

The Influence of Frequency, Intensity, Volume and Mode of Strength Training on Whole Muscle Cross-Sectional Area in Humans

Mathias Wernbom,¹ Jesper Augustsson^{1,2} and Roland Thomeé^{1,2}

- 1 Lundberg Laboratory for Human Muscle Function and Movement Analysis, Department of Orthopaedics, Sahlgrenska University Hospital, Göteborg University, Göteborg, Sweden
- 2 SportRehab Physical Therapy and Sports Medicine Clinic, Göteborg, Sweden

Contents

Abstract	226
1. Methods	227
1.1 Literature Search	227
1.2 Classification of Muscle Actions, Training Methods and Modalities	228
1.3 Quantification of Exercise Frequency, Intensity and Volume	229
1.4 Classification of Training Status	230
1.5 Calculation of Changes and Rate of Changes in Muscle Cross-Sectional Area (CSA)	230
2. Results Part 1: Quadriceps Studies	231
2.1 Quadriceps Studies: Dynamic External Resistance	231
2.1.1 Length of Training Period, Average Increase in CSA and CSA Per Day	232
2.1.2 Rate of Gain in CSA: Men versus Women	232
2.1.3 Frequency	232
2.1.4 Intensity	232
2.1.5 Volume	232
2.2 Quadriceps Studies: Accommodating Resistance	233
2.2.1 Length of Training Period, Average Increase in CSA and CSA Per Day	233
2.2.2 Frequency	233
2.2.3 Velocity	234
2.2.4 Torque	234
2.2.5 Volume	234
2.2.6 Total Duration Per Session	235
2.2.7 Time-Torque Product Per Session	235
2.3 Quadriceps Studies: Isometric Resistance	235
2.3.1 Length of Training Period, Average Increase in CSA and CSA Per Day	235
2.3.2 Frequency	235
2.3.3 Intensity	235
2.3.4 Volume	235
2.4 Quadriceps Studies: Combined Strength and Endurance Training	236
2.4.1 Rate of Gain in CSA: Combined Training versus Pure Strength Training	236
2.4.2 Length of Training Period and Increase in CSA	236
2.5 Quadriceps Studies: All Voluntary Training Modes	236
2.5.1 Length of Training Period and Increase in CSA	236
2.6 Quadriceps Studies: Strength Training as a Countermeasure During Unloading	236

2.6.1	Unloading versus Unloading and Exercise Countermeasure	236
2.7	Quadriceps Studies: Electromyostimulation	237
3.	Results Part 2: Elbow Flexor Studies	237
3.1	Elbow Flexor Studies: Dynamic External Resistance	237
3.1.1	Length of Training Period, Average Increase in CSA and CSA Per Day	238
3.1.2	Frequency	238
3.1.3	Intensity	238
3.1.4	Volume	238
3.2	Elbow Flexor Studies: Accommodating Resistance	239
3.3	Elbow Flexor Studies: Isometric Resistance	239
4.	Discussion	239
4.1	Frequency	239
4.2	Intensity	242
4.3	Volume	244
4.4	Mode of Training and Type of Muscle Action	245
4.5	Rest Periods and the Role of Fatigue	247
4.6	Interactions Between Frequency, Intensity, Volume and Mode	249
4.7	Time Course of Muscle Hypertrophy	251
4.8	Hypertrophic Response of the Quadriceps versus the Elbow Flexors	252
4.9	The Stimulus for Muscle Hypertrophy in Strength Training	253
4.10	Suggestions for Future Research	254
4.11	Limitations	256
4.12	Training Implications and Recommendations	257
5.	Conclusions	258

Abstract

Strength training is an important component in sports training and rehabilitation. Quantification of the dose-response relationships between training variables and the outcome is fundamental for the proper prescription of resistance training. The purpose of this comprehensive review was to identify dose-response relationships for the development of muscle hypertrophy by calculating the magnitudes and rates of increases in muscle cross-sectional area induced by varying levels of frequency, intensity and volume, as well as by different modes of strength training.

Computer searches in the databases MEDLINE, SportDiscus® and CINAHL® were performed as well as hand searches of relevant journals, books and reference lists. The analysis was limited to the quadriceps femoris and the elbow flexors, since these were the only muscle groups that allowed for evaluations of dose-response trends. The modes of strength training were classified as dynamic external resistance (including free weights and weight machines), accommodating resistance (e.g. isokinetic and semi-isokinetic devices) and isometric resistance. The subcategories related to the types of muscle actions used. The results demonstrate that given sufficient frequency, intensity and volume of work, all three types of muscle actions can induce significant hypertrophy at an impressive rate and that, at present, there is insufficient evidence for the superiority of any mode and/or type of muscle action over other modes and types of training. Tentative dose-response relationships for each variable are outlined, based on the available evidence, and interactions between variables are discussed. In addition, recommendations for training and suggestions for further research are given.

Strength training has become increasingly popular in recent decades. Whereas previously strength training had been used by a few selected athletes to improve their strength and size, it is now an important component in training for most sports as well as for injury prevention and rehabilitation.^[1-3] Quantification of the dose-response relationships between the training variables (e.g. intensity, frequency and volume) and the outcome (e.g. strength, power and hypertrophy) is fundamental for the proper prescription of resistance training.^[4] Several meta-analyses^[4-8] and numerous reviews^[1,3,9-11] have dealt with various aspects of optimising strength; however, with the exception of a paper by Fry,^[12] few systematic reviews have focused on the issue of how to train specifically for muscle hypertrophy. The review of Fry^[12] discussed the role of training intensity on hypertrophy as measured by increases in muscle fibre area (MFA).

Implicit in many articles in the literature are the following assumptions: (i) training for strength and training for hypertrophy is essentially one and the same thing; and (ii) the programme that yields the largest increases in strength also results in the largest increases in muscle mass. These assumptions are not necessarily true in all situations. For example, studies by Choi et al.^[13] and Masuda et al.^[14] showed smaller increases in one repetition maximum (1RM) and isometric strength, but greater increases in quadriceps muscle area (as measured by magnetic resonance imaging [MRI]) and MFA after a typical moderate-load bodybuilding regimen when compared with a high-intensity powerlifting programme. Schmidtbleicher and Buehrle^[15] showed greater increases for triceps brachii muscle area (as measured by CT scanning) for a group that trained with 3 sets of 12 repetitions at 70% of 1RM when compared with a group that trained with 7 sets of 1–3 repetitions at 90–100% of 1RM, while the strength increases for the groups were similar. Thus, it is apparent from these and other studies that the training prescription for hypertrophy may differ somewhat from the prescription for maximum strength. This observation has been taken into account in various models of periodisation,^[16,17] where

training periods or training sessions aimed at stimulating maximum hypertrophy by high volume and moderate loads are followed by periods or sessions aimed at increasing maximum strength by moderate volume and heavy loads. The latter type of workout presumably acts by optimising neural adaptations,^[11] although marked hypertrophy can also occur if the volume is sufficient.^[12,15,18]

Scanning methods such as MRI and CT are regarded as the gold standard for assessing whole muscle size.^[19,20] To our knowledge, no systematic review has been published that has analysed the impact of several important training variables such as frequency, intensity and volume on changes in muscle area or volume as measured by scanning methods. Such a review could provide evidence-based guidelines for the prescription of strength training for increasing muscle mass. Establishing efficient models of strength training for hypertrophy in humans could also be of value for the study of the physiological mechanisms of the hypertrophy process. Therefore, the purpose of the present study was to identify dose-response relationships for the development of muscle hypertrophy by calculating the rates and magnitudes of increases in muscle cross-sectional area (CSA) or muscle volume induced by varying levels of frequency, intensity and volume, as well as by different modes of strength training.

1. Methods

1.1 Literature Search

Computer searches in the MEDLINE/PubMed, SportDiscus® and CINAHL® databases were performed for articles from 1970, when the first training study using scanning techniques to evaluate changes in anatomical muscle CSA was published.^[21] In addition, hand searches of relevant journals and books as well as the reference lists of articles already obtained were performed. The data reviewed in this article was accumulated as a result of literature searches conducted for this and other projects over a period of several years. The last search was performed on 3 December 2006. As the search progressed, it quickly became apparent that

the quadriceps was by far the most studied muscle group in humans undergoing strength training and that the elbow flexors (biceps brachii and brachialis) were the second most studied muscle group. Currently, these are probably the only muscle groups that allow for meaningful evaluation of dose-response trends. Therefore, the present review is focused on the human quadriceps and elbow flexors.

Criteria for inclusion were as follows:

1. Studies must have examined the effects of strength training on anatomical muscle area or muscle volume by a scanning method (i.e. MRI, CT or ultrasound [UL]).
2. Studies must have been conducted on healthy and uninjured participants between 18 and 59 years of age.
3. Sufficient data to calculate changes in muscle area or volume must have been reported.
4. Sufficient information regarding the training variables (in particular: frequency, intensity and volume) and the type and mode of exercise employed must have been reported to allow for replication of the study.

Exclusion criteria were as follows:

1. The subjects received supplements (e.g. creatine monohydrate, amino acids, proteins) or anabolic hormones and/or growth factors that could potentially have influenced the neuromuscular adaptations to strength training. Such study groups (but not necessarily other groups from the same study) were excluded from the current review.
2. The subjects were in negative energy balance (i.e. on a weight-loss diet).
3. The data from the study have been published before. However, sometimes it was necessary to collect data from several different papers from the same study.
4. Only part of the muscle group (e.g. vastus lateralis) was scanned. Alternatively, only data for the total muscle CSA of the limb (e.g. total thigh muscle area) was reported without specifying CSAs for the individual muscles (e.g. quadriceps).

1.2 Classification of Muscle Actions, Training Methods and Modalities

For the purposes of this review, the terminology of Knuttgen and Komi^[22] was adopted for the classification of muscle actions. Accordingly, exercise can be classified as either static (involving isometric muscle actions) or dynamic (involving concentric and/or eccentric muscle actions). During an isometric muscle action, the muscle develops force but no external movement occurs and the length of the muscle-tendon complex does not change. During a concentric action, the muscle produces force while shortening. An eccentric muscle action refers to a situation where the muscle produces force while lengthening.

In resistance exercise, training methods or modalities are often classified according to the type of resistance used. In his 1981 review, arguably the first systematic look at strength training, Atha^[9] divided the training modes into three main categories: (i) isotonic; (ii) isokinetic; and (iii) isometric. Isometric training obviously involves isometric actions. Isotonic training refers to dynamic exercise in which the muscle(s) exerts a constant tension.^[22] In various textbooks of physiology, an isotonic muscle action is often illustrated by an isolated muscle that is shortening or lengthening against a constant load, thus developing a constant force. This is not true in the intact muscle of a person performing an exercise because of biomechanical factors such as changes in the lengths of the lever arms of the muscle and of the resistance, and also the accelerations and decelerations that occur during dynamic exercise. Thus, even if the external resistance remains constant, the muscle will not develop a constant level of force.^[22,23] For this reason, the term 'isotonic' is often replaced by the term 'dynamic constant external resistance' (DCER).^[23] In DCER exercise, the absolute load is constant throughout the movement, as when lifting a dumbbell. Further examples of DCER would be simple cable pulley systems with no lever arms and machines with circle shaped cams. The term 'variable resistance' is used when the resistance throughout the range of motion is varied, for example by an irregularly shaped camwheel or a lever arm.^[23] The

idea with variable resistance is to closely match the resistance with the strength of the subject throughout the range of motion.^[24] However, because many dynamic training studies did not specify if the resistance was constant or variable, no distinction between these subcategories was made in the present review. The overall category for both these subcategories is termed dynamic external resistance (DER).

In isokinetic training, muscle actions are performed at a constant angular velocity, which is controlled by the machine. Unlike dynamic external resistance training, there is no set resistance to overcome; however, since the velocity is controlled, any force applied against the equipment results in an equal and opposite reaction force.^[23] Since the subject can freely vary the level of effort in the entire movement to accommodate for pain or weakness in certain regions of the range of motion, the isokinetic mode is very useful in rehabilitation.^[24] Isokinetics are sometimes sorted into a category called 'accommodating resistance'.^[25] Also included in this category are devices in which the resistance is provided by hydraulic cylinders, which function by limiting the flow through an adjustable aperture. Although not providing a strictly isokinetic movement, the resistance setting on these machines can be adjusted to limit the velocity within relatively narrow ranges.^[25] These devices are sometimes also referred to as semi-isokinetic.^[26] For the purposes of this review, the term 'accommodating resistance' was chosen for the main category. Another form of strength training uses the inertia of a flywheel for resistance. In this type of ergometer, the force exerted by the subject is transferred to a strap being wound around the axle of a fixed flywheel.^[27] A concentric muscle action unwinds the strap and overcomes the inertia of the flywheel, setting it spinning on low friction bearings. The rotating flywheel soon causes the strap to start winding up again; therefore, the machine returns the stored energy of the spinning flywheel via the strap and the subject tries to resist the returning movement by performing an eccentric muscle action. Caruso et al.^[28] have used the term 'isoinertial' to describe this

type of training, but Murphy and Wilson^[29] have used the exact same term to describe DCER training. With isoinertial flywheel ergometers, as with isokinetic training, the resistance is effort dependent for each type of action. Therefore, this mode of exercise will be included in the 'accommodating resistance' category.

1.3 Quantification of Exercise Frequency, Intensity and Volume

Regarding exercise intensity in dynamic external resistance training, we chose to express intensity as a function of 1RM in the exercise(s) performed for the muscle group in question (e.g. 80% of 1RM in the squat). In many of the studies, the authors provided exact percentages or at least estimates of the percentage. In cases where the intensity was expressed only as a function of how many repetitions the subjects were able to perform (e.g. 8RM), we estimated the relative intensity based on data on the relationship between the number of repetitions performed and the 1RM for the same or similar exercises.^[2,30-33] For the squat, we used the RM tables of Wathan,^[32] which have been shown to be accurate for the squat in previously untrained subjects.^[33] For the leg press, knee extension and arm curl exercises, we used data from Hoeger et al.^[30] The intensity for isometric training was quantified as a function of the maximum force achieved during a maximal voluntary isometric action (MVIA).

While the quantification of exercise intensity in conventional resistance training and isometric training is relatively straightforward, how to express the intensity or load for isokinetic and other accommodating training modes is less obvious. The force-velocity relationship of skeletal muscle dictates that as the velocity of the concentric muscle action increases, the maximum possible force decreases.^[34,35] Depending on the training status, the maximum torque developed by the quadriceps during eccentric muscle actions is slightly higher (trained subjects) or not significantly higher (sedentary subjects) than the maximum isometric torque.^[35] In cases where the peak torque during eccentric muscle actions exceeds that of isometric muscle actions, the peak torque

increases only marginally with increasing velocity and appears to reach a plateau at relatively low velocities.^[35] The amount of force developed by the muscle is generally regarded as an important stimuli for muscle hypertrophy.^[36] Since maximum effort (and therefore, recruitment of the greatest number of motor units possible) was used in most accommodating training studies, an estimate of the torque developed in relation to the isometric maximum could provide some insight into the level of force necessary to produce hypertrophy as a consequence of accommodating resistance training. Therefore, in addition to listing the training velocity, level of effort and type(s) of muscle action(s), we estimated the relative level of torque normalised to the maximum isometric torque based on the peak torque data for the quadriceps in untrained subjects from Amiridis et al.^[35] For the elbow flexors, data from Hortobagyi and Katch^[37] and Paddon-Jones et al.^[38] were used.

Training volume is a measure of the total amount of work (joules) performed in a given time period.^[23] In this review, training volume refers to a single session. In a less strict sense, volume can be estimated by the sum of repetitions^[23] or even by the number of sets performed.^[4] While simply stating the number of sets may seem a crude measure of volume, several meta-analyses^[4-6,8] have shown significant differences in strength gains between training with single and multiple sets in favour of multiple sets, particularly for trained subjects. Theoretically, a given exercise volume can be distributed in many different ways and as a consequence result in different adaptations. Therefore, several estimates of volume (number of sets, total number of repetitions, total duration of work and total work) were used in this review. However, instead of expressing the total amount of work performed in joules, work was calculated in arbitrary units (sets \times repetitions \times intensity).^[25] If several exercises were performed for the muscle group (e.g. leg presses and knee extensions for the quadriceps), the volumes for each of these were summed to yield the total volume for the muscle group. Regarding the training frequency, we have chosen to report frequency as the number of

sessions per muscle group per week, as opposed to training days per week. For example, a training group may have trained the quadriceps twice a day, three days a week. The frequency then is reported as six times per week. We are aware of the possibility that the physiological responses may differ between training once a day six times per week and twice a day three times per week.

1.4 Classification of Training Status

In the majority of the studies, the subjects were reported as either untrained/sedentary or as physically active. Physically active subjects generally performed some form of endurance training, but not any systematic strength training. Since many studies reported varying levels of activity among the participants and because endurance training induces little if any muscle hypertrophy,^[39] the categories 'untrained' and 'physically active' were combined for analyses. Deschenes and Kraemer^[40] made the following classification of training status with reference to resistance training: untrained, moderately trained, trained, advanced and elite. They suggested that the window of adaptation for strength becomes progressively smaller as the subject progresses. However, because of the lack of studies involving athletes of different training status, data from studies with trained, advanced and elite athletes are discussed together in the present review. In cases where the strength training status of the subjects was uncertain, information was sought regarding the CSA of the exercised muscles and comparisons were made with data from previously untrained individuals^[41-45] and resistance-trained subjects and strength athletes.^[41,45-47]

1.5 Calculation of Changes and Rate of Changes in Muscle Cross-Sectional Area (CSA)

In most of the studies reviewed here, the authors reported the changes in CSA or at least the pre- and post-training values. Sometimes, figures were used instead of numerical data; in such cases the graphs were measured if possible. The relative changes were calculated by simply dividing the post- with

the pre-training values. To allow for comparisons between studies of different length, percent changes per day were calculated by dividing the change in area with the length of the training period in days. Although some studies^[43,48] have shown preferential hypertrophy of individual muscles in a muscle group and of different levels in the same muscle, no consistent pattern has yet emerged. Furthermore, data from other studies^[44,49] suggest that changes in muscle CSA at the middle level and muscle volume after a training period are of a similar magnitude. In addition, studies by Aagaard and co-workers^[50] and Tracy et al.^[51] have confirmed that quadriceps muscle volume can be accurately predicted from a single scan at the middle level. Therefore, no distinction was made in this review between muscle volume and CSA as indexes of muscle size. A further discussion on the subject is provided by Tracy and colleagues.^[52]

There are several reasons for focusing mainly on changes in whole muscle CSA and not MFA. As argued by Narici and colleagues^[43] and D'Antona et al.,^[47] care should be taken when drawing conclusions concerning the whole muscle mass from changes occurring at a single biopsy site. In the study of Narici et al.,^[43] the changes in mean fibre area (2% increase in MFA) were not representative of either the vastus lateralis at the same level as the biopsy site (7.5% increase in muscle CSA by MRI), or of the quadriceps as a whole ($\approx 16\%$ increase in muscle CSA). Apart from the obvious risk of not detecting hypertrophy because of sampling muscle tissue from just a single site in a very large and architecturally complex muscle group such as the quadriceps, the lower limit for the increase in fibre size that can be detected is 10%. Furthermore, the coefficient of variation between repeated biopsies is quite large, $\approx 15\text{--}20\%$ (see Narici et al.^[43] for discussion). Thus, hypertrophic changes that are detectable at the whole muscle level may go unnoticed if only fibre areas are measured. Finally, as discussed by McCall and colleagues,^[53] one should be cautious in ruling out hyperplasia (an increase in the number of muscle fibres in a muscle) as a possible

contributing mechanism for whole muscle hypertrophy.

