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SYSTEMATIC REVIEW

Chronic Adaptations to Eccentric Training: A Systematic Review

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Abstract

Background Resistance training is an integral component of physical preparation for athletes. A growing body of evidence indicates that eccentric strength training methods induce novel stimuli for neuromuscular adaptations.

Objective The purpose of this systematic review was to determine the effects of eccentric training in comparison to concentric-only or traditional (i.e. constrained by concentric strength) resistance training.

Methods Searches were performed using the electronic databases MEDLINE via EBSCO, PubMed and SPORTDiscus via EBSCO. Full journal articles investigating the long-term ($\geq$4 weeks) effects of eccentric training in healthy (absence of injury or illness during the 4 weeks preceding the training intervention), adult (17–35 years), human participants were selected for the systematic review. A total of 40 studies conformed to these criteria.

Results Eccentric training elicits greater improvements in muscle strength, although in a largely mode-specific manner. Superior enhancements in power and stretch-shortening cycle (SSC) function have also been reported. Eccentric training is at least as effective as other modalities in increasing muscle cross-sectional area (CSA), while the pattern of hypertrophy appears nuanced and increased CSA may occur longitudinally within muscle (i.e. the addition of sarcomeres in series). There appears to be a preferential increase in the size of type II muscle fibres and the potential to exert a unique effect upon fibre type transitions. Qualitative and quantitative changes in tendon tissue that may be related to the magnitude of strain imposed have also been reported with eccentric training.

Conclusions Eccentric training is a potent stimulus for enhancements in muscle mechanical function, and muscle-tendon unit (MTU) morphological and architectural adaptations. The inclusion of eccentric loads not constrained by concentric strength appears to be superior to traditional resistance training in improving variables associated with strength, power and speed performance.

Key Points

- Eccentric training can improve muscle mechanical function to a greater extent than other modalities.
- Novel muscle-tendon unit adaptations associated with a faster (i.e. explosive) phenotype have been reported.
- Eccentric training may be especially beneficial in enhancing strength, power and speed performance.

1 Background

Resistance training has become a ubiquitous component of physical preparation programmes for athletic populations [1]. It has been well established that resistance training can

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improve a host of neuromuscular variables relevant to athletic performance across a continuum of strength, power, and endurance events [1–3]. Traditional resistance training typically includes both eccentric and concentric phases of movement across a set of repetitions. Eccentric muscle actions occur when the load applied to the muscle exceeds the force produced by the muscle itself, resulting in a lengthening action [4]. Therefore, muscle forces tend to be highest during lengthening actions [5]. The prescription of load is dictated by concentric strength and thus tends to insufficiently load the eccentric phase of movement. A growing body of evidence indicates that resistance training programmes that sufficiently load the eccentric phase of movement can elicit superior neuromuscular adaptations compared with concentric-only or traditional resistance training constrained by concentric strength [6–8]. The training stress and physiological strain imposed by eccentric training induces an adaptive response conducive to enhancements in muscle mechanical function, and alterations in muscle-tendon unit (MTU) morphology and architecture. Metrics of strength, power and stretch-shortening cycle (SSC) function appear to be particularly responsive to eccentric stimuli. The purpose of this review was to systematically retrieve and collate studies that directly compared eccentric training with concentric or traditional resistance training.

2 Methods

The review was conducted according to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines for systematic reviews [9]. One reviewer performed initial database searches for articles investigating the chronic (i.e. ≥4 weeks) adaptations to eccentric training interventions on in vivo muscle-tendon properties and performance in human subjects (last search April 2016). Searches were performed using the electronic databases MEDLINE via EBSCO (1950–present), PubMed (1950–present) and SPORTDiscus via EBSCO (1985–present). Key search terms were grouped and searched within the article title, abstract, and keywords using the search conjunctions ‘OR’ and ‘AND’. Combinations of the following terms were used as search terms: ‘eccentric exercise’, ‘eccentric training’, ‘eccentric contraction’, ‘lengthening contraction’, ‘negative work’ and ‘passive work’ in conjunction with the terms ‘muscle’, ‘tendon’, ‘strength’, ‘power’, ‘speed’, ‘hypertrophy’, ‘force’, ‘velocity’ and ‘performance’. Key journals identified were also searched using the keyword ‘eccentric’. Furthermore, the reference lists of articles retrieved were screened for additional eligible articles. Full journal articles investigating the long-term effects of eccentric training (≥4 weeks) in healthy (i.e. the absence of injury or illness during the 4 weeks preceding the training intervention), adult (i.e. 17–35 years), human participants were selected for systematic review (Fig. 1). Articles were excluded if the aforementioned criteria were not fulfilled, training was performed less than twice weekly, eccentric exercise intensity was not quantified or was below the relative concentric exercise intensity, or no concentric or traditional resistance training control group was included.

3 Results and Discussion

3.1 Participant and Intervention Characteristics

Across the 40 studies included for review, 1150 participants (406 females and 744 males) with a mean age of 23.9 years (range 17.6–35.0) were recruited. The majority of investigations (32/40; 80 %) recruited untrained participants, four (10 %) recruited participants with resistance training experience (3 months to 1 year), and the remaining four (10 %) recruited participants who were either moderately trained or participated in elite sport. The majority of investigations compared eccentric training (i.e. eccentric contractions at an intensity above the relative concentric training intensity, performed alone or in conjunction with concentric contractions) of various volumes and intensities with traditional resistance training (i.e. mixed eccentric and concentric contractions limited by concentric intensity) and/or concentric training (i.e. concentric contractions only). A non-training control group was included in 17 (43 %) studies. Other training variables compared included the magnitude of overload (i.e. intensity; heavy vs. light), contraction velocity (i.e. tempo; fast vs. slow) and the additional effects of whey protein hydrolysate supplementation. The average intervention duration was 9.8 weeks (range 5–20), with a training frequency of 2.9 sessions per week (range 2.0–4.2). Single-joint movements were predominantly investigated (32 studies; 80 %) and isokinetic modalities were used more (26 studies; 65 %) than isoinertial modalities.

3.2 Muscle Mechanical Function

Eccentric training has been consistently reported to increase concentric [10–32], isometric [18, 23, 25, 29, 33–37], and eccentric [11, 13–15, 17, 18, 21–25, 27–29, 31, 37–42] strength when assessed via isoinertial (i.e. repetition maximum [RM] testing) or isokinetic (i.e. maximal voluntary contraction [MVC] testing) modalities (Table 1). Concentric training also elicits increases in concentric [11, 13–18, 21–32, 37–41], isometric [18, 23, 29, 33, 37, 40] and eccentric

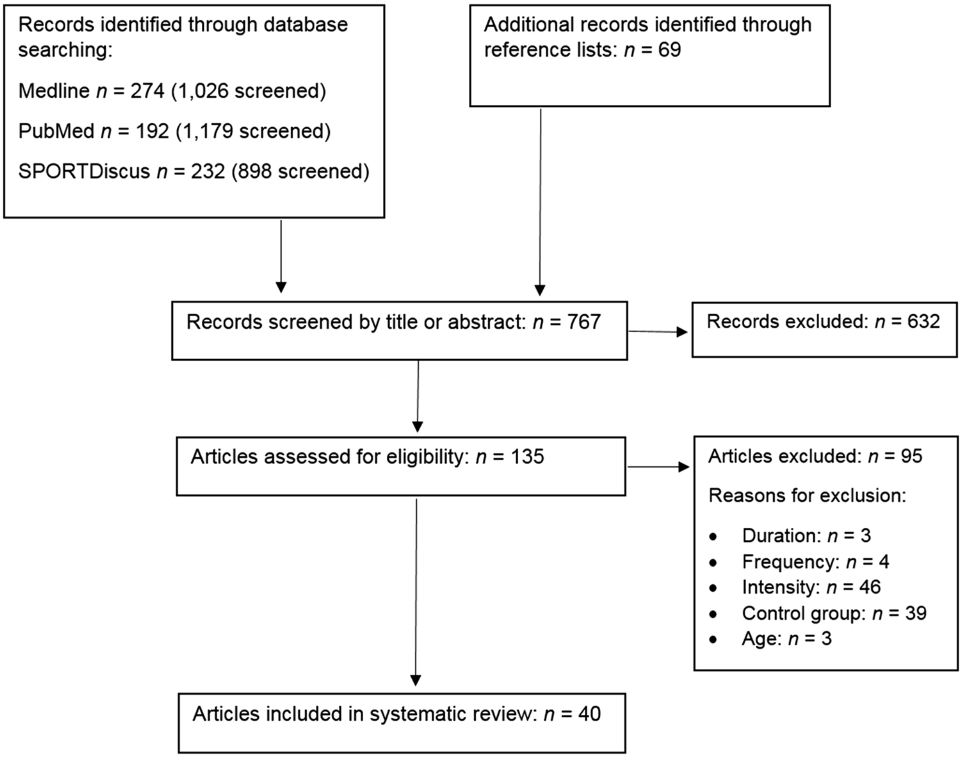

Fig. 1 Search strategy

[11, 13–15, 17, 18, 21, 23, 25, 27–29, 39, 42] strength, while increases in concentric [10, 12, 19, 20, 23], isometric [23, 34] and eccentric strength [23] are similarly observed following traditional resistance training (Table 1). Strength increases have been proposed to be largely mode-specific [8], and while some studies reported that eccentric training increased eccentric strength to a greater extent compared with concentric training [13, 21, 22, 25, 27, 31, 38, 39, 41], and vice versa [11, 38–41], others found no differences between modalities [10, 12, 14, 15, 19, 20, 23, 24, 28–30, 32–34, 42, 43]. A number of studies investigating eccentric training included the concentric portion of the movement in addition to the overloaded eccentric portion [10, 12–14, 19, 20, 23, 24, 32, 34, 42, 43], which may partly explain the mixed findings compared with previous reviews that compared eccentric-only with concentric-only modalities [6, 8]. When using eccentric loads greater than maximal concentric strength (e.g. 1RM or MVC), eccentric training generally leads to greater overall strength increases (i.e. combined concentric, isometric and eccentric strength) than concentric and traditional training [12, 16, 17, 21–23, 25–27, 30, 31]. Furthermore, studies directly comparing heavier with lighter eccentric loads found that heavier eccentric training induced greater increases in eccentric strength [16, 26]. Muscle contraction velocity used within training can also influence strength adaptations, and greater increases in eccentric strength have been observed with fast versus slow eccentric training [17], while increases in eccentric strength with eccentric training become more pronounced when the testing velocity corresponds to that used within training [8]. Greater increases in contralateral eccentric strength (i.e. cross-education) have been reported with fast (i.e. 180°/s) versus slow (i.e. 30°/s) eccentric training [44], although improvements can also occur following training at moderate (i.e. 60°/s) contraction speeds [45]. Fast contractions have also been proposed to allow for a greater transfer of eccentric training to concentric strength [7].

