



Review

Non-uniform muscle adaptations to eccentric exercise and the implications for training and sport

Nosratollah Hedayatpour^a, Deborah Falla^{b,c,*}^a Department of Physical Education and Sport Sciences, University of Bojnord, Bojnord, Iran^b Pain Clinic, Center for Anesthesiology, Emergency and Intensive Care Medicine, University Hospital Göttingen, Göttingen, Germany^c Department of Neurorehabilitation Engineering, Bernstein Focus Neurotechnology (BFNT) Göttingen, Bernstein Center for Computational Neuroscience, University Medical Center Göttingen, Georg-August University, Göttingen, Germany

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ABSTRACT

Due to the variations in morphological and architectural characteristics of fibers within a skeletal muscle, regions of a muscle may be differently affected by eccentric exercise. Although eccentric exercise may be beneficial for increasing muscle mass and can be beneficial for the treatment of tendinopathies, the non-uniform effect of eccentric exercise results in regional muscle damage and as a consequence, non-uniform changes in muscle activation. This regional muscle weakness can contribute to muscle strength imbalances and may potentially alter the load distribution on joint structures, increasing the risk of injury.

In this brief review, the non-uniform effects of eccentric exercise are reviewed and their implications for training and sport are considered.

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1. Introduction

Structural and functional muscle adaptations occur in response to training and the nature of the exercise determines the type of adaptation. For example, an increase in aerobic metabolism and consequently enhanced respiratory capacity occurs in skeletal muscles following long term endurance training (Hamel et al., 1986). On the contrary, heavy resistance exercise increases neural inputs to motor neurons (Semmler et al., 2004) and also induces

changes in the ionic membrane permeability of muscle fibers, which in turn stimulates an increase in gene expression and protein synthesis, and the development of cellular hypertrophy of muscle fibers (Cureton et al., 1988; Goldspink et al., 1992; Shoenberger et al., 2003). In particular, high load eccentric exercise is commonly used by weight lifters and body-builders to increase muscle size and maximum force capacity. Moreover, many movements in various sports, such as jumping, landing, and abrupt changes of direction, requires eccentric contractions and therefore eccentric exercises are commonly incorporated into training regimes. However, eccentric exercise is also associated with muscle fiber damage, pain, reduced fiber excitability and initial muscle weakness (Felicetti et al., 1997; Fridén and Lieber, 1992; Sbriccoli et al., 2001; Semmler et al., 2007; Hedayatpour et al., 2009), which may delay or inhibit neuromuscular responses at injured sites (Semmler

* Corresponding author at: Department of Neurorehabilitation Engineering, Bernstein Focus Neurotechnology (BFNT) Göttingen, Bernstein Center for Computational Neuroscience, University Medical Center Göttingen, Georg-August University, Von-Siebold-Str. 4, 37075 Göttingen, Germany. Tel.: +49 (0) 551 3920109; fax: +49 (0) 551 3920110.

E-mail address: deborah.falla@bccn.uni-goettingen.de (D. Falla).

et al., 2007; Hedayatpour et al., 2008b). Thus, when athletes with muscle pain are faced with actions that may challenge joint stability during exercise and/or routine activities of daily living, the unprepared neuromuscular system may be incapable of appropriately providing joint support, thereby exposing joint structures to abnormal load and overtime the development of musculoskeletal disorders (Navasier, 1991; Myers and Laudner, 2006).

Recent studies show that different regions of the skeletal muscle are more affected by repeated, intensive, eccentric exercise (Hedayatpour et al., 2008b, 2009, 2010; Piitulainen et al., 2009; Binderup et al., 2010) potentially resulting in an imbalance of muscle activity and alteration of the load distribution on joints. Non-uniform adaptations to eccentric exercise are attributed to the variation in morphological and architectural characteristics of muscle fibers depending on their location within a skeletal muscle (Lexell and Taylor, 1991; Blazevich et al., 2006) and consequent uneven activation of muscle regions during exercise.

This paper provides a brief overview of studies documenting non-uniform activation of skeletal muscles in response to exercise and training, especially following eccentric exercise. Although eccentric exercise can increase muscle mass (Roig et al., 2009) and can be beneficial for the treatment of tendinopathies (Woodley et al., 2007), the non-uniform effect of eccentric exercise results in non-uniform changes in muscle activation (Semmler et al., 2007; Hedayatpour et al., 2008b), alternative muscle synergies (Semmler, 2002) and strength imbalances, potentially altering the load distribution on joint structures and increasing the risk of injury. These implications are considered.

