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The Influence of Eccentric Muscle Actions on Concentric Muscle Strength: An Exception to the Principle of Specificity?

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ABSTRACT

The principle of specificity suggests that the largest changes in strength occur when training resembles the specific strength test. A one-repetition maximum (1RM) test, which tests the maximal concentric strength, is commonly used as a surrogate for strength adaptation. When separating muscle actions into concentric or eccentric phases, multiple lines of evidence suggest that eccentric muscle actions possess several distinct physiological properties compared with concentric actions. In accordance, there are instances where the increases in 1RM strength test were similar between eccentric-only and concentric-only resistance training. This is at odds with the principle of specificity which suggests that individuals who trained with concentric actions would be expected to have an advantage in that specific task. Although the mechanistic reasons why eccentric-biased training carries over to maximal concentric strength remains to be elucidated, the lack of discernible differences in strength gains with eccentrically-biased training (e.g., eccentric-only and accentuated eccentric training) may imply that the effects of eccentric loading in training are transferable to concentric strength. Our review revisits the role of eccentric loading in enhancing concentric maximal muscle strength. We also speculate on potential physiological factors (i.e., molecular and neural factors) that may differentiate the effects of eccentric and concentric resistance training on the changes in muscle strength. Currently, the majority of the studies investigating the changes in strength have been conducted using isokinetic eccentric training. This is important as there is a viewpoint that the magnitude of chronic adaptations with different modalities of eccentric exercises (i.e., isotonic, isokinetic, and isoinertial training) may also differ from each other. While it has been suggested that eccentric action has a greater transferable capacity for strength adaptations compared to concentric actions, future investigations are warranted to investigate with different modalities of eccentric exercises. There also remains a host of unanswered questions related to the role of eccentric action for maximal concentric strength. For example, future studies may examine whether the eccentric action would be additive when the training is already maximally loaded during the concentric action for increasing concentric maximal strength. We suggested a few different designs that could be used to answer some of these questions in future studies.

INTRODUCTION

The principle of specificity in strength training suggests that the greatest change in strength is generally expected in the specific task that was trained [1, 2]. For example, it has been repeatedly observed that high-load resistance training (e.g., ≥70% one-repetition maximum; 1RM) induces greater changes in 1RM strength when compared with low-load training (e.g., ≤30% 1RM) [3-6]. However, some data suggest that the difference in 1RM strength changes between high-load and low-load training can largely be abolished if the low-load group is exposed to additional maximal strength tests [7, 8], reinforcing the concept of specificity (i.e., strength testing itself may provide a training stimulus for adaptation) [8]. Another example of specificity is that a greater change in specific strength is expected within the type of muscle action trained where strength is assessed in a manner that the group is accustomed to. This was illustrated by the observations that 4 sets of dynamic exercise using an 8 – 12RM led to robust changes in concentric 1RM strength, without any detectable changes in isokinetic strength (i.e., non-specific strength) [9]. Additional support was published in a recent meta-analysis, which quantified the effects of isotonic strength training on specific (isotonic) and non-specific (isokinetic/isometric) strength relative to a non-exercise control group [2]. It was reported that strength training increased both the specific and non-specific strength, yet the smaller effect on non-specific strength demonstrates that specificity is a primary determinant of strength adaptations [2].

According to the principle of specificity, participants trained with concentric actions should be expected to have an advantage in a concentric 1RM test compared to eccentric-only training [1]. However, there are some instances where the increases in maximal concentric strength, a 1RM test, were similar between eccentric-only and concentric-only resistance training [10, 11]. The lack of discernible differences in strength gain in these studies may imply that adaptive signals within the neuromuscular system may cause eccentric loading in training to be transferable to concentric strength. When separating muscle actions into concentric or eccentric phases, multiple lines of evidence suggest that eccentric muscle actions possess several distinct physiological properties compared with concentric actions [12-15]. Previous work has also shown that training exclusively with eccentric loading as opposed to concentric loading may elicit greater increases in concentric, eccentric, and isometric muscular strength gains [16, 17]. Thus, although the generality of strength adaptation (i.e., the change in strength on a task that was not trained) often follows a predictable pattern where increases in strength diminish as the strength test becomes farther from the actual training stimulus [18], this does not always seem to hold true for eccentric muscle actions. In this context, the principle of specificity may require additional refinement. The present review explores the role of eccentric loading in enhancing maximal concentric muscle strength. In addition, we provide some speculation on potential physiological factors that may differentiate the effects of eccentric and concentric resistance training on the changes in maximal muscle strength, as well as suggestions for future research. Here, we mainly focus on literature demonstrating the benefits of eccentric loading on the changes in 1RM strength, a commonly used surrogate for strength adaptation.

