1

Ageing and recovery after resistance exercise-induced muscle damage:

Current evidence and implications for future research

Abstract

Ageing is anecdotally associated with a prolonged recovery from resistance training, though current literature remains equivocal. This brief review considers the effects of resistance training on indirect markers of muscle damage and recovery (i.e. muscle soreness, blood markers and muscle strength) in older males. With no date restrictions, four databases were searched for articles relating to ageing, muscle damage and recovery. Data from 11 studies was extracted for review. Of these four reported worse symptoms in older compared to younger populations, while two have observed the opposite, and the remaining studies (n = 6) proposing no differences between age groups. It appears that resistance training can be practiced in older populations without concern for impaired recovery. To improve current knowledge, researchers are urged to utilise more ecologically valid muscle damaging bouts and investigate the mechanisms which underpin the recovery of muscle soreness and strength after exercise in older populations.

Key words

Fatigue, muscle soreness, muscle strength, sarcopenia, dynapenia

Introduction

It is predicted that the global population will grow to 11.18 billion by the year 2100 (United Nations, 2017). This growth will incorporate an increasing proportion of people classified as older adults, with those over the age of 60 expected to increase from 0.91 billion in 2015 to 3.14 billion (United Nations, 2017). Improvements in medical care, a decline in the leading causes of mortality and a better appreciation of the factors that enhance longevity contribute to such demographic transformations (Baker & Tang, 2010; Ferrucci, Giallauria, & Guralnik, 2008). Despite these demographic transformations, the ageing process remains associated with losses in muscle mass (i.e. sarcopenia) (Lexell, Taylor, & Sjöström, 1988), and strength and power (i.e. dynapenia) (Fernandes, Lamb, & Twist, 2018a). In addition, these losses are not uniform with strength and power declining faster than muscle mass into older age (Clark & Manini, 2008, 2012), and lower-body regions displaying greater rates of sarcopenia and dynapenia than the upper-body (Fernandes et al., 2018a; Frontera et al., 2000). For the general population, sarcopenia and dynapenia have a negative impact on quality of life and daily functioning (Cruz-Jentoft et al., 2010) and, for the growing numbers of ageing athletes (Lepers, Rüst, Stapley, & Knechtle, 2013; Tanaka & Seals, 2008), are likely contributors to age-related declines in athletic performance (Baker & Tang, 2010; Pantoja, Saez De Villarreal, Brisswalter, Peyré-Tartaruga, & Morin, 2016). Resistance training provides a potent method of offsetting these age-associated changes (Bottaro, Machado, Nogueira, Scales, & Veloso, 2007; Kongsgaard, Backer, Jørgensen, Kjær, & Beyer, 2004; Newton et al., 2002; Sayers & Gibson, 2010, 2014) and, as such, is included in national physical activity guidelines (Department of Health and Social Care, 2019). However optimal

management of resistance training dosing for older populations remains challenging given concerns around impaired recovery.

An acute consequence of unaccustomed resistance training is exerciseinduced muscle damage (EIMD) which involves damage to the muscle ultrastructure, particularly when it comprises high-volume and/or eccentrically biased muscle actions (Hortobágyi et al., 1998; Roth et al., 1999). During the eccentric component of muscle actions, lengthening is non-uniform and weaker sarcomeres extend beyond their myofilament overlap and fail to re-interdigitate (Hyldahl & Hubal, 2014; Morgan & Proske, 2004). This causes an increased stress per myofibre that is consistent with eccentric contractions and is known as the 'popping-sarcomere hypothesis' (Morgan & Proske, 2004). Thereafter, a loss of calcium homeostasis leads to excitation-contraction (E-C) coupling dysfunction and a prolonged loss of muscle strength (Damas, Nosaka, Libardi, Chen, & Ugrinowitsch, 2016; Hyldahl & Hubal, 2014; Morgan & Proske, 2004). Irrespective of the mechanisms, indirect markers of EIMD such as muscle soreness, and intramuscular enzymes in the blood are commonly used to indicate EMID (Damas et al., 2016; Fernandes, Lamb, & Twist, 2018b; Hyldahl & Hubal, 2014). These indirect markers are highly individualised and often do not reflect the magnitude of EIMD (Damas et al., 2016; Fridén & Lieber, 2001; Nosaka, Newton, & Sacco, 2002), such that quantifying changes in muscle function (i.e. strength and power) offers the most relevant marker of EIMD (Damas et al., 2016). This notwithstanding, best practice, from a research and practitioner perspective often takes a holistic view and measures a variety of indirect markers when assessing EIMD.

Muscle damage is a natural response to resistance training leading to cellular, mechanical and neural changes that enhance muscle function, reduce damage in

subsequent bouts of resistance training (Burt, Lamb, Nicholas, & Twist, 2015; Hyldahl, Chen, & Nosaka, 2017; McHugh, 2003) and might be a key requirement for skeletal muscle hypertrophy (Schoenfeld, 2010). Exposure to muscle damage should therefore not be discouraged in older populations. However, ageing is anecdotally associated with an impaired recovery from resistance induced muscle damage. The responses to EIMD in older individuals remain equivocal, with some research reporting worse symptoms of EIMD in older compared to young populations (Chapman, Newton, McGuigan, & Nosaka, 2008; Fernandes, Lamb, & Twist, 2019; Nikolaidis, 2017; Nikolaidis et al., 2013), some suggesting worse symptoms in young compared to old (Lavender & Nosaka, 2006, 2007), and others proposing no age differences in EIMD (Arroyo et al., 2017; Buford et al., 2014; Gordon III et al., 2017; Heckel et al., 2019; Lavender & Nosaka, 2008). These discrepancies between studies might be attributable to factors such as different protocols (e.g. single- versus multi-jointed), muscle groups used (e.g. upper- versus lower-body), activity status of the participants (e.g. trained versus untrained) and large inter-individual variability in the indirect markers of muscle damage measured (Damas et al., 2016). Therefore, a review of the current literature is required to provide sport and clinical practitioners with a greater understanding of EIMD and recovery time course for older adults. Moreover, greater understanding of the fatigue and recovery time course with ageing would provide older populations, clinicians and practitioners with a framework to facilitate the prescription of appropriate targeted recovery strategies and periodisation of resistance training within a micro-cycle (Clifford, 2019). As such, the aim of this review was to explore the effects of resistance training on indirect markers of EIMD (i.e. muscle function, soreness and circulating proteins) throughout the recovery process in older males. Additionally, the review sought to describe the

current limitations within this area of investigation and subsequently provide scope for future research.