This is of course not to say that changes in fibre area are irrelevant as an index of muscle mass. Ideally, a training study would include measurements at both the cellular level and at the whole muscle level. Also, it should be noted that the relative changes in mean fibre area are usually of a larger magnitude than the changes in anatomical muscle area.^[44] However, we feel that the focus on changes in whole muscle CSA and volume, as measured by scanning techniques, is justified since these are arguably the most sensitive and representative measures of whole muscle mass, even though they may underestimate the changes at the cellular level. Regarding training issues where the evidence at the whole muscle level is limited, we will discuss relevant studies, if any, which have measured MFA changes.

2. Results Part 1: Quadriceps Studies

2.1 Quadriceps Studies: Dynamic External Resistance

After application of the inclusion and exclusion criteria, the literature search resulted in 44 original articles^[13,43-46,54-92] investigating quadriceps muscle CSA or volume before and after DER training. Because there were often more than one training group or more than one limb that received training, these 44 articles yielded 65 datapoints for CSA. Five of the articles (seven datapoints) involved trained to elite strength athletes. These were too few to allow for any meaningful analysis and will be discussed briefly in sections 4.1 and 4.6. Five studies dealt with pure concentric and/or eccentric training, with four datapoints for concentric training and three for eccentric training. Four datapoints from four different studies involved training where the subjects finished each set with several repetitions in reserve. Since stopping well short of muscular failure has been shown to yield modest hypertrophy in comparison with performing each set to muscular failure,^[85] even when the total volume is similar, these study groups were excluded. As a result, except where

otherwise indicated, the analysis for DER deals with training using combined concentric-eccentric muscle actions (47 datapoints), with previously untrained subjects.

2.1.1 Length of Training Period, Average Increase in CSA and CSA Per Day

The average length of the training period was 79 days. The shortest study was 14 days and the longest lasted 6 months. The average increase in quadriceps CSA was 8.5% (range: 1.1–17.3%). The average increase per day in CSA for training with combined concentric-eccentric muscle actions (47 datapoints) was 0.12% per day (range: 0.04–0.55%). If the study of Abe et al.^[84] is excluded as an ‘outlier’ because of the unusually high training frequency and rate of gain, the average increase was 0.11% per day (range: 0.04–0.26%). For pure concentric training, the increase was 0.06% per day and for pure eccentric training 0.03% per day.

2.1.2 Rate of Gain in CSA: Men versus Women

In six studies, groups of men and groups of women followed exactly the same training programmes. The average increases in CSA per day in these studies were 0.13% for men and 0.14% for women. Because these differences were considered as negligible and because several studies contained groups consisting of both men and women, data from all studies were pooled in the analysis for DER training (section 2.1).

2.1.3 Frequency

The mean training frequency was 2.8 times a week. The most common frequency was three times a week (22 of 47 datapoints), followed by two times a week (17 datapoints). Frequencies between and above these (2.3–4 times per week) were noted in a few cases. No studies were found that involved training at frequencies of more than two times per week. A plot of frequency versus percentage increase in quadriceps CSA per day is shown in figure 1. The highest rate of increase (0.55% per day) was reported for the training study^[84] with the highest frequency (12 times per week). For the frequency of two sessions per week, the average increase was 0.11% per day (range: 0.03–0.21%); for three ses-

sions per week, the increase was 0.11% per day (range: 0.04–0.26%).

2.1.4 Intensity

The mean peak intensity (the highest value reached during a session, averaged over the entire period) was 73% of 1RM. The average intensity (the mean of all training sets) was 66% of 1RM. Inspection of figure 2 reveals a tendency for greater rates of increase for intensities >60% of 1RM when compared with intensities below this level; however, it should be noted that only six datapoints involved training with mean peak intensities <60% of 1RM. The study of Abe et al.^[84] is not shown because of the unusually high training frequency (12 times per week) and very high rate of increase. The peak intensity in this study was 20% of 1RM.

2.1.5 Volume

The mean number of sets was 6.1 and the mean number of total repetitions was 60. The results are shown in figure 3. The study of Abe et al.^[84] was not included in the following analysis of volume. Inspection of the datapoints revealed four identifiable ‘clusters’ in the range of total repetitions. Fourteen datapoints were found in the range of 21–39 repetitions, 14 datapoints in the range of 40–60 repetitions, 11 datapoints in the 66–90 repetition range and finally 6 datapoints in the range ≥ 100 repetitions per session. The average rate of increase of CSA for each cluster was as follows: 21–39 repetitions = 0.12% per day; 40–60 repetitions = 0.13% per day; 66–90 repetitions = 0.08% per day; and ≥ 100 repetitions = 0.12% per day. No studies were found that

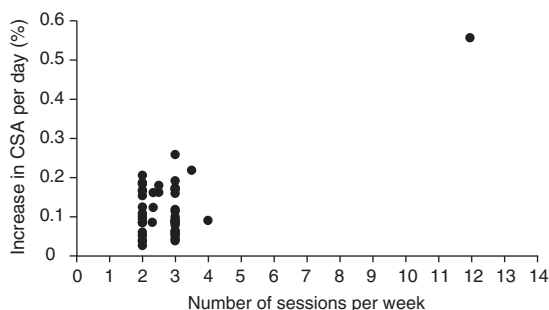


Fig. 1. Frequency of training vs percentage increase in cross-sectional area (CSA) per day of the quadriceps during dynamic external resistance training (number of study groups = 47).

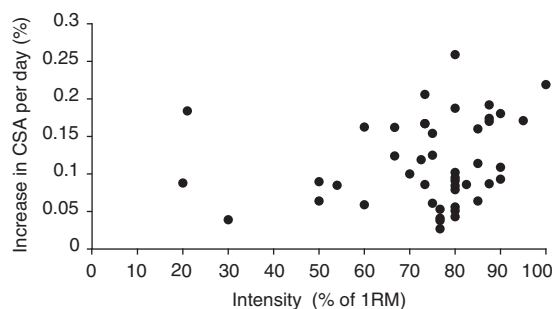


Fig. 2. Peak intensity of training vs percentage increase in cross-sectional area (CSA) per day of the quadriceps during dynamic external resistance training (number of study groups = 46). **RM** = repetition maximum.

involved <21 repetitions per session on average. For the number of sets, the following groupings were made: 3 sets (average CSA increase = 0.09% per day); 4 sets (0.13% per day); 5–6 sets (0.13% per day); 7–9 sets (0.09% per day); and ≥ 10 sets (0.14% per day). No studies were found which involved <3 sets. When training volume was expressed in arbitrary units [sets \times repetitions \times intensity], no apparent relation was found between the volume and increases in CSA per day (data not shown).

2.2 Quadriceps Studies:

Accommodating Resistance

The literature search resulted in 17 original articles^[27,42,48,87,93-105] investigating quadriceps muscle CSA or volume before and after an accommodating resistance-training programme. These 17 articles yielded 21 datapoints for CSA. Of these, 14 datapoints involved pure concentric training, three involved pure eccentric training and four involved training with combined concentric-eccentric muscle actions. Some of the studies^[93,95-98] included subjects with strength training experience. Based on anthropometric and quadriceps muscle CSA data, they were considered as ‘moderately trained’ and are included in the analysis in sections 2.2.1–2.2.7, together with previously untrained and physically active individuals.

2.2.1 Length of Training Period, Average Increase in CSA and CSA Per Day

The average length of the training period was 52 days. The shortest study was 13 days and the longest lasted 84 days. The mean total increase in CSA was 5.8% (range: 2.5–18.4%) for all types muscle action combined. For pure concentric training, the mean total CSA increase was 6.1% (range: 2.5–18.4%), for pure eccentric training the mean increase was 4.2% (range: 2.5–6.2%) and for combined concentric-eccentric training, the corresponding figures were 6.0% (range: 4.1–7.4%). The mean CSA increase per day for pure concentric training was 0.13% (range: 0.05–0.44%), for pure eccentric training 0.06% (range: 0.04–0.09%) and for combined concentric-eccentric training 0.16% (range: 0.06–0.21%). The average CSA increase for all the accommodating resistance modes combined was 0.13% per day.

2.2.2 Frequency

The mean frequency for concentric training was 3.4 times a week. Three sessions (nine datapoints) per week yielded an average increase in CSA of 0.13% per day and 3.5–4 sessions per week (four datapoints) yielded an average increase in CSA of 0.12% per day. Five sessions (one datapoint) per week yielded an average increase in CSA of 0.22% per day. The largest rate of CSA increase (0.44% per day) was noted in a study^[104] using three sessions per week. No concentric training studies were found with training frequencies below three sessions per week or above five sessions per week. The frequen-

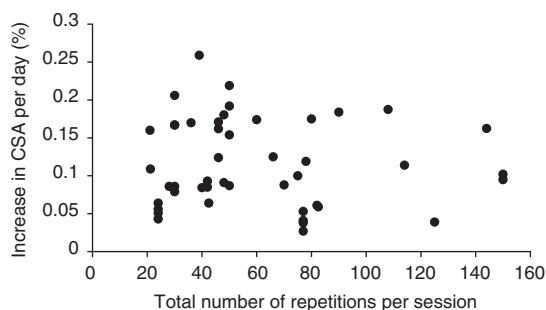


Fig. 3. Total number of repetitions vs percentage increase in cross-sectional area (CSA) per day of the quadriceps during dynamic external resistance training (number of study groups = 45).

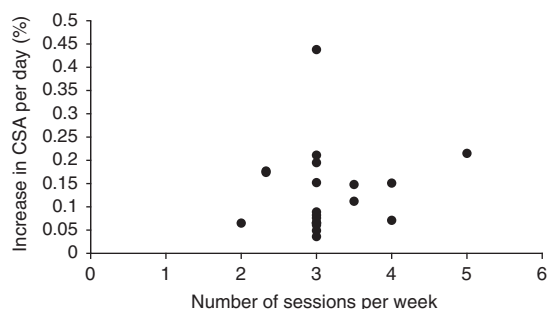


Fig. 4. Frequency of training vs percentage increase in cross-sectional area (CSA) per day of the quadriceps during accommodating concentric and/or eccentric training (number of study groups = 21).

cy for pure eccentric training was three times per week in all studies (three datapoints). For the combined concentric-eccentric training regimens, the frequencies were two (one datapoint), 2.3 (two datapoints) and three (one datapoint) times per week. The frequency plot for all categories combined is shown in figure 4. No relationship between the frequency and the rate of CSA increase is apparent from figure 4.

2.2.3 Velocity

For pure concentric training, the most common velocities were 60°/s (seven datapoints, 0.13% increase in CSA per day) and 120°/s (four datapoints, 0.16% increase in CSA per day). Two studies used 180°/s (0.14% increase in CSA per day) and one study used 90°/s (0.05% increase in CSA per day). The velocities for eccentric training and combined concentric-eccentric training were in the range between 45 and 90°/s.

2.2.4 Torque

Data from Amiridis et al.^[35] on untrained subjects suggests that the isokinetic concentric peak torque of the quadriceps expressed as a percentage of maximum isometric torque is ≈59%, 69%, 77% and 88% at the velocities of 180°/s, 120°/s, 90°/s and 60°/s, respectively. When these percentage values were applied to the concentric training studies, no relation was found between the level of torque developed and the rate of increase in CSA. The eccentric peak torque of the quadriceps in relation to the maximum isometric torque is ≈104%, 106% and 104% at the velocities of 30°/s, 60°/s and 90°/s, respectively.

When the percentage values for eccentric torque were applied and all accommodating modes and types of muscle actions were combined, no relation was found between the maximum torque developed during training and the rate of increase in quadriceps CSA (see figure 5).

2.2.5 Volume

For pure concentric training, the largest increases occurred when the total number was between 50 and 60 muscle actions (six datapoints, 0.19% increase in CSA per day [0.13% increase in CSA per day without the studies of Akima et al.^[103] and Rafeei^[104]]). Two datapoints were found in the interval of 30–40 muscle actions (0.06% increase in CSA per day) and six datapoints between 120 and 480 muscle actions (0.10% increase in CSA per day). If studies with pure eccentric and combined concentric-eccentric muscle actions are included in the analysis, the increases still tend to reach their maximum in the range between 50 and 60 muscle actions per session (ten datapoints, 0.18% increase in CSA per day). See figure 6.

Regarding the number of sets for pure concentric training, one datapoint was found for 3 sets, one for 4 sets, six for 5–6 sets, none for 7–9 sets and six for ≥10 sets. The highest increase occurred at 5–6 sets (0.19% increase in CSA per day [0.13% increase in CSA per day minus Akima et al.^[103] and Rafeei^[104]]). The increase in CSA for ≥10 sets was 0.10% per day and the increase for 3–4 sets was 0.06%. If studies with pure eccentric and combined

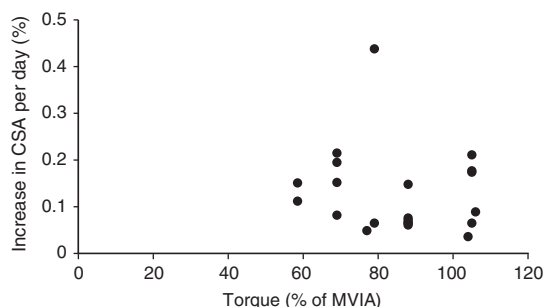


Fig. 5. Torque vs percentage increase in cross-sectional area (CSA) per day of the quadriceps during accommodating concentric and/or eccentric training (number of study groups = 21). **MVIA** = maximal voluntary isometric action.

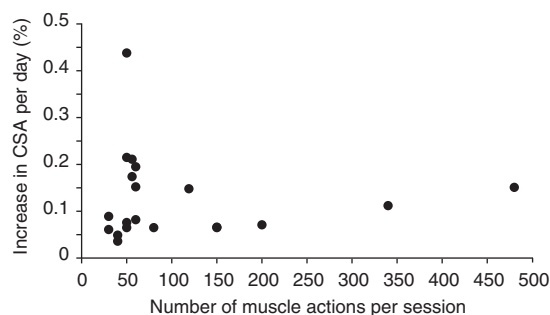


Fig. 6. Number of muscle actions vs percentage increase in cross-sectional area (CSA) per day of the quadriceps during accommodating concentric and/or eccentric training (number of study groups = 21).

concentric-eccentric muscle actions are included in the analysis, the results are as follows: 3 sets (two datapoints) = 0.08% increase in CSA per day; 4 sets (six datapoints) = 0.12% increase in CSA; 5–6 sets (seven datapoints) = 0.17% increase in CSA (0.11% without the studies of Akima et al.^[103] and Rafeei^[104]); and ≥ 10 sets (six datapoints) = 0.10% increase in CSA per day.

2.2.6 Total Duration Per Session

For pure concentric training, eight datapoints were distributed between 37.5 and 75 seconds of total duration of muscle work. The average increase in CSA for these datapoints was 0.16% per day. The other six datapoints were distributed between 170 and 300 seconds. The average increase in CSA for these datapoints was 0.09% per day. For the pure eccentric and combined concentric-eccentric training groups taken together, the seven datapoints (average of 0.12% increase in CSA per day) were distributed between 40 and 84 seconds.

2.2.7 Time-Torque Product Per Session

The time-torque product per session was calculated by multiplying the total duration with the estimated peak torque (with maximum isometric torque assigned a value of 1) and is reported here in arbitrary units. No relation was found between the time-torque product and the rate of gain in CSA, regardless of whether eccentric and combined concentric-eccentric training was included in the analysis or not (data not shown). For all types of muscle actions combined, ten datapoints were in the interval be-

tween 25 and 50 units (0.14% increase in CSA per day), six between 50 and 100 units (0.14% increase in CSA per day) and five in the interval between 100 and 265 units (0.10% increase in CSA per day).

2.3 Quadriceps Studies: Isometric Resistance

The literature search resulted in six original articles^[55,106–110] investigating quadriceps muscle CSA or volume before and after an isometric resistance training programme, yielding nine datapoints for CSA.

2.3.1 Length of Training Period, Average Increase in CSA and CSA Per Day

The average length of the training period was 84 days. The shortest study was 56 days and the longest lasted 98 days. The mean increase in total CSA after the training period was 8.9% (range: 4.8–14.6%) and the average rate of CSA increase was 0.11% per day (0.06–0.26%).

2.3.2 Frequency

Three sessions per week (four datapoints) resulted in an increase in CSA of 0.12% per day and four sessions per week (five datapoints) resulted in an increase in CSA of 0.11% per day. The largest rate of gain (0.26% increase in CSA per day) was reported in a study^[106] using three sessions per week.

2.3.3 Intensity

The most common intensity was 70% of MVIA (seven datapoints), the intensity in the other two cases was 80% and 100%, respectively. The largest rate of CSA increase (0.26% per day) was found in the study^[106] that used the highest training intensity (100% of MVIA).

2.3.4 Volume

The total number of repetitions ranged between 4 and 150. The time each repetition was held ranged between 1 and 30 seconds, while the total duration of muscle work per session was between 80 and 150 seconds. No relation was found between the number of repetitions and the increase per day in CSA. Similarly, when volume was expressed as the total duration per session and as the product of intensity and total duration, no apparent relation between volume and rate of increase in CSA was observed,

although the highest rate of increase in CSA (0.26% per day) was observed for the training study^[106] with the largest product of intensity and duration.

2.4 Quadriceps Studies: Combined Strength and Endurance Training

The literature search resulted in seven original articles^[77,78,86,96,111-113] investigating quadriceps muscle CSA or volume before and after a combined training programme, yielding ten datapoints. Some of the studies included groups that performed only strength training, these have been included in sections 2.1 and 2.2. Because of the limited data and different modes of endurance training (rowing, running and cycling), as well as the different modes of strength training, no analysis was performed regarding frequency, intensity and volume.

2.4.1 Rate of Gain in CSA: Combined Training versus Pure Strength Training

In four of seven studies,^[77,78,96,111] comparisons were made between pure strength training and combined training regarding increases in quadriceps CSA. If these are summarised, the resulting average increases are as follows: pure strength training = 0.09% increase in CSA per day; and combined training = 0.10% increase in CSA per day. If the combined training groups of the other three studies^[86,112,113] are included, the average rate of CSA increase for combined training becomes 0.12% per day.

2.4.2 Length of Training Period and Increase in CSA

The shortest study was 70 days and the longest lasted 168 days. The mean total increase in CSA after the training period was 15.1%. The largest increase in CSA was 34% (0.24% per day) and the smallest was 3.9% (0.05% per day).

2.5 Quadriceps Studies: All Voluntary Training Modes

2.5.1 Length of Training Period and Increase in CSA

Longer training periods generally tended to result in larger increases in CSA. Accordingly, the greatest

increase in quadriceps CSA (34%) was noted in one of the longer studies,^[112] after 20 weeks of training (see figure 7). There was also an apparent tendency for the rate of increase in CSA to decrease with increasing lengths of the training period (figure 8). If one regards the studies of Abe et al.^[84] and Rafeei^[104] as outliers because of their unusually high rates of increase, the slope becomes less steep.

2.6 Quadriceps Studies: Strength Training as a Countermeasure During Unloading

The literature search resulted in eight original articles^[114-121] investigating quadriceps muscle CSA or volume before and after a resistance training programme as a countermeasure during otherwise unloaded conditions (bed rest or limb suspension). These eight papers yielded nine datapoints for CSA for the training groups and nine datapoints for the control groups, which performed no training. One study (one datapoint) used isometric training as a countermeasure, one study (one datapoint) used vibration combined with isometric training, four studies (five datapoints) used dynamic external resistance with coupled concentric-eccentric muscle actions and two studies (two datapoints) used accommodating resistance with coupled concentric-eccentric muscle actions.

