Neuromuscular Adaptations to Isoload versus Isokinetic Eccentric Resistance Training

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ABSTRACT

GUILHEM, G., C. CORNU, N. A. MAFFIULETTI, and A. GUÉVEL. Neuromuscular Adaptations to Isoload versus Isokinetic Eccentric Resistance Training. Med. Sci. Sports Exerc., Vol. 45, No. 2, pp. 326–335, 2013. Purpose: The purpose of this study was to compare neuromuscular adaptations induced by work-matched isoload (IL) versus isokinetic (IK) eccentric resistance training. Methods: A total of 31 healthy subjects completed a 9-wk IL (n = 11) or IK (n = 10) training program for the knee extensors or did not train (control group; n = 10). The IL and IK programs consisted of 20 training sessions, which entailed three to five sets of eight repetitions in the respective modalities. The amount of work and the mean angular velocity were strictly matched between IL and IK conditions. Neuromuscular tests were performed before and after training and consisted of the assessment of quadriceps muscle strength, muscle architecture (vastus lateralis), EMG activity, and antagonist coactivation. Results: IL, but not IK, eccentric resistance training enhanced eccentric strength at short muscle length (+20%), high-velocity eccentric strength (+15%), muscle thickness (+10%), and fascicle angle measured at rest (+11%; P < 0.05). Agonist EMG activity increased almost similarly for the two modalities, whereas antagonist coactivation was unaffected by training. Conclusions: IL proved to be more effective than IK training for improving quadriceps muscle strength and structure. It is conjectured that the rapid acceleration of the load in the early phase of IL eccentric movements (i.e., at short muscle lengths), which results in greater torque and angular velocities compared with IK actions, is the main determinant of strength and neuromuscular adaptations to eccentric training. These findings have important consequences for the optimization of IL and IK eccentric exercise for resistance training and rehabilitation purposes. Key Words: LENGTHENING CONTRACTION, STRENGTH TRAINING, EMG, ULTRASONOGRAPHY

Eccentric contractions are characterized by the production of force while lengthening the muscle-tendon complex. This forced and active stretch creates high levels of tension that can cause cytoskeletal damage (4) and, in turn, trigger local inflammation and muscle remodeling (3). Although these perturbations can have detrimental short-term effects on performance, repeated eccentric exercise increases neural activation and triggers long-term adaptations at the cellular level (20,24,29). Mechanical overload has been suggested to influence gene expression via mechanotransduction pathways (29), resulting in skeletal muscle hypertrophy, strengthening of the musculotendinous tissue, and thus protection of the muscle–tendon complex against further injury (21,30). These neuromuscular adaptations induced by eccentric training are responsible for strength improvements (12) that are recognized to be greater than those induced by concentric training (34).

Lengthening contractions may be used to control the displacement of a constant external load (isoinertial or isoload) or to resist a constant angular velocity movement (isokinetic) (16,26). Muscles are differently solicited when exposed to these two exercise modalities, as illustrated by different torque–angle and velocity–angle relationships (15,18). Another distinction between the two lengthening–contraction behaviors is the extent to which the muscle activation is modulated during contraction because muscles elicit different neural patterns when the load forcibly lengthens the muscles versus when the load is voluntarily lowered against gravity (7). Indeed, the intensity of the activation signal changes minimally when resisting an imposed load, in contrast to the amount that it can vary when a load is being displaced (7). Although the neuromuscular adaptations specifically induced by each modality are not identified, isoload (IL) and isokinetic (IK) eccentric training are respectively used to improve muscle strength (8,9,20,24,28,39), to restore muscle function after injury (26) and in the management of tendinopathies (30). A review of the literature recently indicated that IL eccentric training appears to be more effective than IK eccentric training in improving muscle strength (16). Nonetheless, to date, no comparative study has determined the effects specifically induced by IL versus IK eccentric training, mainly because of methodological difficulties in matching the amount of work between the two modalities.

