of the functional and biological decrements attributed to ageing. This review demonstrates that chronic exercise may delay age-associated decrements in physical function in an exercise-mode specific manner and also protects against unfavourable changes in body composition.

Current physical activity guidelines for older adults suggest 150 minutes per week of moderate-to-vigorous physical activity per week, unless chronic conditions prevent them doing so (American College of Sports, 2009). Guidelines also recommend that older adults incorporate some form resistive based exercise at least twice a week. However, the prevalence of functional impairment and reduced independence in older age suggests many older individuals are not meeting these criteria. The master athlete cohorts included in this review provide evidence that canonical age-related impairments in physical function, cardiorespiratory fitness, muscular strength and body composition can be delayed through chronic training, in an exercise mode-specific manner. The continuation of endurance type exercise to maintain high levels of cardiorespiratory fitness and strength/power training to preserve muscular strength offers a viable strategy to extend the health-span of older individuals, compressing the area under the morbidity curve and allowing maintenance of functional independence and good quality of life. It is apparent that few high quality studies

have been conducted in unique master athlete cohorts, and that further research studies encompassing a comprehensive selection of sophisticated measurement tools need to be conducted in order to fully characterise specific benefits of strength/power training and endurance training. Finally, the inclusion of only 268 females in this review reflects a preponderance of males included in the study of master athletes. This disparity warrants further investigation, as it has been documented that men and women may undergo somewhat divergent deterioration in skeletal muscle mass and strength with advancing age, perhaps due to reductions in sex-specific hormones (Hansen and Kjaer, 2014; Kim et al., 2016; Smith et al., 2008). As such, the development of sex-specific exercise training interventions, or manipulation of certain training variables, may be an important consideration.

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Contributions

All authors gave their final approval of the version of the article to be published. JM, LB, BJS and CG conceived and designed the search strategy and protocol. JM and BJS conducted the search. JM and BJS carried out the data analysis and prepared the figures. JM, LB, BJS and CG interpreted the results and drafted the manuscript.

Disclosures

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Appendices

Appendices A) Systematic Review search strategy

References

- Aagaard, P., Magnusson, P.S., Larsson, B., Kjaer, M., Krstrup, P., 2007. Mechanical muscle function, morphology, and fiber type in lifelong trained elderly. *Medicine and Science in Sports and Exercise* 39, 1989-1996.
- Abe, T., DeHoyos, D.V., Pollock, M.L., Garzarella, L., 2000. Time course for strength and muscle thickness changes following upper and lower body resistance training in men and women. *Eur J Appl Physiol* 81, 174-180.
- Alkner, B.A., Tesch, P.A., 2004. Knee extensor and plantar flexor muscle size and function following 90 days of bed rest with or without resistance exercise. *Eur J Appl Physiol* 93, 294-305.
- American College of Sports, M., 2009. American College of Sports Medicine position stand. Progression models in resistance training for healthy adults. *Medicine and science in sports and exercise* 41, 687-708.
- Anselme, F., Caillaud, C., Couret, I., Rossi, M., Prefaut, C., 1994. Histamine and exercise-induced hypoxemia in highly trained athletes. *Journal of Applied Physiology* 76, 127-132.
- Arbab-Zadeh, A., Dijk, E., Prasad, A., Fu, Q., Torres, P., Zhang, R., Thomas, J.D., Palmer, D., Levine, B.D., 2004. Effect of aging and physical activity on left ventricular compliance. *Circulation* 110, 1799-1805.
- Ari, Z., Kutlu, N., Uyanik, B.S., Taneli, F., Buyukyazi, G., Tavli, T., 2004. Serum testosterone, growth hormone, and insulin-like growth factor-1 levels, mental reaction time, and maximal aerobic exercise in sedentary and long-term physically trained elderly males. *International Journal of Neuroscience* 114, 623-637.
- Ballor, D.L., Keesey, R.E., 1991. A meta-analysis of the factors affecting exercise-induced changes in body mass, fat mass and fat-free mass in males and females. *Int J Obes* 15, 717-726.
- Bhella, P.S., Hastings, J.L., Fujimoto, N., Shibata, S., Carrick-Ranson, G., Palmer, M.D., Boyd, K.N., Adams-Huet, B., Levine, B.D., 2014. Impact of lifelong exercise "dose" on left ventricular compliance and distensibility. *Journal of the American College of Cardiology* 64, 1257-1266.
- Bjork, L., Jenkins, N.T., Witkowski, S., Hagberg, J.M., 2012. Nitro-Oxidative Stress Biomarkers in Active and Inactive Men. *International Journal of Sports Medicine* 33, 279-284.
- Blair, S.N., 2009. Physical inactivity: the biggest public health problem of the 21st century. *Br J Sports Med* 43, 1-2.
- Booth, F.W., Roberts, C.K., Laye, M.J., 2012. Lack of Exercise Is a Major Cause of Chronic Diseases. *Comprehensive Physiology* 2, 1143-1211.
- Buford, T.W., Cooke, M.B., Manini, T.M., Leeuwenburgh, C., Willoughby, D.S., 2010. Effects of Age and Sedentary Lifestyle on Skeletal Muscle NF-kappa B Signaling in Men. *Journals of Gerontology Series a-Biological Sciences and Medical Sciences* 65, 532-537.
- Buyukyazi, G., 2004. Differences in the cellular and humoral immune system between sedentary and endurance-trained elderly males. / *Appareil immunitaire cellulaire et*

- humoral: comparaison entre sujets ages sedentaires et endurants. *Science & Sports* 19, 130-135.
- Carrick-Ranson, G., Hastings, J.L., Bhella, P.S., Fujimoto, N., Shibata, S., Palmer, M.D., Boyd, K., Livingston, S., Dijk, E., Levine, B.D., 2014a. The effect of lifelong exercise dose on cardiovascular function during exercise. *J Appl Physiol* (1985) 116, 736-745.
- Carrick-Ranson, G., Hastings, J.L., Bhella, P.S., Fujimoto, N., Shibata, S., Palmer, M.D., Boyd, K., Livingston, S., Dijk, E., Levine, B.D., 2014b. The effect of lifelong exercise dose on cardiovascular function during exercise. *J Appl Physiol* 116, 736-745.
- Coggan, A.R., Spina, R.J., Rogers, M.A., King, D.S., Brown, M., Nemeth, P.M., Holloszy, J.O., 1990. Histochemical and enzymatic characteristics of skeletal muscle in master athletes. *J Appl Physiol* 68, 1896-1901.
- Coupe, C., Svensson, R.B., Grosset, J.F., Kovanen, V., Nielsen, R.H., Olsen, M.R., Larsen, J.O., Praet, S.F., Skovgaard, D., Hansen, M., Aagaard, P., Kjaer, M., Magnusson, S.P., 2014. Life-long endurance running is associated with reduced glycation and mechanical stress in connective tissue. *Age* 36, 9665.
- Cristea, A., Korhonen, M.T., Häkkinen, K., Mero, A., Alén, M., Sipilä, S., Viitasalo, J.T., Koljonen, M.J., Suominen, H., Larsson, L., 2008. Effects of combined strength and sprint training on regulation of muscle contraction at the whole-muscle and single-fibre levels in elite master sprinters. *Acta Physiologica* 193, 275-289.
- Cruz-Jentoft, A.J., Baeyens, J.P., Bauer, J.M., Boirie, Y., Cederholm, T., Landi, F., Martin, F.C., Michel, J.P., Rolland, Y., Schneider, S.M., Topinkova, E., Vandewoude, M., Zamboni, M., European Working Group on Sarcopenia in Older, P., 2010. Sarcopenia: European consensus on definition and diagnosis: Report of the European Working Group on Sarcopenia in Older People. *Age Ageing* 39, 412-423.
- Daskalopoulou, C., Stubbs, B., Kralj, C., Koukounari, A., Prince, M., Prina, A.M., 2017. Physical activity and healthy ageing: A systematic review and meta-analysis of longitudinal cohort studies. *Ageing Res Rev* 38, 6-17.
- Delmonico, M.J., Harris, T.B., Visser, M., Park, S.W., Conroy, M.B., Velasquez-Mieyer, P., Boudreau, R., Manini, T.M., Nevitt, M., Newman, A.B., Goodpaster, B.H., Health, A., Body, 2009. Longitudinal study of muscle strength, quality, and adipose tissue infiltration. *Am J Clin Nutr* 90, 1579-1585.
- Doering, T.M., Reaburn, P.R., Phillips, S.M., Jenkins, D.G., 2015. Post-Exercise Dietary Protein Strategies to Maximize Skeletal Muscle Repair and Remodeling in Masters Endurance Athletes: A Review. *Int J Sport Nutr Exerc Metab*.
- Doherty, T.J., 2003. Invited review: Aging and sarcopenia. *J Appl Physiol* (1985) 95, 1717-1727.
- DubÉ, J.J., Broskey, N.T., Despines, A.A., Stefanovic-Racic, M., Toledo, F.G.S., Goodpaster, B.H., Amati, F., 2016. Muscle Characteristics and Substrate Energetics in Lifelong Endurance Athletes. *Medicine & Science in Sports & Exercise* 48, 472-480.
- Ekelund, U., Besson, H., Luan, J.A., May, A.M., Sharp, S.J., Brage, S., Travier, N., Agudo, A., Slimani, N., Rinaldi, S., Jenab, M., Norat, T., Mouw, T., Rohrmann, S., Kaaks, R., Bergmann, M.M., Boeing, H., Clavel-Chapelon, F., Boutron-Ruault, M.C., Overvad, K., Jakobsen, M.U., Johnsen, N.F., Halkjaer, J., Gonzalez, C.A., Rodriguez, L., Sanchez, M.J., Arriola, L., Barricarte, A., Navarro, C., Key, T.J., Spencer, E.A., Orfanos, P., Naska, A., Trichopoulou, A., Manjer, J., Lund, E., Palli, D., Pala, V., Vineis, P., Mattiello, A., Tumino, R., Bueno-De-Mesquita, H.B., van den Berg, S.W., Odysseos, A.D., Riboli, E., Wareham, N.J., Peeters, P.H., 2011. Physical activity and