Compared with changes in muscle strength, relatively few studies investigated changes in muscle power [13, 14, 19, 34, 46, 47] or contractile rate of force development (RFD) [27, 33]. Muscle power, as assessed primarily by lower body jump variations, increased with eccentric training within a number of studies, while concentric or traditional training had no clear effect [13, 34, 46, 47]. Furthermore, the finding of Colliander and Tesch [14], where vertical jump increased following concentric, but not eccentric, training, may have been a statistically spurious observation. Closer inspection of their data indicates that eccentric training was, at least practically, superior to concentric training (i.e. 8 vs. 4 %; Cohen's *d* 0.36). Vertical jump performance involves an SSC component, and variables associated with SSC performance appear to improve to a greater extent with eccentric training. SSC efficiency (i.e. taken as the ratio of countermovement to squat jump performance), drop jump

Table 1 Studies comparing the effects of eccentric-overload and coupled maximal eccentric and concentric contractions with traditional and concentric-only resistance training on muscle mechanical function

Study, year	Population	Muscle groups (modality)	Intervention	Training duration	Training effect ($p < 0.05$)
Barstow et al. [43], 2003	ECC n = 13, TRAD n = 13, CONT n = 13 (8F, 31M); mean age: 22.2 years; training status: 3 months' resistance training	EF (isoinertial; single-joint)	Volume: 3 sets of 8 repetitions; intensity: ECC group: 100/60 % 1RM, TRAD group: 60 % 1RM; tempo: 2 s ECC, 2 s CONC	12 weeks (2 sessions per week)	No differences in CONC EF strength (1RM) between ECC (16 %), TRAD (14 %) or CONT (10 %)
Ben-Sira et al. [10], 1995	$\text{ECC}_{\text{Heavy}}$ n = 8, TRAD n = 8, $\text{ECC}_{\text{Light}}$ n = 10, CONC n = 12, CONT n = 10 (48F); mean age: 21.1 years; training status: untrained	KE (isoinertial; single-joint)	Volume: $\text{ECC}_{\text{Heavy}}$ group: 3 sets of 5 repetitions, TRAD, $\text{ECC}_{\text{Light}}$ and CONC group: 3 sets of 10 repetitions; intensity: $\text{ECC}_{\text{Heavy}}$ group: 135/65 % 1RM, TRAD, $\text{ECC}_{\text{Light}}$ and CONC groups: 65 % 1RM; tempo: 3 s ECC, 1 s CONC	8 weeks (2 sessions per week)	Increase in CONC KE strength (1RM) with $\text{ECC}_{\text{Heavy}}$ (23 %) and TRAD (19 %) vs. CONT (4 %), no difference between interventions
Blazevich et al. [11], 2007	ECC n = 11, CONC n = 10, CONT n = 9 (16F, 14 M); mean age: 22.8 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 5 sets of 6 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 30°/s	10 weeks (3 sessions per week)	Increase in CONC KE strength (MVC) with ECC (16 %) and CONC (24 %) vs. CONT (1 %), but greater increase with CONC Increase in ECC KE strength (MVC) with ECC (39 %) and CONC (36 %) vs. CONT (3 %), no difference between interventions
Blazevich et al. [33], 2008	ECC n = 11, CONC n = 10 (11F, 10 M); mean age: 22.8 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 5 sets of 6 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 30°/s	10 weeks (3 sessions per week)	Increase in ISO KE strength (MVC) with ECC (10 %) and CONC (13 %), no difference between interventions Increase in RFD 30 ms ($\text{N}\cdot\text{s}^{-1}$) with ECC (28 %) and CONC (50 %), greater increase with CONC vs. ECC
Brandenberg and Docherty [12], 2002	ECC n = 8, TRAD n = 10 (18 M); mean age: NR, university students; training status: 1 year resistance training	EF and EE (isoinertial; single-joint)	Volume: ECC group: 3 sets of 10 repetitions, TRAD group: 4 sets of 10 repetitions; intensity: ECC group: 115/75 % 1RM, TRAD group: 75 % 1RM; tempo: 2 s ECC, 2 s CONC	9 weeks (2.8 sessions per week)	Increase in CONC EF strength (1RM) with ECC (9 %) and TRAD (11 %), no difference between interventions Increase in CONC EE strength (1RM) with ECC (24 %) and TRAD (15 %), but greater increase with ECC training
Colliander and Tesch [13], 1990	ECC + CONC n = 11, CONC n = 11, CONT n = 7 (29 M); mean age: 26.3 years; training status: untrained	KE (isokinetic; single-joint)	Volume: ECC + CONC group: 4.8 sets of 6 CONC repetitions and 6 ECC repetitions, CONC group: 4.8 sets of 12 CONC repetitions; intensity: ECC + CONC group: ECC and CONC MVC, CONC group: CONC MVC; tempo: 60°/s	12 weeks (3 sessions per week)	Increase in ECC KE strength (MVC) with ECC + CONC (36 %) and CONC (19 %), no change with CONT (−5 %), greater increase with ECC + CONC vs. CONC Increase in CONC KE strength (MVC) with ECC + CONC (25 %) and CONC (14 %), no change with CONT (−2 %), no difference between interventions Increase in lower body strength (back squat 3RM) with ECC + CONC (25 %) and CONC (15 %), no change with CONT (2 %), no difference between interventions Increase in lower body power (vertical jump; cm) with ECC + CONC (8 %), no change with CONC (3 %) or CONT (−1 %), no difference between interventions

Table 1 continued

Study, year	Population	Muscle groups (modality)	Intervention	Training duration	Training effect ($p < 0.05$)
Colliander and Tesch, [14] 1992	ECC + CONC n = 10, CONC n = 8, CONT n = 7 (25 M); mean age: 26.6 years; training status: untrained	KE (isokinetic; single-joint)	Volume: ECC + CONC group: 4.8 sets of 6 CONC repetitions and 6 ECC repetitions, CONC group: 4.8 sets of 12 CONC repetitions; intensity: ECC + CONC group: ECC and CONC MVC, CONC group: CONC MVC; tempo: 60°/s	12 weeks (3 sessions per week)	Increase in ECC KE strength (MVC) with ECC + CONC (37 %) and CONC (18 %), no change with CONT (NR), no difference between interventions Increase in CONC KE strength (MVC) with ECC + CONC (26 %) and CONC (13 %), no change with CONT (NR), no difference between interventions Increase in lower body strength (back squat 3RM) with ECC + CONC (23 %) and CONC (13 %), no change with CONT (NR), no difference between interventions Increase in lower body power (vertical jump; cm) with CONC (4 %), no change with ECC + CONC (8 %) or CONT (NR), no difference between interventions
Duncan et al. [38], 1989	ECC n = 16, CONC n = 14, CONT n = 18 (48 M); mean age: 23.9 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 1 set of 10 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 120°/s	6 weeks (2 sessions per week)	Increase in ECC KE strength (MVC; 60, 120 and 180 °/s) with ECC (29 %), no change with CONC (7 %) or CONT (−1 %) Increase in CONC KE strength (MVC; 180 °/s) with CONC (8 %), no change with ECC (1 %) or CONT (−5 %)
Ellenbecker et al. [15], 1988	ECC n = 11, CONC n = 11 (22F and M); mean age: NR, university students; training status: varsity tennis athletes	ER and IR (isokinetic; single-joint)	Volume: 6 sets of 10 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: pyramid across six sets (60, 180, 210, 210, 180, 60°/s)	6 weeks (2 sessions per week)	Increase in CONC ER strength (MVC; 60, 180, 210°/s) with ECC (NR) and CONC (NR), no difference between interventions Increase in CONC IR strength (MVC; 60, 180, 210°/s) with ECC (NR) and CONC (NR), no difference between interventions Increase in ECC ER strength (MVC; 210°/s) with ECC (NR) and CONC (NR), no difference between interventions Increase in ECC IR strength (MVC; 60 and 180°/s) with CONC (8 %), no change with ECC (NR)
Elmer et al. [46], 2012	ECC n = 6, CONC n = 6 (12 M); mean age: 25.0 years; training status: untrained	HE and KE (isokinetic cycling; multi-joint)	Volume: 21 min; intensity: ECC group: 30 % concentric cycling peak power, CONC group: 19 % concentric cycling peak power; tempo: 60 rpm	7 weeks (3 sessions per week)	Increase in leg spring stiffness (kN/m) with ECC (10 %) vs. CONC (−2 %) Increase in jumping power (W) with ECC (7 %) vs. CONC (−2 %)
English et al. [16], 2014	ECC_{138} n = 8, ECC_{100} n = 8, $CONC_{66}$ n = 8, $CONC_{33}$ n = 8, CONC n = 8 (40 M); mean age: 34.9 years; training status: untrained	HE, KE and AE (isokinetic leg press; multi-joint)	Volume: 3.75 sets of 5 repetitions; intensity: ECC_{138} group: 138/76 % 1RM, ECC_{100} group: 100/76 % 1RM, $CONC_{66}$ group: 66/76 % 1RM, $CONC_{33}$: 33/76 % 1RM, CONC: 0/76 % 1RM; tempo: NR	8 weeks (3 sessions per week)	Increase in CONC HE and KE strength (leg press 1RM) with ECC_{138} (20 %), ECC_{100} (13 %), $CONC_{66}$ (8 %), $CONC_{33}$ (8 %) and CONC (8 %), but ECC_{138} greater than $CONC_{66}$, $CONC_{33}$ and CONC Increase in CONC AE strength (calf raise 1RM) with ECC_{138} (11 %), ECC_{100} (12 %), $CONC_{66}$ (7 %) and $CONC_{33}$ (8 %), no change with CONC (5 %), no difference between interventions