On the basis of the principle of strength training specificity, it has been postulated that IL and IK eccentric actions provide a different stimulus to the neuromuscular system and, therefore, could produce different structural and/or neural adaptations (15,18). In the IL modality, mechanical overloading...
due to gravity induces a greater initial limb acceleration compared to IK eccentric contractions, which stretches the elastic component of the muscle–tendon unit. This rise in stretching velocity increases passive torque, especially at high torque levels (31). Hence, the IL modality creates greater torque levels than the IK modality at short muscle lengths (15). Moreover, quadriceps EMG activity has been shown to be greater at the beginning of IL eccentric actions compared with IK, despite similar behavior of muscle fascicles during the two contraction modalities (15). These biomechanical differences suggest that specific neural adaptations could occur at short muscle lengths after IL training, in comparison to IK training (16,18). The faster angular velocity coupled with greater torque levels at the onset of IL contractions could also stimulate muscle hypertrophy to a greater extent compared to IK eccentric actions (11,15,39).

Thus, the purpose of the present study was to compare neuromuscular adaptations of knee extensor muscles induced by IL versus IK eccentric resistance training, continuously standardized for total angular work and average velocity. Determining the effectiveness and the specific adaptive processes induced by respective loading modalities is important, considering that IL and IK training are used interchangeably (albeit probably erroneously) for athletic or clinical purposes. We hypothesized that, compared to IK, IL eccentric training would induce greater strength gains and neural adaptations at short muscle lengths, as well as greater overall increases in muscle mass.

**METHODS**

**Subjects**

A total of 31 healthy men with no previous history of knee injury volunteered to participate in this study. None of them had previously participated in systematic resistance training. Subjects were randomly assigned to one of three groups: IL (n = 11, 21 ± 2 yr, 177 ± 3 cm, 76 ± 9 kg), IK (n = 10, 20 ± 1 yr, 179 ± 5 cm, 74 ± 10 kg), or control (C; n = 10, 20 ± 1, 181 ± 7.0 cm, 75 ± 11 kg). The three groups were homogeneous in terms of age, height, weight, and isometric maximal voluntary contraction (MVC) torque of the knee extensors (IL: 278 ± 29 N·m; IK: 297 ± 42 N·m; C: 312 ± 62 N·m). All participants were informed regarding the nature, aims, and risks associated with the experimental procedure before they gave their written consent to participate. The study was approved by the local ethical committee and was conducted in accordance with the Helsinki Declaration.

**Study Design**

The study was spread over 18 wk (Fig. 1). During week 1, participants attended a familiarization session that was dedicated to evaluate and carefully accustom them with eccentric exercise and testing procedures. The next 17 wk were dedicated to IL (weeks 2–12) and IK (weeks 3–13) training and testing, whereas C group did not train and was tested at weeks 8 and 18. To equalize the average mechanical stimulus associated with IL and IK training, both subject groups performed the same amount of external angular work at the same mean angular velocity for each set of eccentric exercise (see below and Guilhem et al. [17] for details). In brief, the IK group started the protocol 1 wk after the IL group to adjust the standardized parameters for the IK sessions. The mean angular velocity of each IL repetition was calculated on the whole range of motion, and values were then averaged per set. The obtained mean angular velocity was then adopted for the IK sessions. The total amount of angular work was also calculated for each IL set, and the amount of work the IK group had to perform was based on the work completed by the IL group 1 wk earlier. All participants were tested before (pre) and 9 wk after (post) the 9-wk training or the control period and were asked not to perform any strenuous exercise for 48 h before each testing session. Because local fluid accumulation may occur after eccentric exercise and this can influence muscle architecture
measurements, the post training tests were performed 4 to 7 d after the last training session to allow the fluid to disperse.

**Eccentric Training**

IL and IK training programs consisted of 20 sessions of eccentric exercise executed on the same ergometer and supervised by the same experimenter, during a 9-wk period (Fig. 1). Each session started with 30 body-weight squats as a warm-up. Subjects were then asked to sit on an isokinetic dynamometer (Biodex System 3 Pro, Shirley, NY) that was specifically modified to achieve IL and IK eccentric contractions in similar conditions (17). They performed eccentric contractions of the right knee extensors from 30° to 90° of flexion (0° = lever arm in the horizontal position). Individual ergometer settings and seat position were recorded during the familiarization session and reproduced for all training sessions. Mechanical signals provided by the dynamometer (i.e., joint position, external torque, and angular velocity) were collected at a sampling frequency of 1000 Hz via an A/D converter (Bagnoli 16 EMG System; Delsys, Boston, MA). IL training sessions consisted of three (week 1), four (week 2), and five (weeks 3–9) sets of eight repetitions at 100% (weeks 1 and 2) and then increased at 120% (weeks 3–9) of the maximal load that subjects could lift concentrically once (one-repetition maximum [1-RM] load), as described in Figure 1. IK training sessions included the same number of sets as IL training; each set was composed of n volitional maximal repetitions performed at a preset velocity of 10–1s to 30–1s.

