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The Role of Resistance Exercise Intensity on Muscle Fibre Adaptations

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Abstract

Although many training variables contribute to the performance, cellular and molecular adaptations to resistance exercise, relative intensity (% 1 repetition maximum [%1RM]) appears to be an important factor. This review summarises and analyses data from numerous resistance exercise training studies that have monitored percentage fibre type, fibre type cross-sectional areas, percentage cross-sectional areas, and myosin heavy chain (MHC) isoform expression. In general, relative intensity appears to account for 18–35% of the variance for the hypertrophy response to resistance exercise. On the other hand, fibre type and MHC transitions were not related to the relative intensity used for training. When competitive lifters were compared, those typically utilising the heaviest loads

(\geq 90% 1RM), that is weightlifters and powerlifters, exhibited a preferential hypertrophy of type II fibres when compared with body builders who appear to equally hypertrophy both type I and type II fibres. These data suggest that maximal hypertrophy occurs with loads from 80–95% 1RM.

One of the most frequently asked questions by those using resistance exercise is "how heavy should I go?". Surprisingly, this is a more complex question than it may at first appear. Over the past several decades, however, a number of resistance exercise training studies have been performed that provide some insight to this question. In recent years, resistance exercise has become one of the fastest growing exercise and fitness activities. Whether the goal is to improve athletic performance, enhance general health and fitness, rehabilitate after surgery or an injury, or just for the pleasure of the exercise, many people now recognise the benefits of the various forms of resistance exercise. Needless to say, resistance exercise can lead to adaptations of many physiological systems;^[1,2] however, the most obvious one is skeletal muscle. Such adaptations can be quite remarkable, both from muscle performance and muscle anatomy and structure perspectives. In light of these observations, the applied muscle physiologist must ask "what is responsible for these adaptations?". Many scientists have addressed this question at the physiological mechanistic level. This is certainly understandable and desirable, since only through a thorough understanding of the underlying physiology can one appreciate exactly what is going on. A logical place to start is with the genetic regulation of skeletal muscle, which has been eloquently addressed in several recent reviews.[3,4] Others for example, have asked this question from either an endocrine viewpoint,^[5] or a neural control perspective.[1,6]

The diverse nature of human muscle is quite amazing,^[7] thus demonstrating how variable and plastic muscle can be to serve its functional role for humans. It has recently been pointed out that animal models can provide much valuable information concerning muscle adaptations to resistance exercise;^[8] however, human studies are still necessary to permit

study of the actual training methods in popular use. While such discussions are absolutely critical to our understanding of the regulating mechanisms of skeletal muscle, the exercise scientist and the practitioner must also be aware of the regulating role of the exercise stimulus itself. While the regulating role of the exercise stimulus should never be completely separated from the physiological mechanisms, it is equally important for those studying the skeletal muscle system to fully appreciate the often subtle, but physiologically different types of resistance exercise in use. Only when knowledge of muscle physiology and the appropriate application of training stimuli are combined can we hope to optimise the adaptation process. Indeed, considerable attempts have been made in this direction,^[9] but much work must be done to completely 'bridge this gap'.

The purpose of this review is to provide a preliminary examination of the role of resistance training load (i.e. intensity) on adaptation of human skeletal muscle. While the load used is only one of many important variables, it is believed to be, perhaps, one of the most critical.

1. Acute Training Variables

One of the fundamental difficulties in describing resistance exercise is the extreme variability of this type of training. Perhaps one of the most thorough descriptions was presented by Fleck and Kraemer^[1,10] when they introduced the five acute training variables for resistance exercise. These include: (i) choice of exercise; (ii) order of exercise; (iii) load or intensity; (iv) volume of exercise; and (v) rest. Each of these items describes an element of a single resistance exercise training session. A close examination reveals that there are many options for each of these variables, the net result being a tremendously huge number of different training sessions possible.^[11] What is even more amazing is the additional variety that results when one considers training variation for the long-term training programme. The often used training principle of periodisation creates just such a variable training scenario.^[12,13] While this variety can be extremely beneficial for individuals performing resistance exercise, such variety also can be very confusing for some. In addition, it is not really possible to completely dissociate the effects of one acute training variable from another. The actual training programme is possible only through the combination of each of the five acute training variables as well as the long-term training programme. On the other hand, a debatable question is "which of these variables is most important?". While this review will not attempt to answer that question, it will try to present some data that emphasises the adaptational role of the load used during resistance exercise.

2. Resistance Exercise Intensity Defined

An often confusing topic is the definition of resistance exercise load or intensity. Many different definitions have been presented for this term, perhaps due to the complex nature of resistance exercise. Obviously, for a review of this type, it is essential to precisely define what is meant by this term. For the purposes of this paper, resistance exercise intensity will be operationally defined as the percentage of maximal strength (%1 repetition maximum [%1RM]) used for a particular exercise.^[10,12,13] This definition is often called relative intensity since it is based on each individual's strength capacity. This is a very convenient way to prescribe relatively similar training loads for people with different strength capabilities. Since not all studies included in this review have used this definition, it has been necessary to convert relative training intensities for some studies to %1RM to provide a uniform unit of measure for this variable. Sometimes relative intensity is expressed as the average or mean relative intensity for an entire training session. Thus, mean intensity provides a measure for the entire session and includes all exercises, sets and repetitions, not just one particular exercise or set. When calculating this value, some coaches will include warm-up sets, but typically only the actual training sets performed after any warm-up are included in this calculation. Another method for quantifying relative intensity is the use of RM loads.^[10,12] Based on the most weight that an individual can lift for a prescribed number of repetitions, RM loads are a convenient method for quantifying the physiological stress encountered. Examples of this type of intensity prescription are 1RM, 10RM or 20RM loads, each of which presents a distinctly different exercise stress. On the other hand, contrary to using relative intensity which attempts to equate individuals with different strength capabilities, absolute intensity is simply the measure of the actual load or resistance used.^[13]