- gain in abdominal adiposity and body weight: prospective cohort study in 288,498 men and women. *American Journal of Clinical Nutrition* 93, 826-835.
- Eskurza, I., Donato, A.J., Moreau, K.L., Seals, D.R., Tanaka, H., 2002. Changes in maximal aerobic capacity with age in endurance-trained women: 7-yr follow-up. *J Appl Physiol* 92, 2303-2308.
- Evans, W.J., Campbell, W.W., 1993. Sarcopenia and age-related changes in body composition and functional capacity. *J Nutr* 123, 465-468.
- Everman, S., Farris, J.W., Bay, R.C., Daniels, J.T., 2018. Elite Distance Runners: A 45-Year Follow-up. *Medicine and Science in Sports and Exercise* 50, 73-78.
- Faulkner, J.A., Davis, C.S., Mendias, C.L., Brooks, S.V., 2008. The aging of elite male athletes: age-related changes in performance and skeletal muscle structure and function. *Clin J Sport Med* 18, 501-507.
- Fitzgerald, M.D., Tanaka, H., Tran, Z.V., Seals, D.R., 1997. Age-related declines in maximal aerobic capacity in regularly exercising vs. sedentary women: A meta-analysis. *Journal of Applied Physiology* 83, 160-165.
- Franzoni, F., Ghiadoni, L., Galetta, F., Plantinga, Y., Lubrano, V., Huang, Y., Salvetti, G., Regoli, F., Taddei, S., Santoro, G., Salvetti, A., 2005. Physical activity, plasma antioxidant capacity, and endothelium-dependent vasodilation in young and older men. *American Journal of Hypertension* 18, 510-516.
- Frontera, W.R., Hughes, V.A., Fielding, R.A., Fiatarone, M.A., Evans, W.J., Roubenoff, R., 2000. Aging of skeletal muscle: a 12-yr longitudinal study. *Journal of Applied Physiology* 88, 1321-1326.
- Galetta, F., Franzoni, F., Femia, F.R., Roccella, N., Pentimone, F., Santoro, G., 2005. Lifelong physical training prevents the age-related impairment of heart rate variability and exercise capacity in elderly people. *Journal of Sports Medicine & Physical Fitness* 45, 217-221.
- Galetta, F., Franzoni, F., Plantinga, Y., Ghiadoni, L., Rossi, M., Prattichizzo, F., Carpi, A., Taddei, S., Santoro, G., 2006. Ambulatory blood pressure monitoring and endothelium-dependent vasodilation in the elderly athletes. *Biomedicine & Pharmacotherapy* 60, 443-447.
- Gava, P., Kern, H., Carraro, U., 2015. Age-associated power decline from running, jumping, and throwing male masters world records. *Experimental aging research* 41, 115-135.
- Gent, D.N., Norton, K., 2013. Aging has greater impact on anaerobic versus aerobic power in trained masters athletes. *J Sports Sci* 31, 97-103.
- Goodpaster, B.H., Park, S.W., Harris, T.B., Kritchevsky, S.B., Nevitt, M., Schwartz, A.V., Simonsick, E.M., Tylavsky, F.A., Visser, M., Newman, A.B., 2006. The loss of skeletal muscle strength, mass, and quality in older adults: the health, aging and body composition study. *J Gerontol A Biol Sci Med Sci* 61, 1059-1064.
- Guralnik, J.M., Fried, L.P., Salive, M.E., 1996. Disability as a public health outcome in the aging population. *Annu Rev Publ Health* 17, 25-46.
- Hairi, N.N., Cumming, R.G., Naganathan, V., Handelsman, D.J., Le Couteur, D.G., Creasey, H., Waite, L.M., Seibel, M.J., Sambrook, P.N., 2010. Loss of muscle strength, mass (sarcopenia), and quality (specific force) and its relationship with functional limitation and physical disability: the Concord Health and Ageing in Men Project. *J Am Geriatr Soc* 58, 2055-2062.
- Hansen, M., Kjaer, M., 2014. Influence of sex and estrogen on musculotendinous protein turnover at rest and after exercise. *Exerc Sport Sci Rev* 42, 183-192.
- Harridge, S.D., Lazarus, N.R., 2017. Physical Activity, Aging, and Physiological Function. *Physiology (Bethesda)* 32, 152-161.

- Hawkins, S.A., Marcell, T.J., Jaque, S.V., Wiswell, R.A., 2001. A longitudinal assessment of change in VO₂max and maximal heart rate in master athletes. *Medicine and Science in Sports and Exercise* 33, 1744-1750.
- Hayes, L.D., Sculthorpe, N., Herbert, P., Baker, J.S., Spagna, R., Grace, F.M., 2015. Six weeks of conditioning exercise increases total, but not free testosterone in lifelong sedentary aging men. *Aging Male* 18, 195-200.
- Holloszy, J.O., 2000. The biology of aging. *Mayo Clin Proc* 75 Suppl, S3-8; discussion S8-9.
- Hung, W.W., Ross, J.S., Boockvar, K.S., Siu, A.L., 2011. Recent trends in chronic disease, impairment and disability among older adults in the United States. *Bmc Geriatrics* 11.
- Janssen, I., Heymsfield, S.B., Wang, Z.M., Ross, R., 2000. Skeletal muscle mass and distribution in 468 men and women aged 18-88 yr. *J Appl Physiol* (1985) 89, 81-88.
- Kadi, F., Charifi, N., Denis, C., Lexell, J., 2004. Satellite cells and myonuclei in young and elderly women and men. *Muscle Nerve* 29, 120-127.
- Katzel, L.I., Fleg, J.L., Busby-Whitehead, M.J., Sorkin, J.D., Becker, L.C., Lakatta, E.G., Goldberg, A.P., 1998. Exercise-induced silent myocardial ischemia in master athletes. *American Journal of Cardiology* 81, 261-265.
- Katzel, L.I., Sorkin, J.D., Fleg, J.L., 2001. A comparison of longitudinal changes in aerobic fitness in older endurance athletes and sedentary men. *Journal of the American Geriatrics Society* 49, 1657-1664.
- Kent-Braun, J.A., Ng, A.V., Young, K., 2000. Skeletal muscle contractile and noncontractile components in young and older women and men. *J Appl Physiol* (1985) 88, 662-668.
- Kim, K.M., Lim, S., Moon, J.H., Choi, S.H., Jang, H.C., 2016. Gender-Specific Associations between Muscle and Bone Losses in Longitudinal Changes of Muscle Mass and Strength, and Bone Mass. *Osteoporosis International* 27, S384-S384.
- Korhonen, M.T., Cristea, A., Alen, M., Hakkinen, K., Sipila, S., Mero, A., Viitasalo, J.T., Larsson, L., Suominen, H., 2006. Aging, muscle fiber type, and contractile function in sprint-trained athletes. *J Appl Physiol* 101, 906-917.
- Korhonen, M.T., Heinonen, A., Siekkinen, J., Isolehto, J., Alen, M., Kiviranta, I., Suominen, H., 2012. Bone density, structure and strength, and their determinants in aging sprint athletes. *Medicine and Science in Sports and Exercise* 44, 2340-2349.
- Kuk, J.L., Katzmarzyk, P.T., Nichaman, M.Z., Church, T.S., Blair, S.N., Ross, R., 2006. Visceral fat is an independent predictor of all-cause mortality in men. *Obesity* 14, 336-341.
- Kuk, J.L., Saunders, T.J., Davidson, L.E., Ross, R., 2009. Age-related changes in total and regional fat distribution. *Ageing Res Rev* 8, 339-348.
- Kumagai, K., Abe, T., Brechue, W.F., Ryushi, T., Takano, S., Mizuno, M., 2000. Sprint performance is related to muscle fascicle length in male 100-m sprinters. *Journal of Applied Physiology* 88, 811-816.
- Kusy, K., Zielinski, J., 2014. Aerobic capacity in speed-power athletes aged 20-90 years vs endurance runners and untrained participants. *Scandinavian Journal of Medicine & Science in Sports* 24, 68-79.
- Larsson, L., Li, X.P., Frontera, W.R., 1997. Effects of aging on shortening velocity and myosin isoform composition in single human skeletal muscle cells. *American Journal of Physiology-Cell Physiology* 272, C638-C649.
- Lazarus, N.R., Harridge, S.D., 2007. Inherent ageing in humans: the case for studying master athletes. *Scand J Med Sci Sports* 17, 461-463.
- Lee, D.C., Artero, E.G., Sui, X., Blair, S.N., 2010. Mortality trends in the general population: the importance of cardiorespiratory fitness. *J Psychopharmacol* 24, 27-35.
- Lee, D.C., Sui, X., Ortega, F.B., Kim, Y.S., Church, T.S., Winnett, R.A., Ekelund, U., Katzmarzyk, P.T., Blair, S.N., 2011. Comparisons of leisure-time physical activity

- and cardiorespiratory fitness as predictors of all-cause mortality in men and women. *Br J Sports Med* 45, 504-510.
- Lexell, J., 1995. Human aging, muscle mass, and fiber type composition. *J Gerontol A Biol Sci Med Sci* 50 Spec No, 11-16.
- MacDonald, A.J., Greig, C.A., Baracos, V., 2011. The advantages and limitations of cross-sectional body composition analysis. *Curr Opin Support Palliat Care* 5, 342-349.
- Mackey, A.L., Karlsen, A., Couppé, C., Mikkelsen, U.R., Nielsen, R.H., Magnusson, S.P., Kjaer, M., 2014. Differential satellite cell density of type I and II fibres with lifelong endurance running in old men. *Acta Physiologica* 210, 612-627.
- Maffulli, N., Testa, V., Capasso, G., 1994. Anaerobic Threshold Determination in Master Endurance Runners. *Journal of Sports Medicine and Physical Fitness* 34, 242-249.
- Malbut, K.E., Dinan, S., Young, A., 2002. Aerobic training in the 'oldest old': the effect of 24 weeks of training. *Age Ageing* 31, 255-260.
- Marcell, T.J., Hawkins, S.A., Tarpenning, K.M., Hyslop, D.M., Wiswell, R.A., 2003. Longitudinal analysis of lactate threshold in male and female master athletes. *Medicine and Science in Sports and Exercise* 35, 810-817.
- Marcell, T.J., Hawkins, S.A., Wiswell, R.A., 2014. Leg strength declines with advancing age despite habitual endurance exercise in active older adults. *Journal of Strength & Conditioning Research* 28, 504-513.
- Matelot, D., Schnell, F., Kervio, G., Ridard, C., Thillaye du Boullay, N., Wilson, M., Carre, F., 2016. Cardiovascular Benefits of Endurance Training in Seniors: 40 is not too Late to Start. *International Journal of Sports Medicine* 37, 625-632.
- Mikkelsen, U.R., Couppe, C., Karlsen, A., Grosset, J.F., Schjerling, P., Mackey, A.L., Klausen, H.H., Magnusson, S.P., Kjaer, M., 2013. Life-long endurance exercise in humans: Circulating levels of inflammatory markers and leg muscle size. *Mechanisms of Ageing and Development* 134, 531-540.
- Mitchell, W.K., Williams, J., Atherton, P., Larvin, M., Lund, J., Narici, M., 2012. Sarcopenia, dynapenia, and the impact of advancing age on human skeletal muscle size and strength; a quantitative review. *Frontiers in Physiology* 3.
- Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G., Group, P., 2009. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLoS Med* 6, e1000097.
- Molmen, H.E., Wisloff, U., Aamot, I.L., Stoylen, A., Ingul, C.B., 2012. Aerobic interval training compensates age related decline in cardiac function. *Scandinavian Cardiovascular Journal* 46, 163-171.
- Mortensen, S.P., Nyberg, M., Winding, K., Saltin, B., 2012. Lifelong physical activity preserves functional sympatholysis and purinergic signalling in the ageing human leg. *J Physiol-London* 590, 6227-6236.
- Mosole, S., Carraro, U., Kern, H., Loeffler, S., Fruhmman, H., Vogelauer, M., Burggraf, S., Mayr, W., Krenn, M., Paternostro-Sluga, T., Hamar, D., Cvecka, J., Sedliak, M., Tirpakova, V., Sarabon, N., Musaro, A., Sandri, M., Protasi, F., Nori, A., Pond, A., Zampieri, S., 2014. Long-Term High-Level Exercise Promotes Muscle Reinnervation With Age. *Journal of Neuropathology and Experimental Neurology* 73, 284-294.
- Mucci, P., Anselme-Poujol, F., Caillaud, C., Couret, I., Rossi, M., Prefaut, C., 1999. Basophil releasability in young highly trained and older athletes. *Medicine & Science in Sports & Exercise* 31, 507-513 507p.
- Murton, A.J., Marimuthu, K., Mallinson, J.E., Selby, A.L., Smith, K., Rennie, M.J., Greenhaff, P.L., 2015. Obesity Appears to Be Associated With Altered Muscle Protein Synthetic and Breakdown Responses to Increased Nutrient Delivery in Older Men, but Not Reduced Muscle Mass or Contractile Function. *Diabetes* 64, 3160-3171.