The number of IK repetitions was adjusted to match the amount of work performed in both training modalities. After each IL and IK eccentric repetition, the dynamometer lever was automatically moved to the starting position at 30°s (passive

**FIGURE 2**—Description of torque and EMG signals processing to determine torque–angle and EMG–angle relationships. A. Torque and EMG data recorded during pre (black line) and post (gray line) tests on VL, VM, RF, ST, and BF during maximal slow eccentric contractions (∼30°s) for a representative subject of the IL group. B. Torque was averaged every 10° throughout the whole range of motion to construct the torque–angle relationship. C. EMG data were RMS with a time averaging period of 100 ms to produce an RMS envelope. D. Maximal M-wave amplitude (Mmax). E. RMS data were normalized to Mmax and averaged every 10° throughout the whole range of motion to construct the EMG–angle relationship.

An example for the 45° value (from 40° to 50°) is depicted as a red area on A and C and as a red point on B and E.
mode), and subjects were consistently asked to relax during this phase (i.e., pure eccentric training). To optimize the effects of resistance training, no training sessions were completed during the fifth week of the training program, as previously recommended (13).

Measurements

Muscle strength. Eccentric and isometric muscle strength of the knee extensor muscles was evaluated on the isokinetic dynamometer in the same conditions used for training. The specific effects of IL and IK training on the torque–angle relationship were determined during eccentric contractions performed at an angular velocity similar to the training velocity (∼30°·s⁻¹; Fig. 2). Knee extensor peak torque was investigated during high-velocity eccentric contractions (∼180°·s⁻¹), during slow (30°·s⁻¹) and fast concentric contractions (180°·s⁻¹), and during isometric MVCs performed at a 70° knee angle. Isometric knee flexion MVCs were performed at a 40° knee angle to normalize EMG activity of knee flexor muscles. Each test condition included three trials and was performed in a randomized order that was individually reproduced during the two test sessions. All strength tests and measurements are summarized in Figure 1.

EMG. Synchronously with mechanical signals, EMG signals were recorded during each strength test using bipolar surface EMG sensors (Delsys) from the vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF), semitendinosus (ST), and long head biceps femoris (BF) muscles (Fig. 2A). Each EMG sensor was made of two parallel silver bars with a length of 10 mm. The interbar distance was 10 mm. Inter-electrode impedance was minimized using standard skin preparation procedures (19). EMG sensors were placed between the distal tendon and the innervation zone of respective muscles, in parallel with the direction of the muscle fibers (19). Maximal M-wave responses (M_max) were evoked at rest using supramaximal single shocks with 1-ms duration (Digitimer DS7A, Hertfordshire, UK). The femoral nerve was stimulated using a cathode ball electrode manually pressed in the femoral triangle. The anode was a rectangular electrode (89 × 50 mm) located in the gluteal fold. EMG signals were preamplified (gain = 10) at the sensor level and sampled at 1000 Hz via an A/D converter (Bagnoli 16 EMG System; Delsys; gain = 1000).

Muscle architecture. In vivo VL muscle architecture was examined at rest and during MVC using ultrasonography (2). The same experimenter completed all the assessments at the pre and post sessions. Real-time longitudinal images were obtained using a two-dimensional B-mode ultrasonographic apparatus (Phillips HD3, Bothell, WA) equipped with a 40-mm linear array probe (7.5 MHz). The probe position was directed onto the right VL at 50% of the distance from the greater trochanter to the lateral condyle of the femur, with the knee flexed at 90° (2,25). Once muscle fascicles were clearly identified on the echographic images, the probe was firmly fixed and its position was labeled, so as to ensure consistent repositioning. Water-soluble gel was applied to the transducer to aid acoustic coupling and to avoid dermal contact. During post tests, on-screen images were compared to pre images to limit possible changes of probe orientation between sessions, which could have resulted in significant muscle architecture variations. Images were acquired at a sampling rate of 25 Hz with commercial software (Pinnacle Studio v10.0; Pinnacle Systems, Mountain View, CA) and were synchronized with torque and EMG data for the MVC trials.