REVISITING THE PRINCIPLE OF SPECIFICITY

Specificity of muscle action type

In alignment with the principle of specificity, one of the early works by Komi and Buskirk [19] highlighted that eccentric-only training led to significantly greater increases in eccentric strength compared to the concentric-only training and control groups. This study also observed that both eccentric-only and concentric-only training groups increased concentric strength over the control group; however, the increase was not significantly different between the eccentric-only and concentric-only training groups following seven weeks of training [19]. The authors concluded that eccentric actions had a greater capacity to increase muscle strength than concentric actions [19]. Since then, many researchers have investigated the use of eccentrically-biased exercise (e.g., eccentric-only or training that employs eccentric overload, also known as accentuated eccentric loading), with an emphasis on leveraging the greater force-generating capacity of eccentric actions [16, 17, 20, 21]. For example, studies that have utilized accentuated eccentric loading resulted in greater strength gains than traditional concentric-eccentric resistance training (i.e., 1:1 concentric: eccentric load ratio) in some movements [22, 23]. In other studies, eccentric-only training was similarly effective for increasing maximal concentric strength as concentric-only [10, 11, 24] and traditional training (i.e., concentric and eccentric) [10, 24].

Observations that a similar or greater increase in maximal concentric strength with eccentrically-biased resistance training is of particular interest from the principle of specificity standpoint. Many resistance training studies include concentric

1RM as a surrogate for strength adaptation [2]. However, the absence of differences in changes in maximal concentric strength between eccentric-only and concentric-only training [10, 11, 24], as well as between traditional resistance training [10, 24], implies that the effects of the eccentric loading in training may carry over to maximal concentric strength. Future studies may quantitatively investigate how much transfer occurs from eccentric resistance training to concentric 1RM strength compared to a control group.

Specificity of load

Maximal strength adaptation largely depends upon exposure to high loads (i.e., % 1RM) [8, 25]. For example, training with 3 – 5 repetitions at 90 % 1RM resulted in superior 1RM strength gains in some testing movements (i.e., 1RM strength in the bench press but not in the squat) compared to training with 10 – 12 repetitions at 70 % 1RM [26], whereas others found no differences in strength gains between 1RM training (i.e., performing up to five heavy single repetitions per session) and training with an 8 – 12RM with the bicep curl exercise [9, 27, 28]. The load threshold necessary to maximize strength gains may be at least partially dependent on the complexity of the skill such that complex movements may benefit from more exposure to heavier loads close to the 1RM in order to maximize strength adaptations compared to simpler movements [7, 18]. Nonetheless, without incorporating some exposure to lifting heavy loads, low-load training alone (e.g., 15% maximal strength) may not always be sufficient to increase maximal strength compared to baseline [4, 5, 29, 30].

It has been speculated that the greater force-generating capacity of the eccentric action may provide a unique stimulus to elicit neuromuscular adaptations and improve strength [16, 17, 21]. When a study compared a training group using 75% of concentric 1RM for both concentric and eccentric actions with an eccentric overload group using 75% of concentric 1RM for concentric and 110 – 120% of concentric 1RM for eccentric actions, it was found that the eccentric overload group induced a greater increase in concentric 1RM strength than a group using lower eccentric loading, albeit not in all tested exercises [22]. In contrast, Tøien et al. [31] reported that eccentric overload (i.e., 150 % of concentric 1RM) did not further improve 1RM strength when compared to a training program that employed a high-load protocol using 90 % of concentric 1RM for both concentric and eccentric actions. Authors concluded that adding greater overload in the eccentric phase may not always induce greater neuromuscular adaptations than what can already be achieved in the concentric phase with a high-load [31]. The relative intensity at which the eccentric overload is not additive for concentric maximal strength is currently unknown and requires additional research, but it may be affected by a factor such as the complexity of movement [18]. However, it is important to note that the relative importance of each action phase (i.e., concentric or eccentric action) cannot be assessed from the study by Tøien et al. [31]. When concentric actions are coupled with eccentric actions, the examination of each muscle action type might be constrained by the muscle contractile properties during its eccentric portion, influencing the subsequent contractile function of its concentric action (e.g., the enhancement of force output due to residual force enhancement and stretch-shortening cycle) [32]. Thus, it is unknown what strength adaptations would look like when compared with a group that only performs concentric-only or eccentric-only actions. Nonetheless, this argument would also be extended to many previous eccentric overloading studies [21], and future experiments may further consider examining the effect of the accentuated eccentric loading-only condition on the changes in maximal concentric strength.