Intensity can also be defined as a function of power. Power is the amount of work performed during a determined time period or work/time. This measure can be helpful for quantifying both the intensity of a particular exercise (exercise intensity) or for the entire training session (training intensity).^[13] Obviously, not all exercises are performed at the same movement velocity. This is due either to the nature of the exercise (e.g. bench press vs power clean) or due to the chosen speed at which the exercise is performed (e.g. maximal velocity vs 'super-slow' training). When considering a single repetition, the exercise that uses a heavier load and/ or a faster velocity will have a greater exercise intensity. Exercises with typically high exercise intensities include the weightlifting-related movements such as cleans, snatches and jerks, as well as exercises such as speed squats or jump squats. Exercise intensity is helpful for comparing different types of exercise. Training intensity, on the other hand, refers to the rate of work performed during a particular training session. This is greatly influenced by the inter-set rest intervals used. In essence, training intensity is simply another way of expressing the equation of work/time, or the actual definition of power. Instead of being measured during a single lifting movement, it is determined over the course of the entire training session.

Numerous other definitions have been presented for exercise intensity. If one considers aerobic exercise, intensity is often defined as a percentage of maximal heart rate (%HRmax) or percentage heart rate reserve.^[14,15] This definition is similar to the above definition of %1RM for resistance exercise, although it is necessarily based on a physiological measure central to cardiovascular fitness (i.e. heart rate). It can also be defined as a percentage of effort,^[15,16] thus relying on each individual's perceptions of their levels of exertion to determine intensity. Such a definition is very similar to the commonly used rating of perceived exertion, which is a convenient and valid measure of exercise intensity for aerobic forms of exercise.^[16] Attempts have been made to utilise perceptions of effort to quantify resistance exercise intensity, but it must be remembered that such measures are always validated by comparisons with actual measurable measures for resistance exercise (i.e. the actual load used). Due to the nature of perception measures, it is possible to have considerable physiological differences in the actual relative resistances used, even though two different lifting tasks may both result in similar perceptions of effort. Perhaps a good illustration of this is performing a 1RM versus a 25RM lifting task. Both lifting tasks result in maximal efforts, but present extremely different forms of physiological stress, and use extremely different loads. If defining resistance exercise intensity as a perception of effort, both the 1RM and the 25RM tasks are maximally difficult, even though different loads are used, different physiological stresses are presented, and the long-term training effects are different.^[17] Each of the above definitions of intensity can be useful, but help illustrate how confusing this term can be. When quantifying an exercise programme, it is critical to carefully define the intensity terminology used. Table I lists the various types of intensity identified in this section.

3. Adaptations to Resistance Exercise

A cursory review of the relevant literature quickly reveals that the physiological and performance adaptations to heavy resistance exercise are many and varied.^[1,2,18] Of particular interest to the present review are performance adaptations such as muscular strength, power and speed.^[1,2,18] Undoubtedly, any performance adaptation is dependent on accompanying physiological adaptations. For example, the endocrine system can have considerable impact on muscle adaptations to resistance exercise,^[5,19] and it is well established that varying the weight training prescription can have a profound impact on the resulting hormonal response and adaptation.^[1,2,20-22] From a different physiological viewpoint, it is well known that human skeletal muscle is very diverse concerning fibre types, sizes and protein make-up.^[7] Such diversity allows humans to successfully meet the various physical demands presented to them. As might be expected, adaptations of the different physiological systems do not respond to exercise independent of other systems, but are often dependent on each other for optimal responses.^[17,21,23] The following section will briefly overview some of the primary physiological and performance adaptations of human skeletal muscle to resistance exercise.

3.1 Muscular Strength

It is a well accepted fact that regular exposure to heavy resistance exercise will result in increases in maximal muscular strength.^[1] Although much overlap exists, many of the initial strength adaptations are due to alterations in the neural regulation of muscular activity, while subsequent adaptations rely more on adaptations of the skeletal muscle system.^[6] Although resistance exercise intensity is one of the most important resistance exercise training variables,^[10,12] relatively few studies have examined intrinsic muscle adaptations to varying loading schemes. Cross-sectional studies of highly trained competitive lifters (i.e. weightlifters, powerlifters) have noted that these individuals who regularly train

Table I. Methods of calculating resistance exercise intensity

| Relative intensity (%RM) |
|--|
| RM load |
| Mean intensity |
| Absolute intensity |
| Exercise intensity |
| Training intensity |
| Perceptions of effort (% effort, RPE) |
| RM = repetition maximum; RPE = rating of perceived exertion. |

with extremely high relative intensities, posses extremely high levels of muscular strength.^[18] Recent studies suggest that there is a dose-response curve that can describe the relationship between relative intensity and the rate of strength adaptations.^[17,24] These studies will be discussed in greater detail later.