Data Processing

Mechanical data. All data were analyzed with custom written scripts (MATLAB, The MathWorks, Natick, MA). Mechanical signals were low-pass filtered (cutoff frequency = 10 Hz). Torque measurements were gravity and inertia corrected (18). Only eccentric strength test trials with the highest peak torque and isometric MVC torque were considered for further analysis. To construct the torque–angle relationship using the best eccentric trial performed at ∼30°·s⁻¹, the mean torque was calculated every 10° throughout the range of motion (e.g., from 30° to 40° for 35°; Fig. 2B).

EMG data. These were band-pass filtered (bandwidth = 6–400 Hz) using a second-order Butterworth filter. Voluntary EMG signals collected during isokinetic and isometric strength tests were consistently analyzed as the root mean square (RMS) amplitude with a time averaging period of 10 ms (Fig. 2C). To assess training-induced changes in the EMG–angle relationship, the average RMS EMG amplitude obtained during the eccentric contraction at ∼30°·s⁻¹ was quantified every 10° throughout the range of motion for VL, VM, and RF muscles (Fig. 2E). Maximal RMS EMG values were calculated over a 100-ms period before maximal torque for VL, VM, and RF muscles. To overcome interindividual variations related to skin impedance and electrode placement during the different testing sessions, RMS EMG values were normalized to M_max amplitude for individual muscles (EMG/ M_max; Fig. 2D) (35). Because voluntary EMG data did not reveal a muscle effect in any of the test conditions (P > 0.05), agonist EMG activity was calculated as the mean of VL, VM, and RF EMG/M_max values. During eccentric and concentric contractions, antagonist coactivation was calculated as a mean EMG value for ST and BF muscles on the isokinetic phase. During MVC, RMS value was calculated over the 1 s before peak torque. These values were subsequently expressed as a fraction of the RMS value recorded during isometric knee flexion MVC, for both ST and BF muscles.

Ultrasonographic data. Ultrasonographic images were analyzed by the same investigator who was blinded to subject’s training group. Three muscle fascicles per image were clearly labeled with the use of common drawing software (Photoshop Elements v4.0; Adobe System Inc., San Jose, CA). The aponeuroses and muscle fascicles were then digitized using public domain image-processing software (ImageJ; National Institute of Health, Bethesda, MD). Measurements of muscle thickness, which is defined as the distance between the superficial and the deep aponeurosis, were made on both sides of the image and averaged, as described elsewhere (15). The fascicle angle was determined as the angle between the fascicle...
and its insertion on the deep aponeurosis. Fascicle length is generally quantified as the length of the fascicular path between the superficial and the deep aponeurosis. Because the VL fascicles were too long to be fully visualized by our probe and therefore impossible to measure from the origin to the insertion, VL fascicle length was estimated assuming its linear continuation (2,15,33). To limit the effect of estimation, the values of three measured fascicles were averaged for each scan. Repeated measurements performed with the present technique previously showed good reproducibility (15).

### Statistical Analyses

Normality of data was tested using a Kolmogorov–Smirnov test. Separate two-way ANOVAs (time [pre, post] × group [IL, IK, C]) with repeated measures were applied to eccentric and concentric peak torque, MVC torque, EMG activity, and muscle architecture variables (VL thickness, VL fascicle angle, and VL fascicle length). Separate three-way ANOVAs (time [pre, post] × angle [35°, 45°, 55°, 65°, 75°, 85°] × group [IL, IK, C]) with repeated measures were performed on torque–angle and EMG–angle relationship data. When the sphericity assumption in repeated-measures ANOVAs was violated (Mauchly’s test), a Geisser–Greenhouse correction was used. Post hoc tests were performed by means of Newman–Keuls procedures. Cohen’s d effect sizes (ES) and thresholds ([G 0.5 [small], 0.5–0.79 [moderate], and [Q 0.8 [large]]) were also used to compare the magnitude of the difference of the change between pre and post training tests (5). For between-condition comparisons, further analyses were conducted to identify the chance that the true (unknown) values for IL or IK were higher (i.e., greater than the smallest practically important difference, or the smallest worthwhile [difference] change, [0.2 multiplied by the between-subject SD, based on Cohen’s ES principle (5)]), similar or lower. Quantitative chances of higher or lower values were assessed qualitatively as follows: <1%, almost certainly not; 1%–5%, very unlikely; 5%–25%, unlikely; 25%–75%, possible; 75%–95%, likely; 95%–99%, very likely; >99%, almost certainly. If the chance of having higher or lower values were both >5%, the true difference was assessed as unclear (22). Analyses were performed with Statistica Version 7.1 (StatSoft, Tulsa, OK). For all tests, the significance level was set at \( P < 0.05 \).