Table 1 continued

Study, year	Population	Muscle groups (modality)	Intervention	Training duration	Training effect ($p < 0.05$)
Farthing and Chilibeck [17], 2003	ECC_{Fast}, $CONC_{Fast}$ $n = 13$ (9F, 4 M), ECC_{Slow}, $CONC_{Slow}$ $n = 11$ (4F, 7 M), CONT $n = 10$ (8F, 2 M); mean age: 22.2 years; training status: untrained	EF (isokinetic; single-joint)	Volume: 4.6 sets of 8 repetitions; intensity: ECC groups: ECC MVC, CONC groups: CONC MVC; tempo: fast groups: 180°/s, slow groups: 30°/s	8 weeks (3 sessions per week)	Increase in CONC EF strength (MVC) with ECC_{Fast} (23 %) greater than $CONC_{Fast}$ (1 %), $CONC_{Slow}$(6 %) and CONT (0 %), but not ECC_{Slow} (16 %) Increase in ECC EF strength (MVC) with ECC_{Fast} (16 %) greater than $CONC_{Fast}$ (−1 %), ECC_{Slow} (6 %), $CONC_{Slow}$(5 %) and CONT (0 %)
Farthing and Chilibeck [44], 2003	ECC_{Fast}, $CONC_{Fast}$ $n = 13$ (9F, 4 M) ECC_{Slow}, $CONC_{Slow}$ $n = 11$ (4F, 7 M), CONT $n = 10$ (8F, 2 M); mean age: 22.2 years; training status: untrained	EF (isokinetic; single-joint)	Volume: 4.6 sets of 8 repetitions; intensity: ECC groups: ECC MVC, CONC groups: CONC MVC; tempo: fast groups: 180°/s, slow groups: 30°/s	8 weeks (3 sessions per week)	Increase in contralateral ECC EF strength (MVC; 180 °/s) with ECC_{Fast} and $CONC_{Fast}$ (23 %), no change with ECC_{Slow}, $CONC_{Slow}$ (−17 %) or CONT (8 %), no difference between interventions
Farup et al. [18], 2014	ECC_{Whey} and ECC$n = 11$, $CONC_{Whey}$ and CONC $n = 11$, within-subject design (22 M); mean age: 23.9 years; training status: untrained	KE (isoinertial; single-joint)	Volume: 9.3 sets of 10.7 repetitions; intensity: ECC groups: 90/75 % 1RM, CONC groups: 75 % 1RM; tempo: ECC: 2 s, CONC: 2 s	12 weeks (2.75 sessions per week)	Increase in CONC KE strength (MVC) with ECC (4 %), $CONC_{Whey}$ (7 %) and CONC (20 %), no change with ECC_{Whey} (2 %), no difference between interventions Increase in ISO KE strength (MVC) with ECC_{Whey} (6 %) ECC (10 %), $CONC_{Whey}$ (17 %) and CONC (20 %), no difference between interventions Increase in ECC KE strength (MVC) with ECC_{Whey} (10 %), ECC (8 %), $CONC_{Whey}$ (8 %) and CONC (19 %), no difference between interventions
Franchi et al. [37], 2014	ECC $n = 6$, CONC $n = 6$ (12 M); mean age: 25.0 years; training status: untrained	HE and KE (isokinetic; multi-joint)	Volume: 4 sets of 9 repetitions; intensity: ECC group: 80 % ECC 1RM, CONC group: 80 % CONC 1RM; tempo: ECC group: 3 s, CONC group: 2 s	10 weeks (3 sessions per week)	Increase in ISO KE strength (MVC) with ECC (11 %) and CONC (9 %), no difference between interventions
Friedmann-Bette et al. [19], 2010	ECC $n = 14$, TRAD $n = 11$ (25 M); mean age: 24.4 years; training status: strength trained	KE (isoinertial; single-joint)	Volume: ECC group: 5 sets of 8 repetitions, TRAD group: 6 sets of 8 repetitions; intensity: ECC: 152/80 % 1RM, TRAD: 80 % 1RM; tempo: NR; explosive ECC and CONC	6 weeks (3 sessions per week)	Increase in CONC KE strength (1RM) with ECC (16 %) and TRAD (19 %), no difference between interventions Increase in squat jump (cm) with ECC (7 %), no change with TRAD (1 %)
Godard et al. [20], 1998	ECC $n = 9$, TRAD $n = 9$, CONT $n = 10$ (17F, 21 M); mean age: 22.4 years; training status: recreationally active	KE (isokinetic; single-joint)	Volume: 1 set of 10 repetitions; intensity: ECC group: 120/80 % 1RM, TRAD group: 80 % 1RM; tempo: 30°/s	10 weeks (2)	Increase in CONC KE strength (MVC) with ECC (81 %) and TRAD (82 %) vs. CONT (7 %), no difference between interventions

Table 1 continued

Study, year	Population	Muscle groups (modality)	Intervention	Training duration	Training effect ($p < 0.05$)
Gross et al. [34], 2010	ECC $n = 8$, TRAD $n = 7$ (15 M); mean age: 17.6 years; training status: junior national skiers	HE and KE (isokinetic and isoinertial; multi-joint)	Volume: ECC group: 12 sets of 30 repetitions weight training and 20 min ECC cycling, TRAD group: 22.5 sets of 30 repetitions; intensity: ECC group: 40 % 1RM weight training and 532 W ECC cycling, TRAD group: 40 % 1RM; tempo: ECC cycling: 70 rpm, weight training: NR	6 weeks (3 sessions per week)	Increase in ISO HE and KE strength (leg press MVC) with ECC (10 %) and TRAD (12 %), no difference between interventions Decrease in squat jump (cm) with TRAD (−4 %), no change with ECC (2 %) Increase in countermovement jump (cm) with ECC (7 %), no change with TRAD (3 %)
Hawkins et al. [21], 1999	ECC $n = 8$, CONC $n = 8$ (within-subject design), CONT $n = 12$ (20F); mean age: 21.4 years; training status: untrained	KEand KF (isokinetic; single-joint)	Volume: ECC group: 3 sets of 3 repetitions, CONC group: 3 sets of 4 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: NR	18 weeks (3 sessions per week)	Increase in CONC KE strength (MVC) with ECC (18 %) and CONC (23 %), no change with CONT (−6 %), no difference between interventions Increase in ECC KE strength (MVC) with ECC (22 %) and CONC (17 %) increased, no change with CONT (−3 %), greater increase with ECC training vs. CONC Increase in CONC KF strength (MVC) ECC (13 %), no change with CONC (6 %) or CONT (NR) Increase in ECC KF strength (MVC) with ECC (14 %) and CONC (13 %), no change with CONT (NR), no difference between interventions
Higbie et al. [39], 1996	ECC $n = 19$, CONC $n = 16$, CONT $n = 19$ (54F); mean age: 20.5 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 3 sets of 10 repetitions; intensity; ECC group: ECC MVC, CONC group: CONC MVC; tempo: 60°/s	10 weeks (3 sessions per week)	Increase in CONC KE strength (MVC) with CONC (18 %), no change with ECC (7 %) or CONT (5 %), greater increase with CONC training vs. ECC Increase in ECC KE strength (MVC) with ECC (36 %) and CONC (13 %), no change with CONT (−2 %), greater increase with ECC training vs. CONC Increase in CONC KE activation (EMG) with CONC (22 %) greater than CONT (−8 %), no change with ECC (7 %) Increase in ECC KE activation (EMG) with ECC (17 %) and CONC (20 %) greater than CONT (−9 %), no difference between interventions

Table 1 continued

Study, year	Population	Muscle groups (modality)	Intervention	Training duration	Training effect ($p < 0.05$)
Hortobagyi et al. [22], 1996	ECC n = 7, CONC n = 8, CONT n = 6 (21 M); mean age: 21.3 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 5.3 sets of 10 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 60°/s	12 weeks (3 sessions per week)	Increase in CONC KE strength (MVC) with ECC (33 %) and CONC (53 %), no change with CONT (NR), no difference between interventions
					Increase in ECC KE strength (MVC) with ECC (116 %), no change with CONC (40 %) or CONT (NR), greater increase with ECC training vs. CONC
					Increase in CONC KE activation (EMG) with CONC (28 %), no change with ECC (62 %) or CONT (NR), no difference between interventions
					Increase in ECC KE activation (EMG) with ECC (188 %), no change with CONC (10 %) or CONT (NR), greater increase with ECC training vs. CONC
Hortobagyi et al. [45], 1997	ECC n = 7, CONC n = 8, CONT n = 6 (21 M); mean age: 21.3 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 5.3 sets of 10 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 60°/s	12 weeks (3 sessions per week)	Increase in contralateral CONC KE Strength (MVC) with CONC (30 %), no change with ECC (18 %) or CONT (0 %), no difference between interventions
					Increase in contralateral ISO KE strength (MVC) with ECC (39 %) and CONC (22 %), no change with CONT (2 %), greater increase with ECC vs. CONC
					Increase in contralateral ECC KE strength (MVC) with ECC (77 %), no change with CONC (18 %) or CONT (4 %), greater increase with ECC vs. CONC
Hortobagyi et al. [23], 2000	ECC n = 12, ECC + CONC n = 12, CONC n = 12, CONT n = 24 (24F, 24 M); mean age: 22.0 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 5.3 sets of 10 repetitions; intensity: ECC group: ECC MVC, ECC + CONC group: ECC and CONC MVC, CONC group: CONC MVC; tempo: 60°/s	12 weeks (3 sessions per week)	Increase in CONC KE strength (MVC) with ECC (25 %), ECC + CONC (40 %) and CONC (44 %), no change with CONT (NR), no difference between interventions
					Increase in ISO KE strength (MVC) with ECC (42 %), ECC + CONC (38 %) and CONC (31 %), no change with CONT (NR), greater increase with ECC and ECC + CONC vs. CONC
					Increase in ECC KE strength (MVC) with ECC (86 %), ECC + CONC (70 %) and CONC (20 %), no change with CONT (NR), no difference between interventions
Kaminski et al. [24], 1998	ECC n = 9, CONC n = 9, CONT n = 9 (27 M); mean age: 22.9 years; training status: untrained	KF (isoinertial; single-joint)	Volume: 2 sets of 8 repetitions; intensity: ECC group: 100/40 % 1RM, CONC group: 80 % 1RM; tempo: NR	6 weeks (2 sessions per week)	Increase in CONC KF strength (1RM/BW) with ECC (29 %) and CONC (19 %), no change with CONT (5 %), no difference between interventions
					Increase in ECC KF strength (MVC) with ECC (30 %), no change with CONC (13 %) or CONT (−5 %), no difference between interventions