2.6.1 Unloading versus Unloading and Exercise Countermeasure

The average length of the training and unloading period was 49 days (range: 20–119 days). The mean decrease in quadriceps CSA for unloading was

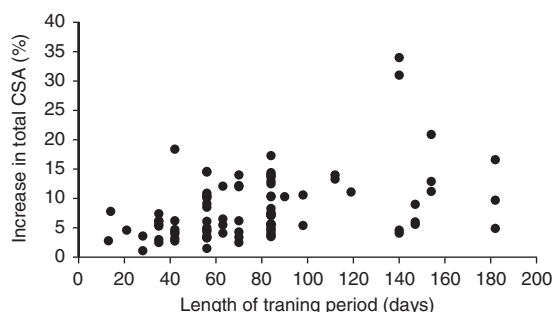


Fig. 7. Training period vs total percentage increase in cross-sectional area (CSA) of the quadriceps during all types of voluntary strength training (number of study groups = 91).

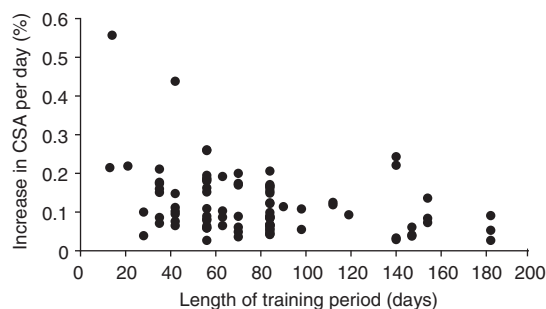


Fig. 8. Training period vs percentage change in cross-sectional area (CSA) per day of the quadriceps during all types of voluntary strength training (number of study groups = 91).

–11.1% and the mean rate of decrease was –0.30% per day. The degree of loss appeared to be related to the length of the unloading period, as the largest decrements in CSA were found in the studies with the longest unloading period. However, the rate of loss in CSA seemed to decrease with the length of the unloading period, so that the longer studies showed lower average rates of change. For the unloading plus strength training countermeasure, the CSA increased by an average of 1.3% (0.03% per day). If the isometric training and the vibration training groups are excluded, the increase in CSA becomes 2.7% (0.09% per day). The largest total CSA increase was 7.7% (0.22% per day) and the largest rate of gain was 0.30% per day (6.0% in total CSA). The greatest total CSA decrement was –3.8% (–0.19% per day) for the isometric countermeasure. The greatest total CSA decrease for the dynamic groups was –1.9% (–0.02% per day). Because of the limited data and differences in both training modes and unloading models, no analysis was performed regarding frequency, intensity and volume. The lowest training frequency was every third day (2.3 times per week) and the highest was twice a day (14 times per week).

2.7 Quadriceps

Studies: Electromyostimulation

The literature search resulted in three original articles^[99,122,123] investigating quadriceps muscle CSA in healthy uninjured subjects before and after a resistance training programme using electromyos-

timulation to evoke muscle actions. In the first of these,^[99] previously untrained subjects performed 3–5 sets of 10 unilateral combined concentric and eccentric actions in an isokinetic dynamometer at a velocity of 75°/s, for two sessions per week for 9 weeks. The increase in quadriceps CSA was 10.1% (0.16% per day). In the second study,^[122] from the same research group, recreationally resistance-trained subjects performed an identical protocol to that in the first study, for two sessions per week for 8 weeks. These subjects continued their normal resistance-training regimens during the study, including exercises for the quadriceps of both sides. The increase in CSA was 9.8% (0.18% per day). The control limb that performed only regular resistance exercise showed no increase in quadriceps CSA. Another group performed exactly the same programme but also received creatine supplementation. This group increased the CSA with 12.1% (0.22% per day) but this was not significantly greater than the other (placebo) group. The control limb that performed regular resistance exercise only showed a slight increase (5%) in quadriceps CSA. In the third study,^[123] electromyostimulation was used to evoke 40 isometric muscle actions per session, four sessions a week for 8 weeks. The increase in CSA was 6% (0.11% per day).

3. Results Part 2: Elbow Flexor Studies

3.1 Elbow Flexor Studies: Dynamic External Resistance

The literature search resulted in 16 original articles^[25,53,124–137] investigating elbow flexor (biceps and brachialis) muscle CSA or volume before and after a DER training programme with specific exercises for the elbow flexors. These papers yielded 36 datapoints for CSA. Three of the papers (seven datapoints) included highly-trained subjects, while one paper included recreationally-trained subjects (one datapoint), who had previously trained without any structured programmes or specific goals. Based on strength and CSA data, the latter group was regarded as ‘moderately trained’ and included in the analysis of ‘untrained’ and ‘physically active’ sub-

jects in sections 3.1.1–3.1.4. Four groups (four datapoints) from three other studies were excluded because they either performed only non-specific exercises for the biceps and brachialis muscles (e.g. latissimus pulldown, dumbbell row) or they did not perform their elbow flexor exercises with near maximal effort or near muscular failure in any set. One group from another study was excluded because the eccentric phase was performed in a plyometric manner with the resistance building up momentum before the subject started to resist it, making it very difficult to estimate the actual intensity. As a result, the analysis in sections 3.1.1–3.1.4 for the variables of frequency, intensity and volume is based on 24 datapoints for training with previously untrained to moderately trained subjects. All studies involved training with combined concentric-eccentric muscle actions, but in one study the eccentric phase was overloaded with $\approx 180\%$ of 1RM.

3.1.1 Length of Training Period, Average Increase in CSA and CSA Per Day

The average length of the training period was 91 days. The shortest study was 30 days and the longest lasted 6 months. The average increase in flexor CSA was 15.8% and the average increase per day in CSA was 0.20%. The highest increase in elbow flexor CSA (33%) was noted in the longest study, after 6 months of training,^[130] although an almost equal increase (32.6%) was observed in another study after 11 weeks.^[125]

3.1.2 Frequency

The results are shown in figure 9. The mean training frequency was 2.9 times a week. The most common frequency was three times a week (17 of 24 datapoints), followed by two times a week (six datapoints). The highest frequency was four times per week. No studies were found that involved training at frequencies of less than two times per week. The highest rate of CSA increase (0.59% per day) was noted for a training study^[128] with a frequency of four times per week. For the frequency of three sessions per week, the average CSA increase was 0.18% per day and for two sessions per week, the CSA increase was 0.18% per day.

3.1.3 Intensity

The mean peak intensity (the highest value reached during a session, averaged over the entire period) was 72%, which was the same as the average intensity (the mean of all training sets), since no study reported using different loads during one and the same session. The highest mean intensity reported was 180% of 1RM, in a study^[126] that used eccentric overload, in addition to performing the concentric phase with a lower resistance. This was also the only study that used such overload; the others used the same resistance in both types of muscle actions. The lowest resistance reported in a study was 10%. When the intensity was plotted against the rate of increase, a tendency was found for the rate to increase with increasing intensity. The highest rates of increase tended to occur around 75% of 1RM (see figure 10).

3.1.4 Volume

The results for the number of repetitions versus CSA per day are shown in figure 11. The mean number of sets was 5.4 and the mean number of total repetitions was 47. Three clusters of datapoints were identified as follows: (i) 7–38 repetitions (ten datapoints); (ii) 42–66 repetitions (nine datapoints); (iii) and 74–120 repetitions (five datapoints). The maximum rate of CSA increase was found in the interval between 42 and 66 repetitions (0.26% per day). For 7–38 repetitions, the CSA increase was 0.15% per day, and for 74–120 repetitions, the rate was 0.18% per day. For total sets, the rate of CSA increase appeared to peak between 4 and 6 sets (nine

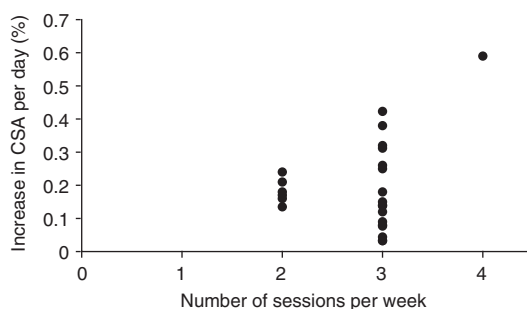
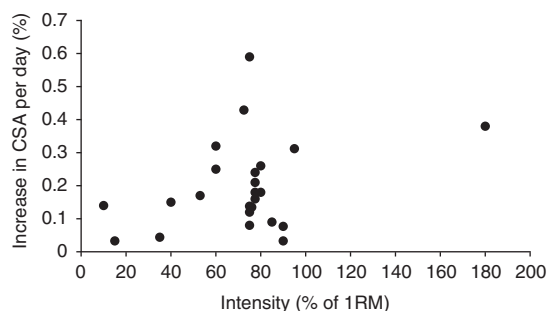


Fig. 9. Frequency of training vs percentage increase in cross-sectional area (CSA) per day of the elbow flexors during dynamic external resistance training (number of study groups = 24).



frequencies in more conventional training. Furthermore, it is interesting to note that there was no difference in the mean rates of increase in CSA between two and three sessions per week for DER quadriceps training (0.11% vs 0.11% per day, respectively). For accommodating resistance training and isometric quadriceps training, it is difficult to evaluate any trend because of the limited number of studies and the smaller range of frequencies. The highest rate of CSA gain in the isometric category (0.26% per day) was achieved in a study^[106] in which the subjects trained three times per week; however, this was also the study with the highest training intensity (100% of MVIA) and the highest product of intensity and total duration. The highest rate of CSA increase for accommodating resistance training (0.44% per day) was noted in a study^[104] that used a frequency of three sessions per week, followed by a study^[103] that used a frequency of five times per week (0.22% increase in CSA per day). High rates of CSA increase (0.17–0.21% per day) were also observed in three studies^[27,87,105] in which training was performed two to three times per week.

For the unloading plus resistance exercise countermeasure studies, the highest rate of CSA gain (0.30% per day) was noted for the study^[115] with the greatest training frequency (14 sessions per week), although a high rate of CSA increase (0.22% per day) was also noted in a study^[118] with a frequency of every third day. However, caution is warranted when comparing the results of these studies because of possible differences in the effects of the different models of unloading and/or the exercise regimens. For example, Tesch and co-workers^[118] employed limb suspension for unloading and knee extensions for the exercise countermeasure and showed a marked hypertrophic response in the quadriceps of the unloading plus exercise limb. In a different study by Alkner and Tesch,^[119] when using bedrest for unloading and horizontal squats, but with the exact same dosage of training as in their other study,^[118] the exercise resulted in no hypertrophy but still managed to completely counteract the atrophy that was evident in the pure bedrest group. Also notable is that in one bedrest study,^[114] which used isometric

training at 100% of MVIA as a countermeasure, training once a day was insufficient to prevent all the atrophy. In yet another bedrest study,^[117] training once a day using a leg press, with coupled concentric-eccentric actions at 90% of 1RM, preserved the muscle volume but failed to induce significant hypertrophy. Further research is obviously needed to address the effects of different exercise modes and regimens (e.g. different frequencies and distributions of the total training volume), as well as the impact of the unloading model employed.

For elbow flexor training with dynamic external resistance, the greatest rate of increase in CSA (0.59% per day; 17.7% total increase in CSA) was observed in a study^[128] with a frequency of four times a week. The second, third, fourth highest increase in CSA rates noted were 0.42%, 0.38% and 0.32% per day, respectively. These three studies^[125,126,132] used a frequency of three times per week. However, with the exception of these three studies, the average values suggest that there is relatively little difference between training the elbow flexors two or three times per week, in terms of the rate of increase in CSA (0.18% per day for both frequencies). However, the highest increase in CSA that was noted for two times per week was 0.24% per day, compared with 0.42% per day for three times per week. As noted in section 3.2, all accommodating resistance training studies involving the elbow flexors used a frequency of three times a week. Regarding frequency for isometric elbow flexor training, the highest rate of CSA increase (0.23% per day) was noted for a study^[21] with a frequency of six times per week, but this was also the study that had the highest intensity (100% of MVIA). Remarkably, this regimen consisted of only three isometric actions per day, each lasting 10 seconds, thus resulting in a total of 30 seconds of maximal isometric activity each day.

While a higher than normal training frequency (four or more times per week) can result in rapid hypertrophy in the initial stage, it should also be noted that several of these studies^[84,115,128] lasted only between 2 and 4 weeks. It is uncertain if training at these high frequencies would continue to

yield very high rates of increases in CSA or perhaps result in diminishing returns or even overtraining after a longer period. Inspection of the data from the study of Abe et al.^[84] suggests that the rate of increase in CSA was considerably slower during the second week compared with the first week, dropping from a maximum of $\approx 1\%$ per day to $\approx 0.25\%$ per day. Using a frequency of three times a week and a protocol of 4 sets of 7 maximal effort concentric-eccentric actions, Seynnes et al.^[105] showed a rate of increase of only $\approx 0.12\%$ per day during the first 10 days, but $\approx 0.25\%$ per day during the last 25 days of a training period that lasted 35 days. Thus, there is a possibility that training with a frequency of two to three times per week may start to produce a high rate of increase after the first two weeks; because of this and the paucity of data regarding long-term training with high frequencies, it is not possible to say which frequency is more optimal in the long run. Nevertheless, a high frequency (four or more times per week), in combination with relatively non-damaging low-to-moderate volume training, may be a good way to 'kick-start' the hypertrophy process. For longer-term training, the studies included in this review show that frequencies between two and four times a week can result in CSA gains for periods of up to 6 months. For previously untrained subjects, no study was found with a training frequency of less than two sessions per week.

Regarding the impact of training frequency in more advanced trainers, we found nine studies^[45,46,56,61,76,79,133,134,137] using scanning methods to monitor changes in CSA in the quadriceps and/or elbow flexors as a result of training in strength-trained subjects and strength/power athletes. In two preliminary reports,^[79,134] different frequencies of training were directly compared. Vikne and co-workers^[79] investigated the effects of squat training with an eccentric overload on quadriceps CSA in subjects that trained one, two and three times a week for 12 weeks. All groups performed 5 sets of 4 repetitions in each session using a squat machine, which was loaded to 50% of 1RM in the concentric phase and to 110–135% of 1RM in the eccentric phase. The groups that trained two and three times

per week gained significantly more in 1RM strength and quadriceps CSA (5.99% and 6.75%, respectively) than the group that trained once a week (3.1% increase in CSA). There was no difference between training two and three times per week. Wirth and colleagues^[134] investigated the effects of frequency on elbow flexor CSA in subjects that trained once, twice and three times a week for 8 weeks. All groups performed several types of arm curls for a total of 5 sets of 8–12 repetitions in each session. The groups that trained two and three times per week gained significantly more in elbow flexor CSA (6.6% and 7.4%, respectively) than the group that trained once a week (3.9%).

The results of Vikne et al.^[79] and Wirth et al.^[134] are remarkably similar despite using different muscle groups and training modes. In both reports, two and three sessions per week yielded almost twice the increase in muscle CSA when compared with one session, with no apparent further advantage for three versus two sessions. This seems logical in view of the typical pattern of changes in muscle protein synthesis after a resistance training session, with peak synthesis rates observed between 3 and 24 hours, and with elevated rates sometimes lasting between 48 and 72 hours after exercise.^[140–143] However, it cannot be excluded that larger volumes and/or different modes of training would yield different results. Furthermore, the total weekly volumes were not matched between the groups in the studies of Vikne et al.^[79] and Wirth et al.^[134] Also, it should be noted that most studies on muscle protein synthesis in humans after resistance exercise have only studied a time span of up to 48 hours post-exercise.

Anecdotally, many bodybuilders and other strength athletes only train each muscle group specifically between one and two times per week, sometimes even less often. On the other hand, weightlifters are known to perform exercises involving their quadriceps for several sessions per training day.^[144] Tesch^[145] has remarked that it is not known if bodybuilding regimens are superior to the training regimens performed by powerlifters and olympic lifters. Training each muscle group once a week has been shown to result in increases in muscle

CSA^[79,134,146] and lean body mass.^[146,147] However, the results of Wirth et al.^[134] and Vikne et al.^[79] are supported by data from McLester et al.,^[147] who using experienced subjects showed superior increases in lean body mass for three training sessions per week versus only one per week per muscle group, even when the total weekly volume remained the same for the two groups.

Häkkinen and Kallinen^[61] also investigated the effects of different distributions of the same total volume, in a group of trained female subjects of which some were competitive strength athletes. These subjects underwent two three-week periods of strength training for the quadriceps, with 3 training days per week. During one period, the subjects trained once each training day and during the second period the same subjects trained with the same total daily volume but separated into two sessions. During the first training period, the subjects did not gain in either strength or quadriceps CSA, but during the second period, the subjects increased significantly in both maximum static strength and CSA (4.0% and 0.19% per day, respectively). Although some interesting trends can be discerned from the data discussed in this section, there is clearly a need for further research on training frequency in both highly-trained and less-trained subjects.

4.2 Intensity

The studies reviewed in this article show that there is a remarkably wide range of intensities that may produce hypertrophy. Still, there seems to be some relationship between the load (or torque) and the rate of increase in CSA, at least for dynamic external resistance training, but this relationship is not a straightforward one. In figure 2 and figure 10, it can be seen that the rates of increase are generally higher for intensities >60% of 1RM than for those <60% of 1RM, although caution is warranted because of the few datapoints <60% of 1RM. However, it appears that intensities of ≈70–85% of 1RM are sufficient to induce high rates of increase and that even heavier loads do not necessarily result in greater CSA gains. In the categories of accommodating resistance, where the effort is usually maxi-

mal from the first repetition, there was no relation between the torque developed and the rate of gain in CSA, regardless of whether eccentric muscle actions were included in the analysis or not. This was true for both the quadriceps (figure 5) and the elbow flexors (data not shown). This is contradictory to some of the studies in the literature,^[148–151] but consistent with other reports.^[55,62,68,69] It should be noted that no accommodating training study was found in which the level of torque was <60% of MVIA.

In contrast, the study of Farthing and Chilibeck^[151] seems to confirm the importance of the force developed during training for the hypertrophic response. In their study, subjects trained their elbow flexors in an isokinetic dynamometer, with concentric actions for one arm and eccentric actions for the other arm. One group trained with fast (180°/s) and another group trained with slow (30°/s) speed, with all groups training three times per week and progressing from 2 to 6 sets of 8 repetitions over the course of the training period, which lasted 8 weeks. The hypertrophic response was evaluated with measurements of muscle thickness by ultrasound. The greatest increase in thickness (≈13% at the middle level) was found in the fast eccentric group, followed by the slow eccentric group (≈7%), the slow concentric group (≈5%) and the fast concentric group (≈2%). The authors interpreted their results as a confirmation of the theory that greater force production leads to greater hypertrophy.

This interpretation may be premature since the protocols differed greatly in terms of torque-time integral and in the volume of work performed. Furthermore, it is possible that a local overtraining response was developing in the slow eccentric group. Support for this possibility comes from an earlier study by Paddon-Jones and colleagues,^[38] who used very similar eccentric training regimens to those in the study of Farthing and Chilibeck.^[151] Their results generally showed increases in elbow flexor torque for both fast and slow eccentric training after 5 weeks of training, but at 10 weeks the torque values of the slow group were either halted or even back to the baseline values while the fast group

continued to gain. The authors suggested that the great cumulative stress of the slow protocol had caused an overtraining-like response. The results of Shepstone et al.^[138] confirmed the findings of Farthing and Chilibeck^[151] regarding the superiority of fast versus slow eccentric training for the hypertrophic response of the elbow flexors. However, this study is open to the same interpretation regarding the possibility of a local overtraining response in the slow eccentric group, since the difference in torque-time integral between the fast and slow protocol was even greater (>10-fold) than in the preceding studies. Moreover, the slight differences in peak torque between the fast and the slow eccentric velocities in the studies mentioned here argues against the level of torque as the primary explanation for the differences observed in the hypertrophy of the elbow flexors. Recruitment differences between fast and slow eccentric velocities cannot be excluded as a contributing factor; however, at present there is not enough evidence to support that this occurs. Nevertheless, the considerable difference in hypertrophy between fast eccentric and both fast and slow concentric training in the study of Farthing and Chilibeck^[151] lends support to the hypothesis that the force developed by the muscle during training is an important factor for hypertrophy.