3.2 Fibre Types

Human skeletal muscle fibre types can be identified based on the histochemical staining properties of the myosin adenosine triphosphatase (ATPase) enzyme found in the globular region of the myosin head, also known as the myosin S-1 unit.^[7] Using this terminology, three major fibre types can be identified, types I, IIA and IIB. Their functional characteristics are based in large part on the speed of enzyme activity. These fibre types form a continuum, from type I which is the slowest, to IIB which is the fastest. Closer scrutiny permits the further classification of hybrid fibres that are intermediate to the three major types. The result is a continuum of types that range from the slowest to the fastest (see equation 1).

$$I \leftrightarrow IC \leftrightarrow IIC \leftrightarrow IIAC \leftrightarrow IIA \leftrightarrow IIAB \leftrightarrow IIB$$
(slowest) (fastest)

(Eq. 1)

In equation 1, the major types that make-up the largest portion of human skeletal muscle are italicised, and possess only one type of myosin ATPase, either I, IIA or IIB. The others represent hybrid fibre types that have various proportions of types I, IIA or IIB myosin ATPase. Although this classification system is sometimes used interchangeably with other classification systems (e.g. red and white, slow and fast twitch, glycolytic and oxidative), it should be noted that each of these different classification systems are based on different physiological or anatomical properties and are not necessarily analogous. Figure 1 illustrates human skeletal muscle with several of these fibre types identified.

It has become quite apparent that alterations in the human fibre type profile can be manifested via resistance exercise.^[1,2,7] In general, there appears to be a conversion of IIB fibres to IIA.[17,23,25-29] Similar responses have been observed when elderly individuals have been studied.[30-32] This conversion can happen relatively rapidly, with significant transitions occurring after only four training sessions in untrained females.^[23] On the other hand, it appears that if the relative intensity is too low (e.g. approx 40% 1RM), this transitions does not occur.^[24] At first glance, it may seem odd that IIB fibres are not preferred for heavy resistance exercise since they are the fastest contracting.^[33-35] It has been theorised that since these fibres are the most difficult to recruit, they are not often used, and may indeed be 'held in reserve' for the time when they are needed on a regular basis.^[7] When heavy resistance exercise is routinely performed, these fibres are regularly recruited provided the intensity is great enough. The net result is that they convert to IIA fibres, suggesting that IIA fibres are the preferred fibres for heavy resistance exercise. Although not all studies have differentiated IIA and IIB fibres.^[36-39] it is repeatedly apparent with heavy resistance exercise that there is no transition from type I to type $II^{[1,2,7,17,23-29,31,32,36-40]}$ within the scopes of these studies. Although it has been suggested that such a I to II transition may occur in other exercise settings,^[41] this result could not be replicated,^[42] and this has never been reported with heavy resistance exercise alone. Cross-sectional comparison of competitive lifters and distance runners has noted significant differences in the I: II ratio, although it was



IIA

Fig. 1. Photomicrograph of human skeletal muscle (vastus lateralis m.) with several different fibre types identified. Bar = $100\mu m$.

beyond the scope of the study to determine the role of the exercise programme in these differences.^[43]

3.3 Hypertrophy

One of the most noticeable physical adaptations to heavy resistance exercise is muscular hypertrophy.^[1,2,7] While not all resistance exercise programmes produce increases in muscular size,^[17,37] most training protocols result in some degree of hypertrophy.^[17,23,25-29,36-39,44-46] This is also evident among elderly populations.^[31,32,40] It appears that eccentric muscle actions are critical to optimise this adaptation.^[26] Furthermore, evidence of protein synthesis begins within 4 hours after a resistance exercise session, indicating how quickly this adaptational response is initiated.^[47] During periods of detraining, human muscle retains much of their training-induced hypertrophy for extensive periods (e.g. 32 weeks), and is capable of returning to previous states of hypertrophy quite rapidly with subsequent training.^[28] Muscle hypertrophy is fibre type-specific in some instances, with type II fibres exhibiting preferential growth.^[17,23,25,27,29,44] In general, females do not exhibit as great an absolute hypertrophic response when compared with males, although relative gains may be similar.^[2,23,29] Additionally, competing forms of exercise (i.e. aerobic activities) can compromise the hypertrophic response that would result from resistance exercise alone.[48]

3.4 Myosin Heavy Chain (MHC) Isoforms

Performance capabilities of human skeletal muscle are dependent in part on the various isoforms of contractile proteins present. One of the critical proteins is the myosin heavy chain (MHC), which consists of primarily the head of the crossbridge (S-1 unit). Mature human MHC isoforms come in three variations in peripheral skeletal muscles, I, IIa and IIb,^[7] and it is the MHC where the myosin ATPase is located. Type I myosin ATPase is typically associated with type I MHC, type IIA myosin ATPase with type IIa MHC, and type IIB myosin ATPase with type IIb MHC.^[44] Since it is the S-1 unit that is intimately involved with the conformational changes associated with the power stroke during muscle contraction, it is important to note that type IIb MHC is capable of the fastest movement, while type I MHC is the slowest.^[7,33-35] This difference in isoform speeds is most likely critical to high power human performances since preliminary data indicate that contractile velocity accounts for 40-55% of the variance in peak human muscular power during typical loads for resistance exercise.^[49] Furthermore, pilot work suggests that in vivo human measures of rate of force development and rate of integrated electromyogram development are significantly correlated with relative MHC content.^[50] These data support reports from in vitro measures on single fibres.^[33-35] Resistance exercise training studies have consistently reported increases in percentage type IIa MHC and decreases in percentage type IIb MHC.^[23,24,26,32,44,51] Changes in relative MHC content are related to fibre hypertrophy, since it has been demonstrated that percentage MHC content is highly correlated with percentage fibre type crosssectional area.^[44] As a result, decreases in type I MHC may be observed when preferential hypertrophy of type IIA and IIB fibres occurs.^[17,48] In general, MHC data provide supporting evidence for percentage fibre type area data.^[7,44] Figure 2 illustrates electrophoretic separation of the three MHC isoforms present in humans.