### RESULTS

The ANOVAs revealed significant time × group interactions for some of the dependent variables considered in the present study (see corresponding sections below). Post hoc tests occasionally showed significant differences between the training groups (IL or IK) and the C group but did not show any significant differences between IL and IK groups at any time point. Thus, the post hoc results presented below correspond to pre-to-post changes within the same group. When only one training modality induced a significant effect, Cohen’s ES and smallest worthwhile changes are presented to further illustrate the differences between IL and IK groups. For all comparisons, further analyses were conducted to identify the chance that the true (unknown) values for IL or IK were higher (i.e., greater than the smallest practically important difference, or the smallest worthwhile [difference] change, [0.2 multiplied by the between-subject SD, based on Cohen’s ES principle (5)]), similar or lower. Quantitative chances of higher or lower values were assessed qualitatively as follows: <1%, almost certainly not; 1%–5%, very unlikely; 5%–25%, unlikely; 25%–75%, possible; 75%–95%, likely; 95%–99%, very likely; >99%, almost certainly. If the chance of having higher or lower values were both >5%, the true difference was assessed as unclear (22). Analyses were performed with Statistica Version 7.1 (StatSoft, Tulsa, OK). For all tests, the significance level was set at \( P < 0.05 \).
the dependent variables, no significant variation over the time was observed for the C group.

**Training stimulus and compliance.** During the 9-wk experimental period, all the trained subjects completed the 20 training sessions, except one subject in the IK group who missed one session. Figure 3 presents the mechanical differences between IL and IK modalities in terms of torque (Figs. 3A and B) and angular velocity (Figs. 3D and E) for representative training sessions (i.e., first and last sessions). Torque and velocity were higher in IL than IK at short muscle lengths, whereas torque was higher in IK around the angle of peak torque (~70°). Training load was progressively increased along the experimental period so that the training stimulus was perfectly matched for IL and IK groups in terms of workload (Fig. 3C) and mean angular velocity (Fig. 3F).

**Slow eccentric contractions (training velocity).** Both IL and IK training induced a rise of the torque–angle relationship to greater torque levels during slow eccentric contractions (Fig. 4A). Eccentric torque at 35° and 45° increased from pre to post for IL (+18% ± 5% and +22% ± 4%, respectively; P < 0.01) but not for IK (P = 0.11). ECCENTRIC TRAINING: LOAD OR VELOCITY? Eccentric torque at 55°, 65°, 75°, and 85° increased from pre to post for both IL and IK (P < 0.01). Qualitative analysis of smallest worthwhile changes suggested that strength improvements at 35° and 45° were higher for IL compared with IK (standardized difference rated as “moderate” and “large,” respectively, and the chances that the true values for IL were higher were 80% and 95%, respectively). The quadriceps femoris EMG/Mₘₐₓ ratio recorded during slow eccentric contractions increased from pre to post on the entire range of motion for IL (Fig. 4B; P < 0.05). IK training increased the EMG/Mₘₐₓ ratio at 35°, 45°, 55°, 65°, and 75° (P < 0.05) but not at 85° (P = 0.06).