Table 1 continued

Study, year	Population	Muscle groups (modality)	Intervention	Training duration	Training effect ($p < 0.05$)
Komi and Buskirk [25], 1972	ECC $n = 11$, CONC $n = 10$, CONT $n = 10$ (31 M); mean age: 19.6 years; training status; untrained	EF (isokinetic; single-joint)	Volume: 1 set of 6 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: NR	7 weeks (4 sessions per week)	Increase in CONC EF strength (MVC) with ECC (16 %) and CONC (12 %) vs. CONT (2 %), no difference between interventions Increase in ISO EF strength (MVC) with ECC (7 %) vs. CONT (1 %), no change with CONC (6 %) Increase in ECC EF strength (MVC) with ECC (16 %) and CONC (7 %) vs. CONT (−4 %), greater increase with ECC vs. CONC
LaStayo et al. [35], 1999	ECC $n = 4$, CONC $n = 5$ (5F, 4 M); mean age: 21.5 years; training status: untrained	HE and KE (isokinetic cycling; multi-joint)	Volume: 27.5 min; intensity: ECC group: 1 L/min O_2 consumption, CONC group: 1.2 L/min O_2 consumption; tempo: 55 rpm	6 weeks (4.2 sessions per week)	Increase in ISO KE strength (MVC) with ECC (27 %), no change with CONC (10 %)
LaStayo et al. [36], 2000	ECC $n = 7$, CONC $n = 7$ (14 M); mean age: 23.9 years; training status: untrained	HE and KE (isokinetic cycling; multi-joint)	Volume: 27.5 min; intensity: 62 % maximum heart rate; tempo: 60 rpm	8 weeks (3.5 sessions per week)	Increase in ISO KE strength (MVC) with ECC (36 %), no change with CONC (2 %)
Liu et al. [47], 2013	ECC + CONC$_{\mathrm{Fast}}$$n = 10$, ECC + CONC$_{\mathrm{Slow}}$$n = 10$, TRAD $n = 10$ (30 M); mean age: 19.5 years; training status: untrained	HE and KE (ECC groups: isokinetic, TRAD group: isoinertial; multi-joint)	Volume: 5 sets of 10 repetitions; intensity; ECC groups: ECC MVC, TRAD group: 70 % 1RM; tempo: ECC$_{\mathrm{Fast}}$: 2.5 Hz, ECC$_{\mathrm{Slow}}$ and TRAD: 0.5 Hz	10 weeks (3 sessions per week)	Increase in lower body power (vertical jump; cm) with ECC + CONC$_{\mathrm{Fast}}$ (4 %) and ECC + CONC$_{\mathrm{Slow}}$(3 %), no change with TRAD (2 %), greater increase with ECC + CONC$_{\mathrm{Fast}}$ vs. ECC + CONC$_{\mathrm{Slow}}$ and TRAD Increase in drop jump (cm) with ECC + CONC$_{\mathrm{Fast}}$ (6 %), no change with ECC + CONC$_{\mathrm{Slow}}$(1 %) or TRAD (1 %), greater increase with ECC + CONC$_{\mathrm{Fast}}$ vs. ECC + CONC$_{\mathrm{Slow}}$ Decrease in 30 m sprint time (s) with ECC + CONC$_{\mathrm{Fast}}$ (−0.23 %), ECC + CONC$_{\mathrm{Slow}}$ (−0.12 %) and TRAD (−0.12 %), greater improvement with ECC + CONC$_{\mathrm{Fast}}$ vs. ECC + CONC$_{\mathrm{Slow}}$ and TRAD Increase in stretch shortening cycle efficiency with ECC + CONC$_{\mathrm{Fast}}$ (11 %), no change with ECC + CONC$_{\mathrm{Slow}}$(4 %) or TRAD (2 %), greater increase with ECC + CONC$_{\mathrm{Fast}}$ vs. ECC + CONC$_{\mathrm{Slow}}$ and TRAD
Malliaras et al. [26], 2013	ECC$_{\mathrm{Heavy}}$$n = 10$, ECC$_{\mathrm{Light}}$$n = 10$, CONC $n = 9$, CONT $n = 9$ (38 M); mean age: 27.5 years; training status: untrained	KE (isoinertial; single-joint)	Volume: ECC$_{\mathrm{Heavy}}$ and CONC groups: 4 sets of 7.5 repetitions, ECC$_{\mathrm{Light}}$ group: 4 sets of 13.5 repetitions; intensity: ECC$_{\mathrm{Heavy}}$ group: 80 % ECC 1RM, ECC$_{\mathrm{Light}}$ and CONC groups: 80 % CONC 1RM; tempo: ECC: 5 s, CONC: 1 s	12 weeks (3 sessions per week)	Increase in CONC KE strength (5RM) with ECC$_{\mathrm{Heavy}}$ (77 %), ECC$_{\mathrm{Light}}$(61 %) and CONC (53 %), no change with CONT (NR), greater increase with ECC$_{\mathrm{Heavy}}$ vs. ECC$_{\mathrm{Light}}$ and CONC

Table 1 continued

Study, year	Population	Muscle groups (modality)	Intervention	Training duration	Training effect ($p < 0.05$)
Miller et al. [27], 2006	ECC n = 17, CONC n = 21 (38F); mean age: 20.0 years; training status: untrained	KF and KE (isokinetic; single-joint)	Volume: 4.5 sets of 6 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 60°/s	20 weeks (3 sessions per week)	Increase in CONC KE strength (MVC) with ECC (15 %) and CONC (10 %), no difference between interventions
					Increase in CONC KF strength (MVC) with ECC (29 %) and CONC (27 %), no difference between interventions
					Increase in ECC KE strength (MVC) with ECC (28 %) and CONC (12 %), greater increase with ECC vs. CONC
					Increase in ECC KF strength (MVC) with ECC (40 %) and CONC (20 %), greater increase with ECC vs. CONC
					Increase in CONC KE RFD (ms) with ECC (14 %) and CONC (14 %), no difference between interventions
					Increase in CONC KF RFD (ms) with ECC (35 %) and CONC (21 %), no difference between interventions
					Increase in ECC KE RFD (ms) with ECC (26 %) and CONC (2 %), greater increase with ECC vs. CONC
					Increase in ECC KF RFD (ms) with ECC (21 %) and CONC (9 %), greater increase with ECC vs. CONC
Mont et al. [28], 1994	ECC n = 8, CONC n = 9, CONT n = 13 (30 M); mean age: 33.0 years; training status: elite tennis players	ER and IR (isokinetic; single-joint)	Volume: 8 sets of 10 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: pyramid across eight sets (90, 120, 150, 180, 180, 180, 120, 90°/s)	6 weeks (3 sessions per week)	Increase in CONC ER strength (MVC) with ECC (9 %) and CONC (7 %) vs. CONT (−9 %), no difference between interventions
					Increase in CONC IR strength (MVC) with ECC (2 %) and CONC (12 %) vs. CONT (−9 %), no difference between interventions
					Increase in ECC ER strength (MVC) with ECC (18 %) and CONC (10 %) vs. CONT (−1 %), no difference between interventions
					Increase in ECC IR strength (MVC) with ECC (5 %) and CONC (18 %) vs. CONT (−4 %), no difference between interventions
Moore et al. [29], 2012	ECC and CONC n = 9, within-subject design (9 M); mean age: 22.0 years; training status: untrained	EF (isokinetic; single-joint)	Volume: ECC group 4.44 sets of 10 repetitions, CONC group: 4.44 sets of 14 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 45°/s	9 weeks (2 sessions per week)	Increase in CONC EF strength (MVC) with ECC (11 %) and CONC (14 %), no difference between interventions
					Increase in ISO EF strength (MVC) with ECC (9 %) and CONC (19 %), no difference between interventions
					Increase on ECC EF strength (MVC) with ECC (8 %) and CONC (11 %), no difference between interventions

Table 1 continued

Study, year	Population	Muscle groups (modality)	Intervention	Training duration	Training effect ($p < 0.05$)
Nickols-Richardson et al. [30], 2007	ECC $n = 33$, CONC $n = 37$ (70F); mean age: 35.0 years; training status: untrained	KF,KE, EF and EE (isokinetic; single-joint)	Volume: 4.5 sets of 6 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 60°/s	20 weeks (3 sessions per week)	Increase in CONC KF and KE strength (MVC) with ECC (29 %) and CONC (19 %), no difference between interventions Increase in CONC EF and EE strength (MVC) with ECC (25 %) and CONC (13 %), greater increase with ECC vs. CONC
Seger et al. [40], 1998	ECC $n = 5$, CONC $n = 5$ (10 M); mean age: 24.5 years; training status: moderately trained	KE (isokinetic; single-joint)	Volume: 4 sets of 10 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 90°/s	10 weeks (3 sessions per week)	Increase in CONC KE strength (MVC; 30 and 90°/s) with CONC (12 %), no change with ECC (4 %) Increase in ISO KE strength (MVC) with CONC (14 %), no change with ECC (6 %) Increase in ECC KE strength (MVC; 30 and 90°/s) with ECC (24 %) and CONC (13 %), no difference between interventions
Spurway [42], 2000	ECC and CONC $n = 20$, within-subject design (10F, 10 M); mean age: 24.0 years; training status: untrained	KE (isoinertial; single-joint)	Volume: 3 sets of 6 repetitions; intensity: ECC group: 85 % ECC 1RM, CONC group: 85 % CONC 1RM; tempo: NR	6 weeks (3 sessions per week)	Increase in ECC KE strength (MVC) with ECC (26 %) and CONC (23 %), no difference between interventions
Tomberlin et al. [41], 1991	ECC $n = 21$, CONC $n = 19$, CONT $n = 23$ (32F, 31 M); mean age: 27.1 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 3 sets of 10 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 100°/s	6 weeks (3 sessions per week)	Increase in CONC KE strength (MVC) with CONC (8 %), no change with ECC (4 %) or CONT (−2 %), greater increase with CONC vs. ECC and CONT Increase in ECC KE strength (MVC) with ECC (21 %) and CONC (11 %), no change with CONT (5 %), greater increase with ECC vs. CONC and CONT
Vikne et al. [31], 2006	ECC $n = 9$, CONC $n = 8$ (17 M); mean age: 27.1 years; training status: resistance trained	EF (isoinertial; single-joint)	Volume: 3.9 sets of 6 repetitions; intensity: ECC group: 94 % ECC 1RM, CONC group: 94 % CONC 1RM; tempo: ECC: 3.5 s, CONC: explosive	12 weeks (2.5 sessions per week)	Increase in CONC EF strength (1RM) with ECC (14 %) and CONC (18 %), no difference between interventions Increase in ECC EF strength (1RM) with ECC (9 %) and CONC (3 %), greater increase with ECC vs. CONC
Yarrow et al. [32], 2008	ECC $n = 10$, CONC $n = 12$ (22 M); mean age: 22.1 years; training status: untrained	Lower Body/Back Squat and Upper Body/Bench Press (isoinertial; multi-joint)	Volume: ECC group: 3 sets of 6 repetitions, CONC group: 4 sets of 6 repetitions; intensity: ECC group: 110/44 % 1RM, CONC group: 65 % 1RM; tempo: 6 s per repetition	5 weeks (3 sessions per week)	Increase in lower body strength (back squat 1RM) with ECC (19 %) and CONC (25 %), no difference between interventions Increase in upper body strength (bench press 1RM) with ECC (9 %) and CONC (10 %), no difference between interventions

°/s degrees per second, *cm* centimetres, *AE* ankle extensors, *CONC* concentric, *CONT* control, *ECC* eccentric, *ECC + CONC* coupled maximal eccentric and concentric contractions, *EE* elbow extensors, *EF* elbow flexors, *EMG* electromyography, *ER* shoulder external rotators, *F* females, *HE* hip extensors, *IR* shoulder internal rotators, *ISO* isometric, *KE* knee extensors, *KF* knee flexors, *kN/m* kilonewtons per metre, *L/m* litres per minute, *M* males, *ms* milliseconds, *MVC* maximum voluntary contraction, *n* number of subjects, $N{\cdot}s^{-1}$ newtons per second, *NR* not reported, *RFD* rate of force development, *RM* repetition maximum, *rpm* revolutions per minute, *s* seconds, *TRAD* traditional resistance training, *W* watts

performance and leg spring stiffness have been found to increase following eccentric, but not concentric or traditional, resistance training [46, 47]. Squat jump performance, which involves no SSC component and therefore reflects muscle power independent of elastic energy utilization and stretch reflex potentiation, may also benefit to a greater extent following eccentric training compared with concentric or traditional resistance training [19, 34]. Aligning with observations on muscle strength, fast eccentric training appears to have a more potent effect on measures of muscle power than slow eccentric training. Vertical jump, drop jump, SSC efficiency and sprinting performance (i.e. 30 m) all improved to a greater extent following fast (i.e. 2.5 Hz isokinetic squat movement) combined eccentric/concentric training compared with slow combined eccentric/concentric (i.e. 0.5 Hz isokinetic squat movement) and traditional resistance training [47]. Improvements in contractile RFD appear to be dependent on the method of assessment. Isometric RFD from 0 to 30 ms increased to a greater extent with concentric versus eccentric training [33], while eccentric training has been found to elicit a greater increase in eccentric RFD (i.e. as inferred from time to peak torque during isokinetic knee extension and flexion) and an equivalent increase in concentric RFD compared with concentric training [27].