When investigating the action type in isolation, incorporating eccentric actions with concentric actions led to a greater increase in concentric strength than concentric-only training, suggesting that eccentric action was additive for strength adaptations [33-35]. For instance, Dudley et al. demonstrated that the increase in 3RM leg press strength was significantly greater for the group performing concentric and eccentric actions (4 – 5 sets of 6 – 12 repetitions) than for the concentric action-only group (8 – 10 sets of 6 – 12 repetitions) [34]. A notable finding was that although the concentric-only group performed double the number of concentric actions than the concentric and eccentric group, this did not lead to a greater increase in 3RM strength. Moreover, a similar increase in bench press estimated 1RM strength was achieved by eccentric-only training with an overloading method (i.e., 5 sets x 6 repetitions at 120 % 1RM) compared with concentric-only (i.e., 6 sets x 7 repetitions at 85% 1RM) and concentric-eccentric (i.e., 4 sets x 5 repetitions at 90 % 1RM) training groups [36]. In this case, the eccentric-only training did not perform concentric actions throughout the training intervention and was more "naïve" to the testing action type. However, a similar increase in estimated 1RM strength was observed between the eccentric-only training and the groups that were repeatedly exposed to concentric actions [36].

The role of eccentric loading in enhancing muscle strength has also been tested by prescribing the same external loads, sets, and repetitions in both eccentric-only and concentric-only training [11, 24, 37, 38]. In this instance, the eccentric-only group could theoretically train at a lower relative intensity (i.e., % maximal eccentric strength) due to inherent differences in force-generating capacity between the two muscle action types [39, 40]. This is the primary reason why the accentuated eccentric loading method is theorized to be beneficial for strength adaptations [21]. Vikne et al. [11] reported that prescribing the training load proportional to the maximal strength of the respective muscle actions resulted in a similar increase in concentric 1RM strength with eccentric-only and concentric-only training (i.e., the same relative load but the prescribed load is greater for eccentric action). Nonetheless, there is evidence to suggest that sub-optimally loaded eccentric training (i.e., a lower relative intensity relative to concentric training) can still induce similar maximal concentric strength adaptations compared with concentric training. For example, Sato et al. [24] demonstrated that using equivalent external loads, sets, and repetitions resulted in similar increases in concentric strength following eccentric-only, concentric-only, or concentric-eccentric resistance training. In that study, the participants in the training groups performed 3 sets of 10 repetitions of dumbbell preacher curl on the dominant arm twice a week for five weeks. As stated above, it would be expected that the eccentric-only group trained at a lower relative percentage of maximal eccentric strength. Despite these differences, the eccentric-only group increased all strength assessments (i.e., concentric, eccentric, and isometric strength) comparable to the groups using concentric actions (i.e., concentric and concentric-eccentric groups). In comparison, the concentric-only group increased concentric strength without any changes in eccentric strength. These findings suggest that "sub-optimally" loaded eccentric training may confer beneficial effects on maximal concentric strength. However, "sub-optimally" loaded concentric training may not provide beneficial effects on eccentric strength adaptations.