Outline of terms

Establishing a definition of what encompasses 'young', 'middle-aged' and 'old' is problematic because chronological and biological age are not always the same (Balcombe & Sinclair, 2001). Moreover, as life expectancy increases and the quality of life of older populations improves, what constitutes these terms will likely change (Orimo et al., 2006). As such, the use of young, middle-aged and old in this manuscript are based upon the age groups used in the reviewed articles. Typically, this constitutes young, middle-aged and old age groups as 18-25, 35-60 and >60 years, respectively. Whilst it would be advantageous to establish definitions of these groups it is beyond the scope of this article.

Methods

With no date restrictions a literature search was conducted between January 2019 and March 2020 on PubMed, Google Scholar, SPORTDiscus and the host institution databases. Search terms included "ageing" OR "age" OR "middle-aged" OR "old" OR "masters" OR "older" OR "veteran" AND "eccentric exercise" OR "lengthening exercise" OR "muscle damage" OR "exercise-induced muscle damage" OR "exercise-induced muscle injury" OR "contraction-induced muscle injury" OR "muscle soreness" OR "delayed onset muscle soreness" OR "creatine kinase" OR "myoglobin" OR "exercise-induced muscle weakness" OR "fatigue" OR "recovery". Only articles in English were considered. Articles were only included if they 1) provided a young versus middle-aged or old comparison, 2) provided recovery

markers beyond ≥ 24 hours, 3) had an all-male sample and 4) did not provide a recovery aid (e.g. cold-water immersion). The reference list of the retrieved articles was examined to identify articles not found during the literature search. All article that were retrieved were included within the review, providing they met the inclusion criteria.

The effects of ageing on indirect markers of EIMD

Muscle soreness

Muscle soreness is the most commonly assessed marker of EIMD (Warren, Lowe, & Armstrong, 1999) though the mechanism for its appearance remains unclear. Sensations of muscle soreness could result from a complex interaction of damage to the muscle structure and connective tissue, disrupted calcium homeostasis, sensitisation of nociceptors from inflammatory cell infiltrates and reductions in range of motion (Hyldahl & Hubal, 2014; Jamurtas et al., 2005; Nogueira et al., 2014; Nosaka et al., 2002). Irrespective of the mechanisms, muscle soreness typically appears between 8 - 24 h after muscle-damaging exercise, peaks between 24 - 48 h and usually subsides within 96 h (Damas et al., 2016; Jones, Newham, & Torgan, 1989). Although muscle soreness does not appear to reflect the magnitude of muscle damage (Damas et al., 2016; Nosaka et al., 2002), it might provide an indication of any physiological changes after exercise.

Several studies have presented equivocal findings on age-related differences in muscle soreness after muscle-damaging resistance training (Table 1). For example, older males (~64 to 70 years) have reported lower muscle soreness than young (~25 years) (Chapman et al., 2008; Lavender & Nosaka, 2006) and middle-aged males (~48 years) (Lavender & Nosaka, 2008) despite having greater force

losses after exercise (at 72 hours post) (Chapman et al., 2008) (Table 2). These data are in contrast to those studies reporting no differences in muscle soreness between age groups (Buford et al., 2014; Gordon III et al., 2017; Heckel et al., 2019), even in the presence of greater force losses in older males (Fernandes et al., 2019; Nikolaidis, 2017; Nikolaidis et al., 2013). Taken collectively, these findings suggest that the mechanisms which lead to soreness are comparable and *potentially* ameliorated after resistance training in older populations.

Circulating proteins

Monitoring of muscle-specific proteins, such as plasma creatine kinase (CK) and serum myoglobin (Mb), are typical when assessing EIMD and generally peak in concentration 2 to 6 days after exercise (Byrne, Twist, & Eston, 2004; Damas et al., 2016; Hyldahl & Hubal, 2014; Warren et al., 1999). Resistance training increases membrane permeability and subsequently leakage of muscle proteins into the blood (Sorichter, Puschendorf, & Mair, 1999). However, muscle-specific proteins demonstrate a poor temporal relationship with muscle function, a high intra- and inter-individual variability (Damas et al., 2016; Fridén & Lieber, 2001), and most likely reflect the occurrence of tissue damage rather than the magnitude (Owens, Twist, Cobley, Howatson, & Close, 2018).

CK (eight studies) and Mb (five studies) are the most frequently investigated muscle-specific proteins in studies of ageing and recovery (Table 1). Whilst several studies have examined the response of CK and Mb to resistance across age groups (Arroyo et al., 2017; Chapman et al., 2008; Fernandes et al., 2019; Gordon III et al., 2017; Lavender & Nosaka, 2006, 2008; Nikolaidis, 2017; Nikolaidis et al., 2013), only two have reported differences in the response of CK (Lavender & Nosaka, 2006) and

Mb (Heckel et al., 2019; Lavender & Nosaka, 2006) to resistance training between younger (~21 to 25 years) and older (~ 65 to 71 years) males (Table 2). Lavender and Nosaka (Lavender & Nosaka, 2006) noted higher CK and Mb activity in young males, after eccentric elbow flexor exercise, than in their older counterparts, whilst Heckel et al. (2019) observed elevated Mb in the older group after knee extension exercise. However, given the commentary above, CK and Mb concentrations were only increased from baseline (i.e. membrane permeability was increased) and do not provide an indication of the magnitude of EIMD between groups.