At present, there are no accommodating resistance training studies that have investigated the impact of different eccentric velocities and/or different levels of torque development during eccentric muscle actions on the CSA of the human quadriceps as measured by scanning methods. There is also a lack of direct comparisons using accommodating concentric training at different velocities and/or different levels of torque development. The studies reviewed in this article suggest that hypertrophy can be induced with a range of concentric velocities. The upper limit of concentric velocity that is still capable of inducing hypertrophy is not known, but type 1 fibre hypertrophy has been observed after training at 240°/s^[152] and type 2 fibre hypertrophy after training at velocities as high as 300°/s.^[153] While being quite high compared with the cadence of conventional resistance training, these velocities are still well be-

low the reported maximum velocity of unloaded knee extensions, which may reach values of $\approx 700^\circ/\text{s}$.^[154]

In support of the use of moderately fast concentric training, an early study by Thomeé et al.^[155] showed a clear trend (but not significant) for hypertrophy of type 2 muscle fibres ($\approx 30\text{--}35\%$) in the vastus lateralis in both the healthy and the injured limbs in individuals undergoing moderately fast (180°/s) isokinetic concentric training after reconstruction of the anterior cruciate ligament (ACL). No such trend was apparent in either limb in the group that trained at a low velocity (60°/s). The training was carried out three times per week for 8 weeks, with the slow velocity group progressing from 3 sets of 10 repetitions to 10 sets of 10 repetitions and the fast group from 3 sets of 15 repetitions to 10 sets of 15 repetitions during the time course of the study. A CT scan was also performed of the quadriceps and vastus lateralis at mid-thigh level, but unfortunately too few scans were available due to problems with the scanner, thus making it impossible to confirm or reject the trend of the fibre CSA data at the whole muscle level. However, a study by Froböse and colleagues^[156] also supports the use of moderately fast concentric training for the quadriceps, at least in the rehabilitation setting. These authors investigated the effects of isokinetic concentric training in patients that had undergone reconstruction of the ACL and they showed hypertrophy of the quadriceps in response to moderate (150°/s) and fast (240°/s) protocols, which was at least equal to that of the slow protocol (60°/s). Thus, it appears that hypertrophy can be induced in the human quadriceps as a result of concentric training at velocities of up to at least 240°/s and torque levels as low as $\approx 50\%$ of MVIA.

However, the largest increase ($\approx 18\%$ at mid-thigh level), as well as the by far highest rate of increase in quadriceps CSA (0.44% per day) for accommodating training, was noted in the study by Rafeei,^[104] who trained subjects with 5 sets of 10 concentric muscle actions at 90% of the maximum torque at 60°/s, three times per week for 6 weeks. An interesting feature of the study of Rafeei^[104] was that

the subjects trained at the same absolute torque throughout the study. Another notable feature was the generous rest periods, with 5 seconds between each concentric action and 120 seconds between each set. The level of effort was probably high enough to recruit most of the motor units, while the high but not maximal force level and the generous rest periods may have minimised muscle damage and fatigue of fast fibres, thus allowing the muscle to hypertrophy already in the initial stages of training.

Regarding dynamic external resistance training, the range of intensities that can produce hypertrophy is even more remarkable than in the case of accommodating resistance. Studies^[83,84] have shown marked increases in CSA in response to loads as low as 20% of 1RM when the exercise has been combined with partial restriction of the blood flow by means of thigh tourniquets. Even so, consideration of the recruitment of motor units during fatiguing exercise with low loads reveals that the results of the studies of Takarada et al.^[83] and Abe et al.^[84] do not necessarily disprove the theory that tension is a major determinant of the hypertrophic response. A study by Greenhaff and co-workers^[157] showed a greatly increased rate of glycogenolysis in type 1 fibres and a marked decline in force and near total depletion of phosphocreatine in both fibre types during intermittent electrical stimulation of the quadriceps with the blood flow occluded. In contrast, the decline in force during the same protocol of stimulation but with intact circulation was ascribed almost solely to fatigue in type 2 fibres. Although Greenhaff et al.^[157] used electrical stimulation instead of voluntary activation, their findings are of relevance for the development of fatigue under circumstances where the blood supply to the working muscle is limited, for example by a tourniquet and/or by the raised intramuscular pressure during the continuously performed coupled concentric-eccentric muscle actions that conventional resistance training usually consists of. With a decline in force in type 1 fibres, more type 2 fibres would have to be recruited and towards the end of each set, the remaining force-producing fibres could be exposed to

relatively high tensions. It is also possible that some fast fibres are preferentially recruited during eccentric actions and that this may occur at loads as low as 25% of MVIA.^[158] Thus, it may be too simplistic to estimate the stress imposed on each muscle fibre merely by the magnitude of the external load.

In summary, although there may well exist a level of tension below which no hypertrophy occurs, the relationship between the training load and the hypertrophic response is complex. Achieving recruitment of the greatest possible number of motor units in the target muscle(s) and making these motor units fire at high rates and for sufficient lengths of time are obvious prerequisites for inducing significant hypertrophy. Still, it appears that maximal loads are not necessary to ensure that these conditions are met providing that the training is performed with close to maximum effort in at least one of the sets. Thus, the results of this review support the typical recommendations with intensity levels of 70–85% of maximum when training for muscle hypertrophy, but also show that marked hypertrophy is possible at both higher and lower loads. However, placing high mechanical stress on the working muscle may result in local overtraining if the duration of work is long. Some of the possible interactions between the level of tension, duration of exercise, mode of exercise and muscle damage will be discussed in section 4.6. The impact of intensity in more advanced athletes remains poorly defined due to the lack of objective scientific data.

4.3 Volume

A notable trend in the several types and modes of strength training reviewed in this article was the occurrence of a plateau in the hypertrophic adaptations after a certain point of volume or duration of work had been reached. In some of the results, there is even a suggestion of a decline when the volume or duration is extended beyond the point of the plateau. Again, it must be noted that no studies were found that investigated the effects of 1 or 2 sets on muscle CSA or muscle volume of the quadriceps or elbow flexors. That said, figure 11, for the total repetitions for DER training of the elbow flexors, suggests a

dose-response curve where greater gains in muscle mass are noted initially with increasing volume (or duration) of work, but with diminishing returns as the volume increases further. Overall, moderate volumes (≈ 30 – 60 repetitions per session for DER training) appear to yield the largest responses.

However, two notable exceptions^[125,126] also appear in figure 11, which demonstrate that high rates of growth can be achieved with a relatively small number (≈ 12 – 14) of repetitions per session under some circumstances. In the first of these studies,^[125] very high loads (≈ 90 – 100% of 1RM) were used for both the concentric and the eccentric phases and in the other study,^[126] extremely high loads (progressing from 130 to 230% of 1RM) were used for the eccentric phase. As can be seen in figure 10, the majority of the other datapoints were distributed between 60 and 90% of 1RM. A further example demonstrating that significant hypertrophy can be induced with a surprisingly small number of muscle actions at very high loads, at least in previously untrained subjects, can be found in a study by Hawkins et al.,^[148] who showed that a total of 9 maximal eccentric muscle actions was sufficient to induce significant increases in thigh lean mass, while 12 maximal concentric actions was not. Thus, the relationship between volume and the hypertrophic response may differ between different levels of torque and/or types and modes of strength training. The discrepancy between different studies in terms of the volume needed to induce hypertrophy may, in part, be related to differences in the total duration of muscle activity per session. In many studies, neither the velocity nor the duration of each repetition were reported.

To date, relatively few studies have directly compared the effects of different volumes of work on the hypertrophic response as measured by scanning methodology. These few studies^[146,159–161] used less accurate measures of muscle mass rather than muscle CSA or volume, or scanned only parts of the muscle groups, and it is therefore difficult to compare these with studies in which whole muscle scans were performed with MRI, CT or UL. However, in two of these studies,^[159,160] significant increases in

muscle thickness were demonstrated after as little as 1 set of 8–12 repetitions of specific exercise per muscle group. Because of this and given the relative paucity of data, especially regarding the early part of the volume continuum (i.e. 1–20 total repetitions), there is clearly a need for further research on the impact of training volume on whole muscle CSA. This appears to be true for both previously untrained and well-trained individuals.

However, recent data from Ronnestad et al.^[162] provide further support to the notion of a dose-response relationship between the training volume and the hypertrophic response of the quadriceps. These authors reported superior increases in quadriceps CSA for a total of 6 sets (11.3%) versus 2 sets (7.6%) of quadriceps exercise (two exercises of 1 or 3 sets each at 7–10RM) at an exercise frequency of three times per week for 11 weeks. It deserves to be noted that the subjects in this study received a protein supplement prior to each workout. Because it is currently unknown how protein supplementation interacts with training volume, these results may not necessarily apply to strength training that is performed without supplementation.

4.4 Mode of Training and Type of Muscle Action

In the scientific literature relating to the area of resistance training, one sometimes finds categorical statements such as ‘eccentric training produces the greatest muscle hypertrophy’. This review demonstrates that given sufficient frequency, intensity and duration of work, all three types of muscle actions can induce significant hypertrophy at impressive rates and that at present, there is insufficient evidence for the superiority of any mode and/or type of muscle action over other modes and types of training in this regard. Using dynamic external resistance training as an example, one would be tempted to conclude that, if anything, pure eccentric training is actually inferior to both concentric and concentric-eccentric training, as judged by the degree and rate of hypertrophy observed in the studies included in this review. If one instead considers concentric and eccentric training with accommodating resistance,

maximal eccentric training has been slightly more effective than maximal concentric training in the few studies that have directly compared these two types of training. However, the hypertrophic response has been modest in many of the studies comparing the effects of pure concentric versus pure eccentric training and this appears to be true both for accommodating resistance and dynamic external resistance training studies. Thus, the protocols that have been compared may not have been the best of each type. Again, it is noteworthy that both the largest total increase in CSA (18.4%) and the highest rate of increase in CSA (0.44% per day) for the quadriceps for the category of accommodating training was noted for a pure concentric training group.^[104] This was also the second highest rate of increase for any mode of quadriceps training, surpassed only by the shorter study of Abe et al.^[84] The findings of Rafeei,^[104] of greater hypertrophy at the whole muscle level as well as at the muscle fibre level for near maximal concentric versus submaximal eccentric training, expanded on an almost identical study from the same research group,^[163] in which greater fibre hypertrophy was found for concentric training when compared with eccentric training when both regimens were performed at the same torque level.

The divergence in the results of concentric versus eccentric training between different modes (DER vs accommodating resistance) may be due to differences in the characteristics of the resistance for each mode. As discussed in the introduction, when using external resistance (e.g. free weights, weight machines), the torque is not necessarily optimally matched throughout the movement to the individual's strength curve. Herzog et al.^[164] calculated that the internal forces of the three vastus muscles of the quadriceps are at their highest at knee angles of $\approx 60\text{--}80^\circ$ of flexion (full extension is defined here as 0° of flexion), whereafter the forces drops to lower levels with decreasing angles of flexion. At $0\text{--}20^\circ$ of flexion, the forces are low, only $\approx 20\text{--}40\%$ of maximum. Similarly, Ichinose et al.^[165] reported that the force of the vastus lateralis was maximal at 70° of flexion.

If force is an important stimuli in resistance training, it follows that a certain level of torque must be reached for some minimum duration for significant hypertrophy to occur. In the pioneering study of Jones and Rutherford,^[55] who compared pure concentric and eccentric regimens using a variable resistance knee extension device, the authors noted that the subjects activation of the quadriceps was high only near the position of full knee extension. Further inspection of their electromyogram data suggests that the eccentric training was accompanied by slightly less activation than the concentric training and also that the duration of high activity was shorter. Thus, it is possible that less than optimal internal force production and short total durations of high activity contributed to the finding of no difference between the eccentric and concentric training, and to the modest hypertrophy for both protocols in their study. The eccentric and concentric exercise regimens in the studies of Housh et al.^[68,69] may have shared the same problem, as the resistance in their device was greatest near full extension. Nonetheless, the studies of Jones and Rutherford,^[55] Smith and Rutherford^[62] and Housh et al.^[68,69] show that at least for the mode of dynamic external resistance training, the greater loads that are possible with eccentric training (compared with concentric training) do not necessarily translate into greater gains in muscle size.

Among the accommodating modes, the isoinertial flywheel knee-extension model of Tesch and colleagues^[27,87,105,118] has so far consistently induced hypertrophy of the quadriceps CSA at high rates (0.17–0.22% per day). It is not immediately obvious why this mode seems to be more effective than most of the isokinetic regimens that have also used maximal eccentric actions. In the flywheel study of Tesch et al.,^[27] the subjects were instructed to resist only gently during the first part of the eccentric action and then apply maximum force. The torque-angle curves in the same study^[27] show that high eccentric forces were reached only during a rather short arc of $\approx 20\text{--}25^\circ$, from $\approx 65\text{--}90^\circ$ of flexion. In contrast, during isokinetic eccentric exercise, maximum effort is usually applied from the start and data^[166,167] col-

lected at similar average velocities show that high eccentric forces can be achieved through an arc of at least 40°. However, maximum eccentric efforts at extended knee angles are often perceived as uncomfortable.^[168] In the isokinetic study of Seger et al.,^[102] four of five subjects in the eccentric training group had frequent complaints of knee pain during the training, which may have affected the hypertrophic adaptations. Interestingly, Holder-Powell and Rutherford^[168] showed that much of the discomfort associated with maximum isokinetic eccentric exercise could be avoided if the subjects started to resist later in the arc of motion, from ≈45° of flexion instead of 15° of flexion. Also, the eccentric peak torque was significantly higher when the range of motion was 45–95°, compared with 15–95° of flexion. It could be that the relatively low volumes and short ranges of high-force eccentric exercise in the flywheel studies worked in favour of producing hypertrophy, whereas the isokinetic-eccentric protocols may have resulted in too much stress and strain on the tissues.

Other factors to consider when comparing the isokinetic and flywheel modes are the accelerations and decelerations that occur in the latter mode but by definition not in the former. It has been hypothesised that accelerative and decelerative forces are important components of the stimulus for muscle hypertrophy in resistance training.^[169] To date, there is little evidence to support this hypothesis. Collectively, the successes of both the dynamic, isokinetic and isometric modes in producing muscle hypertrophy does not appear to support accelerations and/or decelerations as being particularly important for the hypertrophic response. However, although the angular velocity in isokinetic training is controlled, the fascicle velocity in the working quadriceps varies markedly through the range of motion.^[170] Furthermore, isokinetics usually involve a brief build up of speed before the isovelocity phase is reached and a short braking period after the isovelocity phase.^[170] Thus, from a muscle point-of-view, accelerations and decelerations occur even during 'isokinetic' exercise. It should also be noted that with weight-based resistance training, accelerations and decelerations

can result in far greater peak loads than the nominal load.^[129] The significance, if any, of these very high but momentary forces for the hypertrophic response remains to be explored. We speculate that differences in torque profile, torque-time integral and motor unit recruitment account for some of the differences in the hypertrophy observed between studies where the training variables have been nominally similar. Also, if strenuous eccentric training is performed at a high frequency, the hypertrophic response may become compromised. These interactions will be discussed in greater detail in section 4.6.

In summary, all modes reviewed here seem capable of inducing marked hypertrophy, at least in the short term. This is not to say that some method or combination of modes will not emerge as superior in the long term. The ideal proportions between the different types of muscle actions are still a subject of debate rather than a scientific certainty.

4.5 Rest Periods and the Role of Fatigue

Because too many studies did not report the rest periods between sets (and repetitions), we opted not to try to evaluate any trends. However, some elaboration regarding the potential impact of rest periods is possible. Closely associated with rest periods is the role of fatigue in strength training. Regarding strength, some studies^[171,172] have shown that short rest periods between sets and/or repetitions are superior to longer ones, whereas other studies^[173] have concluded that longer periods are superior to shorter ones, while yet other studies^[174] have reported no difference. Upon closer examination, it appears that when maximal or near-maximal efforts are used, it is advantageous to use long periods of rest. This is logical in light of the well known detrimental effects of fatigue on force production and electrical activity in the working muscle. If high levels of force and maximum recruitment of motor units are important factors in stimulating muscle hypertrophy, it makes sense to use generous rest periods between sets and repetitions of near-maximal to maximal efforts.

It is interesting that for the accommodating and isometric categories, the studies in which the highest

rates of muscle growth were found^[104,106] did include long rest periods. Furthermore, in the DER training study^[92] that reported the highest rate of CSA increase (0.26% per day), very long rest periods (10 minutes) between working sets were used, but in this study the volume was periodised, which may also have impacted on the results. It is also worth noting that maximum isokinetic-concentric exercise performed with little rest between each muscle action is associated with a marked decline in peak torque during each working set, whereas little or no decline occurs during maximum eccentric exercise.^[175-177] Hence, it can be hypothesised that if the rest periods are too short during near-maximal concentric exercise, the training effects will be compromised.

Although eccentric exercise generally produces little acute fatigue, it appears that it is dependent on the training velocity (and probably also the work-to-rest ratio), with faster eccentric velocities producing less fatigue than slower velocities (see Tesch et al.^[175] for a discussion). The difference in acute fatigue development between concentric and eccentric muscle actions and also between fast and slow eccentric muscle actions have obvious implications for comparisons between these modes in regard to training effects. On the other hand, when using submaximal resistance, the size principle dictates that motor unit recruitment and firing rates are probably far from maximal until the muscle is near fatigue or unless the repetitions are performed with the intention to execute the movement very quickly.

The importance of exercising with near-maximal effort when using submaximal resistance in conventional strength training has been elegantly demonstrated by Goto and co-workers.^[85] In their study, two groups of untrained subjects performed 5 sets of 10 repetitions of dynamic knee extensions at a load of 10RM ($\approx 75\%$ of 1RM), two times per week for 12 weeks. One group performed all 10 repetitions in each set in a continuous manner to muscular failure, while the other group performed 5 repetitions and then rested for 30 seconds before performing the remaining 5 repetitions. Thus, although the volume was matched between the groups, the subjects of the

latter group trained with considerably less effort in comparison to the first group. The results showed a dramatic difference in the extent of hypertrophy in favour of the group that trained in a continuous manner (12.9% increase in quadriceps CSA), versus the group that rested in the middle of each set (4.0% increase in quadriceps CSA). The authors speculated that both increased recruitment of motor units and a greater acute hormonal response could have contributed to the greater hypertrophy seen after the continuous protocol. However, along with the increased stress on the muscle with shorter rest periods at submaximal resistance, the potential for overtraining may also increase. In a study by Folland and colleagues,^[174] conventional resistance training with multiple sets to muscular failure and very short rest periods (30 seconds) led to considerable delayed onset muscle soreness during the first week of training. With this type of training, caution with the training frequency and volume appears to be warranted.

