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Review

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

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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.

Contents

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; Shoepe 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 (Felici 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

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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

even greater reduction of the pressure pain threshold at the same region both 24 and 48 h post eccentric exercise (Hedayatpour et al., 2008b).

The greatest tenderness and muscle swelling occurs around the distal region of the biceps brachii muscle after eccentric exercise of the elbow flexors (Cleak and Eston, 1992) and pressure pain threshold mapping of the trapezius shows that hyperalgesia develops in a heterogeneous manner over the muscle in response to eccentric exercise (Binderup et al., 2010). Variation in tenderness is also seen between synergistic muscles. For example, the rectus femoris and biceps femoris muscle are more vulnerable to the strain compared to the vastus medialis and semitendinosus respectively (Greco et al., 1991). Inter- and intramuscular variation in tenderness after eccentric exercise may be explained by a non-uniform vulnerability of muscle fibers to damage (Takekura et al., 2001). This non-uniformity in susceptibility to damage can be related to the mechanical and metabolic capacity of muscle fibers in producing tension, temperature (Nadel et al., 1972), activation of phospholipase A2 (Palmer et al., 1983), and lipid peroxidation from oxygen radicals (Jenkins, 1988). This would result in a site specific production of inflammatory agents (e.g., prostaglandins) in response to eccentric exercise, which sensitizes nociceptors to varying degrees, depending on the location within the muscle (Ostrowski et al., 1998). Using EMG and pressure pain threshold topographical mapping of the quadriceps muscle, we have observed that the distal location of the quadriceps is the site where the EMG amplitude displays the greatest decrease over the duration of sustained knee extension contractions after eccentric exercise (Fig. 1) and this site coincides with the greatest reduction in pressure pain threshold (Fig. 2) (Hedayatpour et al., 2008b).

Furthermore, muscle fiber conduction velocity is reduced during sustained knee extension contractions after eccentric exercise

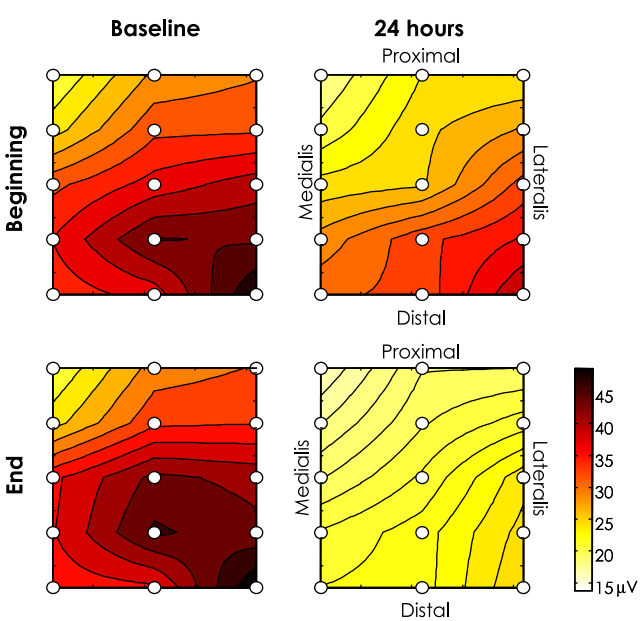

Fig. 1. Average rectified value (ARV) obtained from 15 locations distributed over the quadriceps (vastus medialis, rectus femoris and vastus lateralis) at the first and last time interval (1 s) of a sustained knee extension contraction at 40% of the maximum voluntary contraction performed until task failure at baseline and 24 h after eccentric exercise. The maps are average values over 11 subjects with values interpolated by a factor 10 for graphical purposes only. The white circles represent the recording points and the values in between are obtained through interpolation. Note the larger decrease in ARV at the distal region of the quadriceps from the beginning to the end of the contraction following eccentric exercise (Hedayatpour et al., 2008b).

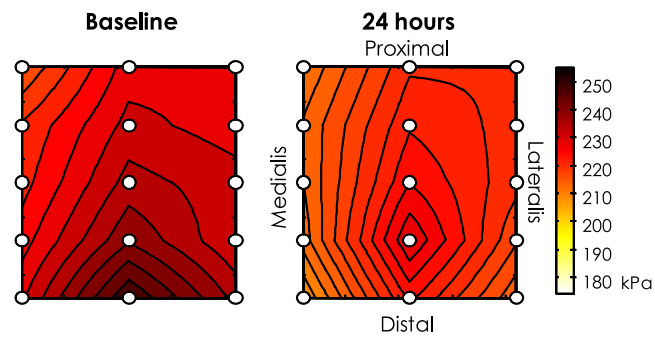

Fig. 2. Pressure pain thresholds (PPT) recorded over the quadriceps (vastus medialis, rectus femoris and vastus lateralis) at baseline and 24 h after eccentric exercise of the quadriceps. The maps are average values over 11 subjects with values interpolated by a factor 10 for graphical purposes only. The white circles represent the assessment points for PPT measures and the values in between are obtained through interpolation. Note the larger decrease in PPT at the distal region of the quadriceps following eccentric exercise (Hedayatpour et al., 2008b).