Muscular strength

Reduced muscle strength (e.g. force or torque) after resistance training is considered the most appropriate indirect marker of EIMD as it demonstrates the lowest interindividual variability (Damas et al., 2016; Paulsen, Mikkelsen, Raastad, & Peake, 2012; Warren et al., 1999). Depending on the type, intensity and duration of the initial exercise bout, strength can decrease by 15-60% after resistance training and can persist for up to ~2 weeks (Hyldahl & Hubal, 2014; Paulsen et al., 2012). The mechanisms that result in decreased force production include physical damage to the sarcomere and sarcolemma from eccentric lengthening and E-C coupling failure (Hyldahl & Hubal, 2014; Morgan & Proske, 2004).

Whether losses in muscle strength differ between age groups after resistance training is currently unclear. Of the 11 available studies (Table 1), four conclude that muscle strength loss after resistance training is greater in older (~40-67 years) compared to younger (~21-25 years) males (Chapman et al., 2008; Fernandes et al., 2019; Nikolaidis, 2017; Nikolaidis et al., 2013), two have reported greater decrements in young (~19 to 20 years) compared to old (~71 years) (Lavender &

Nosaka, 2006, 2007) and the remainder observed no differences between age groups (Arroyo et al., 2017; Buford et al., 2014; Gordon III et al., 2017; Heckel et al., 2019; Lavender & Nosaka, 2008) (Table 2). The reasons for the discrepancy between these studies are unclear but might be due to differences in physical activity and resistance training status of the participants. For example, when controlling for physical activity, Buford and colleagues (2014) observed similar recovery of isometric plantar flexion force in younger (~23 years) and older (~76 years) adults males after eccentric unilateral plantar flexion exercise. More recently, two studies have investigated the recovery profiles of young (~22 years) and middle-aged (~47 years) recreationally resistance trained males (Arroyo et al., 2017; Gordon III et al., 2017), both of which reported no difference in the recovery profile of muscle strength markers (e.g. peak and mean knee extensor torque and power) after eccentric knee extension exercise (Arroyo et al., 2017; Gordon III et al., 2017). These studies suggest that when physical activity/training status is matched, recovery of muscle strength is similar between age groups. Conceptually, these data *might* suggest that impairments in the recovery of muscle strength can be attributed to a lack of training, rather than ageing.

Another factor that could influence the time course of recovery between younger and older males after resistance training could be exercise selection. For healthy males, multi-jointed exercise (e.g. squats, bench press) are preferred to single-jointed exercises (e.g. knee extensions, bicep curls), especially in the strength and conditioning settings (Allison, Brooke-Wavell, & Folland, 2013; American College of Sports Medicine, 2002, 2009). When comparing the recovery of muscle function from squatting exercise (10 x 10 squats at 60% one repetition maximum (1RM)), Fernandes et al. (2019) reported greater losses in isometric force in

resistance trained middle-aged males (~40 years) compared to their younger (~22 years) counterparts. These data are supported by Nikolaidis (2017) who observed greater isometric force loss in older males (~67 years) after squatting exercise than young males (~21 years). Uniquely, Fernandes and colleagues (2019) also noted moderately greater losses in squatting peak power at 20 and 80% 1RM after exercise for middle-aged males (~40 years) compared to younger participants (~22 years) (Fernandes et al., 2019). Tentatively, these data *might* suggest that activity status and exercise type (e.g. single- versus multi-jointed) mediate the recovery of muscle strength loss between younger and older males after resistance training. Given the positive relationship between power and sporting tasks/playing standard (Cronin & Hansen, 2005; Fernandes, Daniels, Myler, & Twist, 2019; Hansen, Cronin, Pickering, & Douglas, 2011), middle-aged males should consider the potential implications of impaired recovery on performance after damaging exercise. However, the paucity of data makes it impractical to draw firm conclusions on muscle strength loss after resistance training.

Age-dependant central and peripheral alterations in muscle function after resistance training

Impaired muscle function in the hours and days after resistance training might be the result of central (e.g. neural impairments and a reduction in excitability to the alpha motor-neuron (Avela, Kyröläinen, Komi, & Rama, 1999; Horita, Komi, Nicol, & Kyröläinen, 1999; Morton et al., 2005)) and/or peripheral perturbations (e.g. disruption of sarcomeres, impaired E-C coupling, accumulation/depletion of metabolites (Allen, Lamb, & Westerblad, 2008; Doguet et al., 2016; Hubal, Rubinstein, & Clarkson, 2007). For example, Macdonald, Button, Drinkwater and

Behm (2014) observed decrements in MVC after muscle-damaging squatting exercise that were accompanied by impairments in voluntary activation (VA; i.e. central alterations) and resting twitch force (i.e. peripheral alterations).

The available data on resistance training induced central and peripheral fatigue alterations between age groups is limited to four studies investigating the immediate post-exercise alterations (Dalton, Power, Paturel, & Rice, 2015; Dalton, Power, Vandervoort, & Rice, 2012; Fernandes et al., 2018b) and one reporting on these alterations in the days after exercise (Fernandes et al., 2019). Dalton et al. (2012) observed no differences in VA or resting twitch torque between these groups (~25 vs 75 year old recreational active males) after slow (60°·s⁻¹), moderate (180°⋅s⁻¹) or unconstrained velocity knee extension exercise. Similarly, Dalton et al. (2015) and Fernandes et al. (2018b) noted a comparable reduction in VA after single- and multi-jointed RT, respectively, in young (~22 to 25 years) and older (~40 to 74 years) recreational active and resistance trained males, respectively. Notably, the younger group was subject to greater losses in resting twitch torque after singlejointed resistance training (Dalton et al., 2015) but experienced inferior symptoms than the older males after multi-jointed exercise (Fernandes et al., 2018b). The reason for these discrepancies is unclear but might be owing to differences in the type of exercise (e.g. single- vs. multi-jointed), contraction type (e.g. isotonic versus isokinetic) and movement velocity (e.g. constrained versus unconstrained), such that the immediate central and peripheral fatigue responses might be task specific (Fernandes et al., 2018b; Petrella, Kim, Tuggle, Hall, & Bamman, 2005). In the only study of its kind, Fernandes and colleagues (2019) noted that the reductions in resting doublet force persisted for three days in resistance trained middle-aged males (~40 years), despite no difference in voluntary activation between age groups

(young = ~22 years), suggesting that force loss is peripherally mediated between these groups. Identifying the mechanism of force loss after resistance exercise might help practitioners when prescribing such exercise with athletes of different ages. For example, different mechanisms of force loss might determine appropriate recovery strategies after exercise, depending whether these are centrally or peripherally orientated (Minett & Duffield, 2014). Further work on the mechanisms of force loss after resistance training in different age groups is needed to confirm these findings.