The impact of rest periods may extend beyond the effects on fatigue and motor unit recruitment. Using a rat muscle model, the research group of Faulkner has, in a series of studies,^[178-180] investigated the effects of electrical stimulation against the deleterious effects of denervation on muscle mass. They showed that denervated muscle is sensitive to both the total number of muscle actions and the distribution of loading. For example, 100 muscle actions per day generated at a constant interval over 24 hours was sufficient to maintain muscle mass and force, but the same number of muscle actions distributed over just 4 hours per day (and consequently 20 hours of rest in between) failed to maintain mass and force. Although these findings may not necessarily extrapolate to intact innervated human muscle, they show that skeletal muscle, at least under some circumstances, is sensitive to both the total number of muscle actions and the distribution of them. Future studies should examine the potential impact of both shorter (seconds) and longer (minutes, hours) rest periods on skeletal muscle hypertrophy and hypertrophic signalling in this light.

4.6 Interactions Between Frequency, Intensity, Volume and Mode

After acknowledging that the training volume seems to influence the hypertrophic response to a certain extent, the question arises of what aspect of volume is the most important determinant of this response? Is it the total mechanical work performed or is it the time-tension integral of the activity? Based on the available evidence, we suggest that the time-tension integral is a more important parameter than the mechanical work output (force \times distance).

The elbow flexor eccentric training studies of Refsnes,^[126] Paddon-Jones et al.,^[38] Farthing and Chilibeck^[151] and Shepstone et al.^[138] provide insight into some of the complex interactions that takes place between the training variables of frequency, intensity, volume and mode of resistance training. If one considers the last two of these studies, one finds that the external work output (expressed as total number of repetitions \times the torque developed) was likely to be similar between the slow and fast eccentric groups because of the marginal difference in maximum torque between the slow and the fast velocities. In contrast, the total duration and the torque-time integral between the groups were vastly different, ≈ 6 – 10 -fold greater for the slow groups compared with the fast groups. The studies of Farthing and Chilibeck^[151] and Shepstone et al.^[138] are difficult to compare with each other in terms of the degree of hypertrophy achieved because different measures of muscle mass were used (muscle thickness vs muscle CSA). Still, the hypertrophic response noted for the fast eccentric group appears to be larger in the Farthing and Chilibeck study^[151] ($\approx 13\%$ increase in muscle thickness) than the 8.5% increase in CSA reported by Shepstone et al.^[138] Because thickness measures only one dimension of the muscle, the increase in elbow flexor CSA was likely to be greater than 13% . If the muscle grew equally in width as it did in thickness, the result would be an increase in CSA of 27.7% . This scenario seems unlikely, because a triceps training study by Kawakami et al.^[181] showed that an increase of 31.7% in elbow extensor area was accompanied by an increase in thickness of 27.0% . If the same ratio

of ≈ 1.17 between the increase in CSA and thickness is applied to the elbow flexors in the study of Farthing and Chilibeck,^[151] one arrives at an estimated increase in CSA of $\approx 15\%$ for the fast eccentric training group.

The training groups of Farthing and Chilibeck^[151] progressed from 2 sets of 8 repetitions to 6 sets of 8 repetitions, resulting in an average total duration of muscle activity per session of 22 and 132 seconds for the fast and slow eccentric groups, respectively. In the study of Shepstone et al.,^[138] the progression was from 1 set of 10 repetitions to 4 sets of 10 repetitions and the corresponding average total durations of muscle activity per session were 14 and 146 seconds for the fast and slow eccentric groups, respectively. We suggest that the slightly greater total duration for the fast group in Farthing and Chilibeck^[151] versus Shepstone et al.^[138] was responsible for the greater hypertrophic response in the former study. On the other hand, with the slow-velocity protocols, the cumulative damaging effects of the long durations of maximum eccentric exercise may have counteracted the hypertrophy so that this became less in comparison with the fast training. The study of Refsnes,^[126] using a dynamic constant resistance training model in which the eccentric phase was overloaded (progressing from 130% to $\approx 230\%$ of 1RM during the time course of the study) also attests to the effectiveness of short durations of maximum eccentric exercise for inducing increases in elbow flexor CSA. In this study, the volume was carefully progressed from 2 sets of 2 repetitions to 5 sets of 4 repetitions during the 8 weeks of the study, resulting in a maximum duration of ≈ 14 – 16 seconds of near-maximal eccentric work. The velocity in the eccentric phase was moderate, ≈ 80 – $90^\circ/\text{s}$. The concentric phase was loaded with only 30% of 1RM, and the contribution of the concentric phase to the hypertrophic response was therefore probably small. The subjects increased their elbow flexor CSA by 21.5% (0.38% per day), an impressive increase especially when considering the very brief duration of work.

The risk for overtraining with long durations of high-force eccentric exercise is supported by a study

by Amiridis *et al.*,^[182] who compared different modes of training in a group of young elite female basketball players after a period of very strenuous training for the knee extensors. During the first 12 weeks, all subjects performed 8 sets of 8 concentric repetitions at 70% of 1RM and 8 sets of 8 eccentric repetitions at 110% of 1RM in the leg press, 4 sessions per week. At 12 weeks, the subjects had significantly reduced performances in both the leg press and the countermovement jump, indicating that they were overtrained. During the second 12 weeks of training, the subjects were divided into three groups that performed different modes of recovery training, 4 sessions per week. The first group trained with 8 sets of 8 concentric repetitions at 70% of 1RM; the second group completed 4 sets of 8 concentric repetitions at 70% of 1RM and 4 sets of 8 eccentric repetitions at 110% of 1RM; and the third group performed 8 sets of 8 eccentric repetitions at 110% of 1RM. Compared with values from the first 12 weeks overtraining, all groups increased their performance in the leg press and the countermovement jump, but only the pure concentric group noted significant increases in leg-press strength (39%), isokinetic strength (11–43%) and vertical jump (15%) in comparison with the pre-training values. Although no morphological data was presented in this study, it is likely that some degree of overtraining at the muscle level was responsible for the poor performance at 12 weeks. It is also interesting to note that despite reduced total volume in comparison with the first 12 weeks, neither the pure eccentric nor the combined concentric-eccentric groups experienced any supercompensation in performance, whereas the pure concentric group did. Thus, it would appear that moderate-force concentric training was better tolerated than high-force eccentric training, at least for the moderately high volumes and the rather high training frequency used in this study. Taken together, the results of these studies support the common recommendation of using somewhat lower frequencies and volumes for high-force eccentric exercise than for conventional resistance training.

On the other hand, studies by LaStayo and colleagues^[183,184] using eccentric cycling at submaximal intensities for long durations (≈ 20 – 30 minutes) have shown very rapid and large gains in MFA (≈ 50 – 60%). Recently, a case report^[185] was published that showed that marked hypertrophy is evident also at the whole muscle level after this type of training. In these regimens, up to ≈ 1000 – 2000 eccentric muscle actions were performed during each training session, three times per week. The absolute intensity level was reported in watts, so it is difficult to quantify the forces in terms of percentage of MVIA. Nevertheless, these studies^[183–185] show that given careful and gradual progression of exercise intensity and duration, human skeletal muscle can tolerate and adapt to prolonged submaximal-eccentric exercise.

Overall, we feel that the trends observed in this review are consistent with the model for training-overtraining continuum proposed by Fry,^[186] where the optimal training volume and also the volume threshold for overtraining decreases with increasing intensity. The study of Abe *et al.*^[84] is especially intriguing in this context because of the combination of very low intensity and extremely high frequency. To the best of our knowledge, no studies to date have investigated the effect of performing two strength training sessions during the same day on skeletal muscle protein synthesis, so it is not known whether there is any additional benefit in doing so compared with performing just a single session. If the sensitivity of skeletal muscle protein synthesis to mechanical stimuli is regained during the same day and if there is room for further elevations of the net protein synthesis, then it would make sense to perform more than one session per day. This could explain the results of Häkkinen and Kallinen,^[61] although the effects of tapering down the volume (and hence, the total stress per session imposed on the muscle) also remain a possibility. As pointed out in the discussion concerning rest periods (section 4.5), mechanistic investigations concerning the effects of different distributions of loads and rest periods on skeletal muscle mass and/or intracellular hypertrophic signalling are largely lacking. It is also

uncertain whether the mechanosensitivity of skeletal muscle decreases with long periods of strength training. Until these and other dose-response relationships become more fully characterised, it will remain difficult to prescribe a proper 'dosage' of training for each mode of training and type of muscle action for the specific purpose of inducing hypertrophy.

Regarding training for hypertrophy in already highly-trained individuals, there is at present insufficient data to suggest any trends in the dose-response curves for the training variables. It has been suggested by some authors^[187] that the volume needed to induce optimal gains in strength, increases with training status, so that advanced trainers and elite athletes will have to perform far more sets (≥ 10 sets per muscle group) than untrained and recreational lifters ($\approx 4\text{--}5$ sets per muscle group). Other authors emphasise the importance of load and the type of muscle action. Refsnes^[188] has reported preliminary findings from unpublished studies, which indicate that very well-trained athletes respond to eccentric overload training with greater hypertrophy than after conventional training. Recently, a study by Vikne and colleagues^[137] demonstrated significantly larger increases in elbow flexor area in well-trained individuals after pure eccentric training (11% increase) than after concentric training (3% increase). It should be noted that the volume was not equalised between the groups and it also seems likely that the total duration of work was markedly longer for the eccentric group, thus resulting in large differences in time-tension integral between the protocols. Hence, although the results suggest a clear superiority of pure eccentric exercise versus pure concentric exercise for inducing hypertrophy in well-trained subjects, other variables cannot be ruled out as contributing factors. Seemingly at odds with the observations of Refsnes^[188] and Vikne et al.,^[137] Brandenburg and Docherty^[133] showed no difference in muscle CSA after eccentric-overload training for the elbow flexors and the elbow extensors compared with conventional training. In their study,^[133] coupled concentric-eccentric repetitions were performed in both groups and the total volume

was similar between the groups. Needless to say, more research is needed regarding interactions between variables in both trained and untrained subjects.

Finally, a comment on the interactions between strength and endurance training is warranted. It has been recommended that both strength and endurance training should be included in a well-rounded training programme.^[189] The additive effects of strength and endurance training on various parameters of health status have been shown in several studies.^[190-192] Recently, it has been demonstrated that while strength training by itself can lead to increased arterial stiffness, this negative effect can be offset if endurance training is performed concurrently.^[193] From a strength training point of view, there is an interest in how to train concurrently without affecting strength and hypertrophy negatively. It has been suggested that strength training should be performed first, in order not to compromise the quality of the strength-training session.^[194] However, this order may not necessarily be the best choice for inducing increases in muscle mass. Deakin^[195] investigated the impact of the order of exercise in combined strength and endurance training and reported that gene expression associated with muscle hypertrophy responded more strongly when cycling was performed before strength training, instead of vice versa. Interestingly, in the study of Sale et al.,^[111] performing cycling first seemed to induce the greatest increase in muscle area. Still, because the lack of studies investigating the effects of the order of exercise in concurrent training on hypertrophy, no firm conclusions can be drawn on this issue.

4.7 Time Course of Muscle Hypertrophy

Strength gains as a result of a period of resistance training are usually attributed to two major factors: (i) neural adaptations; and (ii) hypertrophy.^[196] Until recently, the prevailing opinion has been that neural adaptations play the dominant role during the first 6–7 weeks of training, during which hypertrophy is usually minor. However, as noted by Staron and co-workers^[196] and by Sale,^[197] it appears that the hy-

hypertrophy process begins earlier than this, as trends for increased fibre CSAs can be observed at 2 weeks into the training period. In the studies of Mayhew et al.^[163] and Rafeei,^[104] significant increases in fibre CSA (type 1 = 12–14%; type 2 = 26–28%) were observed for the concentric training groups as early as 4 weeks into the training. In the latter study,^[104] further hypertrophy had occurred at 6 weeks, which was also manifested at the whole muscle level ($\approx 18\%$ increase in quadriceps CSA at mid-thigh level). In the study of Abe et al.,^[84] significant increases in muscle volume were noted after just 2 weeks and several other investigations^[13,27,54,87,105,118,128] have also demonstrated significant hypertrophy at the whole muscle level after short periods of training (3–5 weeks). Thus, there is now plenty of evidence that significant hypertrophy can take place early on given proper frequency, intensity and volume of training.

Based on the observation of positive muscle-protein balance after an isolated session of resistance exercise, Phillips^[198] has proposed that a gain in active force-producing myofibrillar proteins could occur after a single strength-training session and that this increase may take place without a change in fibre CSA. In line with this idea, Willoughby and Taylor^[199] reported an increase in myofibrillar content in muscle biopsies obtained from previously untrained young men after just three strength-training sessions, with sessions separated by 48 hours of rest. As argued by Phillips,^[198] the idea that early gains in strength are due exclusively to neural adaptations seems doubtful. Judging from the studies included in this review, the hypertrophy process actually seems to be most rapid during the first 6 weeks, after which the rate declines slowly. Because the majority of studies have only investigated a time period of up to 12 weeks, it is difficult to assess how the rate of protein accretion is affected by longer periods of training. A study by Sale et al.^[112] suggests that relatively high rates of increase in muscle CSA (0.22–0.24% per day) may be possible to maintain for periods of up to 20 weeks, but unfortunately no mid-point data were available from this investigation. Therefore, it cannot be excluded

that the majority of the increase took place during the first 10 weeks of training.

Little is also known about how different training variables and modes interact with the length of the training period. In some strength-training studies, the increase in muscle volume is delayed, while in others, the rate of growth is rapid. We speculate that less-damaging training modes may allow the hypertrophy response to start earlier. Regimens that include eccentric muscle actions, especially those involving maximal effort, appear to require a careful initiation and progression of training to avoid muscle damage and muscle protein breakdown. In line with the results of Foley et al.,^[200] who noted a long-lasting decrease in elbow flexor muscle volume after an acute session of high-force eccentric exercise, Willoughby et al.^[201] found decreased myofibrillar protein content in muscle biopsies taken from the vastus lateralis after an acute session of 70 near-maximal eccentric actions for the knee extensors. This decrease was accompanied by increases in caspase 3 activity and in the expression of ubiquitin, which the authors interpreted as indicating that apoptosis and increased proteolysis had occurred in the exercised muscle. They also reported a repeated bout effect for most of the parameters after a second session of an identical eccentric protocol. Nevertheless, a trend towards decreased myofibrillar content was evident even after the second session, although this was not significant and certainly of a smaller magnitude than after the first session. In contrast, in the study of Willoughby and Taylor,^[199] where a conventional resistance-training model for the quadriceps was employed, the myofibrillar content appeared to increase from the very first workout, reaching significance after the second session. Clearly, more research into the time course of the hypertrophic process is needed, especially with reference to the effects of different regimens and modes.

4.8 Hypertrophic Response of the Quadriceps versus the Elbow Flexors

It has long been recognised that some muscles are very responsive to the stimulus of strength training,

while others seem more stubborn. One explanation to this phenomenon could be that muscles that are frequently used in everyday activities are already in a trained state, thus leaving less room for improvements in strength and size. For example, the soleus muscle appears to be relatively unresponsive to resistance exercise in comparison with the vastus lateralis and the biceps brachii.^[202] Regarding the latter two muscles, it is commonly held that the elbow flexors are in a less-trained state than the quadriceps.^[128,203] Studies where the hypertrophic response of the quadriceps and the elbow flexors to similar training regimens have been directly compared tend to support this theory.^[48,66,204] The trends reported in this review for conventional resistance training for the quadriceps versus the elbow flexors lend support to this observation, as the CSA of the elbow flexors tended to increase at a greater rate (0.20% per day) than the quadriceps (0.11% per day). Further support comes from a study by Turner and co-workers,^[203] who found marked hypertrophy in the elbow flexors (24% increase in CSA) in response to endurance training for the upper limb (arm cycling to exhaustion for 30 minutes, five times per week for 6 weeks), while leg cycling at the same relative intensity and duration had negligible effects on the mass of the lower limb. Notably, the rate of CSA hypertrophy for the elbow flexors observed in this study (0.57% per day) surpasses all strength-training studies included in this review, except that of Narici and Kayser.^[128] The differences between various muscle groups in the physiological response to similar training regimens warrants some caution in generalising findings from one muscle group to another. Future investigations should study whether the dose-response relationships differ between the elbow flexors and the quadriceps in regard to the major training variables.

4.9 The Stimulus for Muscle Hypertrophy in Strength Training

It is beyond the scope of this article to discuss in any detail the pathways or networks of intracellular signals leading to hypertrophy as a result of a period of increased loading of the muscle(s) involved. Sev-

eral excellent reviews^[205-208] and original investigations^[91,209-213] on various aspects of this topic are available. However, a brief discussion of some of the physiological stimuli occurring during resistance training that may trigger the hypertrophic pathways is relevant. Over 30 years ago, it was suggested by Goldberg and co-workers^[214] that increased tension development (either passive or active) is the critical event in initiating compensatory growth. MacDougall^[215] noted that the loading of the muscle must be very high in order to result in hypertrophy, but that the total duration during which the muscle develops tension also affects the magnitude of the hypertrophy response. He supported this observation with the results of the study of Sale and colleagues,^[125] who showed a tendency for training with 6 sets of 10–12RM to result in larger increases in elbow flexor muscle CSA than training with 6 sets of 1–3RM (33% vs 24%).

Two studies by Martineau and Gardiner^[216,217] have provided insight into how different levels of force and different durations of tension may affect hypertrophic signaling in skeletal muscle. Using rat muscle preparations, these authors noted that mechanically sensitive pathways reacted in a dose-dependent manner to the level of force, so that larger increases in intracellular signaling were seen after eccentric actions when compared with isometric and concentric actions.^[216] In a follow-up study,^[217] they showed that the same pathways were also sensitive to the time-tension integral in a dose-dependent manner. Interestingly, this was the case regardless of whether the total duration was distributed into a few long durations of stretch or many short ones. Also, the rate of stretch had no effect on these pathways. In the latter study,^[217] they remarked that both peak tension and time-tension integral must be included in the modelling of the mechanical stimulus response of skeletal muscle. Some of the pathways that are now recognised as crucial for the hypertrophic response were not assessed in the studies of Martineau and Gardiner,^[216,217] and little is currently known about the response of these pathways to the variables of peak tension and time-tension integral. One of these is the phosphatidylinositol-3 kinase/

protein kinase B/mammalian target of rapamycin pathway,^[205-208] which has several downstream targets, among them the signaling molecule p70 S6 kinase (p70S6K). A recent study by Eliasson et al.^[218] showed that the phosphorylation of p70S6K in the human quadriceps 2 hours after resistance exercise was greater after a total of 24 maximal-eccentric actions compared with 24 maximal-concentric actions and to 24 submaximal eccentric actions. However, this was in the absence of nutritional supply. In contrast, Cuthbertson and colleagues^[219] demonstrated similar increases in p70S6K and muscle protein synthesis after eccentric and concentric exercise. Importantly, in this study the subjects received protein and carbohydrate supplementation immediately post-exercise. Another difference is that a much greater volume of work was performed compared with the study of Eliasson et al.^[218]

Based on the data reviewed in this paper, we speculate that hypertrophic signalling in human skeletal muscle is very sensitive to the magnitude of tension developed in the muscle. Hence, for very short durations of work, the increase in muscle size will be greater for maximal-eccentric exercise than for maximal-concentric exercise of similar durations, as in the studies of Farthing and Chilibeck^[151] and Hawkins et al.^[148] The response is presumably also dependent on the total duration of work and increases initially with greater durations. Thus, both short durations of maximal eccentric exercise and somewhat longer durations of concentric, isometric and conventional dynamic resistance exercise can result in impressive increases in muscle volume. However, especially with maximal eccentric exercise, damage also seems to come into play as the duration of work increases even further and the acute and/or cumulative damage may eventually overpower the hypertrophic process. This could be an explanation for the modest hypertrophy reported in several isokinetic training studies where the eccentric component has been maximal and of moderate-to-long total durations. As discussed by Rennie and colleagues^[205] and Jones and Folland,^[220] other physiological events associated with muscle activa-

tion (e.g. temporarily increased Ca^{2+} levels in the cytosol, metabolite accumulation, ischaemia and acute hormonal changes) may also act as signals for adaptation and interactions between these and mechanically-induced signaling seem plausible. The potential role of acute hormonal responses has been reviewed by Kraemer and Ratamess.^[221]

Apart from mechanical forces, growth factors and hormones, another exercise-related stimuli that has been shown to affect the hypertrophic signaling in skeletal muscle (as assessed by phosphorylation of p70S6K) is heat stress.^[222] Interestingly, both in cultured muscle cells and in skeletal muscle, heat stress and mechanical stretch has been shown to interact so that protein expression and concentration is higher after a combination of the two stimuli than either alone.^[223,224] These authors suggested that a stress-induced heat-shock response may modulate the exercise-induced adaptations of skeletal muscles, for example when combining vascular occlusion with resistance exercise. If an interaction between heat stress and mechanical stimuli occurs during strength training with restricted blood flow, it could, at least in part, explain the success of low-to-moderate intensity training during these conditions in inducing hypertrophy,^[83,84,131] even in highly-trained athletes.^[76,225]

4.10 Suggestions for Future Research

The trends observed in this review could serve as a starting point for experiments aiming to establish efficient models of training for the purpose of gaining and/or preserving muscle mass. Major challenges for future research are to isolate the impact of each of the resistance training variables and to investigate the interactions between them, as well as the effects of various training strategies (e.g. periodization, tapering, changes in type and mode of exercise in order to 'shock' the muscles). We also recommend that future investigations should describe the exercise protocols in greater detail than has generally been the case up until recently. Consequently, variables such as speed, range and duration of each repetition and rest periods between repetitions and sets should also be reported in addition to

the commonly recognised variables of frequency, intensity, volume and mode of exercise.