Furthermore, a series of studies illustrated that moderate load resistance training (i.e., 3 – 4 sets of 8 – 12RM) for three sessions a week resulted in similar improvements in 1RM strength compared with a training group performing up to five single repetitions per session [9, 28, 41]. Considering the observation that moderate load resistance training with concentric and eccentric actions elicited similar increases in concentric 1RM strength as the 1RM training group, it is tempting to assert the potential roles of eccentric loading in an individual's propensity for strength adaptations. While this may simply be that the training load of 8 – 12RM in these studies was sufficiently loaded enough to induce neuromuscular adaptations similar to the 1RM training group, the importance of incorporating eccentric loading for maximal strength improvement was noted in previous literature when compared with concentric-only training [33-35]. Thus, it is possible that eccentric actions made up for the moderate loading to induce similar strength gains as the 1RM training group. Future studies should examine the role of the eccentric action for concentric 1RM strength when the training protocol is maximally loaded during the concentric action. This would allow us to examine whether the eccentric action can be further additive to the increase in maximal strength. One way to address this is to compare a 1RM training protocol with or without eccentric actions. Another concept to examine the effect of eccentric actions on concentric 1RM strength gains is to explore whether frequent exposure to high-load eccentric singles-only (e.g., relative to concentric 1RM or eccentric 1RM if possible) can achieve comparable "practice" effects to those identified in the training literature, where frequent exposure to the concentric 1RM test appears to largely eliminate the strength differences between high- and low-load resistance training protocol [8]. Likewise, it might be worth exploring how much eccentric actions play a role in improvements in 1RM strength with moderate loads. One way to test this is to use the aforementioned study protocols (i.e., sets of 8 – 12RM) [9, 27, 28, 41] with eccentric actions and compare changes in 1RM to the same 8 – 12RM protocol without eccentric actions. Given that the load threshold necessary to maximize strength may be partially dependent on the complexity of the movement [7, 18], future studies may also examine these designs with a number of different exercises (i.e., isolated vs. compound movement).

INSIGHT FROM ISOKINETIC TRAINING LITERATURE

So far, the information regarding adaptations in maximal strength with eccentric actions has mainly focused on the isotonic resistance training literature. However, compared with isotonic eccentric training, most studies investigating the changes in strength have been conducted using isokinetic eccentric training [16, 17]. Thus, we believe that some of the unanswered questions related to the role of eccentric action for concentric 1RM strength could be addressed by the aforementioned proposed study designs. While our focus is to highlight literature demonstrating the benefits of eccentric loading on the changes in 1RM strength, isokinetic training literature has also provided insights into the role of eccentric action on changes in maximal concentric strength. Isokinetic actions involve contracting against a lever arm moving at a constant velocity, and each repetition can be performed maximally throughout a given range of motion [42]. Conversely, isotonic actions have to overcome a preset resistance, and the force required to move the resistance varies depending on factors such as joint angle and the length of the agonist muscle. Thus, depending on the resistance exercise (e.g., free-weight vs. machine), isotonic action may produce the greatest loading on the neuromuscular system at the weakest point of the range of motion, leaving the rest of the joint angles working inherently submaximal [43]. When examining the effects of eccentric actions, one of the limitations of isotonic resistance training is that constant loading does not accommodate the difference in force-generating capacity between the concentric and eccentric phases of an exercise [20]. Consequently, repetition failure occurs when muscle force falls below the necessary level to overcome the resistance during the concentric phase. This means that eccentric actions can continue with the same load while not reaching eccentric failure. Although there is data to suggest that training with the same external loads, sets, and repetitions induced similar increases in concentric strength following eccentric-only and concentric-only training [24], it is ultimately uncertain at what percentage of relative eccentric 1RM individuals are training during the eccentric phase. This would hinder the assessment of eccentric action capacity and its associated adaptations at different relative load. Isokinetic training may bypass this limitation by allowing one to perform each repetition maximally. It can be postulated that differences in the motor unit recruitment [44] and active muscle mass [45] would be minimized between the isokinetic concentric and eccentric actions.