**Fast eccentric contractions.** IL training increased the eccentric peak torque measured at 180° s⁻¹, which may be considered as a high (above 120° s⁻¹) velocity (+15 ± 4%; P < 0.01; Fig. 5A), whereas IK training did not modify this variable (P = 0.54). The increase in high-velocity eccentric peak torque was “almost certainly” higher after IL than IK training, with “large” standardized difference (ES = 1.21). This was concomitant to an increase in EMG/Mₘₐₓ ratio for IL (+16%; P = 0.02) but not for the IK group (P = 0.54; Fig. 5B). This increase was “possibly” higher for IL compared with IK, with “small” difference. Peak torque measured during high-velocity concentric contractions was not significantly affected by either IL (from 151.3 to 162.6 Nm) or IK training (from 144.7 to 145.5 Nm).

**Isometric contractions.** Isometric MVC torque increased from pre to post for both IL (+16% ± 3%; P < 0.001) and IK (+14% ± 3%; P < 0.001; Fig. 5C). This was associated with an increase in EMG/Mₘₐₓ ratio for both IL and IK groups (P < 0.05; Fig. 5D).

**Slow concentric contractions.** Peak torque measured during slow concentric contractions increased after IL (+18% ± 3%; P < 0.001) and IK (+8% ± 3%; P < 0.05) training (Fig. 5E). The concomitant quadriceps femoris EMG activity also increased for both groups (P < 0.05; Fig. 5F).

**FIGURE 4**—Torque–angle (A) and quadriceps femoris EMG/Mₘₐₓ-angle (B) relationships in slow isokinetic eccentric conditions performed at −30° s⁻¹ for IL (left), IK (center), and C (right) groups at pre (straight line) and post (dashed line) tests. *Significant difference between pre- and posttest values (P < 0.05). Data are presented as mean ± SE.
Antagonist coactivation. No significant difference in average hamstring coactivation was observed between pre- and posttraining tests in any of the tested conditions for IL (0.074 ± 0.005 at pre vs 0.071 ± 0.003 at post) and IK (0.072 ± 0.003 at pre vs 0.072 ± 0.003 at post; \( P < 0.05 \)).

Muscle architecture. Whereas no change in VL thickness was found for the IK group (\( P = 0.26 \)), a significant increase of 10% ± 4% was observed after IL training (\( P < 0.001 \); Fig. 6A). This rise in VL thickness after IL training was “possibly” higher compared to that in IK (the chance that the true values for IL were higher was 65%). No significant change in VL fascicle angle was observed for the IK group both at rest (\( P = 0.83 \)) and during MVC (\( P = 0.11 \)), whereas IL training significantly increased VL fascicle angle both at rest (\( +11\% ± 6\% \); \( P < 0.01 \); Fig. 6B) and during MVC (\( +26\% ± 5\% \); \( P < 0.05 \); Fig. 6C). IL training “possibly” increased fascicle angle more than IK training did, with standardized difference rated as “large.” VL fascicle length was unchanged after both IL (from 16.6 to 16.1 mm) and IK (from 14.6 to 15.1 mm) training.

DISCUSSION

The present study produced several important findings. IL, but not IK, eccentric resistance training increased (i) eccentric strength at shorter muscle lengths, (ii) high-velocity eccentric
strength, and (iii) vastus lateralis muscle thickness and fascicle angle, whereas training-induced changes in EMG activity and isometric MVC torque were almost comparable for the two training modalities. As previously reported (18), instantaneous torque levels and angular velocities were higher at the beginning of IL eccentric actions in comparison with IK, throughout the training program. Consequently, although total work and mean angular velocity were standardized for the two modalities, IL and IK training resulted in different mechanical strain at short muscle lengths. The greater initial acceleration of the load in IL conditions imposed unique neuromuscular demands at short muscle lengths that are likely responsible for the different adaptive response to IL versus IK eccentric training.

According to the principle of strength training specificity, in the present study, we observed the greatest strength gains at the eccentric velocity closer to the one used for both training modalities (34). Interestingly, moreover, eccentric strength measured at faster velocity increased after IL, but not IK, eccentric resistance training. As discussed above, IL exercise is able to stress the contractile apparatus at high velocities in the early phase of the eccentric movement (15), which could account, at least in part, for such distinctive adaptation. In line with this hypothesis, it has recently been demonstrated that fast eccentric training created a sevenfold greater gain in muscle strength at high velocity in comparison to slow eccentric training (39). Comparative analysis of muscle activity performed in a previous study (15) suggested a preferential increase in agonist EMG activity after IL training. Simultaneously with greater peak torque increases, we observed an increase in quadriceps femoris EMG activity at the high eccentric velocity after IL training compared to IK. These results suggest that the higher angular velocity and external torque at the beginning of IL movements required greater motor unit activation than the IK modality, which could have resulted in an increased EMG activity after training. This enhanced recruitment was not observed during isometric contractions because EMG activity increases did not differ between the two training modalities. IK exercise allows for a maximal muscular involvement through the whole range of motion with higher activity around the angle of peak torque (26). This could potentially counterbalance the lower neural demand achieved at the beginning of the eccentric movement in comparison to IL exercise.