3.2.1 Muscle Strength

The mechanisms underpinning strength improvements with eccentric training are likely a combination of neural, morphological and architectural factors (Sect. 3.3), although relatively few studies have investigated the possible neural adaptations following eccentric training [22, 25, 39]. The mode-specificity of strength improvements in conjunction with cross-education supports the importance of neural mechanisms, while other evidence indicates that changes in eccentric strength are attained via increased agonist voluntary activation [48, 49] and decreased antagonist coactivation [50]. The inability to fully activate muscle during eccentric contractions [51], particularly in untrained subjects [52], may explain the large improvements in eccentric strength and the observation that eccentric training increases eccentric strength to a greater degree than concentric training increases concentric strength [22, 39]. In support of an improved neural drive, Vangsgaard et al. [49] found 5 weeks of eccentric training of the trapezius muscle increased muscle excitability (i.e. inferred from maximal evoked H-reflex) in concert with a 26 % increase in MVC, aligning with previous findings [53]. Improvements in agonist voluntary activation during eccentric contractions may result from a disinhibition of presynaptic Golgi Ib and joint afferents known to inhibit excitatory muscle spindle Ia afferents [54]. Surface electromyography (EMG) has been found to increase during eccentric contractions, but not concentric contractions, following eccentric training [22, 39], although conflicting findings have been reported [39]. Maximal EMG (i.e. peak root mean square [RMS] values and integrated voltage from the EMG [iEMG]) following training is proposed to reflect the electrical excitation of muscle, which is influenced by the number and size (i.e. type I vs. type II fibres) of recruited motor units, motor unit discharge rate and synchrony [22, 39]. Based on findings using the twitch interpolation technique, motor unit activation during an isometric MVC can be, although not in all cases, maximal in untrained subjects during single joint movements [55]. It has been proposed that increases in EMG with eccentric training result from increases in motor unit discharge rate [39]. Contrary to reports on isometric contractions, maximal activation is typically inhibited during maximal eccentric contractions with untrained subjects [54], which indicates that both motor unit recruitment and discharge rates could contribute to increases in strength. The relative contribution of motor unit activation to the voluntary activation deficit may increase during compound multi-joint movements [55], but methodological limitations with measuring motor unit activity make it challenging to corroborate this supposition. Nonetheless, it is believed that the motor unit discharge rate is the primary inhibitory mechanism constraining voluntary activation during eccentric contractions [52], and thus the neural factor that contributes most to increased eccentric strength following eccentric, or heavy, resistance training [54].

3.2.2 Muscle Power and Stretch-Shortening Cycle Performance

Increases in muscle power following chronic resistance training are generally expected, particularly for subjects with a limited training history [56]. Muscle power is dictated by the force–velocity relationship and therefore the capacity of muscle to both produce force and shorten rapidly [3]. The neural mechanisms underpinning improvements in strength, along with morphological and architectural adaptations (Sect. 3.3), probably contribute to improvements in muscle power with eccentric training [3]. Increases in muscle power will largely arise from improvements in the capability to rapidly recruit larger motor units (i.e. type IIa and IIx) and increases in motor unit firing frequency [3]. Faster recruitment of larger motor units may be achieved by lowering the threshold of recruitment [57], or via a preferential recruitment. Experimental evidence supporting a preferential recruitment is not compelling [52], and therefore a lower threshold of recruitment seems most plausible in explaining a training-induced improvement in rapid motor unit recruitment [3].

Increases in motor unit firing frequency could also contribute to enhancements in eccentric power (i.e. during a vertical jump), and would align with the purported effects of motor unit discharge rates on eccentric strength [54]. Improvements in motor unit synchronization (i.e. intramuscular coordination) and intermuscular coordination (i.e. improved synergist coactivation and decreased antagonist coactivation) could also play a role in the expression of neuromuscular power [3, 58]. Improved eccentric force control is a postulated adaptation to eccentric training [56] and it is possible that increased eccentric coordination could contribute to SSC performance. SSC performance during various outcome measures (i.e. vertical jump, drop jump and SSC efficiency) can be enhanced by modulating the eccentric phase of the movement [46, 47, 59, 60]. Papadopoulos and colleagues [59] found an eccentric leg-press training protocol elicited smaller changes in ankle, hip and knee angles during the eccentric phase of a drop jump that corresponded to improved jump height, power and contact time. The increased joint stiffness during the eccentric phase of the SSC probably enhanced the utilization of elastic energy [59] and allowed the muscle to operate closer to its optimum length and shortening velocity [60]. These adaptations appear to translate to functional performance such as sprinting, particularly with inclusion of fast mixed eccentric/concentric contractions in the training protocol [47]. Cook et al. [61] found that 3 weeks of controlled tempo eccentric training in semi-professional rugby players improved back squat, bench press and countermovement jump performance to a greater extent than traditional resistance training. However, the authors found that the addition of overspeed sprint and power training was necessary to elicit increases in 40-m sprint performance with eccentric training [61]. A 3.3 % increase in flying 10 m sprint time has also been reported in well-trained soccer players following 10 weeks of eccentric flywheel training [62], but contraction speed was not reported. While further research is necessary, it may be postulated that fast contraction velocities optimize the transfer of eccentric-related adaptations to sprint performance involving a fast SSC component.

3.2.3 *Contractile Rate of Force Development*

The lack of studies investigating the effects of eccentric training on RFD, combined with divergent methods of assessment, make it difficult to draw firm conclusions in this area. Contractile RFD is influenced by muscle strength, cross-sectional area (CSA), fibre type and myosin heavy chain (MHC) composition, MTU viscoelastic properties, and neural drive [63, 64]. The relative contribution of these factors probably depends on the RFD time interval assessed. A combination of neural drive and intrinsic muscle properties (i.e. MHC composition) appears to play a marked role during early-phase (i.e. <100 ms) RFD [65], which is unsurprising given the cross-bridge cycling rates of both IIx and IIa fibres are substantially greater than type I fibres [66, 67]. Improvements in late-phase (i.e. >100 ms) RFD may be more related to neural drive, muscle CSA and tendon/aponeurosis stiffness [65]. Indeed, Andersen and Aagaard [64] found that very early RFD (i.e. <40 ms) was related to twitch RFD more so than maximal strength, and from 90 ms onwards strength accounted for 52–81 % of the variance in voluntary RFD. Furthermore, tendon and aponeurosis stiffness has been demonstrated to account for up to 30 % of the variance in RFD from 0 to 200 ms [63]. Training interventions that change these underlying mechanisms could plausibly influence early- and late-phase RFD to differing extents [68]. Six weeks of fast concentric (i.e. 180°/s) training can improve early-phase RFD by 33–56 %, independent of any change in late-phase RFD or strength, a finding that has been attributed to changes in neural drive [69]. Fast eccentric (i.e. 180°/s) resistance training has been similarly demonstrated to improve early-phase RFD by 30 %, but also in conjunction with a 28 % improvement in strength [65]. The mechanisms by which eccentric training improve early-phase RFD may be a combination of intrinsic muscle and neural adaptations. Similar to improvements in muscle strength and power, the unique neural strategies involved with eccentric training may improve RFD via both increased volitional supraspinal drive and spinal reflex disinhibition [65]. Late-phase improvements in RFD have been demonstrated to occur in parallel with improvements in strength with heavy resistance training [64], and therefore the increases in strength observed with eccentric training may contribute to enhanced late-phase RFD. Isometric training that includes the intention to contract explosively (i.e. ‘ballistic-intended’) has been found to improve both early and late RFD [70], and it has been proposed that the intention to act explosively is more important than the type of contraction performed [69]. Further research is necessary to determine best practice in maximizing improvements in RFD; as long as there is maximal intent to contract explosively, eccentric, isometric and concentric training protocols can lead to performance enhancements.

3.2.4 *Summary of Eccentric Training Effects on Muscle Mechanical Function*

In summary, eccentric training may improve overall strength to a greater extent than concentric and traditional modalities, although there is a mode-specificity (i.e. contraction type and velocity) of improvements [8]. Increases in strength result from a combination of neural, morphological and architectural adaptations. Increased voluntary activation of agonists during eccentric contractions via a disinhibition of excitatory inflow to spinal motor neurons may underpin the marked increases in eccentric strength observed following training [54]. Based on EMG experiments, an increase in motor unit discharge rate appears to play a more important role than changes in motor unit recruitment [39], although further research is necessary to determine whether this observation holds during compound, multi-joint movements [55]. Eccentric training improves muscle power and SSC performance to a greater extent than concentric or traditional modalities, while reports on changes in RFD have been mixed. Improvements are likely related to increases in eccentric and concentric strength, an improved ability to rapidly recruit fast motor units, a shift towards a faster muscle phenotype (Sect. 3.3), and an enhanced eccentric phase within the SSC. Given the mode-specificity of adaptations, dedicated concentric training should be performed in addition to eccentric training if improvements in concentric strength, and possibly power, are of importance. In practice, traditional resistance training combining eccentric and concentric actions remains most prevalent. The use of traditional exercises with additional overload above the concentric maximum during the eccentric phase may therefore maximize outcomes across concentric, isometric and eccentric strength [16]. Furthermore, fast eccentric velocities may induce greater strength, power and SSC improvements than slow eccentric velocities [17, 47]. It has also been suggested that the optimal duration between the cessation of eccentric training and performance assessment may necessarily differ from concentric training in expressing improvements in muscle mechanical function [71]. More research is needed to determine the fatigue, recovery and adaptation time-course, as well as subsequent performance responses, with eccentric training.