Fig. 2. Relative amounts of the three myosin heavy chain (MHC) isoforms found in human skeletal muscle can be visualised using SDS-PAGE techniques. All three isoforms have a similar molecular weight of approximately 200 kDa. Type I MHC, however, is the lightest and migrates the farthest down into the gel, while type IIb is the heaviest and migrates the least distance.

4. Analysis of Resistance Exercise Studies

Given what is known regarding physiological and performance adaptations to resistance exercise, the purpose of this review is to examine the scientific literature concerning the role of resistance exercise intensity on cellular and molecular adaptations of human skeletal muscle. Very few studies have controlled for relative intensity for comparative purposes.^[17] Such a review obviously comes with a number of confounding variables that can not be ignored. These limitations must be acknowledged in order to properly interpret these data.

4.1 Limitations

Although this review is attempting to limit discussion to the role of relative intensity, it is impossible to completely separate this training variable from the other important acute training variables for resistance exercise as identified by Fleck and Kraemer.^[10] As previously mentioned, these include choice of exercise, order of exercise, volume of exercise and inter-set rest intervals. It has been pointed out that with all the options for each of these resistance exercise variables, it is possible to develop over a million different training sessions.^[11] Moreover, when one considers the long-term training programme and all the variability possible,^[10,11] the number of possible chronic exercise protocols becomes astronomical. Considering this, this review will account for only the relative intensity used in the training programme. Undoubtedly, any or all of the other acute training variables or the long-term characteristics of the training programme could have contributed in some manner to the muscle adaptations reported. The studies included in this review utilised a variety of training programme durations, exercises, rest intervals, training volumes and frequencies, etc. The subjects used in each of the training studies, however, were all previously untrained. Whether the conclusions reached for these studies would apply to an advanced training population is beyond the scope of this paper, although it is speculated that some of the results could be extrapolated to chronically trained individuals. Although

males have larger muscles and fibre cross-sectional areas, relative growth of the muscle fibres has been reported to be comparable between sexes,^[52] so both sexes have been included in these analyses.

This review has also been limited to studies analysing the vastus lateralis muscle. While a number of excellent studies have been performed on other musculature,^[27,53,54] these muscles exhibit different physiological, anatomical and performance characteristics, and would make interpretation of the data difficult. Studies also were not included if: (i) inadequate information was presented concerning the exercise stimulus; (ii) subjects using different types of resistance exercise training programmes were grouped together; (iii) the prescribed training programme utilised various relative intensities via a periodised training programme; (iv) a dietary intervention was part of the study design; or (v) muscle characteristics were quantified by a method other than biopsies. Any of these situations would again make it difficult to interpret the physiological responses to a particular training variable. For similar reasons, studies using isokinetic exercise modalities were excluded due to the difficulty in determining relative exercise intensities.^[30] Since some of the studies included did not differentiate between type IIA and IIB fibres, these studies have been analysed and presented separately from those that did account for both IIA and IIB fibre types. Furthermore, many of the reports included presented fibre-type data using different classification systems (e.g. slow and fast twitch). When appropriate, these classifications have been reclassified using the myosin ATPase classification most similar (i.e. I, IIA or IIB). In this review, the original fibre classification system developed for human muscles, which includes the classification the fastest fibres in humans as IIB, has been used. Although it has become popular in recent years to adopt the terminology developed for rodents, which includes classifying the fastest fibres as IIX, it has been pointed out that human IIB and rodent IIX (or IID) are similar, but not identical.^[55]

While all of the studies included resistance exercise for the lower limbs, not all studies performed identical exercises. Additionally, not all studies included in this review expressed the relative training intensity in a similar manner. Specifically, some studies used RM loads while others used %RM loads. Using previous guidelines,^[56,57] the relative training intensities for all studies not reporting intensity as a percentage of 1RM were estimated. Furthermore, it is assumed that all training studies included required their subjects to exert a maximal effort, and that none of the loads prescribed involved sub-maximum efforts. Finally, the data presented from elite competitive lifters do not account for the possible use of exogenous pharmaceutical ergogenic aids contributing to performances or muscle fibre characteristics. Undoubtedly, such factors warrant serious consideration when attempting to account for the adaptational process, but the exact contributions can not be discerned from the data provided.