To date, the vast majority of the research concerning the effects of manipulating training variables have been carried out using DER training. For example, we were unable to locate any accommodating training study that directly compared the effects of different volumes on the hypertrophic response. Because the accommodating training modes can induce hypertrophy at rates comparable to those of conventional weight training, and because the training parameters are easily standardised, these modes are well suited for experiments designed to provide insight into the nature of the dose-response relationships.

In humans, electromyostimulation (EMS) has been proven to result in increases in muscle volume comparable to those seen after voluntary strength training. Since EMS bypasses the CNS, the level of activation of a particular muscle group can be standardised. Combining EMS with isokinetic dynamometry could provide an opportunity to gain further insight into many of the issues discussed in this review, such as the effects of the level of torque, the type of muscle action (concentric vs isometric vs eccentric) and the total duration of activity. However,

because EMS involves motor-unit firing patterns, which are usually very different from those occurring in voluntary exercise, findings from such studies may not necessarily apply to voluntary strength training.

As noted in section 2.1, investigations concerning very well-trained individuals are largely lacking, as are studies extending for longer than the typical 8–12 weeks. Because of this, the knowledge regarding the dynamics of the hypertrophy process past this point is limited. In short-term studies, large increases in the training loads for lower-body exercises such as squats, leg presses and knee extensions are often reported, sometimes on the order of 100–200%.^[18,55,196] Since the gain in quadriceps muscle volume during the same time period rarely exceeds $\approx 15\%$, the stress per unit of muscle area should increase by almost as much as the increase in training weight. The significance of the large increase in the stress on the muscles and its interactions with the volume and frequency of training in terms of the hypertrophic response and the risk for overtraining remains to be explored. Although not discussed in this article, the issue of dose-response effects needs to be addressed in the training of other

Table 1. Recommendations for dynamic external resistance training (e.g. weight-based resistance) for hypertrophy

	Moderate load slow-speed training	Conventional hypertrophy training	Eccentric (ecc) overload training
Muscle action	Con and ecc	Con and ecc	Ecc (con = optional)
Exercise	Single and/or multiple joint	Single and/or multiple joint	Single and/or multiple joint
Load	$\approx 50\%$ of 1RM	8–10RM (range: 6–12) $\approx 75\text{--}80\%$ of 1RM	Ecc = $>105\%$ of 1RM Con = 60–75% of 1RM
Repetitions	8–14 to muscular failure	8–10 to muscular failure or near	4–6
Sets	1–3 per exercise Progression from 1 to 3–4 sets in total per muscle group	1–3 per exercise Progression from 1–2 to 3–6 sets in total per muscle group	1–5 per exercise Progression from 1–2 to 3–5 sets in total per muscle group
Velocity and duration per repetition	Slow Ecc = 2–3 seconds Con = 2–3 seconds	Moderate Ecc = 1–2 seconds Con = 1–2 seconds	Slow/moderate Ecc = 2–4 seconds Con = 1–2 seconds
Rest between sets	30–60 seconds	60–180 seconds	120–180 seconds
Frequency	2–3 sessions per muscle group/week	2–3 sessions per muscle group/week	1–3 sessions per muscle group/week
Comments	Suitable training method for beginners and individuals who cannot tolerate high forces	These recommendations are for novice to moderately trained individuals. Well trained athletes may need increased variation in intensity and volume	Mainly for advanced to elite athletes. Progressive but careful increase of the load and volume for the eccentric phase

Con = concentric; RM = repetition maximum.

Table II. Recommendations for accommodating training for hypertrophy

	Moderately fast concentric (con) training	Slow concentric training	Accommodating eccentric (ecc) overload
Mode	Isokinetic or hydraulic	Isokinetic or hydraulic	Isokinetic or isoinertial flywheel
Muscle actions	Con	Con	Ecc and con (con is optional in isokinetics)
Exercise	Single and/or multiple joint	Single and/or multiple joint	Single and/or multiple joint
Effort ^a	90–100%	90%	Ecc = up to 100% Con = up to 100%
Repetitions	10–15	10	6–8
Sets	3–6 per exercise Progression from 3 to 4–6 sets in total per muscle group	3–5 per exercise Progression from 3 to 5 sets in total per muscle group	1–5 per exercise Progression from 1–2 to 4–5 sets in total per muscle group
Velocity	120–240°/s	45–60°/s	45–60°/s
Rest between repetitions and sets, respectively	1–2 seconds, 60–120 seconds	5 seconds, 120 seconds	0–5 seconds, 120 seconds
Frequency	3–5 sessions per muscle group/week	3 sessions per muscle group/week	2 sessions per muscle group/week

a indicates level of torque in relation to the maximum possible torque at the specified velocity.

populations, such as the elderly and individuals recovering from sports injuries.

4.11 Limitations

We recognise that it is obviously very difficult to separate the impact of each training variable from the effects of the other training variables. For example, if one increases the training load (percentage of 1RM) in conventional weight training, it will also affect the volume of training, unless this is compensated for by increasing the number of sets performed. Furthermore, we acknowledge that the main objective of many of the studies included in this review was not necessarily to maximise the hypertrophic response and that the motivational level of the subjects may well have differed considerably between different studies. Closely associated with motivation is whether the training is performed under supervision or not. Direct supervision of the workout has been shown to result in superior increases in strength when compared with unsupervised training.^[226] The level of supervision during training varied among the studies included in this review.

Apart from the training regimen, the training status is also likely to have an impact on the hypertrophic response. Theoretically, a muscle that is already somewhat hypertrophied has less potential

to hypertrophy further in relative terms than a previously untrained muscle. Conversely, a muscle that has atrophied because of disuse or detraining has a large growth potential and merely getting it back to its previous level will represent an increase in muscle volume if the atrophied state is taken as a baseline. Thus, even slight variations in training status may affect the hypertrophic response to a given resistance training regimen. Also, the method of measuring muscle volume or CSA may influence the results. With earlier scanning techniques, the anatomical CSA of the muscle was measured without correcting for intramuscular fat. Recent methods of MRI and CT allow for measurements of interstitial fat, as well as muscle, and consequently for calculation of adipose tissue-free muscle.^[227] In young healthy subjects, the anatomical muscle area is only slightly larger than adipose tissue-free muscle area.^[227] Hence, any increase in muscle volume as a result of strength training will mainly reflect an increase in adipose tissue-free muscle mass. Therefore, the data from the studies included in this review were pooled irrespective of the muscle-scanning method used. However, because of the factors discussed here and the many other confounding factors that inevitably are present when summarising and comparing the results of many different studies, the dose-response trends and recommenda-

tions outlined in the present review should be regarded as tentative.

4.12 Training Implications and Recommendations

Preliminary recommendations for each mode are given in table I, table II and table III. These are based on the evidence outlined in this article, as well as on training protocols that have been shown to increase muscle mass. However, the tables should not be interpreted as stating that all modes and methods are equally effective in increasing muscle mass. Rather, the aim is to summarise different methods that may be suitable in different situations and for specific populations. For example, fatiguing, low-to-moderate load, slow-speed resistance training^[75,88,92,130] has potential applications for the rehabilitation of patients for whom the high forces of conventional heavy-resistance exercise are contraindicated. For patients who can tolerate relatively high forces, but for whom the metabolic and cardiovascular demands of traditional strength training are too severe, pure eccentric exercise may be an alternative because of the low energy demands of this type of exercise.^[183] Our recommendations for conventional hypertrophy training are similar to those presented in the American College of Sports Medicine posi-

tion stand^[3] and by Kraemer and Ratamess.^[11] We also agree with these authors on the importance of progression and individualisation of the exercise prescription. Regarding progression, we recommend low volumes (e.g. 1–2 sets) in the initial stages of training, when performing eccentric-muscle actions, because low volumes have been shown to be sufficient to induce hypertrophy in the early stages of training and because exercise adherence may be improved if the workout is relatively brief. Also, avoiding unnecessary damage may allow hypertrophy to take place earlier. As the individual adapts to the stimulus of strength training, the overall volume and/or intensity may have to be gradually increased to result in continued physiological adaptations and other strategies (e.g. periodisation) can also be introduced if even further progress is desired.

In this context, it is essential that the trainer or therapist is aware of possible interactions between the training variables and how these, in turn, interact with the exercise tolerance of the individual. For example, a training volume that is appropriate at a frequency of two sessions per muscle group per week may become excessive at three sessions per week. Conversely, a volume that is sufficient at three sessions per week may be less than optimal at two sessions per week. The workout structure (e.g.

Table III. Recommendations for isometric training for hypertrophy

	Low-intensity isometric training	High-intensity isometric training	Maximum-intensity isometric training
Exercise selection	Single and/or multiple joint	Single and/or multiple joint	Single and/or multiple joint
Torque level	30–50% of MVIA	70–80% of MVIA	100% of MVIA
Repetitions	1	1	10
Sets	2–6 per exercise Progression from 2 to 4–6 sets in total per muscle group	2–6 per exercise Progression from 2 to 4–6 sets in total per muscle group	1–3 per exercise Progression from 1 to 3 sets in total per muscle group
Duration per repetition	40–60 seconds, and to muscular failure during the final 1–2 sets	15–20 seconds, and to muscular failure during the final 1–2 sets	3–5 seconds
Rest between repetitions and sets, respectively	30–60 seconds	30–60 seconds	25–30 seconds, 60 seconds
Frequency	3–4 sessions per muscle group/week	3–4 sessions per muscle group/week	3 sessions per muscle group/week
Comments	Suitable for individuals who cannot tolerate high forces and with restricted range of movement due to pain and/or injury	Suitable for individuals who cannot tolerate near-maximal forces	Care should be taken to avoid excessive breath-holding and very high blood pressures

MVIA = maximal voluntary isometric action.

whole-body workout versus single muscle-group training) also has a direct bearing on the appropriate dosage of training. Table I, table II and table II are intended as guidelines for single muscle-group training. If whole-body workouts are performed, the volume of specific work per muscle group may have to be reduced so that the overall volume does not become excessive. For further discussion on the topic of workout design, we refer to the paper of Kraemer and Ratamess.^[1]

5. Conclusions

This review demonstrates that several modes of training and all three types of muscle actions can induce hypertrophy at impressive rates and that, at present, there is insufficient evidence for the superiority of any mode and/or type of muscle action over other modes and types of training. That said, it appears that exercise with a maximal-eccentric component can induce increases in muscle mass with shorter durations of work than other modes. Some evidence suggests that the training frequency has a large impact on the rate of gain in muscle volume for shorter periods of training. Because longer studies using relatively high frequencies are lacking, it cannot be excluded that stagnation or even overtraining would occur in the long term. Regarding intensity, moderately heavy loads seem to elicit the greatest gains for most categories of training, although examples of very high rates were noted at both very low and very high intensities when the sets were performed with maximum effort or taken to muscular failure. Thus, achieving recruitment of the greatest number of muscle fibres possible and exposing them to the exercise stimulus may be as important as the training load *per se*. For the total volume or duration of activity, the results suggest a dose-response curve characterised by an increase in the rate of growth in the initial part of the curve, which is followed by the region of peak rate of increase, which in turn is followed by a plateau or even a decline.

It is recognised that the conclusions drawn in this paper mainly concern relatively short-term training in previously untrained subjects and that in highly-

trained subjects or for training studies extending for several months, the dose-response trends and the hypertrophic effects of different modes and types of strength training may be very different. The same may well be true for other populations, such as elderly and injured individuals.

Acknowledgements

No sources of funding were used to assist in the preparation of this review. The authors have no conflicts of interest that are directly relevant to the content of this review.

References

1. Kraemer WJ, Ratamess NA. Fundamentals of resistance training: progression and exercise prescription. *Med Sci Sports Exerc* 2004; 36: 674-88
2. Escamilla R, Wickham R. Exercise-based conditioning and rehabilitation. In: Kolt GS, Snyder-Mackler L, editors. *Physical therapies in sports and exercise*. London: Churchill Livingstone, 2003: 143-64
3. Kraemer WJ, Adams K, Cafarelli E, et al. American College of Sports Medicine Position Stand: progression models in resistance training for healthy adults. *Med Sci Sports Exerc* 2002; 34: 364-80
4. Rhea MR, Alvar BA, Burkett LN, et al. A meta-analysis to determine the dose response for strength development. *Med Sci Sports Exerc* 2003; 35: 456-64
5. Rhea MR, Alvar BA, Burkett LN. Single versus multiple sets for strength: a meta-analysis to address the controversy. *Res Q Exerc Sport* 2002; 73: 485-8
6. Peterson MD, Rhea MR, Alvar BA. Maximizing strength development in athletes: a meta-analysis to determine the dose-response relationship. *J Strength Cond Res* 2004; 18: 377-82
7. Rhea MR, Alderman BL. A meta-analysis of periodized versus nonperiodized strength and power training programs. *Res Q Exerc Sport* 2004; 75: 413-22
8. Wolfe BL, LeMura LM, Cole PJ. Quantitative analysis of single- vs multiple-set programs in resistance training. *J Strength Cond Res* 2004; 18: 35-47
9. Atha J. Strengthening muscle. *Exerc Sports Sci Rev* 1981; 9: 1-73
10. Behm DG. Neuromuscular implications and applications of resistance training. *J Strength Cond Res* 1995; 9: 264-74
11. Häkkinen K. Neuromuscular adaptation during strength training, aging, detraining, and immobilization. *Crit Rev Phys Rehab Med* 1994; 6: 161-98
12. Fry AC. The role of resistance exercise intensity on muscle fibre adaptations. *Sports Med* 2004; 34: 663-79
13. Choi J, Takahashi H, Itai Y, et al. The difference between effects of 'power-up type' and 'bulk-up type' strength training exercises: with special reference to muscle cross-sectional area, muscular strength, anaerobic power and anaerobic endurance. *Jpn J Phys Fitness Sports Med* 1998; 47 (1): 119-29
14. Masuda K, Choi JY, Shimojo H, et al. Maintenance of myoglobin concentration in human skeletal muscle after heavy resistance training. *Eur J Appl Physiol* 1999; 79: 347-52
15. Schmidtbleicher D, Buehrle M. Neuronal adaptation and increase of cross-sectional area studying different strength train-