When individuals performed the same number of total sets and repetitions (2 – 6 sets of 8 repetitions) completed maximally with either isokinetic concentric-only or eccentric-only training, Farthing et al. [46] found that changes in concentric strength and muscle growth were significantly greater with eccentric-only training groups (fast or slow velocity) compared to concentric-only training (fast or slow velocity) and control group following 8 weeks of training. Because eccentric actions produced greater torque in each repetition than concentric actions, overall training volume was higher in the eccentric-only group despite the same total training sets and repetitions across training. It was speculated that these results were attributed to the greater force produced and muscle growth with eccentric actions compared with concentric actions [46]. Although the increases in maximal strength might not be contingent on the training volume with isotonic training [47, 48], the possibility remains that the total volume performed may influence the change in maximal strength with isokinetic training. In addition, the mechanistic role of exercise-induced growth for changes in muscle strength is contentious (discussed below) [49-53]. Nevertheless, when a study accounted for both training intensity (i.e., maximal effort in each repetition) and total training volume between isokinetic concentric-only and eccentric-only conditions, increase in isokinetic concentric peak torque was still similar between concentric-only and eccentric-only training [40]. They also reported that the concentric-only training condition required 40% more repetitions to perform the equivalent amount of work as the eccentric-only training condition. Taking into account these studies above [40, 46] as well as its lower fatiguability [54] and metabolic cost (estimated via net oxygen consumption) [55], eccentric actions could be considered more efficient and advantageous to induce strength adaptations. However, it should also be noted that there is a viewpoint that the magnitude of chronic adaptations with different modalities of eccentric exercises (i.e., isotonic, isokinetic, and isoinertial training) should be differentiated due to their recruitment strategy and biomechanical characteristic differences (e.g., the load forcibly lengthens the muscles versus the load is voluntarily lowered against gravity, along with different torque-angle and velocity-angle relationships) [56-59].

HOW MIGHT ECCENTRIC TRAINING CONTRIBUTE TO CHANGES IN CONCENTRIC MUSCLE STRENGTH?

The mechanistic reasons why eccentric-biased training has been observed to carry over to maximal concentric strength remain to be elucidated. Eccentric actions differ from concentric or isometric actions on the level of mechanical (e.g., a greater force-generating capacity) [39], metabolic (e.g., a reduced estimated metabolic energy expenditure) [55], neural (e.g., a decline in the discharge rate of motor units) [60], and intrinsic (e.g., increased number of attached cross-bridges and the average force per cross-bridge) [15] factors. To what extent these factors contribute to resistance training-induced increases in maximal concentric strength is not known; however, it has been suggested that these unique acute responses to eccentric exercises may underpin the chronic adaptations observed with eccentric training [12]. The following mechanisms are speculative and by no means exhaustive.

Molecular mechanisms

Historically, the cross-bridge theory of muscle contraction has predominantly focused on the actin-myosin complex and its regulatory proteins within the contractile units referred to as sarcomeres [61-63]. The existing theories regarding muscle contraction (shortening or lengthening) suggest that the primary source of mechanical energy driving the sliding filaments in a contracting muscle is attributed to the power stroke of the myosin motors [64]. However, the cross-bridge theory alone is insufficient to explain the following with eccentric actions: the greater force-generating capacity [65], the reduced energy expenditure [15], and the residual force enhancement (i.e., an increase in the steady state isometric force following an eccentric action compared with the corresponding isometric force not preceded by an eccentric action) during eccentric actions [66]. Alternatively, a three-filament model of muscle contraction (actin, myosin, and titin) has been proposed to explain how the third myofilament, titin, can actively participate in muscle force generation by changing its stiffness in the stretched and activated (i.e., high intracellular calcium concentration) state [67-69]. Titin is the largest known protein, with a capacity to contribute to passive muscle tension, sarcomere integrity, and transmission of cross-bridge force to the z-disk [70]. Although there are several theories for how titin might generate force during a muscle contraction [66, 70, 71], the active function of titin on force generation in muscle shortening (i.e., concentric action) has been highlighted more recently [72-74]. A working model for titin-enhanced muscle contraction states that the unfolding and refolding titin immunoglobulin (Ig) domains generate mechanical work that assists muscle contraction [69, 75]. Upon calcium release, actin-myosin motor cross-bridge forms, but the motor can only generate a certain amount of force (described as stalled myosin motors). The refolding of Ig domains was proposed to be an “extra kick” in the force output during muscle shortening by relieving strain on the myosin motor, permitting the completion of power stroke [69, 75]. From this mechanism, it was suggested that titin is considered an active component of the sarcomere that works with actin and myosin in muscle shortening and lengthening [69]. In this light, it has been suggested that titin stiffness plays a critical role in regulating transmission of cross-bridge force during eccentric actions [65, 76]. Titin stiffness increases with muscle force production, providing a mechanism that explains two major properties of eccentric actions: their high force-generating capacity and low energetic cost [70]. The changes in titin stiffness likely are multifactorial, and they can be acutely modulated by calcium binding to titin upon muscle activation [77], titin phosphorylation [78], and titin-actin interaction (i.e., attaching itself to the actin) [79]. The changes in titin stiffness are also thought to be part of mechanisms responsible for the force enhancement properties during the subsequent concentric actions (i.e., increased concentric force output when followed by eccentric actions) [32, 80]. This was illustrated by the reduction of force enhancement following active stretch with the titin mutation, presumably due to the impairment of transmission of cross-bridge forces in sarcomeres [76, 81]. Within traditional resistance exercise (i.e., concentric-eccentric coupled), it could be hypothesized that force enhancement properties of eccentric actions may overload concentric actions that indirectly support strength adaptations. Such a magnitude might be small, but this may partially explain why incorporating eccentric actions to concentric actions led to a greater increase in concentric maximal strength than concentric-only training [33-35].