- Narici, M.V., Maffulli, N., 2010. Sarcopenia: characteristics, mechanisms and functional significance. *Br Med Bull* 95, 139-159.
- Newman, A.B., Kupelian, V., Visser, M., Simonsick, E.M., Goodpaster, B.H., Kritchevsky, S.B., Tylavsky, F.A., Rubin, S.M., Harris, T.B., 2006. Strength, but not muscle mass, is associated with mortality in the health, aging and body composition study cohort. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences* 61, 72-77.
- Newton, R.U., Hakkinen, K., Hakkinen, A., McCormick, M., Volek, J., Kraemer, W.J., 2002. Mixed-methods resistance training increases power and strength of young and older men. *Med Sci Sports Exerc* 34, 1367-1375.
- Niccoli, T., Partridge, L., 2012. Ageing as a Risk Factor for Disease. *Curr Biol* 22, R741-R752.
- Nyberg, M., Blackwell, J.R., Damsgaard, R., Jones, A.M., Hellsten, Y., Mortensen, S.P., 2012. Lifelong physical activity prevents an age-related reduction in arterial and skeletal muscle nitric oxide bioavailability in humans. *Journal of Physiology-London* 590, 5361-5370.
- Ojanen, T., Rauhala, T., Häkkinen, K., 2007. Strength and power profiles of the lower and upper extremities in master throwers at different ages. *Journal of Strength & Conditioning Research (Allen Press Publishing Services Inc.)* 21, 216-222 217p.
- Ortega, F.B., Silventoinen, K., Tynelius, P., Rasmussen, F., 2012. Muscular strength in male adolescents and premature death: cohort study of one million participants. *BMJ* 345, e7279.
- Pereira, F.B., Leite, A.F., de Paula, A.P., 2015. Relationship between pre-sarcopenia, sarcopenia and bone mineral density in elderly men. *Arquivos Brasileiros De Endocrinologia E Metabologia* 59, 59-65.
- Peterson, M.D., Rhea, M.R., Sen, A., Gordon, P.M., 2010. Resistance exercise for muscular strength in older adults: a meta-analysis. *Ageing Res Rev* 9, 226-237.
- Piasecki, M., Ireland, A., Coulson, J., Stashuk, D.W., Hamilton-Wright, A., Swiecicka, A., Rutter, M.K., McPhee, J.S., Jones, D.A., 2016a. Motor unit number estimates and neuromuscular transmission in the tibialis anterior of master athletes: evidence that athletic older people are not spared from age-related motor unit remodeling. *Physiol Rep* 4.
- Piasecki, M., Ireland, A., Jones, D.A., McPhee, J.S., 2016b. Age-dependent motor unit remodelling in human limb muscles. *Biogerontology* 17, 485-496.
- Piasecki, M., Ireland, A., Stashuk, D., Hamilton-Wright, A., Jones, D.A., McPhee, J.S., 2015. Age-related neuromuscular changes affecting human vastus lateralis. *J Physiol.*
- Pollock, M.L., Foster, C., Knapp, D., Rod, J.L., Schmidt, D.H., 1987. Effect of age and training on aerobic capacity and body composition of master athletes. *J Appl Physiol* (1985) 62, 725-731.
- Pollock, R.D., Carter, S., Velloso, C.P., Duggal, N.A., Lord, J.M., Lazarus, N.R., Harridge, S.D.R., 2015. An investigation into the relationship between age and physiological function in highly active older adults. *J Physiol-London* 593, 657-680.
- Power, G.A., Dalton, B.H., Behm, D.G., Doherty, T.J., Vandervoort, A.A., Rice, C.L., 2012. Motor Unit Survival in Lifelong Runners Is Muscle Dependent. *Medicine and Science in Sports and Exercise* 44, 1235-1242.
- Power, G.A., Dalton, B.H., Behm, D.G., Vandervoort, A.A., Doherty, T.J., Rice, C.L., 2010a. Motor Unit Number Estimates in Masters Runners: Use It or Lose It? *Medicine and Science in Sports and Exercise* 42, 1644-1650.

- Power, G.A., Dalton, B.H., Behm, D.G., Vandervoort, A.A., Doherty, T.J., Rice, C.L., 2010b. Motor unit number estimates in masters runners: use it or lose it? *Med Sci Sports Exerc* 42, 1644-1650.
- Prasad, A., Popovic, Z.B., Arbab-Zadeh, A., Fu, Q., Palmer, D., Dijk, E., Greenberg, N.L., Garcia, M.J., Thomas, J.D., Levine, B.D., 2007. The Effects of Aging and Physical Activity on Doppler Measures of Diastolic Function. *American Journal of Cardiology* 99, 1629-1636.
- Prefaut, C., Anselme, F., Caillaud, C., Masse-Biron, J., 1994. Exercise-induced hypoxemia in older athletes. *Journal of Applied Physiology* 76, 120-126.
- Proctor, D.N., Joyner, M.J., 1997. Skeletal muscle mass and the reduction of VO₂max in trained older subjects. *J Appl Physiol* 82, 1411-1415.
- Rantalainen, T., Duckham, R.L., Suominen, H., Heinonen, A., Alen, M., Korhonen, M.T., 2014. Tibial and fibular mid-shaft bone traits in young and older sprinters and non-athletic men. *Calcified Tissue International* 95, 132-140.
- Rittweger, J., di Prampero, P.E., Maffulli, N., Narici, M.V., 2009. Sprint and endurance power and ageing: an analysis of master athletic world records. *Proceedings of the Royal Society B-Biological Sciences* 276, 683-689.
- Rivier, A., Pene, J., Chanez, P., Anselme, F., Caillaud, C., Prefaut, C., Godard, P., Bousquet, J., 1994. Release of cytokines by blood monocytes during strenuous exercise. *International Journal of Sports Medicine* 15, 192-198.
- Rodeheffer, R.J., Gerstenblith, G., Becker, L.C., Fleg, J.L., Weisfeldt, M.L., Lakatta, E.G., 1984. Exercise Cardiac-Output Is Maintained with Advancing Age in Healthy-Human Subjects - Cardiac Dilatation and Increased Stroke Volume Compensate for a Diminished Heart-Rate. *Circulation* 69, 203-213.
- Rogers, M.A., Hagberg, J.M., Martin, W.H., 3rd, Ehsani, A.A., Holloszy, J.O., 1990. Decline in VO₂max with aging in master athletes and sedentary men. *J Appl Physiol* (1985) 68, 2195-2199.
- Ruiz, J.R., Sui, X., Lobelo, F., Morrow, J.R., Jackson, A.W., Sjöström, M., Blair, S.N., 2008. Association between muscular strength and mortality in men: prospective cohort study. *BMJ* 337.
- Sallinen, J., Ojanen, T., Karavirta, L., Ahtiainen, J.P., Hakkinen, K., 2008. Muscle mass and strength, body composition and dietary intake in master strength athletes vs untrained men of different ages. *Journal of Sports Medicine and Physical Fitness* 48, 190-196.
- Sanada, K., Miyachi, M., Tabata, I., Suzuki, K., Yamamoto, K., Kawano, H., Usui, C., Higuchi, M., 2009. Differences in body composition and risk of lifestyle-related diseases between young and older male rowers and sedentary controls. *Journal of Sports Sciences* 27, 1027-1034.
- Schmidt, J.F., Andersen, T.R., Andersen, L.J., Randers, M.B., Hornstrup, T., Hansen, P.R., Bangsbo, J., Krstrup, P., 2015. Cardiovascular function is better in veteran football players than age-matched untrained elderly healthy men. *Scand J Med Sci Spor* 25, 61-69.
- Seals, D.R., Justice, J.N., LaRocca, T.J., 2015. Physiological geroscience: targeting function to increase healthspan and achieve optimal longevity. *J Physiol*.
- Shibata, S., Levine, B.D., 2012. Effect of exercise training on biologic vascular age in healthy seniors. *American Journal of Physiology - Heart & Circulatory Physiology* 302, H1340-1346.
- Sipila, S., Suominen, H., 1991. Ultrasound imaging of the quadriceps muscle in elderly athletes and untrained men. *Muscle & Nerve* 14, 527-533.

- Smeuninx, B., McKendry, J., Wilson, D., Martin, U., Breen, L., 2017. Age-Related Anabolic Resistance of Myofibrillar Protein Synthesis Is Exacerbated in Obese Inactive Individuals. *Journal of Clinical Endocrinology & Metabolism* 102, 3535-3545.
- Smith, G.I., Atherton, P., Villareal, D.T., Frimel, T.N., Rankin, D., Rennie, M.J., Mittendorfer, B., 2008. Differences in Muscle Protein Synthesis and Anabolic Signaling in the Postabsorptive State and in Response to Food in 65-80 Year Old Men and Women. *Plos One* 3.
- Sonn, U., 1996. Longitudinal studies of dependence in daily life activities among elderly persons - Methodological development, use of assistive devices and relation to impairments and functional limitations. *Scandinavian Journal of Rehabilitation Medicine*, 1-35.
- Stenroth, L., Cronin, N.J., Peltonen, J., Korhonen, M.T., Sipila, S., Finni, T., 2016. Triceps surae muscle-tendon properties in older endurance- and sprint-trained athletes. *J Appl Physiol* 120, 63-69.
- Strasser, E.M., Draskovits, T., Praschak, M., Quittan, M., Graf, A., 2013. Association between ultrasound measurements of muscle thickness, pennation angle, echogenicity and skeletal muscle strength in the elderly. *Age (Dordr)* 35, 2377-2388.
- Sundstrup, E., Jakobsen, M.D., Andersen, J.L., Randers, M.B., Petersen, J., Suetta, C., Aagaard, P., Krstrup, P., 2010. Muscle function and postural balance in lifelong trained male footballers compared with sedentary elderly men and youngsters. *Scand J Med Sci Spor* 20, 90-97.
- Suominen, H., Rahkila, P., 1991. Bone mineral density of the calcaneus in 70- to 81-yr-old male athletes and a population sample.[Erratum appears in *Med Sci Sports Exerc* 1992 Mar;24(3):401]. *Medicine & Science in Sports & Exercise* 23, 1227-1233.
- Taaffe, D.R., Henwood, T.R., Nalls, M.A., Walker, D.G., Lang, T.F., Harris, T.B., 2009. Alterations in Muscle Attenuation following Detraining and Retraining in Resistance-Trained Older Adults. *Gerontology* 55, 217-223.
- Tanaka, H., Desouza, C.A., Jones, P.P., Stevenson, E.T., Davy, K.P., Seals, D.R., 1997. Greater rate of decline in maximal aerobic capacity with age in physically active vs. sedentary healthy women. *J Appl Physiol* 83, 1947-1953.
- Tanaka, H., Seals, D.R., 2008. Endurance exercise performance in Masters athletes: age-associated changes and underlying physiological mechanisms. *J Physiol* 586, 55-63.
- Tarpenning, K.M., Hamilton-Wessler, M., Wiswell, R.A., Hawkins, S.A., 2004a. Endurance training delays age of decline in leg strength and muscle morphology. *Medicine & Science in Sports & Exercise* 36, 74-78 75p.
- Tarpenning, K.M., Hamilton-Wessler, M., Wiswell, R.A., Hawkins, S.A., 2004b. Endurance training delays age of decline in leg strength and muscle morphology. *Med Sci Sports Exerc* 36, 74-78.
- Thom, J.M., Morse, C.I., Birch, K.M., Narici, M.V., 2007. Influence of muscle architecture on the torque and power-velocity characteristics of young and elderly men. *European Journal of Applied Physiology* 100, 613-619.
- Thomas, B.P., Yezhuvath, U.S., Tseng, B.Y., Liu, P., Levine, B.D., Zhang, R., Lu, H., 2013. Life-long aerobic exercise preserved baseline cerebral blood flow but reduced vascular reactivity to CO₂. *Journal of Magnetic Resonance Imaging* 38, 1177-1183.
- Trappe, S., Hayes, E., Galpin, A., Kaminsky, L., Jemio, B., Fink, W., Trappe, T., Jansson, A., Gustafsson, T., Tesch, P., 2013. New records in aerobic power among octogenarian lifelong endurance athletes. *J Appl Physiol* 114, 3-10.
- Wilson, T.M., Tanaka, H., 2000. Meta-analysis of the age-associated decline in maximal aerobic capacity in men: relation to training status. *American Journal of Physiology-Heart and Circulatory Physiology* 278, H829-H834.