Gaps within the research literature and future directions

Given that single-jointed, isolated dynamometry does not reflect common training practices, Gordon and colleagues (2017) proposed that future work should use more ecologically valid protocols (i.e. dynamic, constant resistance and multi-jointed exercises) to study the impact of EIMD and fatigue on older athletes. To date, only two studies have investigated the recovery response from multi-jointed dynamic RT in older participants (Fernandes et al., 2019; Nikolaidis, 2017). These studies reported greater losses in isometric force (Fernandes et al., 2019; Nikolaidis, 2017) and peak power (Fernandes et al., 2019) in middle-aged and older populations compared to younger ones. Given that the lower-body undergoes greater losses in muscle mass (Lexell, 1995), strength and power (Fernandes et al., 2018a) than the upper-body, these data have important implications for programming and periodising resistance training with older populations. However, such findings cannot be applied to the upper-body and currently data on the recovery from multi-jointed upper-body resistance training between age groups is lacking. Further investigations are required to understand the muscle damage response of different limbs in older participants, especially given that the upper-body is more susceptible to muscle damage than the lower-body because of the daily exposure of the lower-body to eccentric contractions (i.e. the lower-body is afforded protection due to the repeated bout effect) (Chen, Lin, Chen, Lin, & Nosaka, 2011; Chen et al., 2019; Jamurtas et al., 2005; Saka et al., 2009).

A lack of data regarding the mechanistic basis for the muscle functional changes after resistance training in older populations remains a key omission. To date, only one study has provided such a comparison (Fernandes et al., 2019) with several studies investigating only the immediate (fatigue) central and peripheral response (Dalton et al., 2015, 2012; Fernandes et al., 2018b; Power, Dalton, Rice, & Vandervoort, 2012). Determining if losses in muscle function after resistance training are centrally or peripherally mediated is important for the provision of recovery modalities (Minett & Duffield, 2014). Researchers should, where possible, provide a mechanistic insight into the changes in muscle function across age groups after RT. When taking a holistic approach to muscle function recovery from resistance training, these studies might also employ methods such as the twitch interpolation technique or transcranial magnetic stimulation to examine the influence of peripheral and central alterations.

EIMD incurred from resistance training has the potential to impair sporting performance in the days after the initial bout (Highton, Twist, & Eston, 2009) and is therefore a potential concern for older athletes engaging in novel training approaches for the first time. Given the majority of studies examining the effects of EIMD in older participants have used relatively 'untrained' males (Buford et al., 2014; Lavender & Nosaka, 2006, 2007, 2008; Nikolaidis, 2017; Nikolaidis et al., 2013), what remains unclear is the recovery to unaccustomed exercise bouts in those aged participants that are habitually trained. Understanding how older athletes, who

continue to engage in frequent training to enhance athletic performance, respond to new or more intense training activities is important and has the potential to inform applied practice of those working with 'masters' athletes. Like Fell and Williams (2008) 12 years ago, we again encourage future work to examine the recovery profiles for those older athletes who habitually resistance train or regularly participate in competitive sport. These studies should use more ecologically valid exercise protocols and, where possible, provide a mechanistic underpinning.

To our knowledge, only three studies have investigated the muscle damage and recovery response in younger and older females (Clarkson & Dedrick, 1988; Dedrick & Clarkson, 1990; Ploutz-Snyder, Giamis, Formikell, & Rosenbaum, 2001). After both forearm flexor (Dedrick & Clarkson, 1990) and knee extensor (Ploutz-Snyder et al., 2001) exercise, the recovery of muscle strength appeared to be slower in older compared to younger females. However, to date, these remain the extent of our empirical understanding of recovery among older females after muscle-damaging exercise. Given the potential for differential responses to EIMD between males and females (Dannecker et al., 2012; Sayers & Clarkson, 2001; Sewright, Hubal, Kearns, Holbrook, & Clarkson, 2008; Stupka, Tarnopolsky, Yardley, & Phillips, 2017), the growing number of older females (United Nations, 2017) and female athletes (Lepers, 2019; Lepers et al., 2013; Lepers & Stapley, 2016), and the importance of resistance training in this group (Ploutz-Snyder et al., 2001), future work should seek to confirm and extend what is currently known about the muscle response to resistance training in older females.

Conclusions

The aim of this review was to compare the effects of resistance training on indirect markers of EIMD (i.e. muscle function, soreness and circulating proteins) throughout the recovery process in older trained and untrained males. The notion that ageing is associated with large changes in markers of muscle damage and a prolonged recovery time has not been reported consistently in the literature. In fact, more than half of the available studies have noted that older males experience similar, and even less severe, symptoms of muscle damage than their younger counterparts. Collectively, these data refute the anecdote that ageing is associated with an impaired recovery from exercise. It is therefore plausible to schedule recovery from resistance training among different age groups in a comparable manner. Considering both the mechanistic and performance-related outcomes, studies of muscle function recovery after multi-jointed resistance training in older athletes should be explored. We also encourage future research to consider how training history and sex influence the responses to training that cause symptoms of EIMD.

REFERENCES

- Allen, D. G., Lamb, G. D., & Westerblad, H. (2008). Skeletal muscle fatigue: cellular mechanisms. *Physiological Reviews*, 88(1), 287–332.
- Allison, S. J., Brooke-Wavell, K., & Folland, J. P. (2013). Multiple joint muscle function with ageing: The force-velocity and power-velocity relationships in young and older men. *Aging Clinical and Experimental Research*, *25*(2), 159–166.
- American College of Sports Medicine. (2002). Progression models in resistance training for healthy adults. *Medicine and Science in Sports and Exercise*, *34*(2), 364–380.