4.2 Variables Measured

Since maximal muscular strength (i.e. 1RM) is a readily apparent result of most resistance exercise programmes,^[1,2] several of the studies included were used to demonstrate an apparent dose-response relationship for strength adaptations. Cellular and molecular variables considered include percentage fibre types, fibre cross-sectional areas, percentage fibre type-specific areas and relative MHC content.^[50] Each of these variables have been implicated as contributors to functional human performance.^[17,23,26-29,31,33,34,36,37,40,46,50,51]

4.3 Statistical Analysis

Pre-training and post-training values for the cellular and molecular variables studied were used to determine percentage change ($\%\Delta$) due to the resistance training programmes. Simple regression analyses were performed to determine the strength and the nature of the relationships between relative intensity and changes in the dependent variable. Relative contributions of intensity to the observed training adaptations were determined from the explained variance (r²).



Fig. 3. Relative (%) improvements in 1 repetition maximum (%1RM) strength for resistance exercise training programmes utilising training loads ranging from 40–95% 1RM. Note that the greatest increases occurred when the greatest relative training loads were used.^[25,37,39,59]

5. Intensity and Strength

Before we examine the skeletal muscle adaptations to varying loads, it is critical to remember that muscular strength (1RM) adaptations are dependent on the training load used. In other words, the largest increases in maximal strength occur with relatively heavier training loads. In making this statement, it must be noted that increases in maximal strength can occur from long-term training with a variety of relative resistance loads. But in general, to maximise the 1RM strength responses to a resistance exercise programme, one must handle relatively heavy loads. This illustration of the training specificity principle can be seen in figure 3. This bar graph clearly illustrates that the largest percentage increases in maximal strength occur with loads approaching maximal capacity (i.e. 100% 1RM), whereas lesser degrees of improvement occur with lighter loads.^[17,24,25] These responses are not due to different levels of effort since each training protocol involved maximal efforts for the conditions of each respective study. Obviously, an individual who is interested in maximal muscular strength can not exclusively use maximal or near-maximal loads without the risk of overtraining.^[11,20] However, a critical amount of training time must be spent with these heavy loads if maximal strength is to be increased.^[10,12,28] The bottom line is that relatively heavy loads must be utilised if maximal strength is

to be increased and/or maintained. It has been theorised that this axiom is even more important for those individuals who are advanced in terms of training experience and history.^[10,12,13,58]

6. Intensity and Hypertrophy

In order to extrapolate the relative (%) hypertrophic responses to different relative training intensities, the mean percentage hypertrophy increases for a number of resistance exercise studies were determined from the reported data.^[17,23-26,28,29,31,36-40,45,46] To more closely determine the intensity-specific training effect, the hypertrophic responses for each of the major fibre types (i.e. I and II, or I, IIA and IIB) was examined. How fibre type-specific relationships with relative intensity were determined is illustrated in figure 4 and figure 5. The mean hypertrophic responses for type I and type II fibres is labelled in a scatterplot with the relative training intensity. As expected, the data are somewhat scattered, undoubtedly due to training factors other than relative intensity. Regardless, the regression line illustrates the 'line of best fit' for this relationship. For both fibre types, greater relative intensities were associated with greater hypertrophic



Fig. 4. Relationship between relative (%) hypertrophy of type I fibres and relative intensity (% 1 repetition maximum [%1RM]) for 16 different resistance exercise training protocols. The simple regression line illustrates this relationship. Relative intensity accounts for 18% of the explained variance ($r^2 = 0.182$). The circled symbol represents two different studies.^[6,8,17,24,25,31,33,34,47-50,59-61]



Fig. 5. Relationship between relative (%) hypertrophy of type II fibres and relative intensity (% 1 repetition maximum [%1RM]) for eight different resistance exercise training protocols. The simple regression line illustrates this relationship. Relative intensity accounts for 35% of the explained variance ($r^2 = 0.349$).^[17,25,31,47,48,57,61]

responses. It should be noted that 16 different training programmes were used to determine this relationship for type I fibres, while only eight were used for type II fibres. This is due to the fact that some studies separately reported the sub-types IIA and IIB.

Close examination of figures 3 and 4 reveal several important factors. First, the hypertrophy response for each fibre type is dependent only in part on the relative intensity. This is evident from the explained variances for type I ($r^2 = 0.182$), and type II ($r^2 = 0.349$) fibres. Thus, as expected, there are numerous other training-related variables that are contributing to the resulting muscle growth. Also apparent is the difference between the hypertrophic response for type I and II fibres. Greater relative growth is apparent for the type II fibres, which is in agreement with the training literature.^[17,23-26,28,29,31,36-40,45,46] Interestingly, some of these findings are supported by the animal resistance exercise literature. The relative load (normalised for body mass) used for weight training exercise for cats explained a similar proportion of the variance $(r^2 =$ 0.212) for hypertrophy of the palmaris longus muscle.^[62]



Fig. 6. Regression lines representing the relationships between relative (%) hypertrophy of types I, II, IIA and IIB fibres and relative intensity (% 1 repetition maximum [%1RM]) for 16 different resistance exercise training protocols. Regression lines for types I and II fibres are identical to what is seen in figures 4 and 5, while regression lines for types IIA and IIB have been added for the studies accounting for these fibre sub-types. Relative intensity accounts for 12% of the explained variance ($r^2 = 0.124$) for type IIA fibres, and for 20% of the explained variance ($r^2 = 0.202$) for type IIB fibres.