A training study in rodents reported an exercise-induced increase in titin stiffness of the diaphragm [82]. Other cytoskeletal proteins (e.g., nebulin, integrins, desmin, and dystrophin) and tendon are also the key components of force transmission within and between muscle fibers [83-86]. Reich et al. [87] quantified the passive and active stiffness of triceps brachii muscles following 8 weeks of eccentric training (downhill treadmill running) in rats. They found that both passive and active force and stiffness increased following training compared to control animals, indicating the possibility that the stiffness of titin or other cytoskeletal proteins increased in response to eccentric training [87]. This was in line with recent findings suggesting that eccentric training (downhill treadmill running) increased the stiffness of passive muscle properties in both single fibers and fiber bundles without changing the titin isoform size [88]. Considering that increases in the lateral force transmission of force from sarcomeres along the length of the muscle fibers might be associated with increased muscle strength with resistance training [89], increases in stiffness in these properties might be considered a favorable adaptation for strength gains with eccentric training. However, data in humans appears less consistent with regard to the changes in tendon stiffness, demonstrating no clear difference between concentric-only and eccentric-only resistance training [90, 91]. It is possible that the loading and strain levels obtained in the animal studies are greater than those obtained in the human studies [92]. Importantly, contributions of these properties to the maximal concentric strength are less understood and require additional research [75, 93].

Muscle growth has also been suggested as one of the mechanisms underpinning strength gains with eccentric training [17]. Some data showed that eccentric training may produce morphological adaptations distinct from other muscle actions [11, 94, 95]. For instance, eccentric training has been shown to induce preferential muscle growth in the type II fiber area compared to concentric training [11, 94]. It has been postulated that eccentric action triggers stretch-sensing molecules (e.g., titin) at the sarcomere level to trigger signaling cascades (e.g., calcineurin/nuclear factor of activated t-cells [NFAT]) to provide a potent stimulus for muscle growth [96, 97]. While preferential increases in the type II fiber area [11, 94] may be seen as a preferable adaptation for muscle strength, it should be acknowledged that whether muscle force-generating capacity can be inferred from myosin isoforms is contentious due to the wide range of approaches used in the literature [98]. It has also been demonstrated that the changes in muscle strength at the fiber level may not always correspond with the changes at the whole muscle level [99]. Importantly, whether exercise-induced changes in muscle size contribute to exercise-induced changes in muscle strength is still debated [49-53]. Although muscle growth remains a candidate, experimental studies have yet to demonstrate that changes in muscle size contribute to changes in muscle strength [9, 27, 28, 41]. Reasons for these findings remain speculative, but there is a viewpoint that newly synthesized myosin molecules from resistance exercise might not be readily available for actin interaction [100]. This could be important for maximal strength in that the force generation is largely dictated by the ability of the myosin heads to bind to actin to cause cross-bridge power strokes [101, 102]. Thus, it may be that changes in muscle and strength with training are separate and even unrelated phenomena [49, 50, 52]. Future research is warranted to investigate if the manner in which the muscle protein accrued with eccentric training is causally linked to the changes in muscle strength (methodological considerations for future research can be found in [100]).