3.3 Muscle-Tendon Unit Morphology and Architecture

Eccentric [11, 13, 16, 17, 19–21, 29, 31, 34, 36, 37, 39, 40, 72, 73], concentric [11, 13, 17, 29, 30, 37, 72, 73] and traditional [19, 20, 39] resistance training have all been found to increase muscle size using a variety of measures (i.e. dual-energy x-ray absorptiometry [DXA], muscle circumference, magnetic resonance imaging [MRI], peripheral computerized tomography [pQCT] and ultrasound) (Table 2). Muscle hypertrophy is a common finding with eccentric and concentric training modalities. Either a greater increase [16, 17, 21, 34, 36, 39, 40], or no difference [11, 13, 29, 30, 37, 72, 73] has been reported following eccentric training. Those comparing eccentric training with traditional resistance training reported no differences between modalities [19, 20]. Contraction type appears to mediate a region-specific hypertrophy; eccentric training tends to induce greater increases in distal muscle size, while mid-muscle hypertrophy occurs to a greater extent following concentric training [37, 40]. It is plausible that reported literature is not entirely representative of the extent of adaptation with eccentric training, given that muscle morphology and architecture are typically assessed at the mid-belly of the muscle. When looking at fibre-type-specific responses (i.e. via muscle biopsy and electron microscopy), greater increases in type II fibre area have been observed with eccentric versus concentric or traditional training [19, 22, 23, 31]. In particular, an improved maintenance of, or increase in, type IIx fibre area has been reported with eccentric training relative to concentric [13] or traditional resistance training [19, 23]. Fibre type composition may be uniquely influenced by eccentric training, and either an improved maintenance of [13, 31], or similar reduction of [22], IIx fibres has been found compared with concentric training. As per changes in muscle strength, the intensity and velocity of muscle contraction influence the magnitude of muscle hypertrophy with eccentric training. Even when all conditions involve supra-maximal loads (i.e. greater than maximal concentric strength), greater increases in hypertrophy have been found with heavier eccentric training conditions [16], while fast eccentric velocities (i.e. 180°/s) also induced larger increases in muscle CSA [17]. The addition of whey protein hydrolysate supplementation in the post-exercise period has been found to increase [73], or have no effect on [72], the hypertrophic response following eccentric training. Few studies investigated changes in muscle architecture [11, 37] or tendon structure and function [26, 72] with differing contraction types. Vastus lateralis fascicle length was found to increase with both eccentric and concentric training [11], or eccentric training only [37]. Conflicting results were reported for vastus lateralis fascicle angle, with increases observed following eccentric training only [11], or concentric training only [37]. The patellar tendon cross-sectional area can increase with eccentric training, while the addition of whey protein hydrolysate supplementation appears necessary to promote increases with concentric training [72]. Patellar tendon Young's modulus at 50–75 % MVC has been demonstrated to increase with both eccentric and concentric training, but only with eccentric training at 75–100 % MVC [26]. Maximal tendon force and stress also increased with eccentric, but not concentric, training. Furthermore, a particularly marked increase was observed with heavier eccentric loading [26].

Table 2 Studies comparing the effects of eccentric-overload and coupled maximal eccentric and concentric contractions with traditional and concentric-only resistance training on muscle tendon unit morphology and architecture

Study	Population	Muscle groups (modality)	Intervention	Training duration	Training effect ($p < 0.05$)
Blazevich et al. [11]	ECC $n = 11$, CONC $n = 10$, CONT $n = 9$ (16F, 14 M); mean age: 22.8 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 5 sets of 6 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 30°/s	10 weeks (3 sessions per week)	Increase in quadriceps CSA (cm^3) with ECC and CONC (average change: 10 %), no change with CONT (NR), no difference between conditions Increase in quadriceps fascicle length (mm) with ECC (3 %) and CONC (6 %), no change with CONT (NR), no difference between conditions Increase in vastuslateralis fascicle angle (°) with ECC (21 %), no change with CONC (13 %) or CONT (NR), no difference between interventions
Colliander and Tesch [13]	ECC + CONC $n = 11$, CONC $n = 11$, CONT $n = 7$ (29 M); mean age: 26.3 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 4.8 sets of 12 repetitions; intensity: ECC + CONC group: ECC and CONC MVC, CONC group: CONC MVC; tempo: 60°/s	12 weeks (3 sessions per week)	Increase in thigh CSA (mm) with ECC + CONC (1 %) and CONC (1 %), no change with CONT (0.2 %), no difference between interventions Decrease in quadriceps type IIx area (µm^2) with CONC (−30 %), no change with ECC + CONC (−34 %) or CONT (−33 %), no difference between interventions Decrease in quadriceps type IIx fibre composition (%) with CONC (−43 %), no change with ECC + CONC (−49 %) or CONT (−75 %), no difference between interventions
English [16]	ECC_{138} $n = 8$, ECC_{100} $n = 8$, CONC_{66} $n = 8$, CONC_{33} $n = 8$, CONC $n = 8$ (40 M); mean age: 34.9 years; training status: untrained	HE, KE and AE (isokinetic leg press; multi-joint)	Volume: 3.75 sets of 5 repetitions; intensity: ECC_{138} group: 138/76 % 1RM, ECC_{100} group: 100/76 % 1RM, CONC_{66} group: 66/76 % 1RM, CONC_{33}: 33/76 % 1RM, CONC: 0/76 % 1RM; tempo: NR	8 weeks (3 sessions per week)	Increase in leg CSA (kg) with ECC_{138} (2.4 %), no change with ECC_{100} (1.5 %), CONC_{66} (2.2 %), CONC_{33} (1.5 %) or CONC (−1.5 %), no difference between conditions
Farthing and Chilibeck [17]	ECC_{Fast}, $\text{CONC}_{\text{Fast}}$ $n = 13$ (9F, 4 M) ECC_{Slow}, $\text{CONC}_{\text{Slow}}$ $n = 11$ (4F, 7 M), CONT $n = 10$ (8F, 2 M); mean age: 22.2 years; training status: untrained	EF (isokinetic; single-joint)	Volume: 4.6 sets of 8 repetitions; intensity: ECC groups: ECC MVC, CONC groups: CONC MVC; tempo: Fast groups: 180°/s, Slow groups: 30°/s	8 weeks (3 sessions per week)	Increase in biceps CSA (mm) with ECC_{Fast} (13 %), $\text{CONC}_{\text{Fast}}$ (3 %), ECC_{Slow} (8 %), $\text{CONC}_{\text{Slow}}$ (5 %), no change with CONT (−1 %), greater increase with ECC_{Fast} vs. $\text{CONC}_{\text{Fast}}$, $\text{CONC}_{\text{Slow}}$ and CONT
Farup et al. [18]	ECC_{Whey} and ECC $n = 11$, $\text{CONC}_{\text{Whey}}$ and CONC $n = 11$, within-subject design (22 M); mean age: 23.9 years; training status: untrained	KE (isoinertial; single-joint)	Volume: 9.3 sets of 10.7 repetitions; intensity: ECC groups: 90/75 % 1RM, CONC groups: 75 % 1RM; tempo: ECC: 2 s, CONC: 2 s	12 weeks (2.75 sessions per week)	Increase in quadriceps type I fibre CSA (µm^2) withECC_{Whey} (14 %), ECC (16 %), $\text{CONC}_{\text{Whey}}$(22 %) and CONC (12 %), no difference between interventions Increase in quadriceps type II fibre CSA (µm^2) with $\text{CONC}_{\text{Whey}}$ (25 %), no change for ECC_{Whey} (1 %), ECC (11 %) or CONC (7 %), greater increase with $\text{CONC}_{\text{Whey}}$ vs. ECC_{Whey} and CONC

Table 2 continued

Study	Population	Muscle groups (modality)	Intervention	Training duration	Training effect ($p < 0.05$)
Farup et al. [72]	ECC$_{Whey}$and ECCn = 11, CONC$_{Whey}$ and CONC n = 11, within-subject design (22 M); mean age: 23.9 years; training status: untrained	KE (isoinertial; single-joint)	Volume: 9.3 sets of 10.7 repetitions; intensity: ECC groups: 90/75 % 1RM, CONC groups: 75 % 1RM; tempo: ECC: 2 s, CONC: 2 s	12 weeks (2.75 sessions per week)	Increase in quadriceps CSA (cm^2) with ECC$_{Whey}$ (6 %), ECC (2 %), CONC$_{Whey}$(5 %) and CONC (3 %), no difference between interventions Increase in patellar tendon CSA (cm^2) with ECC$_{Whey}$ (15 %), ECC (10 %) and CONC$_{Whey}$(15 %), no change with CONC (7 %), no difference between interventions
Franchi et al. [37]	ECC n = 6, CONC n = 6 (12 M); mean age: 25.0 years; training status: untrained	HE and KE (isokinetic; multi-joint)	Volume: 4 sets of 9 repetitions; intensity: ECC group: 80 % ECC 1RM, CONC group: 80 % CONC 1RM; tempo: ECC group: 3 s, CONC group: 2 s	10 weeks (3 sessions per week)	Increase in quadriceps CSA (cm^3) with ECC (6 %) and CONC (8 %), no difference between interventions
					Increase in quadriceps fascicle length (cm) with ECC (12 %) and CONC (5 %), greater increase with ECC vs. CONC Increase in vastuslateralis fascicle angle (°) with CONC (30 %), no change with ECC (5 %), greater increase with CONC vs. ECC
Friedmann-Bette et al. [19]	ECC n = 14, TRAD n = 11 (25 M); mean age: 24.4 years; training status: strength trained	KE (isoinertial; single-joint)	Volume: ECC group: 5 sets of 8 repetitions, TRAD group: 6 sets of 8 repetitions; intensity: ECC: 152/80 % 1RM, TRAD: 80 % 1RM; tempo: NR; explosive ECC and CONC	6 weeks (3 sessions per week)	Increase in quadriceps CSA (cm^2) with ECC (6 %) and TRAD (8 %), no difference between interventions Increase in quadriceps type IIx fibre CSA (μm^2) with ECC (20 %), no change with TRAD (10 %), no difference between interventions
Godard et al. [20]	ECC n = 9, TRAD n = 9, CONT n = 10 (12F, 16 M); mean age: 22.4 years; training status: recreationally active	KE (isokinetic; single-joint)	Volume: 1 set of 10 repetitions; intensity: ECC group: 120/80 % 1RM, TRAD group: 80 % 1RM; tempo: 30°/s	10 weeks (2 sessions per week)	Increase in thigh CSA (mm) with ECC (5 %) and TRAD (6 %) vs. CONT (1 %), no difference between interventions
Gross et al. [34]	ECC n = 8, TRAD n = 7 (15 M); mean age: 17.6 years; training status: junior national skiers	HE and KE (isokinetic and isoinertial; multi-joint)	Volume: ECC group: 12 sets of 30 repetitions weight training and 20 min ECC cycling, TRAD group: 22.5 sets of 30 repetitions; intensity: ECC group: 40 % 1RM weight training and 532 W ECC cycling, TRAD group: 40 % 1RM; tempo: ECC cycling: 70 rpm, weight training: NR	6 weeks (3 sessions per week)	Increase in leg lean mass (g) with ECC (2 %), no change with TRAD (NR), no difference between interventions
Hawkins et al. [21]	ECC n = 8, CONC n = 8 (within-subject design), CONT n = 12 (20F); mean age: 21.4 years; training status: untrained	KF and KE (isokinetic; single-joint)	Volume: ECC group: 3 sets of 3 repetitions, CONC group: 3 sets of 4 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: NR	18 weeks (3 sessions per week)	Increase in leg lean mass (g) with ECC (4 %), no change with CONC (2 %) or CONT (1 %), no difference between interventions