Isometric MVC strength of the knee extensor muscles increased similarly after IL and IK training (+16% and +14%, respectively). Although static strength gains induced by comparable high-resistance training appear relatively variable in the literature (24,28,32), our findings are included in the average variations observed after IK and IL eccentric training (+4%–38%) (16). Moreover, isometric strength gains were accompanied by increased quadriceps femoris EMG activity for both training modalities, which is in accordance with most of the studies focused on resistance training effects (9,20,24,28,32,36), and confirm the important role played by neural mechanisms in mediating strength increases. The increase in quadriceps EMG/M\text{max} ratio observed in the present study reveals an increase in the descending neural drive (9,32) that could be due to an increase in the discharge rate of active motor units and/or the recruitment of additional units (24,32). Even assuming that the discharge rate would have been modified by the present eccentric training programs, it has been suggested that such process could only contribute to the final 15% of maximal force in large muscles (e.g., quadriceps femoris), which is a small contribution to the isometric strength gains (24). Alternative hypotheses have been suggested to marginally influence EMG amplitude such as the summation of action potentials or the synchronization of activated motor units (10), which have been shown to increase after resistance training (37).

A decrease in antagonist coactivation has also been proposed to be among the neural mechanisms that could be responsible for strength gains because the external torque is the resultant of the torque produced by agonist muscles minus the torque produced by antagonist muscles (32). However, both of the resistance training modalities considered in the current investigation did not affect hamstring coactivation during isokinetic and isometric contractions. These results are consistent with most of the studies that investigated the effect of eccentric training on antagonist coactivation (24,36).

Numerous authors have identified a link between the mechanical stress applied to the contractile apparatus and muscle hypertrophy (11,38,39). More precisely, it is known that muscle stretch combined to overloading is the most effective stimulus for muscle growth (14). On the basis of torque–angle and velocity–angle relationships previously obtained in the two modalities (18), we hypothesized that IL eccentric training would have promoted muscle hypertrophy to a greater extent compared to IK training. In the current study, we observed a significant 10% increase in VL thickness after IL training, whereas no change was noticed after IK training. Our results are in line with previous studies that have reported an average hypertrophy of 3%–11% after IL eccentric training programs lasting 8 wk (16,40). Similar increases in muscle mass (3%–13%) have also been observed after IK eccentric training, although most of these protocols used training velocities exceeding −60° s\text{−1}. These studies showed that high-velocity eccentric contractions promoted greater muscle hypertrophy compared to slow eccentric contractions (11,39), which suggests that high angular velocity may be a factor favoring protein synthesis resulting in muscle growth (39). As suggested above, the IL modality is able to create higher angular velocities and torques than IK does in the early phase of the eccentric movement (15). On one hand, the high external torque associated with the relatively high instantaneous velocity (up to 100° s\text{−1} for some subjects) in IL at short muscle lengths may stimulate muscle hypertrophy. On the other hand, the lower velocity imposed throughout IK contractions (22° s\text{−1}) could explain the lack of muscle hypertrophy with this training modality. So far, having received little consideration with respect to muscle hypertrophy, the angular velocity, associated with relatively
high torque, seems to have a major effect on this structural adaptive process.