If we take the regression lines for types I and II plotted in figures 3 and 4, add regression lines for the sub-types IIA and IIB, and extend them for relative intensities ranging from 40-95% 1RM, we see the results illustrated in figure 6. In general, similar patterns are seen when including the subtypes. Although the growth response for type I fibres is less than for type II fibres at most intensities, hypertrophy is nevertheless apparent. The important message from figure 6 is that heavy intensities must be used to result in a maximal growth response as measured at the cellular level. Based on the intersecting lines for the type IIB and IIA fibres, one might be tempted to conclude that type IIB fibres possess the greatest potential for growth. However, it must be remembered that there is a consistent transition of IIB fibres to IIA with heavy resistance exercise.^[17,23,25-32] Thus, although these fibres might possess considerable growth potential, they are also disappearing in number due to this transition.

7. Intensity and Fibre Type Transitions

While the load is critical for the hypertrophy response, it is less critical for fibre type transformations. As previously mentioned, it is well established that resistance exercise can convert IIB fibres to IIAB and eventually to IIA. Provided that the effort is maximal or near-maximal, this transition is evident at all loads ranging from 40-95% 1RM. Figure 7 illustrates the regression lines for relative fibre type transitions for various resistance exercise training intensities.^[17,23-26,28,29,31,36-40,45,46] Since type I fibres have not been shown to transition to type II with this type of exercise stimulus, a regression line for type I fibres has not been included. A quick examination of figure 7 reveals that regardless of the relative intensity used, the pattern of fibre type conversion is relatively constant. Chronic resistance exercise training results in a decrease in percentage IIB fibres, and a concomitant increase in percentage IIAB and IIA fibres. Studies that have examined IIAB fibres have suggested that converting fibres



Fig. 7. Regression lines representing the relationships between relative (%) change of types IIA, IIAB and IIB fibres, and relative intensity (% 1 repetition maximum [%1RM]) for eight different resistance exercise training studies. The horizontal nature of the regression lines suggests that relative intensity is not a major contributor to fibre type transitions. Since significant changes for type I fibres have not been reported in the resistance exercise training literthis regression not ature. line has been included [6,8,13,17,24,25,31,33,34,47-50,59,60]

must progress from IIB to IIAB (a hybrid of IIA and IIB) to IIA.^[7,17,23,26,28,29,44,48] It is speculated that a more critical training factor for fibre type conversion is the presence of a maximal effort for the number of prescribed repetitions or the prescribed %1RM. As long as the individual lifts until failure, or near-failure, a conversion of fibres in the direction of IIB to IIA may occur. On the other hand, such fibre type conversions may not be accompanied by maximal hypertrophic responses as illustrated in figures 4 to 6. It should also be noted that the limited data available at low relative intensities (e.g. 40% 1RM) suggest that the fibre transitional response may be slower compared with training at high intensities.^[24,37] Further study is needed to definitively clarify this relationship, as well as to determine the contributing roles of factors such as training volume (e.g. 1 set programmes).

8. Intensity and MHC Expression

The expression in human skeletal muscle of the three different isoforms of the MHC protein (I, IIa, IIb) is closely related to the relative (%) crosssectional area of each major fibre type.^[44] As previously reported, few changes occur to the percentage MHC I with resistance exercise, while increases in percentage MHC IIa and decreases in the percentage MHC IIb are typically observed.^[23,24,26,32,44,51] Figure 8 illustrates the relationship between relative MHC isoform transitions and training intensity. As with fibre type transitions, the load is critical for the hypertrophy response, but less critical for MHC isoform transformations. The horizontal nature of the regression lines in figure 8 indicate that MHC transitions can occur at all training intensities (40-95% 1RM) provided a maximal, or near-maximal effort if used. As with the fibre-type data reported in section 7, this transition is apparent at all loads examined, but it has been suggested that the magnitude of change may be slightly less at lighter loads (e.g. 40% 1RM).^[24,37] The similarities between the fibre type and the MHC transitions are not unexpected since relative MHC content is so closely related to relative cross-sectional areas for the different fibre types.[44]



Fig. 8. Regression lines representing the relationships between relative (%) change of myosin heavy chain (MHC) isoforms I, IIa and IIb, and relative intensity (% 1 repetition maximum [%1RM]) for five different resistance exercise training studies. The horizontal nature of the regression lines suggests that relative intensity is not a major contributor to MHC isoform transitions.^[6,11,24,37,51]

9. Types of Competitive Lifters

In addition to longitudinal resistance exercise training studies, insight on the long-term training effect on muscle fibre characteristics may be extrapolated from descriptive studies of athletes from the competitive lifting sports: weightlifting, powerlifting and body building. Athletes in each of these sports utilise heavy resistance exercise to permit optimal adaptations for their respective sports.

9.1 Weightlifters

Weightlifting, also known as Olympic-style weightlifting, is the only competitive lifting sport contested in the Olympic Games, and is the most popular lifting sport in most parts of the world. The two lifts contested are the snatch, and the clean and jerk lifts. Both of these lifts are characterised by extremely high levels of power. While heavy loads are lifted by elite heavy weight lifters (e.g. >250kg for the clean and jerk; >200kg for the snatch), very high barbell velocities are also observed (e.g. >2 m/ sec).^[59,63] Athletes excelling in this sport often use very high relative intensities (>90% 1RM), with

increased intensities most apparent as major competitions approach.^[18] Repetitions per set are often fairly low due to the importance of maintaining proper lifting technique (i.e. ≤ 5 repetitions), while inter-set rest intervals are often up to 3 minutes for the heaviest loads to permit adequate recovery between sets.^[18,59]

9.2 Powerlifters

Powerlifting is the most popular lifting sport in North America. Athletes compete in three lifts: (i) the barbell squat; (ii) the bench press; and (iii) the dead lift.^[18] Maximal efforts for each of these lifts are characterised by extremely heavy loads and low velocities. For example, world records for heavyweight powerlifters exceed 450kg for the squat, 320kg for the bench press and 410kg for the dead lift.^[18] In many ways, powerlifters train in a somewhat similar manner to weightlifters, although the absolute loads are greater and the velocities are much lower.