Table 2 continued

Study	Population	Muscle groups (modality)	Intervention	Training duration	Training effect ($p < 0.05$)
Higbie et al. 1996 [39]	ECC $n = 19$, CONC $n = 16$, CONT $n = 19$ (54F); mean age: 20.5 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 3 sets of 10 repetitions; intensity; ECC group: ECC MVC, CONC group: CONC MVC; tempo: 60°/s	10 weeks (3 sessions per week)	Increase in quadriceps CSA (cm^2) with ECC (7 %) and CONC (5 %), no change with CONT (−1 %), greater increase with ECC vs. CONC
Hortobagyi et al. [22]	ECC $n = 7$, CONC $n = 8$, CONT $n = 6$ (21 M); mean age: 21.3 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 5.3 sets of 10 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 60°/s	12 weeks (3 sessions per week)	Increase in quadriceps type II fibre CSA (μm^2) with ECC (38 %), no change with CONC (3 %) or CONT (NR), greater increase with ECC vs. CONC
					Increase in quadriceps type IIa fibre composition (%) with ECC (31 %) and CONC (22 %), no change with CONT (NR), no difference between interventions
					Decrease in quadriceps type IIx fibre composition (%) with ECC (−48 %) and CONC (−60 %), no change with CONT (NR), no difference between interventions
Hortobagyi et al. [23]	ECC $n = 12$, ECC + CONC $n = 12$, CONC $n = 12$, CONT $n = 24$ (24F, 24 M); mean age: 22.0 years; training status: untrained	KE (isokinetic; single-joint)	Volume: 5.3 sets of 10 repetitions; intensity: ECC group: ECC MVC, ECC + CONC group: ECC and CONC MVC, CONC group: CONC MVC; tempo: 60°/s	12 weeks (3 sessions per week)	Increase in quadriceps type I fibre CSA (μm^2) with ECC (10 %), ECC + CONC (11 %) and CONC (4 %), no change with CONT (NR), no difference between interventions
					Increase in quadriceps type IIa fibre CSA (μm^2) with ECC (16 %), ECC + CONC (9 %) and CONC (5 %), no change with CONT (NR), greater increase with ECC and ECC + CONC vs. CONC
					Increase in quadriceps type IIx fibre CSA (μm^2) with ECC (16 %), ECC + CONC (10 %) and CONC (5 %), no change with CONT (NR), greater increase with ECC vs. ECC + CONC and CONC
LaStayo et al. [36]	ECC $n = 7$, CONC $n = 7$ (14 M); mean age: 23.9 years; training status: untrained	HE and KE (isokinetic cycling; multi-joint)	Volume: 27.5 min; intensity: 62 % maximum heart rate; tempo: 60 rpm	8 weeks (3.5 sessions per week)	Increase in quadriceps muscle fibre CSA (μm^2) with ECC (52 %), no change with CONC (11 %), no difference between interventions
Malliaras et al. [26]	$\mathrm{ECC}_{\mathrm{Heavy}} n = 10$, $\mathrm{ECC}_{\mathrm{Light}} n = 10$, CONC $n = 9$, CONT $n = 9$ (38 M); mean age: 27.5 years; training status: untrained	KE (isoinertial; single-joint)	Volume: $\mathrm{ECC}_{\mathrm{Heavy}}$ and CONC groups: 4 sets of 7.5 repetitions, $\mathrm{ECC}_{\mathrm{Light}}$ group: 4 sets of 13.5 repetitions; intensity: $\mathrm{ECC}_{\mathrm{Heavy}}$ group: 80 % ECC 1RM, $\mathrm{ECC}_{\mathrm{Light}}$ and CONC groups: 80 % CONC 1RM; tempo: ECC: 5 s, CONC: 1 s	12 weeks (3 sessions per week)	Increase in patellar tendon Young's modulus (MPa; 50–75 %) with $\mathrm{ECC}_{\mathrm{Heavy}}$(87 %), $\mathrm{ECC}_{\mathrm{Light}}$ (59 %) and CONC (81 %) vs. CONT (−3 %), no difference between interventions
					Increase in patellar tendon Young's modulus (MPa; 75–100 %) with $\mathrm{ECC}_{\mathrm{Heavy}}$ (84 %) vs. CONT (3 %), no change with $\mathrm{ECC}_{\mathrm{Light}}$ (59 %) or CONC (71 %), no difference between interventions
					Increase in tendon force (N) with $\mathrm{ECC}_{\mathrm{Heavy}}$ (31 %) and $\mathrm{ECC}_{\mathrm{Light}}$ (16 %), no change with CONC (18 %) or CONT (4 %), $\mathrm{ECC}_{\mathrm{Heavy}}$ greater than CONT, no difference between interventions
					Increase in tendon stress (%) with $\mathrm{ECC}_{\mathrm{Heavy}}$ (24 %), no change with $\mathrm{ECC}_{\mathrm{Light}}$(13 %), CONC (14 %) or CONT (2 %), no difference between interventions

Table 2 continued

Study	Population	Muscle groups (modality)	Intervention	Training duration	Training effect ($p < 0.05$)
Moore et al. [29]	ECC and CONC $n = 9$, within-subject design (9 M); mean age: 22.0 years; training status: untrained	EF (isokinetic; single-joint)	Volume: ECC group 4.44 sets of 10 repetitions, CONC group: 4.44 sets of 14 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 45°/s	9 weeks (2 sessions per week)	Increase in biceps CSA (nm^2) with ECC (7 %) and CONC (5 %), no difference between interventions
Nickols-Richardson et al. [30]	ECC $n = 33$, CONC $n = 37$ (70F); mean age: 35.0 years; training status: untrained	KF,KE, EF and EE (isokinetic; single-joint)	Volume: 4.5 sets of 6 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 60°/s	20 weeks (3 sessions per week)	Increase in lean body mass (kg) with ECC (2 %) and CONC (2 %), no difference between interventions
Rahbek et al. [73]	$ECC_{Whey}$and ECC$n = 12$, $CONC_{Whey}$ and CONC $n = 12$, within-subject design (24 M); mean age: 23.9 years; training status: untrained	KE (isoinertial; single-joint)	Volume: 9.3 sets of 10.7 repetitions; intensity: ECC groups: 90/75 % 1RM, CONC groups: 75 % 1RM; tempo: ECC: 2 s, CONC: 2 s	12 weeks (2.75 sessions per week)	Increase in quadriceps CSA (cm^2) with ECC_{Whey} (8 %), ECC (3 %), $CONC_{Whey}$ (6 %) and CONC (4 %), greater increase with ECC_{Whey} and $CONC_{Whey}$ vs. ECC and CONC
Seger et al. [40]	ECC $n = 5$, CONC $n = 5$ (10 M); mean age: 24.5 years; training status: moderately trained	KE (isokinetic; single-joint)	Volume: 4 sets of 10 repetitions; intensity: ECC group: ECC MVC, CONC group: CONC MVC; tempo: 90°/s	10 weeks (3 sessions per week)	Increase in quadriceps CSA (cm^2) with ECC (4 %), no change with CONC (3 %), no difference between interventions
Vikne et al. [31]	ECC $n = 9$, CONC $n = 8$ (17 M); mean age: 27.1 years; training status: resistance trained	EF (isoinertial; single-joint)	Volume: 3.9 sets of 6 repetitions; intensity: ECC group: 94 % ECC 1RM, CONC group: 94 % CONC 1RM; tempo: ECC: 3.5 s, CONC: explosive	12 weeks (2.5 sessions per week)	Increase in biceps CSA (cm^2) with ECC (11 %), no change with CONC (3 %), greater increase with ECC vs. CONC Decrease in biceps type I fibre CSA (μm^2) with ECC (−9 %), no change with CONC (−1 %), no difference between interventions Increase in biceps type II fibre CSA (μm^2) with ECC (9 %), no change with CONC (1 %), no difference between interventions Decrease in biceps type IIx fibre composition (%) with CONC (−3 %), no change with ECC (1 %), no difference between interventions

°/s degrees per second, *µm* micrometre, *cm* centimetres, *CONC* concentric, *CONT* control, *CSA* cross-sectional area, *ECC* eccentric, *ECC + CONC* coupled maximal eccentric and concentric contractions, *F* females, *kg* kilograms, *M* males, *mm* millimetres, *MPa* megapascal, *ms* milliseconds, *MVC* maximum voluntary contraction, *n* number of subjects, *N* newtons, $N{\cdot}s^{-1}$ newtons per second, *NR* not reported, *RM* repetition maximum, *rpm* revolutions per minute, *s* seconds, *TRAD* traditional resistance training, *W* watts

3.3.1 *Muscle Cross-Sectional Area (CSA) and Architecture*

Increased muscle CSA is generally expected following a resistance training intervention of sufficient duration, and is directly related to an increase in workload and tension development [17]. The number of muscle fibres does not appear to increase during postnatal growth or as a result of training in humans [74]; however, the CSA of existing fibres increases considerably (i.e. via increased myofibril content) in response to mechanical loading [74]. Muscle hypertrophy with heavy resistance training is a product of increased protein translation, upregulation of genes involved in anabolic mechanisms, and satellite cell activation/proliferation [19, 74]. The conversion of a mechanical signal (i.e. generated during contraction) to a molecular event involves the upregulation of primary and secondary messengers within a signalling cascade to activate and/or repress pathways that regulate gene expression and protein synthesis/degradation [75]. Proteins are constantly being synthesized and broken down, even in adult muscle, therefore protein accumulation results from an increased rate of proteins being synthesized and a decreased rate of protein degradation [74]. Three factors are believed to mediate the hypertrophic signalling response to training; mechanical tension, muscle damage (i.e. exercise induced muscle damage [EIMD]) and metabolic stress [76]. The apparent superiority of eccentric training [8], or at least the inclusion of eccentric contractions (i.e. traditional training), may therefore be due to higher levels of both mechanical tension and EIMD than concentric training [77]. High levels of tension induce a mechanochemical signal to upregulate anabolic molecular and cellular activity within myofibres and satellite cells; the combined effects of active tension from contractile elements and passive tension (i.e. stretch-induced strain) from collagen content within the extracellular matrix and titin are believed to induce a more potent signal for protein synthesis [78]. Indeed, stretch-induced strain from eccentric contractions, sensed within the Z-line region of titin [79], appears to elicit a specific anabolic signalling response [75, 80]. Chronic stretch of muscle per se upregulates protein synthesis and increases the number of sarcomeres in series [74]. These observations may explain not only the increases in CSA but also the increases in fascicle length with eccentric training [11, 37, 81–85].

Franchi et al. [37] postulated that increased distal muscle hypertrophy with eccentric training reflects an increased CSA via sarcomeres in series in contrast to the addition of sarcomeres in parallel with concentric training. This mechanism would also explain the increased fascicle angle with concentric training [37], although increases in fascicle angle have also been reported following eccentric training [11, 71, 84, 85], and it is likely that these adaptations can occur in concert to varying degrees. It is not entirely clear which mechanisms instigate the hypertrophic response in the presence of EIMD, and increases in muscle size can still occur in the absence of muscle damage [86]. Nonetheless, it is posited as an additive factor with eccentric training. The acute inflammatory response associated with eccentric contractions and EIMD is believed to induce a release of growth factors that regulate satellite cell activation/proliferation and anabolic signalling [76]. Increased cytokine activity (i.e. monocyte chemotactic protein-1 [MCP-1] and interferon gamma-induced protein 10 [IP-10]) has been reported following eccentric, but not concentric, exercise [87]. IP-10 within skeletal muscle is postulated to recruit T lymphocytes [87, 88], and T-cell infiltration has been found to enhance satellite cell activation and muscle regeneration in mice [89]. Both heavier eccentric loading and fast eccentric contractions involve high levels of tension generation per active motor unit [90, 91], and influence the magnitude of EIMD [92, 93], which may explain the enhanced hypertrophic response when these two variables are emphasized [16, 17, 94]. A greater resistance to fatigue has been observed across a series of maximal contractions [95], and it is probable that metabolic stress will be lower during eccentric versus concentric training [96]. Interestingly, the utilization of extended-duration eccentric cycling (i.e. 20–30 min) of a relatively low contraction intensity per repetition has been demonstrated to lead to increases in muscle CSA [34, 36]. It is possible that under these conditions there is a progressive recruitment and fatigue of higher threshold motor units, which in turn can instigate a marked hypertrophic response independent of high levels of mechanical tension [97]. Therefore, the inclusion of concentric contractions (i.e. traditional resistance training), eccentric contractions to fatigue, or a combination of eccentric loading and blood-flow restriction [98], may be warranted if maximal hypertrophy is the objective.