- ing methods. In: Jonsson GB, editor. *Biomechanics X-B*, volume 6-B. Champaign (IL): Human Kinetics, 1987: 615-20
16. Stone MH, O'Bryant HS. *Weight training: a scientific approach*. Minneapolis (MI): Bellweather press, 1987
 17. Poliquin C. Five steps to increasing the effectiveness of your strength training program. *Natl Strength Cond Assoc J* 1988; 10: 34-9
 18. Campos GE, Luecke TJ, Wendeln HK, et al. Muscular adaptations in response to three different resistance-training regimens: specificity of repetition maximum training zones. *Eur J Appl Physiol* 2002; 88: 50-60
 19. Reeves ND, Maganaris CN, Narici MV. Ultrasonographic assessment of human skeletal muscle size. *Eur J Appl Physiol* 2004; 91: 116-8
 20. Miyatani M, Kanehisa H, Kuno S, et al. Validity of ultrasonograph muscle thickness measurements for estimating muscle volume of knee extensors in humans. *Eur J Appl Physiol* 2002; 86: 203-8
 21. Ikai M, Fukunaga T. A study on training effect on strength per unit cross-sectional area of muscle by means of ultrasonic measurement. *Eur J Appl Physiol* 1970; 28: 173-80
 22. Knuttgen HG, Komi PV. Basic considerations for exercise. In: Komi PV, editor. *Strength and power in sport*. 2nd ed. Oxford: Blackwell scientific publications, 2003: 3-7
 23. Fleck SJ, Kraemer WJ. *Designing resistance training programs*. 2nd ed. Champaign (IL): Human Kinetics, 1997
 24. Grimby G. Clinical aspects of strength and power training. In: Komi PV, editor. *Strength and power in sport*. Oxford: Blackwell scientific publications, 1992: 338-54
 25. O'Hagan FT, Sale DG, MacDougall JD, et al. Comparative effectiveness of accommodating and weight resistance training modes. *Med Sci Sports Exerc* 1995; 27: 1210-9
 26. Baker D, Wilson G, Carlyon B. Generality versus specificity: a comparison of dynamic and isometric measures of strength and speed-strength. *Eur J Appl Physiol* 1994; 68: 350-5
 27. Tesch PA, Ekberg A, Lindquist DM, et al. Muscle hypertrophy following 5-week resistance training using a non-gravity-dependent exercise system. *Acta Physiol Scand* 2004; 180: 89-98
 28. Caruso JF, Hamill JL, Hernandez DA, et al. A comparison of isoloal and isoinertial leg press training on bone and muscle outcomes. *J Strength Cond Res* 2005; 19: 592-8
 29. Murphy AJ, Wilson GJ. The assessment of human dynamic muscular function: a comparison of isoinertial and isokinetic tests. *J Sports Med Phys Fitness* 1996; 36: 169-77
 30. Hoeger WWK, Hopkins DR, Barette SL, et al. Relationship between repetitions and selected percentages of one repetition maximum: a comparison between untrained and trained males and females. *J Appl Sports Sci Res* 1990; 4: 47-54
 31. Hickson RC, Hidaka K, Foster C. Skeletal muscle fiber type, resistance training, and strength-related performance. *Med Sci Sports Exerc* 1994; 26: 593-8
 32. Wathan D. Load assignment. In: Baechle T, editor. *Essentials of strength training and conditioning*. Champaign (IL): Human Kinetics, 1994: 435-9
 33. LaSuer DA, McCormick JH, Mayhew JL, et al. The accuracy of prediction equations for estimating 1-RM performance in the bench press, squat, and deadlift. *J Strength Cond Res* 1997; 11: 211-3
 34. Dudley GA, Harris RT, Duvoisin MR. Effect of voluntary vs artificial activation on the relationship of muscle torque to speed. *J Appl Physiol* 1990; 69: 2215-21
 35. Amiridis IG, Martin A, Morlon B, et al. Co-activation and tension-regulating phenomena during isokinetic knee extension in sedentary and highly skilled humans. *Eur J Appl Physiol* 1996; 73: 149-56
 36. MacDougall JD. Adaptability of muscle to strength training: a cellular approach. In: Saltin B, editor. *Biochemistry of Exercise VI*. Champaign (IL): Human Kinetics, 1986: 501-13
 37. Hortobagyi T, Katch FI. Eccentric and concentric torque-velocity relationships during arm flexion and extension: influence of strength level. *Eur J Appl Physiol* 1990; 60: 395-401
 38. Paddon-Jones D, Leveritt M, Lonergan A, et al. Adaptation to chronic eccentric exercise in humans: the influence of contraction velocity. *Eur J Appl Physiol* 2001; 85: 466-71
 39. Atherton PJ, Babraj J, Smith K, et al. Selective activation of AMPK PGC-1 α or PKB-TSC2-mTOR signaling can explain specific adaptive responses to endurance or resistance training-like electrical muscle stimulation. *FASEB J* 2005; 19: 786-8
 40. Deschenes MR, Kraemer WJ. Performance and physiologic adaptations to resistance training. *Am J Phys Med Rehabil* 2002; 81 (11 Suppl.): S3-16
 41. Maughan RJ, Watson JS, Weir J. Muscle strength and cross-sectional area in man: a comparison of strength-trained and untrained subjects. *Br J Sports Med* 1984; 18: 149-57
 42. Narici MV, Roi GS, Landoni L, et al. Changes in force, cross-sectional area and neural activation during strength training and detraining of the human quadriceps. *Eur J Appl Physiol* 1989; 59: 310-9
 43. Narici MV, Hoppeler H, Kayser B, et al. Human quadriceps cross-sectional area, torque and neural activation during 6 months strength training. *Acta Physiol Scand* 1996; 157: 175-86
 44. Aagaard P, Andersen JL, Dyhre-Poulsen P, et al. A mechanism for increased contractile strength of human pennate muscle in response to strength training: changes in muscle architecture. *J Physiol* 2001; 534: 613-23
 45. Ahtiainen JP, Pakarinen A, Alen M, et al. Muscle hypertrophy, hormonal adaptations and strength development during strength training in strength-trained and untrained men. *Eur J Appl Physiol* 2003; 89: 555-63
 46. Ahtiainen JP, Pakarinen A, Alen M, et al. Short vs long rest period between the sets in hypertrophic resistance training: influence on muscle strength, size, and hormonal adaptations in trained men. *J Strength Cond Res* 2005; 19: 572-82
 47. D'Antona G, Lanfranconi F, Pellegrino MA, et al. Skeletal muscle hypertrophy and structure and function of skeletal muscle fibres in male body builders. *J Physiol* 2006; 570: 611-27
 48. Housh DJ, Housh TJ, Johnson GO, et al. Hypertrophic response to unilateral concentric isokinetic resistance training. *J Appl Physiol* 1992; 73: 65-70
 49. Tracy BL, Ivey FM, Hurlbut D, et al. Muscle quality: II. Effects of strength training in 65- to 75-yr-old men and women. *J Appl Physiol* 1999; 86: 195-201
 50. Aagaard P, Simonsen EB, Andersen JL, et al. MRI assessment of quadriceps muscle size before and after resistance training: determination of volume vs single-site CSA. *Med Sci Sports Exerc* 2001; 33 (5 Suppl.): S147
 51. Tracy BL, Ivey FM, Metter EJ, et al. Muscle volume measurement: single vs multiple axial MRI slices. *Med Sci Sports Exerc* 1999; 31 (5 Suppl.): S384
 52. Tracy BL, Ivey FM, Metter EJ, et al. A more efficient magnetic resonance imaging-based strategy for measuring quadriceps muscle volume. *Med Sci Sports Exerc* 2003; 35: 425-33

53. McCall GE, Byrnes WC, Dickinson A, et al. Muscle fiber hypertrophy, hyperplasia, and capillary density in college men after resistance training. *J Appl Physiol* 1996; 81: 2004-12
54. Young A, Stokes M, Round JM, et al. The effect of high-resistance training on the strength and cross-sectional area of the human quadriceps. *Eur J Clin Invest* 1983; 13: 411-7
55. Jones DA, Rutherford OM. Human muscle strength training: the effects of three different regimes and the nature of the resultant changes. *J Physiol* 1987; 391: 1-11
56. Häkkinen K, Kallinen M, Komi PV, et al. Neuromuscular adaptations during short-term 'normal' and reduced training periods in strength athletes. *Electromyogr Clin Neurophysiol* 1991; 31: 35-42
57. Rutherford OM, Jones DA. Measurement of fibre pennation using ultrasound in the human quadriceps in vivo. *Eur J Appl Physiol* 1992; 65: 433-7
58. Sale DG, Martin JE, Moroz DE. Hypertrophy without increased isometric strength after weight training. *Eur J Appl Physiol* 1992; 64: 51-5
59. Häkkinen K, Pakarinen A, Kallinen M. Neuromuscular adaptations and serum hormones in women during short-term intensive strength training. *Eur J Appl Physiol* 1992; 64: 106-11
60. Ploutz LL, Tesch PA, Biro RL, et al. Effect of resistance training on muscle use during exercise. *J Appl Physiol* 1994; 76: 1675-81
61. Häkkinen K, Kallinen M. Distribution of strength training volume into one or two daily sessions and neuromuscular adaptations in female athletes. *Electromyogr Clin Neurophysiol* 1994; 34: 117-24
62. Smith RC, Rutherford OM. The role of metabolites in strength training: part I. A comparison of eccentric and concentric contractions. *Eur J Appl Physiol* 1995; 71: 332-6
63. Häkkinen K, Häkkinen A. Neuromuscular adaptations during intensive strength training in middle-aged and elderly males and females. *Electromyogr Clin Neurophysiol* 1995; 35: 137-47
64. Häkkinen K, Kallinen M, Linnamo V, et al. Neuromuscular adaptations during bilateral versus unilateral strength training in middle-aged and elderly men and women. *Acta Physiol Scand* 1996; 158: 77-88
65. Hisaeda H, Miyagawa K, Kuno S, et al. Influence of two different modes of resistance training in female subjects. *Ergonomics* 1996; 39: 842-52
66. Welle S, Totterman S, Thornton C. Effect of age on muscle hypertrophy induced by resistance training. *J Gerontol A Biol Sci Med Sci* 1996; 51: M270-5
67. McCarthy JP, Bammann MM, Yelle JM, et al. Resistance exercise training and the orthostatic response. *Eur J Appl Physiol* 1997; 76: 32-40
68. Housh DJ, Housh TJ, Weir JP, et al. Effects of unilateral concentric-only dynamic constant external resistance training on quadriceps femoris cross-sectional area. *J Strength Cond Res* 1998; 12: 185-91
69. Housh DJ, Housh TJ, Weir JP, et al. Effects of unilateral eccentric-only dynamic constant external resistance training on quadriceps femoris cross-sectional area. *J Strength Cond Res* 1998; 12: 192-8
70. Häkkinen K, Newton RU, Gordon SE, et al. Changes in muscle morphology, electromyographic activity, and force production characteristics during progressive strength training in young and older men. *J Gerontol A Biol Sci Med Sci* 1998; 53: B415-23
71. Häkkinen K, Kallinen M, Izquierdo M, et al. Changes in agonist-antagonist EMG, muscle CSA, and force during strength training in middle-aged and older people. *J Appl Physiol* 1998; 84: 1341-9
72. Ivey FM, Roth SM, Ferrell RE, et al. Effects of age, gender, and myostatin genotype on the hypertrophic response to heavy resistance strength training. *J Gerontol A Biol Sci Med Sci* 2000; 55: M641-8
73. Izquierdo M, Häkkinen K, Ibanez J, et al. Effects of strength training on muscle power and serum hormones in middle-aged and older men. *J Appl Physiol* 2001; 90: 1497-507
74. Häkkinen K, Pakarinen A, Hannonen P, et al. Effects of strength training on muscle strength, cross-sectional area, maximal electromyographic activity, and serum hormones in premenopausal women with fibromyalgia. *J Rheumatol* 2002; 29: 1287-95
75. Takarada Y, Ishii N. Effects of low-intensity resistance exercise with short inter-set rest period on muscular function in middle-aged women. *J Strength Cond Res* 2002; 16: 123-8
76. Takarada Y, Sato Y, Ishii N. Effects of resistance exercise combined with vascular occlusion on muscle function in athletes. *Eur J Appl Physiol* 2002; 86: 308-14
77. McCarthy JP, Pozniak MA, Agre JC. Neuromuscular adaptations to concurrent strength and endurance training. *Med Sci Sports Exerc* 2002; 34: 511-9
78. Häkkinen K, Alen M, Kraemer WJ, et al. Neuromuscular adaptations during concurrent strength and endurance training versus strength training. *Eur J Appl Physiol* 2003; 89: 42-52
79. Vikne H, Refsnes PE, Medbø JJ. Effect of training frequency of maximum eccentric strength training on muscle force and cross-sectional area in strength-trained athletes [abstract no. RR-PL-0517]. In: Book of abstracts, 14th International WCPT Congress; 2003 June 7-12; Barcelona
80. Friedmann B, Kinscherf R, Borisch S, et al. Effects of low-resistance/high-repetition strength training in hypoxia on muscle structure and gene expression. *Pflügers Arch* 2003; 446: 742-51
81. Friedmann B, Kinscherf R, Vorwald S, et al. Muscular adaptations to computer-guided strength training with eccentric overload. *Acta Physiol Scand* 2004; 182: 77-88
82. Goto K, Nagasawa M, Yanagisawa O, et al. Muscular adaptations to combinations of high- and low-intensity resistance exercises. *J Strength Cond Res* 2004; 18: 730-7
83. Takarada Y, Tsuruta T, Ishii N. Cooperative effects of exercise and occlusive stimuli on muscular function in low-intensity resistance exercise with moderate vascular occlusion. *Jpn J Physiol* 2004; 54: 585-92
84. Abe T, Yasuda T, Midorikawa T, et al. Skeletal muscle size and circulating IGF-1 are increased after two weeks of twice daily Kaatsu resistance training [online]. *Int J Kaatsu Training Res* 2005; 1: 7-14. Available from URL: http://kaatsu.jp/english/j01_1.html [Accessed 2005 April 25]
85. Goto K, Ishii N, Kizuka T, et al. The impact of metabolic stress on hormonal responses and muscular adaptations. *Med Sci Sports Exerc* 2005; 37: 955-63
86. Izquierdo M, Häkkinen K, Ibanez J, et al. Effects of combined resistance and cardiovascular training on strength, power, muscle cross-sectional area, and endurance markers in middle-aged men. *Eur J Appl Physiol* 2005; 94: 70-5
87. Norrbrand L, Pozzo M, Tesch P. Jämförelse av tränings effekter efter 5 veckors styrketräning med två olika belastningsstrategier (in Swedish) [abstract]. *Svensk Idrottsmedicin* 2005; 24 (4): 30-1

88. Tanimoto M, Ishii N. Effects of low-intensity resistance exercise with slow movement and tonic force generation on muscular function in young men. *J Appl Physiol* 2006; 100: 1150-7
89. Coburn JW, Housh DJ, Housh TJ, et al. Effects of leucine and whey protein supplementation during 8 weeks of unilateral resistance training. *J Strength Cond Res* 2006; 20: 284-9
90. Kubo K, Komuro T, Ishiguro N, et al. Effects of low-load resistance training with vascular occlusion on the mechanical properties of muscle and tendon. *J Appl Biomech.* 2006; 22: 112-9
91. Leger B, Cartoni R, Praz M, et al. Akt signalling through GSK-3{beta}, mTOR and foxo1 is involved in human skeletal muscle hypertrophy and atrophy. *J Physiol* 2006; 576: 923-33
92. Popov DV, Swirkun DV, Ntetreba AI, et al. Hormonal adaptation determines the increase in muscle mass and strength during low-intensity strength training without relaxation. *Human Physiology* 2006; 32 (5): 609-14
93. Petersen SR, Bagnall KM, Wenger HA, et al. The influence of velocity-specific resistance training on the in vivo torque-velocity relationship and the cross-sectional area of quadriceps femoris. *J Orthop Sports Phys Ther* 1989; 11: 456-62
94. Petersen S, Wessel J, Bagnall K, et al. Influence of concentric resistance training on concentric and eccentric strength. *Arch Phys Med Rehabil* 1990; 71: 101-5
95. Petersen SR, Bell GJ, Bagnall KM, et al. Influence of concentric resistance training on eccentric peak torque and muscle cross-sectional area. *J Orthop Sports Phys Ther* 1991; 13: 132-7
96. Bell GJ, Petersen SR, Wessel J, et al. Physiological adaptations to concurrent endurance training and low velocity resistance training. *Int J Sports Med* 1991; 12: 384-90
97. Bell GJ, Petersen SR, Wessel J, et al. Adaptations to endurance training and low velocity resistance training performed in a sequence. *Can J Sport Sci* 1991; 16: 186-92
98. Bell GJ, Petersen SR, MacLean I, et al. Effect of high velocity resistance training on peak torque, cross sectional area and myofibrillar ATPase activity. *J Sports Med Phys Fitness* 1992; 32: 10-8
99. Ruther CL, Golden CL, Harris RT, et al. Hypertrophy, resistance training, and the nature of skeletal muscle activation. *J Strength Cond Res* 1995; 9: 155-9
100. Higbie EJ, Cureton KJ, Warren GL, et al. Effects of concentric and eccentric training on muscle strength, cross-sectional area, and neural activation. *J Appl Physiol* 1996; 81
101. Housh DJ, Housh TJ, Weir JP, et al. Concentric isokinetic resistance training and quadriceps femoris cross-sectional area. *Isokin Exerc Sci* 1996; 6: 101-8
102. Seger JY, Arvidsson B, Thorstensson A. Specific effects of eccentric and concentric training on muscle strength and morphology in humans. *Eur J Appl Physiol* 1998; 79: 49-57
103. Akima H, Takahashi H, Kuno SY, et al. Early phase adaptations of muscle use and strength to isokinetic training. *Med Sci Sports Exerc* 1999; 31: 588-94
104. Rafeei T. The effects of training at equal power levels using concentric and eccentric contractions on skeletal muscle fiber and whole muscle hypertrophy, muscle force and muscle activation in human subjects [dissertation]. Richmond (VA): Virginia Commonwealth University, 1999
105. Seynnes OR, de Boer M, Narici MV. Early skeletal muscle hypertrophy and architectural changes in response to high-intensity resistance training. *J Appl Physiol.* Epub 2006 Oct 19
106. Garfinkel S, Cafarelli E. Relative changes in maximal force, EMG, and muscle cross-sectional area after isometric training. *Med Sci Sports Exerc* 1992; 24: 1220-7
107. Schott J, McCully K, Rutherford OM. The role of metabolites in strength training: II. Short versus long isometric contractions. *Eur J Appl Physiol* 1995; 71: 337-41
108. Kubo K, Kanehisa H, Fukunaga T. Effects of different duration isometric contractions on tendon elasticity in human quadriceps muscles. *J Physiol* 2000; 536: 649-55
109. Kubo K, Ohgo K, Takeishi R, et al. Effects of isometric training at different knee angles on the muscle-tendon complex in vivo. *Scand J Med Sci Sports* 2006; 16: 159-67
110. Kubo K, Yata H, Kanehisa H, et al. Effects of isometric squat training on the tendon stiffness and jump performance. *Eur J Appl Physiol* 2006; 96: 305-14
111. Sale DG, MacDougall JD, Jacobs I, et al. Interaction between concurrent strength and endurance training. *J Appl Physiol* 1990; 68: 260-70
112. Sale DG, Jacobs I, MacDougall JD, et al. Comparison of two regimens of concurrent strength and endurance training. *Med Sci Sports Exerc* 1990; 22: 348-56
113. Kraemer WJ, Nindl BC, Ratamess NA, et al. Changes in muscle hypertrophy in women with periodized resistance training. *Med Sci Sports Exerc* 2004; 36: 697-708
114. Akima H, Kubo K, Kanehisa H, et al. Leg-press resistance training during 20 days of 6 degrees head-down-tilt bed rest prevents muscle deconditioning. *Eur J Appl Physiol* 2000; 82: 30-8
115. Akima H, Kubo K, Imai M, et al. Inactivity and muscle: effect of resistance training during bed rest on muscle size in the lower limb. *Acta Physiol Scand* 2001; 172: 269-78
116. Schulze K, Gallagher P, Trappe S. Resistance training preserves skeletal muscle function during unloading in humans. *Med Sci Sports Exerc* 2002; 34: 303-13
117. Kubo K, Akima H, Ushiyama J, et al. Effects of resistance training during bed rest on the viscoelastic properties of tendon structures in the lower limb. *Scand J Med Sci Sports* 2004; 14: 296-302
118. Tesch PA, Trieschmann JT, Ekberg A. Hypertrophy of chronically unloaded muscle subjected to resistance exercise. *J Appl Physiol* 2004; 96: 1451-8
119. Alkner BA, Tesch PA. Efficacy of a gravity-independent resistance exercise device as a countermeasure to muscle atrophy during 29-day bed rest. *Acta Physiol Scand* 2004; 181: 345-57
120. Shackelford LC, LeBlanc AD, Driscoll TB. Resistance exercise as a countermeasure to disuse-induced bone loss. *J Appl Physiol* 2004; 97: 119-29
121. Mulder ER, Stegeman DF, Gerrits KH, et al. Strength, size and activation of knee extensors followed during 8 weeks of horizontal bed rest and the influence of a countermeasure. *Eur J Appl Physiol.* 2006; 97: 706-15
122. Stevenson SW, Dudley GA. Dietary creatine supplementation and muscular adaptation to resistive overload. *Med Sci Sports Exerc* 2001; 33: 1304-10
123. Gondin J, Guette M, Ballay Y, et al. Electromyostimulation training effects on neural drive and muscle architecture. *Med Sci Sports Exerc* 2005; 37: 1291-9
124. Fukunaga T, Sugiyama M. The effect of static and dynamic strength training on absolute muscle strength. *Jap J Phys Educ* 1978; 22: 343-9
125. Sale D, MacDougall D, Alway S, et al. Effect of low vs high repetition weight training upon strength, muscle size and muscle fiber size [abstract]. *Can J Spt Sci* 1985; 10 (4): 27P
126. Refsnes PE. En treningsmetode, hvor en aktivert muskel strekkes forut for forkortning, og denne treningsmetodens innvirkning på 1RM og vinkelhastighet ved lett belastning (in Norwe-