1.1. Non-uniform activation of muscle regions during exercise

Skeletal muscle is a heterogeneous tissue (Lexell and Taylor, 1991; Blazevich et al., 2006). In broad muscles individual fibers are not mechanically equivalent with respect to their direction of force, and the relative distribution of fast and slow twitch fibers varies between muscle regions (Lexell and Taylor, 1991; Suter et al., 1993). The accumulation of metabolites during a muscle contraction depends on the number of active motor units under anaerobic conditions and this may also vary in different muscle regions. During sustained fatiguing contractions, local accumulation of metabolites reduces the pH of the extra-cellular environment and increases K^+ permeability in the muscle fiber membrane as a consequence of stimulation of the ATP-dependent and/or Ca^{2+} -dependent K^+ channels (Castle and Haylett, 1987), which in turn increases the excitation threshold and decreases muscle fiber excitability (Jones, 1981; Hedayatpour et al., 2007). The speed of metabolite removal may also depend on the location within the muscle due to regional capillary and oxidative enzyme supply to muscle fibers (Tesch and Wright, 1983).

Variation in morphological and architectural characteristics of muscle fibers within a muscle implies a site-dependent change in muscle activity during exercise and fatigue. Accordingly, non-uniform EMG amplitude is detected over the quadriceps muscle group during fatiguing contractions (Kinugasa et al., 2006; Hedayatpour et al., 2008a,b) with the greatest EMG amplitude and greatest reduction in EMG amplitude over time occurring in regions with a higher proportion of fast twitch muscle fibers (Hedayatpour et al., 2008a,b). Fast twitch fibers are known to produce higher tension (Edström and Kugelberg, 1968) and higher lactate (Essen and Haggmark, 1975) contributing to lower pH (Troup et al., 1986) during both dynamic and static contractions to exhaustion resulting in more rapid fatigue. Similarly, the recovery process following fatiguing contractions of the quadriceps muscle is associated with non-uniform EMG responses of different muscle regions (Hedayatpour et al., 2008a, 2010). Variation in the activation of muscle regions is seen in several other muscles including the trapezius

during dynamic (Falla et al., 2007), ramped, and sustained isometric contractions (Holtermann and Roeleveld, 2006), triceps surae (Löscher et al., 1994), biceps brachii (Sakurai et al., 1998) and masseter muscle (Schumann et al., 1994) during fatiguing contractions.

1.2. Non-uniform muscle adaptations to training

Due to the architectural complexity of muscles and the non-uniform distribution of motor unit activation, the morphological and biochemical adaptations to training do not occur uniformly within the skeletal muscle. Region-specific changes of muscle fiber types are observed after high intensity training (Sakuma et al., 1995) and selective increases of muscle fiber cross sectional area within the quadriceps are reported in response to heavy resistance training (Häkkinen et al., 2001). Local expression of insulin-like growth factor-I (IGF-I) mRNA involved in protein synthesis, is also related to this region-specific hypertrophy following training (Borst et al., 2001; Yamaguchi et al., 2003). Accordingly, long term weight training of the quadriceps muscle results in larger increases in cross sectional area at the proximal and distal regions (19%) compared to the central portion (13%) (Narici et al., 1996), and hypertrophy of the vastus medialis and intermedius muscle is greater than the rectus femoris and vastus lateralis muscles (Narici et al., 1989). Similarly, resistance training of the knee flexors induces hypertrophy of the biceps femoris (middle level) and semitendinosus (distal level) but not the semimembranosus (Housh et al., 1992). Similar variability can be observed in upper limb muscles. The middle region of the triceps brachii shows greater hypertrophy following training than the proximal or distal portions (Kawakami et al., 1995), and the hypertrophic response is greater for the biceps brachii muscle compared to the brachialis muscle following resistance training of the elbow flexors (McCall et al., 1996).

1.3. Non-uniform muscle adaptations to eccentric exercise

Takekura et al. (2001) reported differences in the structural disruption of fast and slow-twitch fibers following eccentric tasks. In general, fast twitch fibers are more susceptible to damage (Fridén and Lieber, 1998) because of their lack of oxidative capacity (Baldwin et al., 1972), higher generated tension (Coyle et al., 1979), and their short fiber length. In a muscle of mixed composition the optimal lengths for different fiber types may not be the same and therefore stretching of the whole muscle results in some fibers being stretched further down the descending limb of their length-tension curve than others. During dynamic contractions the frequency of exposure to stretch as a result of the change in fiber pennation angle (Herbert and Gandevia, 1995) may also expose specific muscle fibers to greater injury. For example, eccentric exercise of the biceps brachii muscle induces greatest damage to the fast twitch fibers (Felici et al., 1997; Sbriccoli et al., 2001). Furthermore, Homonko and Theriault (2000) observed preferential damage after downhill running within an area of the rat medial gastrocnemius, which was compartmentalized with fast twitch fibers. In humans when the gastrocnemius muscle is injured, damage typically occurs around the myotendinous junction and in the relatively fast twitch medial head rather than the lateral head (Weishaupt et al., 2001).

After high tension eccentric exercise, delayed onset muscle soreness (DOMS) usually manifests at the injured sites due to necrosis of the contractile elements and inflammation (Nosaka and Clarkson, 1996). Eccentric exercise of the quadriceps femoris induces initial tenderness in the distal portion of the muscle group (Newham et al., 1983). In accordance with this observation, lower pressure pain thresholds are observed in the distal region of the quadriceps after eccentric exercise of the knee extensors, with an

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