9.3 Body Builders

Success in the sport of body building is primarily based on muscular hypertrophy, although muscular symmetry, leanness and presentation style are also critical.^[64] Although actual lifting is not part of competition, athletes in this sport train extensively with heavy resistance exercises. Training programmes are typically of very high volume (i.e. total number of repetitions) and often utilise relatively lower training intensities when compared with weightlifters or powerlifters.^[61] In addition, body builders tend to use more small muscle mass and single-joint exercises than do athletes in the other lifting sports.

10. Muscle Characteristics of Competitive Lifters

Comparing the skeletal muscle characteristics of these competitive lifting populations can help shed light on the role of training load. While the number of studies on these athletes is limited, important training-related information may be deduced.

Figure 9 illustrates the fibre type profiles for powerlifters and body buildweightlifters. ers.^[18,43,54,65-69] Although few studies are available on elite level athletes in these sports, it appears that weightlifters and powerlifters have a greater percentage type II fibres than type I fibres. On the other hand, the limited data for body builders indicates an opposite pattern, that is a greater percentage type I fibres than percentage type II fibres. It is beyond the scope of these cross-sectional studies as to whether these differences are due to the long-term training programme, or if there is a genetic predisposition for these respective fibre characteristics. However, it should be noted that the athletes who require great levels of muscular force and power (weightlifters and powerlifters) are the ones who also possess the greatest content of the fibres capable of producing the greatest force and power. This ability to produce high force and power is due to both the size of the fibre, the fibre type and the contractile protein isoforms present.[33-35]

10.2 Percentage Fibre Type Areas

As seen in figure 10, the percentage cross-sectional area for type II fibres is considerably greater than for type I fibres for weightlifters and powerlifters.^[18,43,54,66,67,69] The opposite pattern is seen for



Fig. 9. Relative (%) fibre type content for competitive lifters (i.e. weightlifters, powerlifters and body builders).^[14,22,23,28,38,44,64,65]



Fig. 10. Relative (%) fibre type area for competitive lifters (i.e. weightlifters, powerlifters and body builders).^[14,22,23,28,38,44,64,65]

body builders.^[54,65,68] When figures 9 and 10 are compared, it is evident that there is a preferential hypertrophy of the type II fibres for the weightlifters and powerlifters, while the body builders have succeeded in increasing the size of both type I and type II fibres equally. As figure 6 illustrates, the weightlifters and powerlifters who routinely train with loads ≥90% 1RM exhibit the greatest growth in the type II fibres. This adaptational difference is less apparent as the relative intensity decreases. Body builders who typically perform a greater number of repetitions per set and much shorter inter-set rest intervals appear to stimulate muscle growth equally in both fibre types. This would be advantageous for a sport dependent on muscle hypertrophy. It is not known if body builders would experience even more hypertrophy of type II fibres if they also included more resistance exercise at very high relative intensities. Furthermore, it has been shown that large muscle mass, multi-joint exercises (i.e. barbell squats) elicit a greater anabolic hormone response than small muscle mass, single joint exercises (i.e. leg extensions, leg curls, hip/back extensions) even when relative intensities are equated.^[60] Thus, it may also be advantageous for body builders to maximise muscular growth by incorporating more large muscle mass, multi-joint exercises into their training programmes. Further study on these aspects of the training programmes are warranted.

10.3 Fibre Type Area Ratios

Perhaps most telling is the difference between weightlifters and powerlifters compared with body builders for the ratio of type II/type I fibre areas. This method of expressing muscle fibre characteristics permits one to see the combined effects of both percentage fibre type and percentage fibre type cross-sectional areas. Figure 11 illustrates the type II/type I area ratios for successful competitive lifters. Both weightlifters and powerlifters have a considerably greater ratio compared with body builders,^[18,54,65-69] again suggesting a preferential hypertrophy of the type II fibres for the type of training they perform. These data do not mean that weightlifters and powerlifters do not experience type I fibre growth, but rather that growth of type I fibres is relatively less than for type II fibres. On the other hand, as seen previously in figures 9 and 10, body builders are successful is attaining growth in both type I and II fibres.