- gian) [dissertation]. Norwegian School of Sport Sciences, Oslo, Norway, 1986
127. Dahl HA, Aaserud R, Jensen J. Muscle hypertrophy after light and heavy resistance training [abstract]. *Med Sci Sports Exerc* 1992; 24 (5 Suppl.): S55
 128. Narici MV, Kayser B. Hypertrophic response of human skeletal muscle to strength training in hypoxia and normoxia. *Eur J Appl Physiol* 1995; 70: 213-9
 129. Moss BM, Refsnes PE, Abildgaard A, et al. Effects of maximal effort strength training with different loads on dynamic strength, cross-sectional area, load-power and load-velocity relationships. *Eur J Appl Physiol* 1997; 75: 193-9
 130. Bembem DA, Feters MG, Bembem MG, et al. Musculoskeletal responses to high- and low-intensity resistance training in early postmenopausal women. *Med Sci Sports Exerc* 2000; 32: 1949-57
 131. Takarada Y, Takazawa H, Sato Y, et al. Effects of resistance exercise combined with moderate vascular occlusion on muscular function in humans. *J Appl Physiol* 2000; 88: 2097-106
 132. Okada J, Fukushima S. Effects of resistance training associated with stretch-shortening cycle exercise on force development and muscle volume in human elbow flexors. *Adv Exerc Sports Physiol* 2001; 7: 65-71
 133. Brandenburg JP, Docherty D. The effects of accentuated eccentric loading on strength, muscle hypertrophy and neural adaptations in trained individuals. *J Strength Cond Res* 2002; 16: 25-32
 134. Wirth K, Atzor KR, Schmidbleicher D. Changes in muscle mass detected by MRI, after an eight week hypertrophy training program. In: Koskolou M, editor. *Proceedings of 7th annual Congress of the European College of Sports Sciences*; 2002 Jul 24-27; Athens, 103
 135. Walker KS, Kambadur R, Sharma M, et al. Resistance training alters plasma myostatin but not IGF-1 in healthy men. *Med Sci Sports Exerc* 2004; 36: 787-93
 136. Hubal MJ, Gordish-Dressman H, Thompson PD, et al. Variability in muscle size and strength gain after unilateral resistance training. *Med Sci Sports Exerc* 2005; 37: 964-72
 137. Vikne H, Refsnes PE, Ekmark M, et al. Muscular performance after concentric and eccentric exercise in trained men. *Med Sci Sports Exerc* 2006; 38: 1770-81
 138. Shephstone TN, Tang JE, Dallaire S, et al. Short-term high- vs low-velocity isokinetic lengthening training results in greater hypertrophy of the elbow flexors in young men. *J Appl Physiol* 2005; 98: 1768-76
 139. Davies J, Parker DF, Rutherford OM, et al. Changes in strength and cross-sectional area of the elbow flexors as a result of isometric strength training. *Eur J Appl Physiol* 1988; 57: 667-70
 140. Chesley A, MacDougall JD, Tarnopolsky MA, et al. Changes in human muscle protein synthesis after resistance exercise. *J Appl Physiol* 1992; 73: 1383-8
 141. MacDougall JD, Gibala MJ, Tarnopolsky MA, et al. The time course for elevated muscle protein synthesis following heavy resistance exercise. *Can J Appl Physiol* 1995; 20: 480-6
 142. Phillips SM, Tipton KD, Aarsland A, et al. Mixed muscle protein synthesis and breakdown after resistance exercise in humans. *Am J Physiol* 1997; 273: E99-107
 143. Miller BF, Olesen JL, Hansen M, et al. Coordinated collagen and muscle protein synthesis in human patella tendon and quadriceps muscle after exercise. *J Physiol* 2005; 567: 1021-33
 144. Garhammer J, Takano B. Training for weightlifting. In: Komi PV, editor. *Strength and power in sport*. Oxford: Blackwell scientific publications, 1992: 357-69
 145. Tesch PA. Strength training and muscle hypertrophy. In: Häkkinen K, editor. *Conference book: international conference on weightlifting and strength training*; Lahti, Finland, 1998 November 10-12; Jyväskylä: Gummerus printing, 1998: 17-22
 146. Ostrowski K, Wilson GJ, Weatherby R, et al. The effect of weight training volume on hormonal output and muscular size and function. *J Strength Cond Res* 1997; 11: 148-54
 147. McLester JR, Bishop P, Williams ME. Comparison of 1 day and 3 days per week of equal-volume resistance training in experienced subjects. *J Strength Cond Res* 2000; 14: 273-81
 148. Hawkins SA, Schroeder ET, Wiswell RA, et al. Eccentric muscle action increases site-specific osteogenic response. *Med Sci Sports Exerc* 1999; 31: 1287-92
 149. Hortobagyi T, Hill JP, Houmard JA, et al. Adaptive responses to muscle lengthening and shortening in humans. *J Appl Physiol* 1996; 80: 765-72
 150. Hortobagyi T, Dempsey L, Fraser D, et al. Changes in muscle strength, muscle fibre size and myofibrillar gene expression after immobilization and retraining in humans. *J Physiol* 2000; 524: 293-304
 151. Farthing JP, Chilibeck PD. The effects of eccentric and concentric training at different velocities on muscle hypertrophy. *Eur J Appl Physiol* 2003; 89: 578-86
 152. Ewing JL, Wolfe DR, Rogers MA, et al. Effects of velocity of isokinetic training on strength, power, and quadriceps muscle fibre characteristics. *Eur J Appl Physiol* 1990; 61: 159-62
 153. Coyle EF, Feiring DC, Rotkis TC, et al. Specificity of power improvements through slow and fast isokinetic training. *J Appl Physiol* 1981; 51: 1437-42
 154. Aagaard P, Simonsen EB, Trolle M, et al. Moment and power generation during maximal knee extensions performed at low and high speeds. *Eur J Appl Physiol* 1994; 69: 376-81
 155. Thomeé R, Renström P, Grimby G, et al. Slow or fast isokinetic training after knee ligament surgery. *J Orthop Sports Phys Ther* 1987; 8: 475-9
 156. Froböse I, Verdonck A, Duesberg F, et al. Effects of various load intensities in the framework of postoperative stationary endurance training on performance deficit of the quadriceps muscle of the thigh [in German]. *Z Orthop Ihre Grenzgeb* 1993; 131: 164-7
 157. Greenhaff PL, Soderlund K, Ren JM, et al. Energy metabolism in single human muscle fibres during intermittent contraction with occluded circulation. *J Physiol* 1993; 460: 443-53
 158. McHugh MP, Tyler TF, Greenberg SC, et al. Differences in activation patterns between eccentric and concentric quadriceps contractions. *J Sports Sci* 2002; 20: 83-91
 159. Starkey DB, Pollock ML, Ishida Y, et al. Effect of resistance training volume on strength and muscle thickness. *Med Sci Sports Exerc* 1996; 28: 1311-20
 160. Pollock ML, Abe T, DeHoyos DV, et al. Muscular hypertrophy responses to 6 months of high or low volume resistance training [abstract]. *Med Sci Sports Exerc* 1998; 30 (5 Suppl.): S116
 161. McBride JM, Blaak JB, Triplett-McBride T. Effect of resistance exercise volume and complexity on EMG, strength, and regional body composition. *Eur J Appl Physiol* 2003; 90: 626-32
 162. Ronnestad RB, Kadi F, Raastad T, et al. Dissimilar effects of 1 and 3 set strength training on strength and muscle mass gains in upper and lower body in untrained subjects. *J Strength Cond Res*. In press

163. Mayhew TP, Rothstein JM, Finucane SD, et al. Muscular adaptation to concentric and eccentric exercise at equal power levels. *Med Sci Sports Exerc* 1995; 27: 868-73
164. Herzog W, Abrahamse SK, ter Keurs HE. Theoretical determination of force-length relations of intact human skeletal muscles using the cross-bridge model. *Pflügers Arch* 1990; 416: 113-9
165. Ichinose Y, Kawakami Y, Ito M, et al. Estimation of active force-length characteristics of human vastus lateralis muscle. *Acta Anat (Basel)* 1997; 159: 78-83
166. Westing SH, Seger JY, Thorstensson A. Effects of electrical stimulation on eccentric and concentric torque-velocity relationships during knee extension in man. *Acta Physiol Scand* 1990; 140: 17-22
167. Dugailly PM, Mouraux D, Llamas N, et al. EMGs and strength patterns of the quadriceps during isokinetic extension of the knee in different contraction mode. *Isokin Exerc Sci* 2002; 10: 21-2
168. Holder-Powell HM, Rutherford OM. Reduction in range of movement can increase maximum voluntary eccentric forces for the human knee extensor muscles. *Eur J Appl Physiol* 1999; 80: 502-4
169. Colliander E. Influence of concentric and eccentric muscle actions on acute strength patterns and adaptive responses to resistance training [dissertation]. Stockholm: Karolinska Institutet, 1992
170. Ichinose Y, Kawakami Y, Ito M, et al. In vivo estimation of contraction velocity of human vastus lateralis muscle during 'isokinetic' action. *J Appl Physiol* 2000; 88: 851-6
171. Rooney KJ, Herbert RD, Balnave RJ. Fatigue contributes to the strength training stimulus. *Med Sci Sports Exerc* 1994; 26: 1160-4
172. Drinkwater EJ, Lawton TW, Lindsell RP, et al. Training leading to repetition failure enhances bench press strength gains in elite junior athletes. *J Strength Cond Res* 2005; 19: 382-8
173. Pincivero DM, Campy RM. The effects of rest interval length and training on quadriceps femoris muscle: part I. Knee extensor torque and muscle fatigue. *J Sports Med Phys Fitness* 2004; 44: 111-8
174. Folland JP, Irish CS, Roberts JC, et al. Fatigue is not a necessary stimulus for strength gains during resistance training. *Br J Sports Med* 2002; 36: 370-3
175. Tesch PA, Dudley GA, Duvoisin MR, et al. Force and EMG signal patterns during repeated bouts of concentric or eccentric muscle actions. *Acta Physiol Scand* 1990; 138: 263-71
176. Grabiner MD, Owings TM. Effects of eccentrically and concentrically induced unilateral fatigue on the involved and uninvolved limbs. *J Electromyogr Kinesiol* 1999; 9: 185-9
177. Kay D, St Clair Gibson A, Mitchell MJ, et al. Different neuromuscular recruitment patterns during eccentric, concentric and isometric contractions. *J Electromyogr Kinesiol* 2000; 10: 425-31
178. Dow DE, Cederna PS, Hassett CA, et al. Number of contractions to maintain mass and force of a denervated rat muscle. *Muscle Nerve* 2004; 30: 77-86
179. Dow DE, Faulkner JA, Dennis RG. Distribution of rest periods between electrically generated contractions in denervated muscles of rats. *Artif Organs* 2005; 29: 432-5
180. Dow DE, Dennis RG, Faulkner JA. Electrical stimulation attenuates denervation and age-related atrophy in extensor digitorum longus muscles of old rats. *J Gerontol A Biol Sci Med Sci* 2005; 60: 416-24
181. Kawakami Y, Abe T, Kuno SY, et al. Training-induced changes in muscle architecture and specific tension. *Eur J Appl Physiol* 1995; 72: 37-43
182. Amiridis IG, Cometti G, Morlon B, et al. Effects of the type of recovery training on the concentric strength of the knee extensors. *J Sports Sci* 1997; 15: 175-80
183. LaStayo PC, Pierotti DJ, Pifer J, et al. Eccentric ergometry: increases in locomotor muscle size and strength at low training intensities. *Am J Physiol Regul Integr Comp Physiol* 2000; 278: R1282-8
184. LaStayo PC, Ewy GA, Pierotti DD, et al. The positive effects of negative work: increased muscle strength and decreased fall risk in a frail elderly population. *J Gerontol A Biol Sci Med Sci* 2003; 58: M419-24
185. Gerber JP, Marcus RL, Dibble LE, et al. Early application of negative work via eccentric ergometry following anterior cruciate ligament reconstruction: a case report. *J Orthop Sports Phys Ther* 2006; 36: 298-307
186. Fry AC. The role of training intensity in resistance exercise overtraining and overreaching. In: Kreider RB, Fry AC, O'Toole ML, editors. *Overtraining in sport*. Champaign (IL): Human Kinetics, 1998: 107-27
187. Peterson MD, Rhea MR, Alvar BA. Applications of the dose-response for muscular strength development: a review of meta-analytic efficacy and reliability for designing training prescription. *J Strength Cond Res* 2005; 19: 950-8
188. Refsnes PE. Testing and training for top Norwegian athletes. In: Müller E, Zallinger G, Ludescher F, editors. *Science in elite sport*. London: E & FN Spon, 1999: 97-114
189. American College of Sports Medicine Position Stand. The recommended quantity and quality of exercise for developing and maintaining cardiorespiratory and muscular fitness, and flexibility in healthy adults. *Med Sci Sports Exerc* 1998; 30: 975-91
190. Wallace MB, Mills BD, Browning CL. Effects of cross-training on markers of insulin resistance/hyperinsulinemia. *Med Sci Sports Exerc* 1997; 29: 1170-5
191. Woods RH, Reyes R, Welsch MA, et al. Concurrent cardiovascular and resistance training in healthy older adults. *Med Sci Sports Exerc* 2001; 33: 1751-8
192. Kraemer WJ, Keuning M, Ratamess NA, et al. Resistance training combined with bench-step aerobics enhances women's health profile. *Med Sci Sports Exerc* 2001; 33: 259-69
193. Kawano H, Tanaka H, Miyachi M. Resistance training and arterial compliance: keeping the benefits while minimizing the stiffening. *J Hypertens* 2006; 24: 1753-9
194. Leveritt M, Abernethy PJ, Barry BK, et al. Concurrent strength and endurance training: a review. *Sports Med* 1999; 28: 413-27
195. Deakin GB. Concurrent training in endurance athletes: the acute effects on muscle recovery capacity, physiological, hormonal and gene expression responses post-exercise (dissertation) [online]. Lismore, Australia: Southern Cross University, 2004. Available from URL: <http://thesis.scu.edu.au/> [Accessed 2006 Dec 3]
196. Staron RS, Karapondo DL, Kraemer WJ, et al. Skeletal muscle adaptations during early phase of heavy-resistance training in men and women. *J Appl Physiol* 1994; 76: 1247-55
197. Sale DG. Neural adaptations to strength training. In: Komi PV, editor. *Strength and power in sport*. 2nd ed. Oxford: Blackwell scientific publications, 2003: 281-314
198. Phillips SM. Short-term training: when do repeated bouts of resistance exercise become training? *Can J Appl Physiol* 2000; 25: 185-93

199. Willoughby DS, Taylor L. Effects of sequential bouts of resistance exercise on androgen receptor expression. *Med Sci Sports Exerc* 2004; 36: 1499-506
200. Foley JM, Jayaraman RC, Prior BM, et al. MR measurements of muscle damage and adaptation after eccentric exercise. *J Appl Physiol* 1999; 87: 2311-8
201. Willoughby DS, Taylor M, Taylor L. Glucocorticoid receptor and ubiquitin expression after repeated eccentric exercise. *Med Sci Sports Exerc* 2003; 35: 2023-31
202. Trappe TA, Raue U, Tesch PA. Human soleus muscle protein synthesis following resistance exercise. *Acta Physiol Scand* 2004; 182: 189-96
203. Turner DL, Hoppeler H, Claassen H, et al. Effects of endurance training on oxidative capacity and structural composition of human arm and leg muscles. *Acta Physiol Scand* 1997; 161: 459-64
204. Abe T, DeHoyos DV, Pollock ML, et al. Time course for strength and muscle thickness changes following upper and lower body resistance training in men and women. *Eur J Appl Physiol* 2000; 81: 174-80
205. Rennie MJ, Wackerhage H, Spangenburg EE, et al. Control of the size of the human muscle mass. *Annu Rev Physiol* 2004; 66: 799-828
206. Glass DJ. Skeletal muscle hypertrophy and atrophy signaling pathways. *Int J Biochem Cell Biol* 2005; 37: 1974-84
207. Nader GA. Molecular determinants of skeletal muscle mass: getting the 'AKT' together. *Int J Biochem Cell Biol* 2005; 37: 1985-96
208. Hornberger TA, Esser KA. Mechanotransduction and the regulation of protein synthesis in skeletal muscle. *Proc Nutr Soc* 2004; 63: 331-5
209. Hameed M, Orell RW, Cobbold M, et al. Expression of IGF-I splice variants in young and old human skeletal muscle after high resistance exercise. *J Physiol* 2003; 547: 247-54
210. Hornberger TA, Chu WK, Mak YW, et al. The role of phospholipase D and phosphatidic acid in the mechanical activation of mTOR signaling in skeletal muscle. *Proc Natl Acad Sci U S A* 2006; 103: 4741-6
211. Boppart MD, Burkin DJ, Kaufman SJ. Alpha7beta1-integrin regulates mechanotransduction and prevents skeletal muscle injury. *Am J Physiol Cell Physiol* 2006; 290: 1660-5
212. Spangenburg EE, McBride TA. Inhibition of stretch-activated channels during eccentric muscle contraction attenuates p70S6K activation. *J Appl Physiol* 2006; 100: 129-35
213. Lange S, Xiang F, Yakovenko A, et al. The kinase domain of titin controls muscle gene expression and protein turnover. *Science* 2005; 308 (5728): 1599-603
214. Goldberg AL, Etlinger JD, Goldspink DF, et al. Mechanism of work-induced hypertrophy of skeletal muscle. *Med Sci Sports* 1975; 7: 185-98
215. MacDougall J. Adaptability of muscle to strength training: a cellular approach. In: Saltin B, editor. *Biochemistry of exercise VI*. Champaign (IL): Human Kinetics, 1986: 501-13
216. Martineau LC, Gardiner PF. Insight into skeletal muscle mechanotransduction: MAPK activation is quantitatively related to tension. *J Appl Physiol* 2001; 91: 693-702
217. Martineau LC, Gardiner PF. Skeletal muscle is sensitive to the tension-time integral but not to the rate of change of tension, as assessed by mechanically induced signaling. *J Biomech* 2002; 35: 657-63
218. Eliasson J, Elfegoun T, Nilsson J, et al. Maximal lengthening contractions increase p70S6 kinase phosphorylation in human skeletal muscle in the absence of nutritional supply. *Am J Physiol Endocrinol Metab* 2006; 291: E1197-205
219. Cuthbertson DJ, Babraj J, Smith K, et al. Anabolic signaling and protein synthesis in human skeletal muscle after dynamic shortening or lengthening exercise. *Am J Physiol Endocrinol Metab* 2006; 290: 731-8
220. Jones DA, Folland JP. Strength training in young adults. In: Maffuli N, Chan KM, Macdonald R, et al., editors. *Sports medicine for specific ages abilities*. Edinburgh: Churchill Livingstone, 2001: 57-64
221. Kraemer WJ, Ratamess NA. Hormonal responses and adaptations to resistance exercise and training. *Sports Med* 2005; 35: 339-61
222. Uehara K, Goto K, Kobayashi T, et al. Heat-stress enhances proliferative potential in rat soleus muscle. *Jpn J Physiol* 2004; 54: 263-71
223. Goto K, Okuyama R, Sugiyama H, et al. Effects of heat stress and mechanical stretch on protein expression in cultured skeletal muscle cells. *Pflügers Arch* 2003; 447: 247-53
224. Goto K, Honda M, Kobayashi T, et al. Heat stress facilitates the recovery of atrophied soleus muscle in rat. *Jpn J Physiol* 2004; 54: 285-93
225. Abe T, Kawamoto K, Yasuda T, et al. Eight days Kaatsu-resistance training improved sprint but not jump performance in collegiate male track and field athletes [online]. *Int J Kaatsu Training Res* 2005; 1: 19-23. Available from URL: http://kaatsu.jp/english/j01_1.html. [Accessed 2005 April 25]
226. Mazzetti SA, Kraemer WJ, Volek JS, et al. The influence of direct supervision of resistance training on strength performance. *Med Sci Sports Exerc* 2000; 32: 1175-84
227. Mitsiopoulos N, Baumgartner RN, Heymsfield SB, et al. Cadaver validation of skeletal muscle measurement by magnetic resonance imaging and computerized tomography. *J Appl Physiol* 1998; 85: 115-22

Correspondence and offprints: *Mathias Wernbom*, Lundberg Laboratory for Human Muscle Function and Movement Analysis, Department of Orthopaedics, Sahlgrenska University Hospital, Gröna Stråket 12, Göteborg, SE-413 45, Sweden.

E-mail: mathias.wernbom@orthop.gu.se