The present study also revealed that the training-induced increase in muscle thickness occurred in parallel with an increase in VL pennation angle at rest for IL but not for IK training. To our knowledge, this is the first time that the effects of pure IL eccentric training were evaluated on VL muscle architecture. The increase in fascicle pennation angle affects the maximum force-generating capacity of a muscle by increasing the amount of parallel contractile material bound to tendon or aponeurosis (2). Fascicle angle also affects the muscle’s architectural gearing ratio (i.e., greater fascicle rotation) that extends the range of optimum lengths and velocities for force production (1,38). These architectural adaptations could explain the eccentric strength gains observed at short muscle lengths after IL training. In accordance with previous findings (8), IL eccentric training increased the fascicle angle at MVC to a greater extent compared to rest conditions (26% vs 11%), illustrating the force-production potential of VL muscle in maximal contraction. Although a shift of the optimum angle for torque generation would have favored a greater sarcomeres overlap, this was not supported by our data. As an alternative hypothesis, an enhancement of muscular perfusion during contraction has been shown to account for short-term changes in VL architecture (6). It is tempting to suggest that the fast overloaded stretch imposed by IL at short muscle length modified the optimal amount of contractile tissue during maximal contractions.

Eccentric training was found to have no effect on fascicle length, whatever the training modality used, concurring with earlier work that reported no increase in sarcomere number and fiber length after eccentric training (27). Previous studies reported fascicle lengthening after resistance training (1,38). Blazevich et al. (1) quantified a VL fascicles lengthening of 90% of initial length during eccentric contractions performed at the same velocity used for training in the present study. Other observations performed in our laboratory showed that fascicle lengthening reached 47% during IK eccentric contractions performed with the same experimental settings as in the present study (15). Because the overloaded stretch is one of the factors favoring changes in muscle architecture, the fascicle lengthening imposed in our study might not have been sufficiently wide to stress the muscle, thus failing to modify VL fascicle length as a result of training. Considering that eccentric contractions started at 30° of knee flexion, significant cross-bridge cycling would only have occurred at long muscle lengths in the IK modality (15). During IL eccentric contractions, however, the “lowering” process would have ensured that even the early part of the contraction (i.e., at short muscle lengths) was performed with active muscle lengthening. Such mechanical differences between IK and IL modalities could explain, at least in part, the specific strength gains observed at short muscle lengths with IL training. Moreover, eccentric and concentric training have been shown to induce similar increases in fascicle length (1). Our study concurs with these data, suggesting that muscle lengthening during training might not be a major factor influencing the length change of whole muscle fascicles in healthy humans (1,27).

In an attempt to compare the two training modalities in standardized conditions, we used a validated procedure to match the mechanical stimulus of IK and IL exercise in terms of workload and mean angular velocity (17). Although this method did not equalize work and velocity at the muscle level, it allowed for a continuous control and a progressive and comparable increase in the external training load for both modalities. Thus, the physiological adaptations observed in this study are mainly the result of the specific mechanical constraints imposed by the respective training modalities (Fig. 3). Although muscle hypertrophy could be nonhomogeneously distributed over the whole quadriceps muscle, in the present study, this parameter was evaluated exclusively for one portion of the quadriceps (VL). VL thickness was quantified using real-time ultrasonography, which gives only partial and indirect quantification of muscle volume (2). The increase in muscle thickness could be reflective of the increase in fascicle angle but might also reveal changes in muscle fluid content (1). Thus, a sufficient delay was observed before posttests to ensure the dispersion of potential fluid accumulation, and validated ultrasonography procedures were adopted to permit simple image acquisition at rest and during MVC without supplemental assessment, in a magnetic resonance imaging coil for instance. Moreover, modifications observed in VL form and function are known to be particularly representative of structural changes occurring in the whole quadriceps (1).

In summary, it is conjectured that the mechanical specificity associated with the early phase of IL contractions (greater instantaneous torque and faster angular velocity than IK) was responsible for eccentric strength gains at short muscle lengths and high velocity and also for structural adaptations. Therefore, because IL eccentric resistance training is effective to improve quadriceps strength at short muscle lengths, this modality could be particularly appropriate for sport activities that impose high mechanical constraints when lower limbs are extended (e.g., long jump, hurdles, floor gymnastics). IL exercise could also be very useful for patients suffering from diseases that specifically affect muscle function at short muscle lengths (e.g., stroke patients [23]). Moreover, because IL eccentric resistance training was effective to promote quadriceps muscle hypertrophy, it could be suitable to sport activities where muscle mass is an important determinant of performance (e.g., contact and combat sports, weight lifting) or to counteract muscle atrophy induced by inactivity or pathology.

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