- Witkowski, S., Lockard, M.M., Jenkins, N.T., Obisesan, T.O., Spangenburg, E.E., Hagberg, J.M., 2010. Relationship between circulating progenitor cells, vascular function and oxidative stress with long-term training and short-term detraining in older men. *Clinical Science* 118, 303-311.
- Wroblewski, A.P., Amati, F., Smiley, M.A., Goodpaster, B., Wright, V., 2011. Chronic exercise preserves lean muscle mass in masters athletes. *Phys Sportsmed* 39, 172-178.
- Yataco, A.R., Busby-Whitehead, J., Drinkwater, D.T., Katzel, L.I., 1997. Relationship of body composition and cardiovascular fitness to lipoprotein lipid profiles in master athletes and sedentary men. *Aging-Clinical & Experimental Research* 9, 88-94.
- Young, A., Stokes, M., Crowe, M., 1984. Size and Strength of the Quadriceps Muscles of Old and Young-Women. *European Journal of Clinical Investigation* 14, 282-287.
- Zampieri, S., Pietrangelo, L., Loeffler, S., Fruhmman, H., Vogelauer, M., Burggraf, S., Pond, A., Grim-Stieger, M., Cvecka, J., Sedliak, M., Tirpakova, V., Mayr, W., Sarabon, N., Rossini, K., Barberi, L., De Rossi, M., Romanello, V., Boncompagni, S., Musaro, A., Sandri, M., Protasi, F., Carraro, U., Kern, H., 2015. Lifelong Physical Exercise Delays Age-Associated Skeletal Muscle Decline. *Journals of Gerontology Series a-Biological Sciences and Medical Sciences* 70, 163-173.

Tables

Author, Year	Fat-Free Mass	Fat Mass	Body Fat	VO _{2max}	Strength	Muscle Architecture	Muscle CSA	Muscle Morphology
(Aagaard et al., 2007)	-	-	Skinfold	Cycle Ergometer	Knee Extension MVC (70° knee angle)	-	-	Muscle Fibre Area, distribution, distribution by area (myofibrillar ATPase staining (Type I, IIa, IIx))
(Anselme et al., 1994)	-	-	-	Cycle Ergometer (30W 3mins, ↑ 30W.min ⁻¹)	-	-	-	-
(Arbab-Zadeh et al., 2004)	-	-	Hydrostatic Weighing	Treadmill (modified Astrand-Saltin)	-	-	-	-
(Ari et al., 2004)	-	-	No Details	Cycle Ergometer (Astrand)	-	-	-	-
(Bhella et al., 2014)	-	-	-	Treadmill (modified Astrand-Saltin)	-	-	-	-
(Bjork et al., 2012)	-	-	7-Site Skinfold	Treadmill (Constant speed, 2% ↑ grad every 2mins)	-	-	-	-
(Buford et al., 2010)	-	-	DXA	Treadmill	-	-	-	-
(Buyukyazi, 2004)	-	-	4-Site Skinfold	Cycle Ergometer (Astrand-Ryhming Sub-max)	-	-	-	-
(Carrick-Ranson et al., 2014a)	Hydrostatic Weighing	-	Hydrostatic Weighing	Treadmill & Upright cycle	-	-	-	-

Author, Year	Fat-Free Mass	Fat Mass	Body Fat	VO _{2max}	Strength	Muscle Architecture	Muscle CSA	Muscle Morphology
(Couppe et al., 2014)	-	-	-	Cycle Ergometer (50/75W start, 25W ↑ .min ⁻¹)	Knee Extension MVC (knee & hip angle 90°, 10 s ramped contraction)	-	Anatomical CSA measured 20 cm proximal to tibia plateau (mid-thigh level) by magnetic resonance imaging (MRI)	-
(Cristea et al., 2008)	-	-	Bioelectrical Impedance	-	-	-	-	Fibre area & distribution (myofibrillar ATPase staining (Type I, IIa, IIx, IIax))
(DubÉ et al., 2016)	DXA Scan	DXA Scan	DXA Scan	Cycle Ergometer (50/75/10W 2mins, 25/50W ↑ every 2 mins)	-	-	-	-
(Franzoni et al., 2005)	-	-	-	Cycle Ergometer	-	-	-	-
((Galetta et al., 2005)	-	-	-	Cycle Ergometer	-	-	-	-
(Galetta et al., 2006)	-	-	-	Cycle Ergometer	-	-	-	-
(Hawkins et	Hydrostatic	-	Hydrostatic	Treadmill	-	-	-	-

Author, Year	Fat-Free Mass	Fat Mass	Body Fat	VO _{2max}	Strength	Muscle Architecture	Muscle CSA	Muscle Morphology
al., 2001)	Weighing		Weighing	(Modified Balke)				
(Hayes et al., 2015)	Bioelectrical Impedance	-	Bioelectrical Impedance	Cycle Ergometer (Ramp)	-	-	-	-
(Katzel et al., 1998)	-	-	Hydrostatic Weighing	Treadmill (Modified Balke)	-	-	-	-
(Katzel et al., 2001)	-	-	-	Treadmill (Modified Balke)	-		-	-
(Korhonen et al., 2006)	-	-	Bioelectrical Impedance	-	Bilateral Isometric MVC (107° knee & 110° hip angle)	Muscle thickness & pennation angle (50% <i>Vastus lateralis</i>)	-	Fibre area & distribution (myofibrillar ATPase staining (Type I, IIa, IIx, IIax))
(Korhonen et al., 2012)	-	-	Bioelectrical Impedance	-	Unilateral Isometric MVC (90° knee & 110° hip angle)	-	-	-
(Larsson et al., 1997)	-	-	-	-	-	-	-	Fibre distribution (myofibrillar ATPase staining (Type I, IIa, IIx, IIax))
(Mackey et al., 2014)	-	-	-	Cycle Ergometer	-	-	-	Fibre Area & distribution (primary/secondary antibodies (Type I & II))
(Marcell et	Hydrostatic		Hydrostatic	Treadmill	-	-	-	-

Author, Year	Fat-Free Mass	Fat Mass	Body Fat	VO _{2max}	Strength	Muscle Architecture	Muscle CSA	Muscle Morphology
al., 2003)	Weighing		Weighing	(Modified Balke)				
(Marcell et al., 2014)	Hydrostatic Weighing	-	Hydrostatic Weighing	Treadmill (Modified Balke)	Unilateral Isometric MVC (60° knee flexion)	-	-	-
(Matelot et al., 2016)	-	-	No Details	Cycle Ergometer	-	-	-	-
(Mikkelsen et al., 2013)	-	-	-	Cycle Ergometer (50/75W start, ↑ 25W.min ⁻¹)	Knee Extension MVC (knee & hip angle 90°, 10 s ramped contraction)	-	Anatomical CSA measured 20 cm proximal to tibia plateau (mid-thigh level) by magnetic resonance imaging (MRI)	-
(Molmen et al., 2012)	-	-	-	Treadmill (Gradient 10% with ↑ speed every min)	-	-	-	-
(Mortensen et al., 2012)	-	-	No Details	Cycle Ergometer		-	-	-
(Mosole et al., 2014)	-	-	-	-	Knee Extension MVC (Relative)	-	-	Fibre distribution (H+E & primary secondary antibodies (type I, II, co-expressing, denervated))

Author, Year	Fat-Free Mass	Fat Mass	Body Fat	VO _{2max}	Strength	Muscle Architecture	Muscle CSA	Muscle Morphology
(Mucci et al., 1999)	-	-	-	Cycle Ergometer (30W 3mins, ↑30W.min ⁻¹)	-	-	-	-
(Nyberg et al., 2012)	-	-	No Details	Cycle Ergometer	-	-	-	-
(Ojanen et al., 2007)	-	-	4-Site Skinfold / Bioelectrical Impedance	-	-	Muscle thickness (<i>Vastus lateralis</i> + <i>Vastus intermedius</i> , lower 1/3 between greater trochanter & lateral joint line of knee)	-	-
(Pollock et al., 2015)	DXA Scan	-	DXA Scan	Cycle Ergometer (50W 3mins, ↑ 1-2W every 3-5s)	Knee Extension MVC (90° Knee angle)	-	-	-
(Power et al., 2012)	-	-	-	-	Bicep Brachii MVC (110° Elbow flexion)	-	-	-
(Power et al., 2010a)	-	-	-	-	Tibialis Anterior MVC	-	-	-
(Prasad et al., 2007)	-	-	-	No details	-	-	-	-
(Prefaut et al., 1994)	-	-	-	Cycle Ergometer (30W 3mins, ↑ 30W.min ⁻¹)	-	-	-	-

Author, Year	Fat-Free Mass	Fat Mass	Body Fat	VO _{2max}	Strength	Muscle Architecture	Muscle CSA	Muscle Morphology
(Proctor and Joyner, 1997)	DXA Scan	-	DXA Scan	Treadmill (2% ↑ grad every other min)	-	-	-	-
(Rantalainen et al., 2014)	-	-	-	-	-	-	Peripheral quantitative computed tomography (p-QCT)	-
(Rivier et al., 1994)	-	-	-	Cycle Ergometer (30W 3mins, ↑ 30W.min ⁻¹)	-	-	-	-
(Sallinen et al., 2008)			4-Site Skinfold	-	-	-	-	-
(Sanada et al., 2009)	DXA Scan	-	DXA Scan	Cycle Ergometer (90W, ↑ 30W.min ⁻¹) Rowing Ergometer 100W start, 50W ↑ .min ⁻¹)	Handheld dynamometer	-	-	-
(Schmidt et al., 2015)	-	DXA Scan	DXA Scan	Cycle Ergometer (40W start, ↑ 20W every 2 mins)	-	-	-	-
(Shibata and Levine, 2012)	-	-	-	No details	-			-
(Sipila and	-	-	-	-	Knee extension	Muscle	Ultrasound	-