- American College of Sports Medicine. (2009). Progression models in resistance training for healthy adults. *Medicine and Science in Sports and Exercise*, *41*(3), 687–708.
- Arroyo, E., Wells, A. J., Gordon, J. A., Varanoske, A. N., Gepner, Y., Coker, N. A., ... Hoffman, J. R. (2017). Tumor necrosis factor-alpha and soluble TNF-alpha receptor responses in young vs. middle-aged males following eccentric exercise. *Experimental Gerontology*, *100*(September), 28–35.
- Avela, J., Kyröläinen, H., Komi, P. V, & Rama, D. (1999). Reduced reflex sensitivity persists several days after long-lasting stretch-shortening cycle exercise. *Journal of Applied Physiology*, 86(4), 1292–1300.
- Baker, A. B., & Tang, Y. Q. (2010). Aging performance for masters records in athletics, swimming, rowing, cycling, triathlon, and weightlifting. *Experimental Aging Research*, *36*(4), 453–477.
- Balcombe, N. R., & Sinclair, A. (2001). Ageing: Definitions, mechanisms and the magnitude of the problem. *Best Practice and Research in Clinical Gastroenterology*, *15*(6), 835–849.
- Bottaro, M., Machado, S. N., Nogueira, W., Scales, R., & Veloso, J. (2007). Effect of high versus low-velocity resistance training on muscular fitness and functional performance in older men. *European Journal of Applied Physiology*, *99*(3), 257–264.
- Buford, T. W., MacNeil, R. G., Clough, L. G., Dirain, M., Sandesara, B., Pahor, M., ... Leeuwenburgh, C. (2014). Active muscle regeneration following eccentric contraction-induced injury is similar between healthy young and older adults. *Journal of Applied Physiology*, 116(11), 1481–1490.
- Burt, D., Lamb, K., Nicholas, C., & Twist, C. (2015). Lower-volume muscle-damaging

- exercise protects against high-volume muscle-damaging exercise and the detrimental effects on endurance performance. *European Journal of Applied Physiology*, *115*(7), 1523–1532.
- Byrne, C., Twist, C., & Eston, R. (2004). Neuromuscular function after exercise-induced muscle damage: theoretical and applied implications. *Sports Medicine*, 34(1), 49–69.
- Chapman, D. W., Newton, M., McGuigan, M. R., & Nosaka, K. (2008). Comparison between old and young men for responses to fast velocity maximal lengthening contractions of the elbow flexors. *European Journal of Applied Physiology*, 104(3), 531–539.
- Chen, T. C., Lin, K. Y., Chen, H. L., Lin, M. J., & Nosaka, K. (2011). Comparison in eccentric exercise-induced muscle damage among four limb muscles. *European Journal of Applied Physiology*, *111*(2), 211–223.
- Chen, T. C., Yang, T. J., Huang, M. J., Wang, H. S., Tseng, K. W., Chen, H. L., & Nosaka, K. (2019). Damage and the repeated bout effect of arm, leg, and trunk muscles induced by eccentric resistance exercises. *Scandinavian Journal of Medicine and Science in Sports*, 29(5), 725–735.
- Clark, B. C., & Manini, T. M. (2008). Sarcopenia ≠ dynapenia. *Journal of Gerontology: MEDICAL SCIENCES*, 63(8), 829–834.
- Clark, B. C., & Manini, T. M. (2012). What is dynapenia? *Nutrition*, *28*(5), 495–503. Retrieved from http://dx.doi.org/10.1016/j.nut.2011.12.002
- Clarkson, P. M., & Dedrick, M. E. (1988). Exercise-induced muscle damage, repair, and adaptation in old and young subjects. *Journal of Gerontology*, *43*(4), 91–96.
- Clifford, T. (2019). Nutritional and pharmacological interventions to expedite recovery following muscle damaging exercise in older adults: A narrative review of the

- literature. Journal of Aging and Physical Activity, 0(0), 1–42.
- Cronin, J. B., & Hansen, K. T. (2005). Strength and power predictors of sports speed. *Journal of Strength and Conditioning Research*, *19*(2), 349–357.
- Cruz-Jentoft, A. J., Baeyens, J. P., Bauer, J. M., Boirie, Y., Cederholm, T., Landi, F., ... Zamboni, M. (2010). Sarcopenia: European consensus on definition and diagnosis. *Age and Ageing*, *39*(4), 412–423.
- Dalton, B. H., Power, G. A., Paturel, J. R., & Rice, C. L. (2015). Older men are more fatigable than young when matched for maximal power and knee extension angular velocity is unconstrained. *Age*, *37*(3), 1–16.
- Dalton, B. H., Power, G. A., Vandervoort, A. A., & Rice, C. L. (2012). The age-related slowing of voluntary shortening velocity exacerbates power loss during repeated fast knee extensions. *Experimental Gerontology*, *47*(1), 85–92.
- Damas, F., Nosaka, K., Libardi, C. A., Chen, T. C., & Ugrinowitsch, C. (2016).

 Susceptibility to exercise-induced muscle damage: A cluster analysis with a large sample. *International Journal of Sports Medicine*, 37(8), 633–640.
- Dannecker, E. A., Liu, Y., Rector, R. S., Thomas, T. R., Fillingim, R. B., & Robinson,
 M. E. (2012). Sex differences in exercise-induced muscle pain and muscle damage. *Journal of Pain*, 13(12), 1242–1249.
- Dedrick, M. E., & Clarkson, P. M. (1990). The effects of eccentric exercise on motor performance in young and older women. *European Journal of Applied Physiology*, *60*, 183–186.
- Department of Health and Social Care. (2019). UK Chief Medical Officers ' Physical Activity Guidelines.
- Doguet, V., Jubeau, M., Dorel, S., Couturier, A., Lacourpaille, L., Guével, A., & Guilhem, G. (2016). Time-course of neuromuscular changes during and after