3.3.2 *Muscle Fibre Size and Composition*

Greater hypertrophy in type II muscle fibres compared with type I muscle fibres is not uncommon with resistance training [99]. Fast contracting fibres are recruited infrequently and their selective hypertrophy is proposed to be an adaptive response to aid power development during periods of near-maximal recruitment [74]. A greater increase in type II fibre area when comparing eccentric with concentric training may reflect the overall greater increase in muscle CSA. It has been further suggested that increased recruitment, tension-generating capacity and predisposition to damage of fast-twitch fibres [81] contribute to the propensity for type IIa [22, 94] and IIx [19, 94] fibre hypertrophy with eccentric training. Eccentric training appears to exert a unique influence on the MHC phenotype shift with either improved maintenance of [13, 31, 100] or increase in [101] IIx fibre composition following training. A shift in fibre type composition (i.e. MHC isoform), particularly a shift from MHC IIx to IIa is commonly reported following resistance training [22, 31, 102], which can be subsequently reversed, or overshoot above pre-existing levels, with detraining [103]. Increased muscle activity via either endurance or traditional resistance exercise appears to switch off the IIx gene in IIx fibres, thus increasing the proportion of IIa fibres at the expense of IIx fibres [102]. It is proposed that both the total number of contractions (i.e. nerve impulses) and maximal tensile load exerted on muscle mediate the MHC shift [102]. The MHC IIx reduction and subsequent overshoot phenomena are not well understood, but it has been postulated that IIx is the 'default' MHC gene [102, 104], and training appears to induce a shift towards a more fatigue-resistant phenotype [103]. Multiple lines of evidence are suggestive of a specific response with eccentric contractions. Friedmann-Bette and colleagues found an increase in IIa in situ hybridizations, or fibres expressing elevated levels of IIx messenger RNA (mRNA), which were postulated to be in transition [19], and a tendency towards an increase in IIx mRNA has also been reported following a submaximal eccentric training protocol [105]. While changes in fibre type and MHC mRNA do not always occur in parallel, long-term steady state levels of mRNA are reasonably well correlated with muscle fibre composition [105]. Furthermore, a 10-week, fast (i.e. 180°/s) isokinetic eccentric training intervention of the elbow flexors was demonstrated to increase type IIx composition by 7 % [101]. These chronic findings align with observations of acute satellite cell [106] and anabolic signalling pathway upregulation [107] in type II fibres following eccentric exercise, and support the proposition of a shift towards a faster phenotype with eccentric training [6].

3.3.3 *Tendon CSA and Qualitative Properties*

Historically, tendon tissue was considered inert, relatively non-vascular and inelastic. However, recent research has highlighted the dynamic nature of the extracellular matrix, and thus adaptive capacity in response to mechanical load [108]. Changes in tendon structure and function appear to be partly mediated by contraction type [26]. Unfortunately, few studies have compared the effects of eccentric training with other resistance training modalities on tendon adaptation. Eccentric loading has gained widespread implementation within the rehabilitation setting as a tool to manage lower limb tendinopathy and improve tendon structure [108, 109]. However, the mechanisms underpinning the improvements with eccentric loading are not well understood [26]. Chronic loading has been demonstrated to increase tendon stiffness, and possibly CSA, and it seems maximizing tendon strain may be necessary in optimizing the adaptive response [26, 85, 110]. In one investigation comparing heavy eccentric, light eccentric and concentric training, only heavy eccentric loading elicited improvements in patellar tendon Young's modulus (75–100 % MVC) and strain (%) without concomitant increases in tendon CSA [26], aligning with a previous report of heavy eccentric training inducing a reduction in elbow flexor series elastic component compliance [111]. In contrast to these findings, a decrease [112], or no change [108], in Achilles tendon stiffness has been reported following the implementation of a popular submaximal eccentric heel drop protocol [113]. These observations may be related to the contraction intensity, and thus provide further support for the importance of load for increasing tendon stiffness. Changes in tendon stiffness in the absence of increases in CSA may be due to increased collagen packing density, alterations in crimp angle, or increased water content [26, 114]. As the tendon is metabolically active [112, 114], adaptation may be driven by changes in rates of protein synthesis and degradation similar to muscle tissue in a coordinated musculo-tendinous response [115]. The cellular tensegrity model proposes that cells (i.e. myofibres and fibroblasts) can respond, in a coordinated fashion, to mechanical stress via integrins located in the plasma membrane and proteins connecting the extracellular matrix to the cytoskeleton, which stimulates functional remodelling of the MTU [115]. The magnitude of mechanical stress may augment the signalling response and thus explain the greater adaptation with heavy versus light eccentric training [26]. The finding that eccentric training can increase tendon CSA [72] is of interest as other acute interventions seem to be less effective at eliciting quantitative changes in tendon tissue. Plyometric training [116] and traditional resistance training [117] have been found to increase Achilles tendon stiffness, but not CSA. Long-term endurance training is associated with increased Achilles tendon CSA [118], which suggests that long-term chronic loading may be necessary to elicit quantitative changes in tendon with submaximal loads. It appears that heavy eccentric training can induce both qualitative and quantitative changes in tendon, although more research is necessary to clarify the optimal loading conditions.

3.3.4 *Summary of Eccentric Training Effects on Muscle-Tendon Unit Morphology and Architecture*

Eccentric training appears to elicit greater increases in muscle CSA than concentric or traditional resistance training.The combination of heavier absolute loads and a smaller number of recruited motor units during eccentric training [52] involves high levels of mechanical tension per motor unit [91] and a greater propensity for EIMD [119]. These factors, combined with stretch-induced strain [78], may stimulate the hypertrophic signalling response to a greater extent than concentric or traditional resistance training [76]. Heavy eccentric loads and fast contraction velocities both appear to further stimulate the adaptive response [16, 17, 94, 101]. The pattern of increased muscle CSA appears to be mediated by contraction type, and eccentric training may promote the addition of sarcomeres in series, as inferred from changes in muscle fascicle length [11, 37]. Selective increases in fast-twitch fibre size have been reported and there is evidence to suggest that a shift towards a fast phenotype can occur as a result of chronic eccentric training [6]. The predisposition for fast-twitch fibre hypertrophy probably results from an increased recruitment with heavy loads, the tension generating capacity and subsequent damage of these fibres [19, 22]. While further research is required, it is possible an upregulation of IIx mRNA signalling can occur with eccentric training [19, 105], leading to an attenuated IIx to IIa shift [13, 31, 100], or an increase in IIx composition with fast contractions [101]. Eccentric training may promote increases in tendon stiffness [26] and CSA [72], which influence the storage and return of elastic strain energy and probably contribute to the observed enhancements in SSC performance. The MTU morphological and architectural adaptations, in conjunction with changes in muscle mechanical function (Sect. 3.2), have important implications for strength, power and speed performance; however, more research is necessary to determine how these findings translate to trained athletes.

4 Conclusions

Eccentric training using external loads greater than the relative concentric training intensity is a potent stimulus for enhancements in muscle mechanical function, and MTU morphological and architectural adaptations. The inclusion of eccentric loads above maximal concentric strength is therefore an avenue to induce novel training stimuli and effect change in key determinants, and functional metrics, of strength, power and speed performance. Strength improvements are largely mode-specific and arise from a combination of neural, morphological and architectural adaptations [8]. Increased agonist volitional drive is posited as the primary contributing factor to the marked increases in eccentric strength observed following training [54]. Eccentric training improves concentric muscle power and SSC performance to a greater extent than concentric or traditional modalities [13, 34, 46, 47]. Reports on changes in RFD have been mixed [27, 33], although limited research in this area has been undertaken. Improvements in muscle power and SSC performance are likely related to improvements in total strength, an improved ability to rapidly recruit fast motor units, qualitative changes to tendon tissue, and an enhanced eccentric phase within the SSC [3]. Eccentric training can elicit greater increases in muscle CSA than concentric or traditional resistance training. High levels of mechanical tension per active motor unit [91], stretch-induced strain [78], and a greater propensity for EIMD [119] with eccentric training may stimulate anabolic signalling to a greater extent than concentric or traditional resistance training [76]. The nature of hypertrophy appears to differ with eccentric training versus concentric training, and the addition of sarcomeres in series, as inferred from changes in muscle fascicle length, may contribute to increases in CSA [11, 37]. A greater number of sarcomeres in series may subsequently increase muscle shortening velocity and increase force production at longer muscle lengths [6]. Fast-twitch fibres hypertrophy to a greater extent as a consequence of eccentric training [19, 22], and while further research is required, it is possible an upregulation of IIx mRNA signalling can occur [19, 105], leading to an attenuated IIx to IIa shift [13, 31, 100], or an increase in IIx composition with fast contractions [101]. An increased number of sarcomeres in series, selective fast-twitch fibre hypertrophy, and possibly increased IIx composition, have been collectively referred to as a shift towards a faster phenotype [6] and may contribute to improvements in speed and power performance with eccentric training. Furthermore, increases in tendon stiffness [26] and CSA [72] will aid the storage and return of elastic strain energy during SSC movements. Particular consideration should be given to contraction velocity; fast eccentric training appears to induce the largest improvements in strength, power and SSC performance [17, 47], and further stimulates increases in muscle CSA [17] and IIx fibre composition [101]. While fast contractions per se are probably an important stimulus, further research is necessary in elucidating the influence of a markedly lower time under tension with such protocols [94]. An acute eccentric training intervention in untrained participants seems to follow the typical adaptive pattern with resistance training. The largest increases in early-phase strength (i.e. 3–4 weeks) are underpinned by neural factors, while MTU morphological and architectural changes require a longer time to materialize [84]. As residual fatigue with eccentric exercise can suppress force production and affect neural control for a period of time following the cessation of training, an appropriate recovery window (i.e. up to 8 weeks) may be necessary to fully realize neuromuscular adaptations [71]. It is less clear how these findings translate to resistance-trained subjects as the majority of investigations have recruited untrained participants; it has been suggested that the pattern of adaptation may be similar, but of a lower magnitude [6]. The heterogeneity of protocols used makes it difficult to elucidate best practice in training volume and frequency. Presently, it would seem that the management of EIMD and delayed-onset muscle soreness should be a primary consideration. Further research is necessary to determine the optimal progression of load and contraction velocity, especially in resistance-trained subjects, for the MTU and performance outcomes.

Compliance with Ethical Standards

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