Author, Year	Fat-Free Mass	Fat Mass	Body Fat	VO _{2max}	Strength	Muscle Architecture	Muscle CSA	Muscle Morphology
Suominen, 1991)					MVC (60° Knee angle)	thickness (no details on site of measurement)	Scanning (midpoint between greater trochanter and knee joint line)	
(Stenroth et al., 2016)	-	-	-	-	Plantar Flexion MVC (ankle 90°, knee full extended, hip 60° angle)	-	-	-
(Sundstrup et al., 2010)	-	-	-	No details	Knee Extension MVC (70° Knee angle)	-	-	Fibre area, distribution, distribution by area (myofibrillar ATPase staining (Type I, IIa, IIx, IIax))
(Suominen and Rahkila, 1991)	-	-	-	Cycle Ergometer (90W start, ↑30W every 2 mins)	Handheld dynamometer	-	-	-
(Tarpenning et al., 2004b)	Hydrostatic Weighing	-	Hydrostatic Weighing	Treadmill (2.5mph start, ↑0.5mph and 2% grade every 2 mins)	-	-	-	Fibre area & distribution (myofibrillar ATPase staining (Type I & II))
(Thomas et al., 2013)	-	-	-	Treadmill (modified Astrand-Saltin)	-	-	-	-
(Trappe et al., 2013)	DXA Scan	-	DXA Scan	Cycle Ergometer (Trained: 50W start ↑15W.min ⁻¹ , 20W	-	-	-	-

Author, Year	Fat-Free Mass	Fat Mass	Body Fat	VO _{2max}	Strength	Muscle Architecture	Muscle CSA	Muscle Morphology
(Witkowski et al., 2010)	-	-	DXA Scan	start ↑10w.min ⁻¹ Cycle Ergometer (50W start ↑15W.min ⁻¹)	-	-	-	-
(Yataco et al., 1997)	Hydrostatic Weighing	Hydrostatic Weighing	Hydrostatic Weighing	Treadmill (Modified Balke)	-	-	-	-
(Zampieri et al., 2015)	-	-	-	-	Knee extension MVC	-	-	Fibre diameter & distribution (H + E, myofibrillar ATPase staining (Type I & II))

Table 1) Included studies and associated measures. DXA, Dual energy x-ray absorptiometry; H + E, Hematoxylin and eosin; MVC, maximal voluntary contraction; W, Watts.

Author, Year	Participant Groups	Number (n)	Sex (M/F)	Age (Years)	Height (m)	Weight (kg)	BMI (Kg.m ²)	Training Experience (years)	Type of Training
(Aagaard et al., 2007)	Older Control	8	M	70.5 (2.8)	1.75 (0.06)	82.9 (6.2)	27.1	-	-
	Master Endurance Athlete	9	M	71.9 (4.3)	1.74 (0.07)	76.0 (8.3)	25.2	>50	Running/Cycling
	Master power athletes	7	M	73.9 (2.2)	1.75 (0.04)	78.7 (20.1)	25.7	>50	Sprinting/Shotput/high- and long-jump
(Anselme et al., 1994)	Young Endurance	7	M	22.2 (3.3)	1.80 (0.05)	68.6 (2.9)	21.3	5 (3.7)	Triathletes
	Master Endurance Athlete	7	M	66.2 (7.8)	1.69 (0.06)	75.4 (5.9)	26.5	30 (13.2)	Cyclists
	Young Control	7	M	23.4 (5.2)	1.75 (0.06)	67.2 (12.0)	22.0	-	Habitually active
	Older Control	7	M	67.6 (7.3)	1.67 (0.04)	67.6 (2.8)	24.1	-	Habitually active
(Arbab-Zadeh et al., 2004)	Older Control	12	M=6 F=6	69.8 (3.0)	1.68 (0.10)	73.3 (10.6)	25.9	-	-
	Young Control	14	M=7 F=7	28.9 (5.0)	1.74 (0.06)	71.2 (4.4)	23.6	-	-
	Master Endurance Athlete	12	M=6 F=6	67.8 (3.0)	1.70 (0.11)	64.6 (13.5)	22.4	23 (8)	Running/Cycling/Swimming
(Ari et al., 2004)	Master Endurance Athlete	10	M	68.0 (6.0)	1.67 (0.08)	71.0 (3.0)	25.5	41 (8)	Aerobic
	Older Control	11	M	65.0 (5.0)	1.69 (0.05)	81.0 (11.0)	28.4	-	-
(Bhella et al., 2014)	Older Control	27	M=15 F=12	68.8 (5.1)	1.70 (0.10)	74.7 (11.2)	26.0	-	-
	Master Endurance Athlete	25	M=17 F=8	67.8 (2.9)	1.71 (0.10)	65.6 (12.1)	22.4	25	Running/Cycling/Swimming

Author, Year	Participant Groups	Number (n)	Sex (M/F)	Age (Years)	Height (m)	Weight (kg)	BMI (Kg.m ²)	Training Experience (years)	Type of Training
(Bjork et al., 2012)	Young Endurance	7	M	25.0 (5.3)	1.83 (0.26)	81.1 (12.7)	24.4	>3	Moderate-high intensity
	Young Control	8	M	25 (2.8)	1.81 (0.28)	77.9 (19.0)	23.6	-	-
	Master Endurance Athlete	12	M	62 (6.9)	1.76 (0.35)	70.7 (10.4)	22.9	>30	Moderate-high intensity
	Older Control	11	M	64 (6.6)	1.75 (0.33)	74.7 (8.0)	24.3	-	-
(Buford et al., 2010)	Young Control	14	M	21.4 (3.8)	1.77 (0.06)	79.6 (17.1)	25.4	-	-
	Older Control	13	M	63.9 (6.6)	1.74 (0.06)	93.7 (15.3)	30.9	-	-
	Master Endurance Athlete	14	M	60.7 (5.5)	1.76 (0.05)	84.2 (7.2)	27.1	23.08 (12.6)	Running/Jogging/Basketball/ Resistance
(Buyukyazi, 2004)	Master Endurance Athlete	11	M	67.1 (6.0)	1.67 (0.08)	70.9 (3.2)	25.5	38.8 (18.5)	Middle/Long-distance Runners
	Older Control	11	M	64.9 (4.6)	1.69 (0.06)	81.6 (11.4)	28.3	-	-
(Carrick-Ranson et al., 2014a)	Older Control	27	M=15 F=12	69 (5.0)	1.69 (0.10)	75.0 (11.0)	26.3	-	-
	Master Endurance Athlete	25	M=17 F=8	68 (3.0)	1.71 (0.10)	66.0 (12.0)	22.6	25	Running/Cycling/ Swimming
(Couppe et al., 2014)	Young Endurance	10	M	26.0 (4.0)	1.79 (0.04)	73.0 (6.0)	23.0	6 (3.16)	Endurance running
	Young Control	12	M	24.0 (3.0)	1.78 (0.06)	70.0 (8.0)	22.0	-	-
	Master Endurance Athlete	15	M	64.0 (4.0)	1.76 (0.05)	71.0 (6.0)	23.0	28 (7.75)	Endurance running

Author, Year	Participant Groups	Number (n)	Sex (M/F)	Age (Years)	Height (m)	Weight (kg)	BMI (Kg.m ²)	Training Experience (years)	Type of Training
	Older Control	12	M	66.0 (4.0)	1.75 (0.04)	75.0 (4.0)	25.0	-	-
(Cristea et al., 2008)	Master power athletes	7	M	66.0 (7.9)	1.73 (0.05)	71.3 (6.6)	23.8	32 (18.5)	Sprint/Strength
	Master power athletes	4	M	71.0 (10.0)	1.71 (0.04)	69.6 (7.2)	23.8	24 (8)	Sprint Strength
(Dub�� et al., 2016)	Young Endurance	14	M=7 F=7	27.8 (4.9)	-	65.7 (10.8)	22.12	5-13	Non-competitive recreational exercise
	Master Endurance Athlete	13	M=9 F=4	64.8 (4.9)	-	68.2 (10.0)	23.76	35-40	Running, Cycling, Swimming, or Aerobic dancing
(Franzoni et al., 2005)	Young Control	16	M	34.1 (7.5)	-	-	23.1	-	-
	Older Control	16	M	63.7 (4.3)	-	-	24.2	-	-
	Young Endurance	16	M	33.4 (6.7)	-	-	23.4	11 (2)	Endurance Running
	Master Endurance Athlete	16	M	63.6 (6.1)	-	-	23.9	37 (5)	Endurance Running
(Galetta et al., 2005)	Master Endurance Athlete	20	M	68.5 (4.5)	-	-	23.4	>40	Endurance Running
	Older Control	20	M	68.2 (3.7)	-	-	24.1	-	-
(Galetta et al., 2006)	Older Control	28	M	65.6 (5.6)	5.60	-	-	-	-
	Master Endurance Athlete	30	M	64.5 (4.5)	4.50	-	-	>40	Endurance Running
(Hawkins et al.,	Master Endurance	34	M	62.2	1.77	77.0	24.5	22.6 (9.3)	Endurance Running

Author, Year	Participant Groups	Number (n)	Sex (M/F)	Age (Years)	Height (m)	Weight (kg)	BMI (Kg.m ²)	Training Experience (years)	Type of Training
2001)	Athlete			(3.5)	(0.02)	(7.6)			
	Master Endurance Athlete	13	M	71.1 (3.2)	1.73 (0.03)	67.5 (9.4)	22.7	21.6 (11.5)	Endurance Running
	Master Endurance Athlete	8	M	82.8 (4.0)	1.73 (0.02)	68.9 (5.9)	23.0	25.9 (22.3)	Endurance Running
(Hayes et al., 2015)	Older Control	28	M	63.0 (5.0)	1.75 (0.06)	90.4 (18.1)	29.5	-	-
	Master Endurance Athlete	20	M	60.0 (5.0)	1.74 (0.06)	79.3 (13.3)	26.2	>30	Water-polo/Triathlon/Sprint cycling/Road cycling/Distance running
(Katzel et al., 1998)	Master Endurance Athlete	70	M	63.0 (6.0)	-	70.0 (8.0)	23.0	>20	Running/Triathlon/Cycling/ Tennis
	Older Control	85	M	61.0 (7.0)	-	83.0 (11.0)	27.0	-	
(Katzel et al., 2001)	Master Endurance Athlete	42	M	63.4 (6.5)		69.4 (7.8)	23.1	>20	Running/Triathlon/Cycling/ Tennis
	Older Control	47	M	61.1 (6.2)		91.4 (11.7)	29.3	-	-
(Korhonen et al., 2006)	Young Power	16	M	24.3 (4.0)	1.78 (0.04)	77.2 (5.6)	24.4	13.2 (5.2)	Sprint/Strength
	Master power athletes	21	M	65.8 (2.8)	1.73 (0.04)	77.2 (4.1)	25.9	35.1 (19.3)	Sprint/Strength
	Master power athletes	20	M	75.3 (4.0)	1.71 (0.05)	69.8 (8.9)	23.8	34.3 (21.9)	Sprint/Strength
(Korhonen et al., 2012)	Young Control	19	M	36.2 (4.4)	1.82 (0.06)	79.2 (6.8)	24.0	-	Ball games/Jogging/Cross-country skiing