with the greatest reduction occurring for the most distal region of the vastus medialis muscle compared to proximal regions (Hedayatpour et al., 2009). The recovery of muscle fiber membrane properties following fatigue is also impaired at different regions of the quadriceps following eccentric exercise, and this impairment is more pronounced for the most distal region of the quadriceps (Hedayatpour et al., 2010) especially for the vastus medialis muscle which is composed of a higher proportion of fast twitch fibers (Travnik et al., 1995).

Site dependent changes in EMG variables after eccentric exercise have also been observed for the biceps brachii (Piitulainen et al., 2009) and the triceps surae (Moritani et al., 1990).

Regional changes in muscle activity and membrane excitability after eccentric exercise indicate that both neuromuscular transmission and membrane properties are altered at the injured sites. Following eccentric exercise, inhibition of specific muscle portions may be attributed to local nociceptive input. Disturbance in postsynaptic regulation of acetylcholine (a major factor for signal transmission) as a result of remodeling of the neuromuscular junction at the injured sites (Warren et al., 1999) may also reduce the discharge rate of motor units, resulting in a regional reduction of muscle activity. The observations reviewed above demonstrate that fatigue and injury resulting from intensive eccentric exercise induces a non-uniform effect on muscle activity both within the muscle and between synergistic muscles.

1.4. Consequences for training and sport

Non-uniform alterations in muscle activation following eccentric exercise may result in muscle strength imbalances, inflexibility and regional muscle weakness over time (Clement et al., 1984; Calhoon and Fry, 1999) contributing to abnormal mechanical loading on joint structures (Kupke et al., 1993). Furthermore, the non-uniform effect of eccentric exercise on synergistic muscles may result in alternative muscle synergies (Semmler, 2002) thereby enhancing the risk of musculoskeletal disorders (Shinohara et al., 2009). As an example, the pectoralis major muscle is subject to significant injury compared to other muscles in the shoulder region during eccentric weight training such as the bench press (Connell et al., 1999), which may result in rupture at its musculotendinous junction or the insertion onto the humerus (Garrett, 1990). Furthermore, rupture of the sternal head of the pectoralis major is more frequent than the clavicular head due to the fiber orientation relative to the direction of force application (Wolfe et al., 1992). Among the elbow flexor muscles the long head of the biceps brachii is comprised primarily of

fast-twitch fibers (Johnson et al., 1973) and is more susceptible to fiber injury and inflammation during high load eccentric strength training (Mariani et al., 1997) which can increase the risk of tendon rupture (Gilcreest, 1933; Morrey, 1993). Impingement syndrome and anterior shoulder instability are common shoulder conditions associated with alternative muscle synergies which can be induced by non-uniform eccentric loading during weight training (Navasier, 1991; Kolber et al., 2009).

Eccentric exercise of the quadriceps results in a greater reduction of vastus medialis activity relative to the other quadriceps components (Hedayatpour et al., 2008b, 2010). An insufficient ability of the vastus medialis muscle to stabilize the patella as result of fatigue may expose structures of the knee to abnormal loading during exercise and may partly explain why soreness, weakness and patellar fatigue fracture are common after intensive fatiguing contractions (Mason et al., 1996). Eccentric exercise also impairs reflex activity in the quadriceps which may contribute to compromised knee stability during perturbations thereby leaving structures of the knee more vulnerable to injury (Hedayatpour et al., 2011).

Due to the morphological and architectural characteristics of their muscle fibers, the rectus femoris, semimembranosus, short head of the biceps femoris and the medial head of the gastrocnemius muscle are also at risk of injury during high load eccentric exercise (Terry and La Prade, 1996; Mallone, 1988; Weishaupt et al., 2001) and can be associated with disruption of tendon and ligament injury (Helms et al., 1995; Sonin et al., 1995; Ross et al., 1997; Chan et al., 1999).

2. Conclusion

The skeletal muscle adapts in a non-uniform manner to exercise and training, especially to 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.

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