- maximal eccentric contractions. Frontiers in Physiology, 7(APR), 1–8.
- Fell, J., & Williams, A. D. (2008). The effect of aging on skeletal-muscle recovery from exercise: Possible implications for aging athletes. *Journal of Aging and Physical Activity*, *16*(1), 97–115.
- Fernandes, J. F. T., Daniels, M., Myler, L., & Twist, C. (2019). Influence of playing standard on upper- and lower-body strength, power, and velocity characteristics of elite rugby league players. *Journal of Functional Morphology and Kinesiology*, *4*(2), 22.
- Fernandes, J. F. T., Lamb, K. L., & Twist, C. (2018a). A comparison of load-velocity and load-power relationships between well-trained young and middle-aged males during three popular resistance exercises. *Journal of Strength and Conditioning Research*, 32(5), 1440–1447.
- Fernandes, J. F. T., Lamb, K. L., & Twist, C. (2018b). Internal loads, but not external loads and fatigue, are similar in young and middle-aged resistance-trained males during high volume squatting exercise. *Journal of Functional Morphology and Kinesiology*, *3*(3), 45.
- Fernandes, J. F. T., Lamb, K. L., & Twist, C. (2019). Exercise-induced muscle damage and recovery in young and middle-aged males with different resistance training experience. *Sports*, 7(6), 132.
- Ferrucci, L., Giallauria, F., & Guralnik, J. M. (2008). Epidemiology of Aging. *Radiologic Clinics of North America*, *46*(4), 643–652.
- Fridén, J., & Lieber, R. L. (2001). Serum creatine kinase level is a poor predictor of muscle function after injury. *Scandinavian Journal of Medicine and Science in Sports*, *11*(2), 126–127.
- Frontera, W. R., Suh, D., Krivickas, L. S., Hughes, V. A., Goldstein, R., & Roubenoff,

- R. (2000). Skeletal muscle fiber quality in older men and women. *American Journal of Physiology Cell Physiology*, 279(3), C611-618.
- Gordon III, J., Hoffman, J. R., Arroyo, E., Varanoske, A., Coker, N., Gepner, Y., ... Fukuda, D. (2017). Comparisons in the recovery response from resistance exercise between young and middle-aged men. *Journal of Strength and Conditioning Research*, 31(12), 3454–3462.
- Hansen, K. T., Cronin, J. B., Pickering, S. L., & Douglas, L. (2011). Do force-time and power-time measures in a loaded jump squat differentiate between speed performance and playing level in elite and elite junior rugby union players?

 **Journal of Strength and Conditioning Research, 0(0), 1–10.
- Heckel, Z., Atlasz, T., Tékus, É., Kőszegi, T., Laczkó, J., & Váczi, M. (2019). Monitoring exercise-induced muscle damage indicators and myoelectric activity during two weeks of knee extensor exercise training in young and old men. *PLoS ONE*, *14*(11), 1–16.
- Highton, J. M., Twist, C., & Eston, R. G. (2009). The effects of exercise-induced muscle damage on agility and sprint running performance. *Journal of Exercise Science and Fitness*, 7(1), 24–30.
- Horita, T., Komi, P. V., Nicol, C., & Kyröläinen, H. (1999). Effect of exhausting stretch-shortening cycle exercise on the time course of mechanical behaviour in the drop jump: Possible role of muscle damage. *European Journal of Applied Physiology and Occupational Physiology*, 79(2), 160–167.
- Hortobágyi, T., Houmard, J., Fraser, D., Dudek, R., Lambert, J., & Tracy, J. (1998).

 Normal forces and myofibrillar disruption after repeated eccentric exercise. *Journal of Applied Physiology*, 84(2), 492–498.
- Hubal, M. J., Rubinstein, S. R., & Clarkson, P. M. (2007). Mechanisms of variability

- in strength loss after muscle-lengthening actions. *Medicine and Science in Sports and Exercise*, *39*(3), 461–468.
- Hyldahl, R. D., Chen, T. C., & Nosaka, K. (2017). Mechanisms and mediators of the skeletal muscle repeated bout effect. *Exercise and Sport Sciences Reviews*, *45*(1), 24–33.
- Hyldahl, R. D., & Hubal, M. J. (2014). Lengthening our perspective: Morphological, cellular, and molecular responses to eccentric exercise. *Muscle and Nerve*, 49(2), 155–170.
- Jamurtas, A. Z., Theocharis, V., Tofas, T., Tsiokanos, A., Yfanti, C., Paschalis, V., ...

 Nosaka, K. (2005). Comparison between leg and arm eccentric exercises of the same relative intensity on indices of muscle damage. *European Journal of Applied Physiology*, *95*(2–3), 179–185.
- Jones, D. A., Newham, D. J., & Torgan, C. (1989). Mechanical influences on long-lasting human muscle fatigue and delayed onset pain. *The Journal of Physiology*, *412*(1), 415–427.
- Kongsgaard, M., Backer, V., Jørgensen, K., Kjær, M., & Beyer, N. (2004). Heavy resistance training increases muscle size, strength and physical function in elderly male COPD-patients A pilot study. *Respiratory Medicine*, *98*(10), 1000–1007.
- Lavender, A. P., & Nosaka, K. (2006). Comparison between old and young men for changes in makers of muscle damage following voluntary eccentric exercise of the elbow flexors. *Applied Physiology, Nutrition, and Metabolism*, *31*(3), 218–225.
- Lavender, A. P., & Nosaka, K. (2007). Fluctuations of isometric force after eccentric exercise of the elbow flexors of young, middle-aged, and old men. *European*