Author, Year	Participant Groups	Number (n)	Sex (M/F)	Age (Years)	Height (m)	Weight (kg)	BMI (Kg.m ²)	Training Experience (years)	Type of Training
(Larsson et al., 1997)	Master power athletes	24	M	65.9 (2.6)	1.72 (0.04)	71.1 (5.6)	24.0	35.1 (18.4)	Sprint/Strength
	Master power athletes	24	M	75.8 (4.3)	1.71 (0.06)	70.3 (8.5)	24.1	34.3 (21.4)	Sprint/Strength
	Young control	4	M	25-31	-	-	-	-	-
	Older Control	2	M	73-81	-	-	-	-	-
	Master Endurance Athlete	2	M	73-81	-	-	-	>50	Endurance Trained/ Competitive Wrestler
(Mackey et al., 2014)	Young Control	12	M	24.0 (3.0)	1.78 (0.06)	70.0 (8.0)	22.2	-	-
	Young Endurance	10	M	26.0 (4.0)	1.79 (0.04)	73.0 (6.0)	22.7	6.0 (2.0)	Endurance Running
	Older Control	12	M	66.0 (4.0)	1.75 (0.04)	75.0 (4.0)	24.5	-	-
(Marcell et al., 2003)	Master Endurance Athlete	15	M	64.0 (4.0)	1.76 (0.05)	71.0 (6.0)	22.9	28.0 (9.0)	Endurance Running
	Master Endurance Athlete	9	M	67.1 (1.2)		70.2 (4.8)	23.2	23.6 (12.6)	Endurance Running
	Master Endurance Athlete	21	M	71.3	1.74	71.3	23.5	24.9	Endurance Running
(Matelot et al., 2016)	Master Endurance Athlete	13	M	62.0 (3.0)	1.72 (0.04)	71.2 (6.1)	24.1	39.0 (4.0)	Endurance Running/Cycling
(Mikkelsen et al., 2013)	Young Control	12	M	24.0 (3.0)	1.78 (0.06)	70.0 (8.0)	22.0	-	-
	Young Endurance	10	M	26.0	1.79	73.0	23.0	6.0 (3.16)	Endurance Running

Author, Year	Participant Groups	Number (n)	Sex (M/F)	Age (Years)	Height (m)	Weight (kg)	BMI (Kg.m ²)	Training Experience (years)	Type of Training
(Molmen et al., 2012)	Older Control	12	M	(4.0) 66.0	(0.04) 1.75	(6.0) 75.0	25.0	-	-
	Master Endurance Athlete	15	M	(4.0) 64.0	(0.04) 1.76	(4.0) 71.0	23.0	28.0 (7.75)	Endurance Running
	Older Control	10	M	(4.0) 71.7	(0.04) (1.3)	(6.0) 76.5	25.0		
	Young Control	10	M	(2.3) 24.8	(16.0) (2.3)	76.0	22.7		
	Master Endurance Athlete	11	M	(1.8) 74.3	(8.3) (1.8)	74.5	23.0	>25	Cross Country Skiers
(Mortensen et al., 2012)	Young Control	8	M	(2.8) 23.0	(0.01) 1.83	(11.3) 79.0	23.6	-	-
	Older Control	8	M	(5.7) 66.0	(0.01) 1.75	(5.7) 79.0	25.8	-	-
	Master Endurance Athlete	8	M	(5.7) 62.0	(0.01) 1.78	(8.5) 76.0	24.0	>30	Endurance trained
(Mosole et al., 2014)	Young Power	5	M	(4.0) 26.2	-	-	-	>5.0	Weightlifting
	Older Control	6	M=4 F=2	(3.5) 71.8	-	-	-	-	-
	Master Endurance Athlete	7	M	(4.0) 68.3	-	-	-	>20	Endurance/Mixed
(Mucci et al., 1999)	Young Athletes	7	M	(3.4) 26.1	(0.10) 1.78	(7.7) 67.8	21.4	4.0 (2.38)	Triathlon/Endurance Running
	Young Control	7	M	(4.0) 23.0	(0.09) 1.83	(10.1) 73.3	21.9	-	-
	Master Endurance	7	M	64.4	1.69	72.3	25.4	25 (5.29)	Cycling

Author, Year	Participant Groups	Number (n)	Sex (M/F)	Age (Years)	Height (m)	Weight (kg)	BMI (Kg.m ²)	Training Experience (years)	Type of Training
(Nyberg et al., 2012)	Athlete			(10.9)	(0.13)	(11.1)			
	Older Control	7	M	61.6 (3.4)	1.69 (0.04)	69.6 (4.2)	24.4	-	-
	Young Control	8	M	23.0 (2.8)	1.83 (0.06)	79.4 (12.2)	23.7	-	-
	Older Control	8	M	66.0 (5.7)	1.75 (0.08)	79.2 (5.1)	25.9	-	-
(Ojanen et al., 2007)	Master Endurance Athlete	8	M	62.0 (5.7)	1.78 (0.06)	75.7 (8.8)	23.9	>30	Endurance trained
	Master power athletes	12	M	60.8 (2.1)	1.78 (0.08)	94.2 (13.4)	29.8	27.5 (14.8)	Shotput / Discus / Hammer
	Master power athletes	9	M	75.0 (4.9)	1.77 (0.05)	87.4 (11.0)	27.8	27.2 (19.8)	Shotput / Discus / Hammer
	Older Control	10	M	61.1 (2.7)	1.77 (0.06)	80.0 (12.2)	25.5	-	-
(Pollock et al., 2015)	Older Control	5	M	69.2 (3.7)	1.75 (0.06)	75.7 (11.1)	24.7	-	-
	Master Endurance Athlete	24	M	62.0 (1.4)	1.70 (0.06)	76.8 (8.5)	24.7	27.6 (17.5)	Cycling
	Master Endurance Athlete	19	M	67.0 (1.2)	1.77 (0.06)	72.6 (7.2)	23.2	26.5 (19.6)	Cycling
	Master Endurance Athlete	19	M	73.4 (2.6)	1.76 (0.06)	74.4 (10.1)	24.1	36.7 (19.5)	Cycling
(Power et al.,	Master Endurance Athlete	15	F	61.9 (1.6)	1.66 (0.06)	60.4 (5.5)	22.1	24.6 (20.3)	Cycling
	Master Endurance Athlete	4	F	75.3 (3.0)	1.61 (0.07)	57.1 (6.4)	22.0	45 (19.6)	Cycling
	Young Control	9	M	27.0	1.81	80.8	24.6	-	-

Author, Year	Participant Groups	Number (n)	Sex (M/F)	Age (Years)	Height (m)	Weight (kg)	BMI (Kg.m ²)	Training Experience (years)	Type of Training
2012)				(5.0)	(0.07)	(9.6)			
	Older Control	9	M	70.0	1.78	90.1	28.5	-	-
				(5.0)	(0.07)	(17.4)			
	Master Endurance Athlete	9	M = 8 F = 1	67.0	1.74	71.3	23.5	>30	Endurance Running
				(4.0)	(0.06)	(10.5)			
(Power et al., 2010a)	Young Control	10	M	27.0	1.78	80.7	25.6	-	-
				(3.0)	(0.08)	(10.0)			
	Older Control	10	M	66.0	1.72	78.8	26.7	-	-
				(3.0)	(0.07)	(10.4)			
	Master Endurance Athlete	10	M = 9 F = 1	64.0	1.77	72.3	23.0	38.2 (6.7)	Endurance Running
				(3.0)	(0.07)	(7.7)			
(Prasad et al., 2007)	Young Control	12	M = 9 F = 3	32.3	-	-	-	-	-
				(9.0)					
	Older Control	13	M = 7 F = 6	69.8	-	-	-	-	-
				(3.0)					
	Master Endurance Athlete	12	M = 6 F = 6	67.8	-	-	-	23.0 (8.0)	Marathons, Triathlons, Middle distance
				(3.0)					
(Prefaut et al., 1994)	Master Endurance Athlete	10	M	65.3	1.68	70.1	24.8	33.0 (18.0)	Cycling
				(8.2)	(0.07)	(4.3)			
	Older Control	10	M	68.3	1.72	74.8	25.3	-	-
				(7.0)	(0.05)	(7.6)			
	Young Endurance	10	M	23.3	1.80	68.8	21.2	-	-
				(3.5)	(0.03)	(6.0)			
(Proctor and Joyner, 1997)	Young Endurance	8	M	24.0	1.80	70.9	21.9	9.0 (3.0)	Running, Cycling, Triathlon
				(4.0)	(0.07)	(7.8)			Running, Cycling, Triathlon

Author, Year	Participant Groups	Number (n)	Sex (M/F)	Age (Years)	Height (m)	Weight (kg)	BMI (Kg.m ²)	Training Experience (years)	Type of Training
(Rantalainen et al., 2014)	Master Endurance Athlete	8	M	64.0 (4.0)	1.78 (0.06)	75.5 (10.2)	23.8	21.0 (5.0)	Running, Cycling, Triathlon
	Young Endurance	8	F	26.0 (4.0)	1.71 (0.05)	60.1 (5.5)	20.6	9.0 (5.0)	
	Young Power	26	M	27.4 (5.1)	1.81 (0.05)	76.7 (5.9)	23.4	15.4 (6.2)	Sprinting
	Young Control	41	M	28.7 (5.8)	1.8 (0.06)	78.1 (9.6)	24.1	-	-
	Master power athletes	35	M	72.4 (5.3)	1.71 (0.05)	70.7 (7.1)	24.2	35.4 (19.1)	Sprinting
	Older Control	24	M	71.6 (4.2)	1.71 (0.06)	75.8 (8.6)	25.9	-	-
(Rivier et al., 1994)	Young Endurance	10	M	23.9 (3.6)	1.78 (0.05)	69.4 (5.8)	21.8	-	Triathlon
	Master Endurance Athlete	6	M	63.7 (5.0)	1.67 (0.06)	75.3 (4.0)	27.0	30.0 (5.0)	Cycling
(Sallinen et al., 2008)	Young Control	10	M	25.7 (3.4)	1.82 (0.04)	77.0 (5.2)	23.3	-	-
	Master power athletes	8	M	71.8 (3.8)	1.75 (0.06)	86.3 (10.7)	28.4	22.8 (14.9)	National level throwers
	Older Control	10	M	70.6 (3.3)	1.70 (0.06)	71.4 (71.4)	24.7	-	-
(Sanada et al., 2009)	Young Control	23	M	25.3 (2.7)	-	70.8 (11.2)	23.5	-	-
	Older Control	22	M	65.2 (4.1)	-	69.7 (8.1)	24.3	-	-

Author, Year	Participant Groups	Number (n)	Sex (M/F)	Age (Years)	Height (m)	Weight (kg)	BMI (Kg.m ²)	Training Experience (years)	Type of Training
(Schmidt et al., 2015)	Young Endurance	26	M	20.3 (1.0)	-	69.3 (5.7)	22.3	3.0	Rowing
	Master Endurance Athlete	24	M	65.7 (3.0)	-	67.9 (8.2)	23.0	46.7 (2.8)	Rowing
	Master Endurance Athlete	17	M	68.1 (2.1)	1.78 (0.03)	78.1 (8.2)	24.6	52.0 (11.0)	Football
	Older Control	26	M	68.2 (3.2)	1.76 (0.03)	84.1 (11.1)	27.2	-	-
(Shibata and Levine, 2012)	Older Control	10	M = 6 F = 4	71.0 (3.0)	1.71 (0.09)	74.0 (10.0)	26	-	-
	Master Endurance Athlete	11	M = 5 F = 6	68.0 (3.0)	1.70 (0.12)	65.0 (14.0)	22.1	23.0 (8.0)	Endurance Running
(Sipila and Suominen, 1991)	Master power athletes	7	M	77.1 (3.5)	1.69 (0.06)	69.8 (9.3)	-	30 to 70	Track and field, Gymnastics
	Master Endurance Athlete	14	M	74.2 (3.0)	1.71 (0.07)	68.7 (8.6)	-	30 to 70	Running, Cross-country Skiing, Cycling, Swimming
	Older Control	11	M	73.4 (2.4)	1.68 (0.04)	74.7 (11.6)	-	-	-
(Stenroth et al., 2016)	Young Control	18	M	23.7 (2.0)	1.81 (0.06)	75.4 (9.0)	23.1	-	-
	Older Control	33	M	74.8 (3.6)	1.73 (0.05)	76.1 (7.7)	25.4	-	-
	Master Endurance Athlete	10	M	74.0 (2.8)	1.75 (0.07)	69.9 (6.9)	22.7	39.4 (20.9)	Endurance Exercise
	Older Power	10	M	74.4 (2.8)	1.76 (0.07)	74.3 (7.1)	24.1	44.7 (19.7)	Sprinting
(Sundstrup et al.,	Master Endurance	10	M	69.6	1.77	83.7	26.8	50.0	Football