Collectively, muscle fibre data from competitive lifters indicate that the greatest difference between weightlifters or powerlifters and body builders is not whether muscle hypertrophy can occur, but rather that there is a preferential hypertrophy of certain fibre types. Obviously, these cellular adaptations must be related to competitive performance; muscular force and power for the weightlifters and power-



Fig. 11. Ratio of type II/type I areas for competitive lifters (i.e. weightlifters, powerlifters and body builders).^[14,22,23,28,44,64,65]

lifters, and muscular size for the body builders. It must also be noted that unlike the previous comparisons of intensity levels ranging from 40-95% 1RM, body builders spend considerable amounts of training time using loads ≥80% 1RM. As a result, examination of the muscle characteristics of athletes in these three lifting sports represents a much smaller range of relative training intensities. On the other hand, weightlifters and powerlifters train specifically to enhance 1RM capabilities, and thus routinely use loads approaching 100% 1RM. Another confounding factor, as previously mentioned, is the potential role of pharmaceutical contributions to these adaptations that can not be determined from most of these studies. Further research would be necessary to determine the pharmaceutical mechanisms for differential adaptations based on resistance exercise intensity.

11. Conclusions

Several conclusions can be deduced from the preceding data. It appears that the muscular hypertrophy response to different relative training intensities follows a dose-response curve. In other words, the greater the %1RM, the greater the hypertrophy response. However, examination of figures 4 and 5 suggest that there may be a threshold for optimal growth responses. Once relative intensity reaches 80% 1RM, it appears that maximal growth is attained. Within the scope of the data available for this review, maximal growth occurs with loads between 80–95% 1RM. This, of course, spans a considerable repetition range that depends on the exercise being used.^[26,48] It is possible that this threshold is simply an artifact of so many of these studies using a relative intensity of approximately 80% 1RM. While some level of hypertrophy is possible at most relative intensities, an adequate load must be used to maximise this response. This concept of a load or intensity threshold for hypertrophy is also supported by animal data where it has been demonstrated that a critical load threshold (i.e. 30% of body mass) exists for weight-trained cats.^[62] Based on the data presented, figure 12 illustrates the optimal relative intensity range for muscular hypertrophy. The range



Fig. 12. Theoretical model of the relationship between relative resistance exercise training intensity (% 1 repetition maximum [%1RM]) and expected degree of muscular hypertrophy.

of hypertrophy indicated for any one intensity represents the range of data from the included studies. As previously mentioned, at best, relative intensity accounts for only 18-35% of the hypertrophy response, meaning that many other variables are likely to contribute to the observed growth responses. Nevertheless, relative intensity is likely to be one of the most important contributing training variables. The levels of hypertrophy for intensities >95% 1RM are theoretical and require further study to determine if the hypertrophy responses drops off as suggested if only using these extremely high relative intensities. However, the curve illustrated in figure 12 is supported by acute hormonal data for extreme levels of relative intensity. When sets of 100% 1RM loads have been used exclusively for a single training session, the responses of anabolic hormones are small or non-existent.^[59] Likewise, the acute anabolic hormonal responses for a training session performed at 40% 1RM loads is also minimal or nonexistent.^[70] Although responses at the cellular or molecular levels were not monitored in either of these studies, these do provide evidence that an anabolic environment is unlikely if exclusively using these extreme intensities.

For those not wanting large levels of muscular hypertrophy (e.g. distance runners, athletes in weight class sports), it must be noted that one does not necessarily want to avoid all resistance exercise \geq 80% 1RM. Rather, it is important to carefully titrate the volume of training performed at or above this intensity. It must be remembered that there are other physiological and performance reasons to train at these intensities besides muscular growth (e.g. muscular strength or power, see figure 3). In addition, the resistance training adaptations for many individuals/athletes may be already compromised by other components of the total training programme (e.g. aerobic conditioning).^[22] Therefore, inclusion of resistance training ≥80% 1RM may be necessary to counter the catabolic effects of other types of exercise.

Resistance exercise-induced fibre type and MHC isoform transitions appear to be less dependent on relative intensity. As figures 7 and 8 illustrate, transitions can occur across the intensity spectrum. It is believed that a critical factor in such transitions is whether the individual exercises to failure or nearfailure. It should be pointed out that whether one trains to this level of exertion or not should be determined by the purposes of the training. Among competitive lifting athletes, muscular growth is apparent for weightlifters, powerlifters and body builders. All of these athletes routinely train with loads at or above 80% 1RM. It appears that those athletes who typically train with the greatest relative intensities (i.e. weightlifters and powerlifters) tend to experience a preferential hypertrophy of type II fibres. It would be a logical assumption that such an adaptation is specific to the requirements of their sports.

12. Training Implications

The preceding data leads one to speculate on potential applications to resistance training programmes. If muscular hypertrophy is an important training goal, relative intensities $\geq 80\%$ 1RM must be routinely used. The same applies if maintenance of muscular mass is a goal. This would apply not only for the athlete who desires to carry a large

muscular mass (e.g. shot putter, American football lineman), but also for the athlete who wishes to simply maintain their existing lean body mass (e.g. distance runner, athlete competing in a particular weight class). Other adaptations such as fibre type or MHC expression are less dependent on relative intensity, but appear to require use of the maximal or near-maximal number of repetitions for a particular load.

An interesting area that requires additional research is the concept of designing the resistance training programme based on an individual's fibre type characteristics. It has been suggested that optimal training programmes must account for the fibre type profile of an individual.^[9] In this manner, different set and repetition schemes and loads may be required for an individual possessing a large percentage type I fibres when compared with an individual with a large percentage type II fibres. Whether such a differentiation is advantageous is beyond the scope of this review, but certainly is worthy of further research. Regardless, depending on the purpose of the resistance exercise training programme, the relative intensity prescribed can have a profound impact on the resulting performance, cellular and molecular adaptations.

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