- Journal of Applied Physiology, 100(2), 161–167.
- Lavender, A. P., & Nosaka, K. (2008). Changes in markers of muscle damage of middle-aged and young men following eccentric exercise of the elbow flexors. *Journal of Science and Medicine in Sport*, 11(2), 124–131.
- Lepers, R. (2019). Sex difference in triathlon performance. *Frontiers in Physiology*, 10(JUL), 1–7.
- Lepers, R., Rüst, C. A., Stapley, P. J., & Knechtle, B. (2013). Relative improvements in endurance performance with age: Evidence from 25 years of Hawaii Ironman racing. *Age*, *35*(3), 953–962.
- Lepers, R., & Stapley, P. J. (2016). Master athletes are extending the limits of human endurance. *Frontiers in Physiology*, 7(DEC), 1–8.
- Lexell, J. (1995). Human aging, muscle mass, and fiber type composition. *Journals of Gerontology Series A Biological Sciences and Medical Sciences*, 50A(December 1995), 11–16.
- Lexell, J., Taylor, C. C., & Sjöström, M. (1988). What is the cause of the ageing atrophy?. Total number, size and proportion of different fiber types studied in whole vastus lateralis muscle from 15- to 83-year-old men. *Journal of the Neurological Sciences*, *84*(2–3), 275–294.
- Macdonald, G. Z., Button, D. C., Drinkwater, E. J., & Behm, D. G. (2014). Foam rolling as a recovery tool after an intense bout of physical activity. *Medicine and Science in Sports and Exercise*, *46*(1), 131–142.
- McHugh, M. P. (2003). Recent advances in the understanding of the repeated bout effect: The protective effect against muscle damage from a single bout of eccentric exercise. *Scandinavian Journal of Medicine and Science in Sports*, 13(2), 88–97.

- Minett, G. M., & Duffield, R. (2014). Is recovery driven by central or peripheral factors? A role for the brain in recovery following intermittent-sprint exercise. Frontiers in Physiology, 5 FEB(February), 1–9.
- Morgan, D. L., & Proske, U. (2004). Popping sarcomere hypothesis explains stretch-induced muscle damage. *Clinical and Experimental Pharmacology and Physiology*, *31*(8), 541–545.
- Morton, J. P., Atkinson, G., MacLaren, D. P. M., Cable, N. T., Gilbert, G., Broome,
 C., ... Drust, B. (2005). Reliability of maximal muscle force and voluntary
 activation as markers of exercise-induced muscle damage. *European Journal of Applied Physiology*, 94(5–6), 541–548.
- Newton, R. U., Häkikinen, K., Häkikinen, A., Mccormick, M., Volek, J., & Kraemer, W. (2002). Mixed-methods of resistance training increases power and strength of young and older men. *Medicine and Science in Sports and Exercise*, *34*(8), 1367-1375.
- Nikolaidis, M. (2017). The effects of resistance exercise on muscle damage, position sense, and blood redox status in young and elderly individuals. *Geriatrics*, *2*(4), 20.
- Nikolaidis, M., Kyparos, A., Spanou, C., Paschalis, V., Theodorou, A. A., Panayiotou, G., ... Vrabas, I. S. (2013). Aging is not a barrier to muscle and redox adaptations: Applying the repeated eccentric exercise model. *Experimental Gerontology*, 48(8), 734–743.
- Nogueira, F. R. D., Libardi, C. A., Nosaka, K., Vechin, F. C., Cavaglieri, C. R., & Chacon-Mikahil, M. P. T. (2014). Comparison in responses to maximal eccentric exercise between elbow flexors and knee extensors of older adults. *Journal of Science and Medicine in Sport*, 17(1), 91–95.

- Nosaka, K., Newton, M., & Sacco, P. (2002). Delayed-onset muscle soreness does not reflect the magnitude of eccentric exercise-induced muscle damage. Scandinavian Journal of Medicine and Science in Sports, 12(6), 337–346.
- Orimo, H., Ito, H., Suzuki, T., Araki, A., Hosoi, T., & Sawabe, M. (2006). Reviewing the definition of elderly. *Geriatrics and Gerontology International*, 43(1), 27–34.
- Owens, D. J., Twist, C., Cobley, J. N., Howatson, G., & Close, G. L. (2018). Exercise-induced muscle damage: What is it, what causes it and what are the nutritional solutions? *European Journal of Sport Science*, *0*(0), 1–15.
- Pantoja, P. D., Saez De Villarreal, E., Brisswalter, J., Peyré-Tartaruga, L. A., & Morin, J. B. (2016). Sprint acceleration mechanics in masters athletes. *Medicine* and Science in Sports and Exercise, 48(12), 2469–2474.
- Paulsen, G., Mikkelsen, U. R., Raastad, T., & Peake, J. M. (2012). Leucocytes, cytokines and satellite cells: What role do they play in muscle damage and regeneration following eccentric exercise? *Exercise Immunology Review*, *18*, 42–97.
- Petrella, J. K., Kim, J., Tuggle, S. C., Hall, S. R., & Bamman, M. M. (2005). Age differences in knee extension power, contractile velocity, and fatigability. *Journal of Applied Physiology*, *98*(1), 211–220.
- Ploutz-Snyder, L. L., Giamis, E. L., Formikell, M., & Rosenbaum, A. E. (2001).

 Resistance training reduces susceptibility to eccentric exercise-induced muscle dysfunction in older women. *Journal of Gerontology: BIOLOGICAL SCIENCES*, 56(9), 384–390.
- Power, G. A., Dalton, B. H., Rice, C. L., & Vandervoort, A. A. (2012). Power loss is greater following lengthening contractions in old versus young women. *Age*, 34(3), 737–750.

- Roth, S. M., Martel, G. F., Ivey, F. M., Lemmer, J. T., Tracy, B. L., Hurlbut, D. E., ... Rogers, M. A. (1999). Ultrastructural muscle damage in young vs. older men after high-volume, heavy-resistance strength training. *Journal of Applied Physiology*, 86(6), 1833–1840.
- Saka, T., Akova, B., Yazici, Z., Sekir, U., Gür, H., & Ozarda, Y. (2009). Difference in the magnitude of muscle damage between elbow flexors and Knee extensors eccentric exercises. *Journal of Sports Science and Medicine*, 8(1), 107–115.
- Sayers, S. P., & Clarkson, P. M. (2001). Force recovery after eccentric exercise in males and females. *European Journal of Applied Physiology*, *84*(1–2), 122–126.
- Sayers, S. P., & Gibson, K. (2010). A comparison of high-speed power training and traditional slow-speed resistance training in older men and women. *Journal of Strength & Conditioning Research*, *24*(12), 3369–3380.
- Sayers, S. P., & Gibson, K. (2014). High-speed power training in older adults: A shift of the external resistance at which peak power is produced. *Journal of Strength and Conditioning Research*, 28(3), 616–621.
- Schoenfeld, B. J. (2010). The mechanisms of muscle hypertrophy and their application to resistance training. *Journal of Strength and Conditioning Research*, 24(10), 2857–2872.
- Sewright, K. A., Hubal, M. J., Kearns, A., Holbrook, M. T., & Clarkson, P. M. (2008).