Author, Year	Participant Groups	Number (n)	Sex (M/F)	Age (Years)	Height (m)	Weight (kg)	BMI (Kg.m ²)	Training Experience (years)	Type of Training
2010)	Athlete			(4.4)	(0.05)	(8.9)			
	Young Control	49	M	32.4	1.82	87.7	26.5	-	-
				(6.3)	(0.05)	(12.6)			
	Older Control	8	M	70.5	1.75	82.9	27.1	-	-
(Suominen and Rahkila, 1991)	Master Endurance Athlete	67	M	73.7	1.71	69.3	23.8	-	Endurance Running, Orienteers, Cross-country Skiers
				(2.7)	(0.07)	(8.6)			
	Master power athletes	14	M	74.3	1.74	82.4	27.1	-	Throwers, Weight Lifters
				(2.9)	(0.06)	(12.5)			
(Tarpennig et al., 2004b)	Master power athletes	16	M	75.5	1.70	69.4	24.1	-	Sprinters, Jumpers
				(3.8)	(0.06)	(12.0)			
	Older Control	42	M	74.2	1.69	76.3	26.7	-	
				(2.8)	(0.07)	(12.0)			
(Thomas et al., 2013)	Master Endurance Athlete	29	M	64.2	1.76	71.5	23.1	20.33 (9.0)	Endurance Running
				(2.3)	(0.07)	(8.1)			
(Thomas et al., 2013)	Master Endurance Athlete	11	M	74.6	1.74	68.6	22.6	24 (20.6)	Endurance Running
				(3.5)	(0.06)	(7.0)			
	Master Endurance Athlete	10	M = 7 F = 3	74.5	-	-	-	23.0 (8.0)	Endurance Running, Swimming, Cycling
				(5.8)					
(Thomas et al., 2013)	Older Control	10	M = 8 F = 2	75.4	-	-	-	-	-
				(5.6)					
	Young Control	9	M = 5 F = 4	27.0	-	-	-	-	-
				(3.6)					
(Trappe et al., 2013)	Master Endurance Athlete	9	M	81.0	1.72	68.0	23.0	>50	Cross-country Skiing, Orienteering, Track and Field
				(3.0)	(0.06)	(9.0)			
(Trappe et al., 2013)	Older Control	6	M	82.0	1.72	77.0	26.0	-	-

Author, Year	Participant Groups	Number (n)	Sex (M/F)	Age (Years)	Height (m)	Weight (kg)	BMI (Kg.m ²)	Training Experience (years)	Type of Training
(Witkowski et al., 2010)	Older Control	11	M	(4.9) 64.0	(0.10) 1.76	(12.2) 73.0	23.6	-	-
	Master Endurance Athlete	12	M	(6.6) 62.0	(0.07) 1.78	(8.0) 70.1	22.0	32.0 (10.4)	Endurance Training
(Yataco et al., 1997)	Master Endurance Athlete	61	M	(6.9) 63.3	(0.10) -	(10.0) 70.1	22.9	>20	Running/Cycling/ Swimming
	Older Control	39	M	(6.1) 60.6	-	(7.1) 77.1	25.6		
(Zampieri et al., 2015)	Young Control	5	M	(5.6) 27.3	(8.5) 1.75	(5.9) 73.8	24.2	-	-
	Older Control	9	M	(4.2) 71.4	(0.04) 1.77	(10.1) 84.9	26.9	-	-
	Master Endurance Athlete	15	M	(3.0) 70.2	(0.08) 1.76	(8.8) 81.7	26.3	>30	Endurance, Strength, Power and Games

Table 2) Anthropometric characteristics and training background of study groups (mean \pm SD) included in this review, (e.g. n, age, height, weight, BMI, years of training, and type of training undertaken).

Study Group	Fat-Free Mass (kg)	Fat Mass (kg)	Body Fat (%)	Muscle Thickness (cm)	Fascicle Length (cm)	Muscle Cross-Sectional Area (mm ²)	Muscle Fibre Area (µm ²)	Muscle Fibre Distribution (%)
Young Controls	53.8 ± 5.7 (1, n=23)	-	17.4 ± 3.0 (8, n=126)	-	-	MRI: 6792 ± 696 (n=12)	Type I: 4282 ± 26 (2, n=28), Type 2: 4783 ± 872 (1, n=12) Type IIa: 4700 ± 560.0 (1, n=16) Type IIx: 3200 ± 2720 (1, n=16) Type IIax: 3700 ± 760 (1, n=16)	Type I: 43.5 ± 4.5 (4, n=37) Type 2: 53.5 ± 5.0 (2, n=17) Type IIa: 35 ± 12 (1, n=16) Type IIx: 7.5 ± 6.4 (2, n=20) Type IIax: 12.0 ± 00 (2, n=20) Denervated: (0.3 ± 0.0 (1, n=5)
Young Endurance	54.8 ± 7.3 (4, n=56)	12.0 ± 4.2 (1, n=14)	14.8 ± 4.9 (8, n=89)	-	-	MRI: 7859 ± 636 (n=10)	Type I: 5550 ± 1337 (1, n=10) Type 2: 5498 ± 1559 (1, n=10)	Type I: 51.5 ± 13.4 (2, n=15) Type 2: 48.6 ± 13.5 (2, n=15) Type IIax: 0.5 ± 0.6 (1, n=5) Denervated: 0.4 ± 0.5 (1, n=5)
Young Power	-	-	-	VL: 2.61 ± 0.08 (n=16)	VL: 7.91 ± 0.49 (n=16)	-	-	-
Older Controls	54.5 ± 7.7 (5, n=122)	20.1 ± 6.3 (2, n=65)	24.5 ± 4.6 (20, n=368)	RF: 2.8 ± 0.56 (n=11)	-	MRI: 5504 ± 727 (n=12) US: 4840 ± 1110 (n=11)	Type I: 5488 ± 459 (3, n=28) Type 2: 4149 ± 903 (1, n=12) Type IIa: 5411 ± 484 (2, n=16) Type IIx: 3974 ± 0 (2, n=16) Type IIax: 4570	Type I: 49.8 ± 4.2 (6, n=45) Type 2: 50.3 ± 4.0 (3, n=27) Type IIa: 23.5 ± 0 (2, n=16) Type IIx: 22.2 ± 13.1 (3, n=18) Type IIax: 5.9 ±

Study Group	Fat-Free Mass (kg)	Fat Mass (kg)	Body Fat (%)	Muscle Thickness (cm)	Fascicle Length (cm)	Muscle Cross-Sectional Area (mm ²)	Muscle Fibre Area (µm ²)	Muscle Fibre Distribution (%)
							± 980 (1, n=4)	5.8 (2, n=8) Denervated: 5.3 ± 1.8 (2, n=15)
Master Endurance	55.2 ± 6.1 (19, n=366)	14.1 ± 3.6 (3, n=91)	19.2 ± 4.1 (38, n=595)	RF: 2.77 ± 0.39 (n=14)	-	MRI: 6481 ± 775 (n=15) US: 5270 ± 880 (n=14)	Type I: 5367 ± 588 (5, n=74) Type 2: 4478 ± 347 (3, n=55) Type IIa: 5043 ± 41 (2, n=19) Type IIx: 3955 ± 88 (2, n=19) Type IIax: 3590 ± 687 (1, n=7)	Type I: 60.8 ± 10.7 (7, n=96) Type 2: 38.4 ± 11.3 (5, n=77) Type IIa: 32.6 ± 10.7 (2, n=19) Type IIx: 10.3 ± 2.7 (3, n=21) Type IIax: 6.3 ± 8.1 (2, n=9) Denervated: 1.9 ± 0.1 (2, n=22)
Master Power	-	-	19.6 ± 5.8 (8, n=125)	VL 60-69: 2.1 ± 0.09 (n=21) VL 70-84: 1.96 ± 0.08 (n=20) RF: 2.73 ± 0.37 (n=7)	VL 60-69: 7.99 ± 0.27 (n=21) VL 70-84: 7.38 ± 0.27 (n=20)	US: 5250 ± 1080 (n=7)	Type I: 4750 ± 1273 (4, n=34) Type IIa: 4755 ± 1404 (4, n=34) Type IIx: 4019 ± 990 (4, n=34) Type IIax: 4120 ± 495 (3, n=27)	Type I: 48.0 ± 8.0 (5, n=59) Type IIa: 31.8 ± 38 (3, n=59) Type IIx: 10.7 ± 4.1 (5, n=59) Type IIax: 11.6 ± 2.6 (2, n=52)

Table 3) Body composition, muscle mass and morphology (mean ± SD) not included in a meta-analysis (e.g. fat-free mass, fat-mass, relative fat-mass

(additional data ineligible to be included in meta-analysis), muscle thickness, fascicle length, muscle CSA, fibre area, fibre distribution). First number in the bracket indicates the number of studies that assessed that particular variable, the second number indicates the number of individuals assessed.

Figures

Figure 1) PRISMA Flowchart detailing the article identification, screening and exclusion process.