Neural mechanism

The neural strategies controlling eccentric actions may differ from those used during concentric and isometric actions [13]. The neural control of the movement may also differ between different modalities of eccentric exercises (i.e., isotonic vs. isokinetic) [57, 59]. However, whether eccentric, concentric, and isometric training shares the same neural adaptations for changes in concentric strength is difficult to examine and currently unknown. Thus, there remains a host of unanswered questions related to this area. Readers are forewarned about this limitation and encouraged to interpret the findings carefully. With this in mind, some acute and chronic data on this topic may provide insights as to why eccentric training provides robust stimulus for increases in concentric muscle strength.

A greater force-generating capacity of the eccentric action has been proposed to generate the same absolute force with fewer motor units recruited for a given submaximal load compared to concentric action [103]. It has been hypothesized that one consequence of the decreased number of recruited motor units might be a higher level of tension per motor unit relative to concentric and isometric action (i.e., a distribution of the mechanical stress on fewer motor units) [104]. Whether increased tension per motor unit provides a potent stimulus for the adaptations observed with eccentric training is currently unknown. A reduced neural drive during eccentric action has also been attributed to the preferential recruitment of high-threshold motor units or lower activation levels of all activated fibers [105, 106]. This increased recruitment was also thought to account for greater neural adaptations (i.e., increased recruitment of those high-threshold motor units) following eccentric training [94, 107]. However, other studies have found little difference in motor unit recruitment order between eccentric and concentric actions [108-110]. Further studies are necessary to investigate the adjustments that may occur with differing eccentric conditions (e.g., preferential recruitment of high-threshold motor units may occur with increasing eccentric action velocities [111]) and how they relate to strength adaptations. In addition, it has been proposed that the differences in the neural control of eccentric and concentric actions may also be due to a combination of cortical and spinal mechanisms [13, 112].

Other factors that could explain increases in concentric strength with eccentric training include increased agonist voluntary activation [113] and decreased antagonist coactivation [114]. Studies suggested that eccentric actions induced greater cortical excitability compared with concentric and isometric actions, which have been postulated as a compensatory response to spinal inhibition [115, 116]. Spinal inhibition is believed to be a part of the mechanism underpinning reduced motor activity during eccentric actions [13]. A 7-week resistance training study reported that the increase in cortical excitability caused a decrease in presynaptic inhibition that could lead to improve muscle recruitment and potentially counteract other inhibitory signals at the spinal level [117]. Such a case could be illustrated in untrained individuals whose voluntary activation is often not maximal during eccentric action (i.e., unable to fully activate during eccentric action) [113]. This deficit in voluntary activation might be reduced with resistance training [113]. To what extent this improved voluntary activation with eccentric training could translate into concentric strength remains to be investigated; however, it has been speculated that incomplete muscle activation in the untrained state may represent a greater reserve for neural adaptations with eccentric training [107]. Thus, there might be greater potential to enhance muscle activation by voluntary command and/or by a modification of the discharge rate of motor units [107]. Further support can be found in the study by Tallent et al. [118]. In that study, 4 weeks of eccentric resistance training resulted in increased volitional drive (V-wave) when tested in both eccentric and concentric actions, but following concentric resistance training, such adaptations were only found in concentric action but not eccentric action [118]. These studies highlight the principle of specificity for concentric training and further suggest that eccentric loading has a greater capacity for neural adaptations. Future investigations should be mindful of this possibility and investigated with different modalities of eccentric exercises (i.e., isotonic, isokinetic, and isoinertial).

CONCLUSION

The principle of specificity suggests that the largest changes in strength occur when interventions resemble the specific strength test. Within traditional training, this is often tested by concentric 1RM testing. As the principle of specificity holds that individuals who trained with concentric actions should be expected to have an advantage in a concentric 1RM, the lack of discernible differences in strength gains with eccentrically-biased training may imply that adaptive signals within the neuromuscular system respond differently to eccentric loading compared to concentric loading. This is not to propose that eccentrically-biased training necessarily replaces traditional resistance training. However, from the principle of specificity standpoint, we view these findings as possible avenues for future studies to investigate potential mechanisms behind exercise-induced increases in muscle strength.

CONFLICTS OF INTEREST

Authors are aware of no competing interests.

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Ethics for this study were approved in line with University's ethics procedure.

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