Ageing Research Reviews 14 (2014) 43–55

Contents lists available at ScienceDirect

Ageing Research Reviews

journal homepage: www.elsevier.com/locate/arr

Review

Aging related changes in determinants of muscle force generating capacity: A comparison of muscle aging in men and male rodents

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ARTICLE INFO

Article history:
Received 15 October 2013
Received in revised form 20 January 2014
Accepted 24 January 2014
Available online 2 February 2014

Keywords:
Muscle aging
Muscle force
Muscle mass
Fiber size
Fiber number
Specific tension

ABSTRACT

Human aging is associated with a progressive decline in skeletal muscle mass and force generating capacity, however the exact mechanisms underlying these changes are not fully understood. Rodents models have often been used to enhance our understanding of mechanisms of age-related changes in human skeletal muscle. However, to what extent age-related alterations in determinants of muscle force generating capacity observed in rodents resemble those in humans has not been considered thoroughly. This review compares the effect of aging on muscle force generating determinants (muscle mass, fiber size, fiber number, fiber type distribution and muscle specific tension), in men and male rodents at similar relative age. It appears that muscle aging in male F344*BN rat resembles that in men most; 32–35-month-old rats exhibit similar signs of muscle weakness to those of 70–80-yr-old men, and the decline in 36–38-month-old rats is similar to that in men aged over 80 yrs. For male C57BL/6 mice, age-related decline in muscle force generating capacity seems to occur only at higher relative age than in men. We conclude that the effects on determinants of muscle force differ between species as well as within species, but qualitatively show the same pattern as that observed in men.

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Contents

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http://dx.doi.org/10.1016/j.arr.2014.01.005

1. Introduction

In humans, aging is accompanied by a progressive decline in muscle mass and force generating capacity, referred to as sarcopenia (Fielding et al., 2011), which starts at the age of 40–60 (Porter et al., 1995; Faulkner et al., 2007). At the age of 80, the muscle force generating capacity is on average approximately 60% of that at the age of 20–30 (Doherty, 2003). This progressive decline in muscle function and muscle mass is presumed to be a significant contributor to the increased incidence of falls, transition to a dependent life-style and reduced quality of life in old age (Roubenoff and Hughes, 2000; Kamel, 2003; Visser and Schaap, 2011). Furthermore, a decrease in muscle mass is associated with an increase in morbidity and mortality (Newman et al., 2001; Morley, 2003; Morley et al., 2006). This and the impact of increased frailty, incidence of falls and associated fractures on the associated cost of care pose an enormous burden on healthcare systems. Moreover, demographic prognoses of economically developed countries worldwide predict that the proportion of older people increases at the fastest pace ever (United Nations, 2011), which makes muscle aging investigations even more urgent.

Clearly, maintenance of muscle mass up to old age or even reversal of the age-related muscle wasting and weakness has important beneficial implications for the quality of life of the older person. To develop adequate strategies to maintain muscle function, a profound understanding of the mechanisms and causes of age-related muscle wasting are a prerequisite. Daily life physical activities require skeletal muscle power, which is the product of muscle force and velocity of contraction. While the force generating capacity is largely determined by the number of sarcomeres arranged in parallel, the maximal shortening velocity is determined by the number of sarcomeres arranged in series and myosin heavy chain (MHC) composition (Larsson and Moss, 1993; Degens and Larsson, 2007). The latter has been reported to shift to a slower profile during aging (Larsson and Ansved, 1995; Degens and Alway, 2006). Thus, not only the age-related decrease in muscle mass, but also slowing of the muscle as a result of a shift to a slower myosin heavy chain profile would negatively impact the ability to produce power (Brooks and Faulkner, 1994a,b).

The age-related muscle wasting (Janssen et al., 2000; Degens and Alway, 2003; Doherty, 2003; Deschenes, 2004; Degens, 2010) is attributable to a loss of muscle fibers and an atrophy of the remaining muscle fibers (Lexell et al., 1988; Larsson and Ansved, 1995; Faulkner et al., 2007). While the loss of muscle mass contributes significantly to muscle weakness in old age, this is aggravated by a reduction in the specific tension, the force generating capacity per cross-sectional area of the remaining muscle tissue (Larsson et al., 1997a,b; Frontera et al., 2000a,b; Gonzalez et al., 2000; Morse et al., 2005; Degens et al., 2009a,b). It is, however, difficult to measure force, and particularly the physiological cross-sectional area of a human muscle in vivo, accurately. This stresses the importance of models investigating sarcopenia. Animal models of sarcopenia may be helpful in overcoming some of these problems. In particular rodents have been used to study the impact of aging on skeletal muscle structure and function. An important question is to what extent the information gained from aging animal models can be translated to humans.

In this review we will address this question by evaluating the similarities in muscle aging in rodents and men. We will give particular attention to the widely used male Fischer344, Fischer344 × Brown Norway (F344*BN) and Wistar rats, and C57BL/6 mice. In addition, the vast majority of the studies on muscle aging in rodents used male animals (~70% vs ~20% female, ~10% is undefined). Therefore, only studies using male rodents were included, because this decreases the variability and complexity of the comparisons. Furthermore, factors influencing the 'rate of muscle aging' (Degens and Korhonen, 2012), such as maximal life span, environment, nutrition and activity levels are discussed. We conclude with a summary of the strengths and weaknesses of these models and discuss to what extent aging rodents can be used as models of muscle aging in men.

2. Advantages of rodent models of muscle aging

Aging rodents have often been used as models to enhance our understanding of processes and biological mechanisms of age-related changes in human skeletal muscle (Cartee, 1995; Alway et al., 2005). The use of rodents to study muscle aging has some obvious advantages. First of all, longitudinal studies in humans require a very long follow-up period, which makes these studies more difficult, in contrast to the relatively short life span of rodents (only 2–3 yrs), which makes it much easier to study the aging process. Secondly, it is ethically less problematical to perform invasive procedures in rodents than in humans (Cartee, 1995). Thirdly, environmental conditions and nutrition can be tightly controlled, and activity can be accurately monitored in laboratory animals, which again is virtually impossible in humans (Alway et al., 2005). Fourthly, terminal experiments can be performed in rodents, allowing one to dissect whole muscles, which increases the opportunities to study whole muscle morphology and cellular and molecular mechanisms, compared to human studies where at best a small muscle biopsy can be analyzed. Finally, laboratory animals have a much more homogeneous gene pool than humans (Alway et al., 2005). Although it may be argued that the experimental control of animal models compromises the validity and relevance of these models to humans (Alway et al., 2005), it is this possibility to control many factors that will help us gain a better understanding of the extent at which various environmental factors contribute to the observed variation in the rate of muscle aging between people (Degens and Korhonen, 2012).

3. Age-related changes in force generating capacity

During aging there is a progressive reduction in the force generating capacity approximately amounting up to 40% when comparing healthy young (20–30 yrs) and old (70–80 yrs) humans (Porter et al., 1995; Doherty, 2003), continuing in the ninth decade and beyond (Murray et al., 1980; Murray and Duthie, 1985; Vandervoort and McComas, 1986).

An important factor to consider when comparing human and rodent aging studies is how a given age of a rodent compares with that of humans. In order to do so we introduce the 'relative age' in this review. 'The relative age' is expressed as a percentage of the mean life span (MLS) of men and rodent species or rodent strain. Table 1 shows values of MLS reported for men, different male rat strains and C57BL/6 mice. Since our interest is aging, relative differences in the duration of the nurture stage and time to reach sexual

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