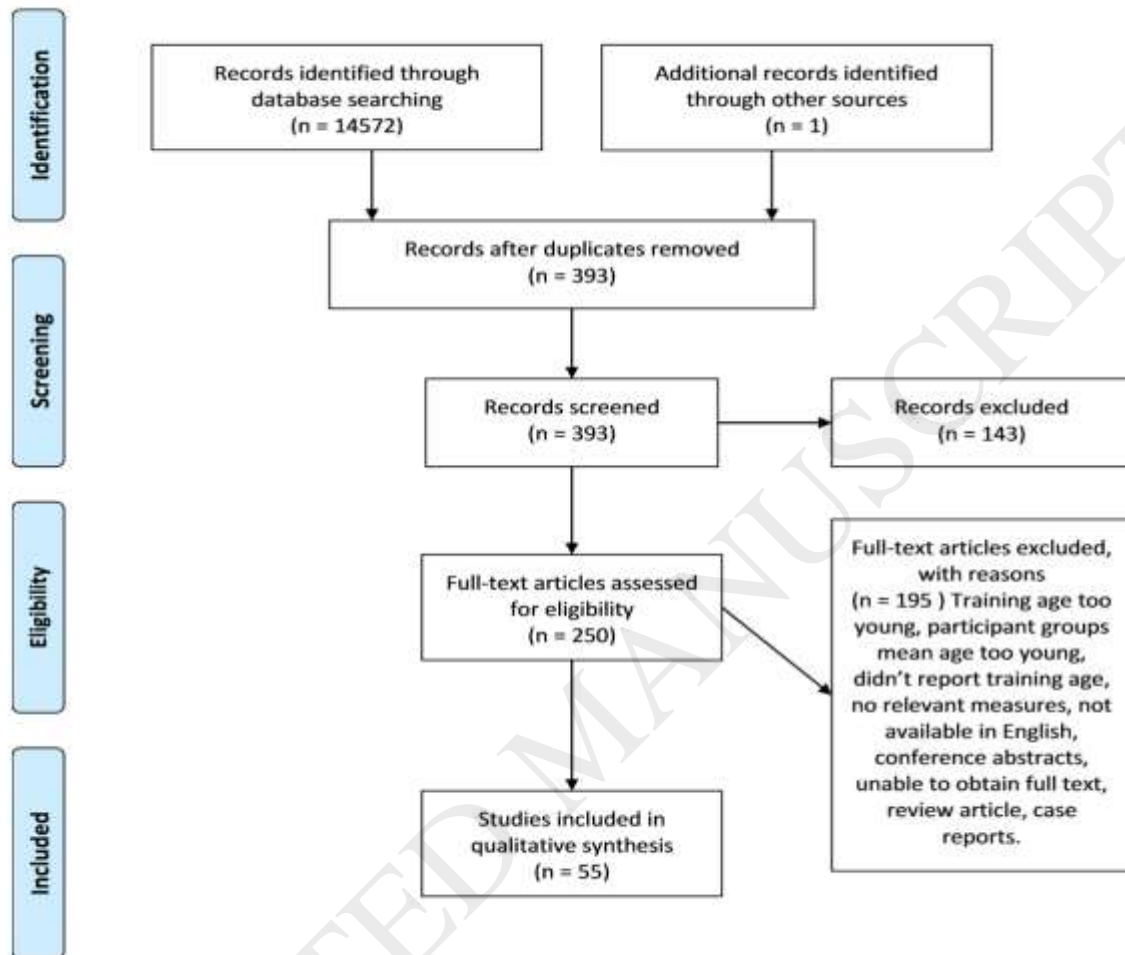


Figure 2) Forest plot of the results from a random-effects meta-analyses shown and mean difference with 95% CI on body fat % in old control, master power athletes, endurance trained young and young control. The vertical dotted line represents the body fat for the master endurance athletes. For each study the square represents the mean difference with the horizontal line indicating the upper and lower limits of the 95% CI. The size of the square indicates the relative weighted contribution of each study to the meta-analyses. The diamond in each section indicates the pooled mean difference for each respective group.

Master endurance athletes vs. old control: Heterogeneity: 7.11 (5.70, 8.52) $\text{Tau}^2 = 5.36$; $\text{Chi}^2 = 71.00$, $\text{df} = 14$ ($P < 0.00001$); $I^2 = 80\%$ Test for overall effect: $Z = 9.89$ ($P < 0.00001$)

Master endurance athletes vs. master power athletes: -1.00 (-7.61, 5.61) Heterogeneity: Not applicable Test for overall effect: $Z = 0.30$ ($P = 0.77$)

Master endurance athletes vs. young control: -0.22 (-3.72, 3.28) Heterogeneity: $\text{Tau}^2 = 13.08$; $\text{Chi}^2 = 17.30$, $\text{df} = 5$ ($P = 0.004$); $I^2 = 71\%$ Test for overall effect: $Z = 0.12$ ($P = 0.90$).

Master endurance athletes vs. young endurance trained: -4.44 (-8.44, -0.43) Heterogeneity: $\text{Tau}^2 = 15.10$; $\text{Chi}^2 = 16.76$, $\text{df} = 4$ ($P = 0.002$); $I^2 = 76\%$ Test for overall effect: $Z = 2.17$ ($P = 0.03$)

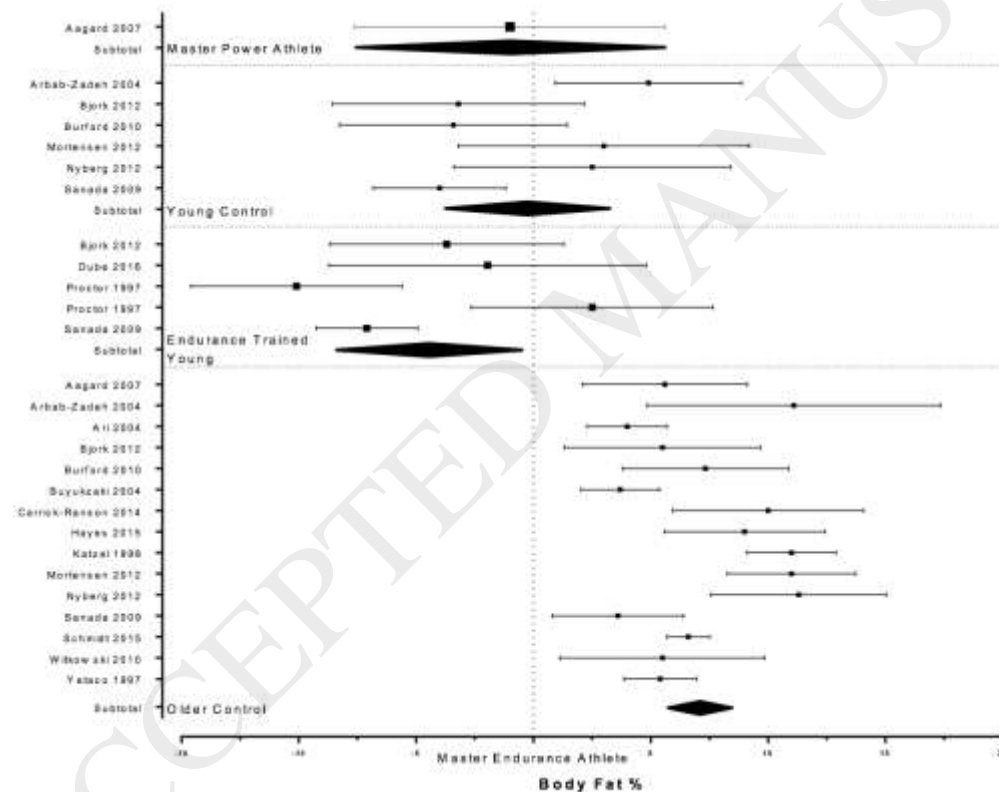


Figure 3) Forest plot of the results from a random-effects meta-analyses shown and mean difference with 95% CI on VO2max (ml.kg-1.min-1) in old control, master power athletes, endurance trained young and young control. The vertical dotted line represents the VO2max for the master endurance athletes. For each study the square represents the mean difference with the horizontal line indicating the upper and lower limits of the 95% CI. The size of the

square indicates the relative weighted contribution of each study to the meta-analyses. The diamond in each section indicates the pooled mean difference for each respective group.

Master endurance athletes vs. old control: -15.41 (-17.39, -13.43) Heterogeneity: $\text{Tau}^2 = 28.97$; $\text{Chi}^2 = 439.62$, $\text{df} = 31$ ($P < 0.00001$); $I^2 = 93\%$ Test for overall effect: $Z = 15.27$ ($P < 0.00001$).

Master endurance athletes vs. master power athletes: -7.77 (-12.03, -3.50) Heterogeneity: $\text{Tau}^2 = 9.37$; $\text{Chi}^2 = 6.54$, $\text{df} = 2$ ($P = 0.04$); $I^2 = 69\%$ Test for overall effect: $Z = 3.57$ ($P = 0.0004$).

Master endurance athletes vs. young control: 0.55 (-4.88, 5.98) Heterogeneity: $\text{Tau}^2 = 116.92$; $\text{Chi}^2 = 547.90$, $\text{df} = 15$ ($P < 0.00001$); $I^2 = 97\%$ Test for overall effect: $Z = 0.20$ ($P = 0.84$).

Master endurance athletes vs. young endurance trained: 16.79 (13.50, 20.09) Heterogeneity: $\text{Tau}^2 = 31.81$; $\text{Chi}^2 = 128.46$, $\text{df} = 12$ ($P < 0.00001$); $I^2 = 91\%$ Test for overall effect: $Z = 9.99$ ($P < 0.00001$).

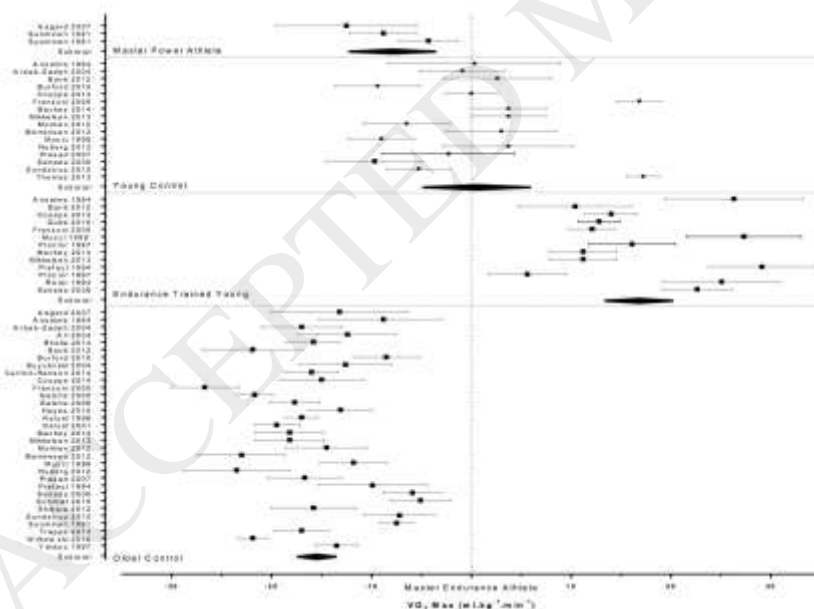


Figure 4) Forest plot of the strength results from random-effects meta-analyses shown presented as standardised mean difference with 95% CI in master power athletes, old control, endurance trained young and young control. The vertical dotted line represents the master

endurance athletes. For each study the square represents the standardised mean difference with the horizontal line indicating the upper and lower limits of the 95% CI. The size of the circle indicates the relative weighted contribution of each study to the meta-analyses. The diamond in each section indicates the pooled mean difference for each respective group.

Master endurance athletes vs. master power athletes: 0.60 [0.28, 0.93] Heterogeneity: $\tau^2 = 0.00$; $\chi^2 = 3.68$, $df = 4$ ($P = 0.45$); $I^2 = 0\%$ Test for overall effect: $Z = 3.63$ ($P = 0.0003$).

Master endurance athletes vs. old control: -0.25 [-0.77, 0.27] Heterogeneity: $\tau^2 = 0.48$; $\chi^2 = 36.17$, $df = 8$ ($P < 0.0001$); $I^2 = 78\%$ Test for overall effect: $Z = 0.93$ ($P = 0.35$).

Master endurance athletes vs. young control: 0.71 [0.06, 1.36] Heterogeneity: $\tau^2 = 0.47$; $\chi^2 = 18.91$, $df = 5$ ($P = 0.002$); $I^2 = 74\%$ Test for overall effect: $Z = 2.13$ ($P = 0.03$).

Master endurance athletes vs. young endurance trained: 0.75 [-0.34, 1.85] Heterogeneity: $\tau^2 = 0.78$; $\chi^2 = 12.12$, $df = 2$ ($P = 0.002$); $I^2 = 84\%$ Test for overall effect: $Z = 1.35$ ($P = 0.18$).