 Sex differences in response to maximal eccentric exercise. *Medicine and Science in Sports and Exercise*, *40*(2), 242–251.
- Sorichter, S., Puschendorf, B., & Mair, J. (1999). Skeletal muscle injury induced by eccentric muscle action: Muscle proteins as markers of muscle fiber injury.

 Exercise Immunology Review, 5, 5–21.
- Stupka, N., Tarnopolsky, M. A., Yardley, N. J., & Phillips, S. M. (2017). Cellular

- adaptation to repeated eccentric exercise-induced muscle damage. *Journal of Applied Physiology*, *91*(4), 1669–1678.
- Tanaka, H., & Seals, D. R. (2008). Endurance exercise performance in Masters athletes: Age-associated changes and underlying physiological mechanisms. *Journal of Physiology*, 586(1), 55–63.
- United Nations, D. of E. and S. A. (2017). World population prospects: The 2017 revision. https://doi.org/10.1017/CBO9781107415324.004
- Warren, G., Lowe, D., & Armstrong, R. (1999). Measurement tools used in the study of eccentric contraction induced injury. *Sports Medicine*, *27*(1), 43–59.

Table 1. Characteristics of studies on ageing and in indirect markers of muscle damage and recovery (i.e. muscle soreness, blood markers and muscle strength) after resistance training.

	Young	Sample size	Old	Sample size	Activity level	Involved muscle	Exercise protocol	Time points
Lavender & Nosaka, 2006	19.4 ± 0.4	10	70.5 ± 1.5	10	Non-RT	EF	6 x 5 ECC at 40% MIVC	Pre, 0, 24, 48, 72, 96, 120 h
Lavender & Nosaka, 2007*	20.4 ± 2.0	10	48.0 ± 7.3	12	Non-RT	EF	6 x 5 ECC at 40% MIVC	Pre, 0, 24, 48, 72, 96, 120, 144, 168 h
			70.5 ± 4.1	10				
Lavender & Nosaka, 2008	19.4 ± 0.4	12	48.0 ± 2.1	12	Non-RT	EF	6 x 5 ECC at 40% MIVC	Pre, 0, 24, 48, 72, 96 h
Chapman et al. 2008	25.0 ± 1.8	10	64.0 ± 1.2	10	Non-RT	EF	5 x 6 ECC at 210 deg×s	Pre, 1, 24, 48, 72 and 96 h
Nikolaidis et al 2013	20.6 ± 0.5	10	64.6 ± 1.1	10	Non-RT	KE	5 x 8 ECC at 60 deg×s	Pre, 0, 48
Buford et al. 2014	22.5 ± 3.7	15	75.8 ± 5.0	15	Non-RT	PF	150 ECC at 110% 1RM	Pre, 48, 168 h
Gordon et al. 2017	21.8 ± 2.0	9	47.0 ± 4.4	10	Rec. RT	KE	8 x 10 ECC-CON at 60 deg×s	Pre, 0, 0.5, 1, 2, 24, 48 h
Arroyo et al. 2017	21.8 ± 2.2	9	47.0 ± 4.4	10	Rec. RT	KE	8 x 10 ECC-CON at 60 deg×s	Pre, 0, 0.5, 1, 2, 24, 48 h
Nikolaidis, 2017	22.1 ± 3.9	10	66.9 ± 5.4	10	Non-RT	KE	5 x 15 ISOT at 75% 1RM	Pre, 48 h
Fernandes et al. 2019	22.3 ± 1.7	9	39.9 ± 6.2	9	RTd	KE	10 x 10 ISOT at 60% 1RM	Pre, 24, 72 h
Heckel et al. 2019	25.1 ± 4.9	10	64.5 ± 5.5	10	Non-RT	KE	4 x 15 ECC at 60 degxs	Pre, 24 48 h

^{*}study contained 3 age groups. RTd, resistance training; RT, resistance training; EF, elbow flexors; KE, knee extensors; PF, plantar flexors; 1RM, one-repetition maximum; MVC, maximal voluntary contraction; MIVC, maximal isometric voluntary contraction; ECC, eccentric contraction; CON, concentric contraction; ISOT, isotonic contraction; VAS, visual analogue scale; CK, creatine kinase; Mb, myoglobin

Table 2. Changes in indirect markers of muscle damage and recovery after resistance training in young and older age groups.

	Muscle damage marker						
	Soreness	Creatine kinase	Myoglobin	Strength			
Lavender & Nosaka, 2006	↑YG	↑YG	↑YG	↓YG			
Lavender & Nosaka, 2007	N/A	N/A	N/A	↓YG			
Lavender & Nosaka, 2008	↑YG	\leftrightarrow	\leftrightarrow	\leftrightarrow			
Chapman et al. 2008	↑YG	\leftrightarrow	N/A	↓og			
Nikolaidis et al. 2013	\leftrightarrow	N/A	N/A	↓og			
Buford et al. 2014	\leftrightarrow	N/A	N/A	\leftrightarrow			
Gordon et al. 2017	\leftrightarrow	\leftrightarrow	\leftrightarrow	\leftrightarrow			
Arroyo et al. 2017	\leftrightarrow	\leftrightarrow	\leftrightarrow	\leftrightarrow			
Nikolaidis, 2017	\leftrightarrow	\leftrightarrow	N/A	↓og			
Fernandes et al. 2019	\leftrightarrow	\leftrightarrow	N/A	↓og			
Heckel et al. 2019	\leftrightarrow	\leftrightarrow	↑og	\leftrightarrow			