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ORIGINAL ARTICLE

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Adaptation to chronic eccentric exercise in humans: the influence of contraction velocity

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Abstract We compared changes in muscle fibre composition and muscle strength indices following a 10 week isokinetic resistance training programme consisting of fast (3.14 rad·s^{-1}) or slow (0.52 rad·s^{-1}) velocity eccentric muscle contractions. A group of 20 non-resistance trained subjects were assigned to a FAST ($n = 7$), SLOW ($n = 6$) or non-training CONTROL ($n = 7$) group. A unilateral training protocol targeted the elbow flexor muscle group and consisted of 24 maximal eccentric isokinetic contractions (four sets of six repetitions) performed three times a week for 10 weeks. Muscle biopsy samples were obtained from the belly of the biceps brachii. Isometric torque and concentric and eccentric torque at 0.52 and 3.14 rad·s^{-1} were examined at 0, 5 and 10 weeks. After 10 weeks, the FAST group demonstrated significant [mean (SEM)] increases in eccentric [29.6 (6.4)%] and concentric torque [27.4 (7.3)%] at 3.14 rad·s^{-1}, isometric torque [21.3 (4.3)%] and eccentric torque [25.2 (7.2)%] at 0.52 rad·s^{-1}. The percentage of type I fibres in the FAST group decreased from [53.8 (6.6)% to 39.1 (4.4)%] while type IIb fibre percentage increased from [5.8 (1.9)% to 12.9 (3.3)%; $P < 0.05$]. In contrast, the SLOW group did not experience significant changes in muscle fibre type or muscle torque. We conclude that neuromuscular adaptations to eccentric training stimuli may be influenced by differences in the ability to cope with chronic exposure to relatively fast and slow eccentric contraction velocities. Possible mechanisms include greater cumulative damage to contractile tissues or stress induced by slow eccentric muscle contractions.

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Introduction

The focus of many resistance training programmes is to target and remedy a perceived weakness or to improve a physical capacity that may be advantageous for a particular sport or activity. Consequently, many applied research programmes focus on manipulating or controlling resistance training variables such as contraction mode or movement velocity in attempts to understand better and optimise the physiological responses to resistance training (Sale and MacDougall 1981; Dudley et al. 1990; Ryan et al. 1991; Behm and Sale 1993; Griffin et al. 1993; Seger et al. 1998).

In previous research, the investigation of velocity-specific responses to concentric resistance training has involved quantifying post-test changes in strength using concentric contraction velocities both faster and slower than the single training velocity. Using this model, comparatively high velocity isokinetic concentric training programmes (i.e. higher than 2.0 rad·s^{-1}) have been shown to increase peak concentric torque production during both slower and faster contraction velocities (Kellis and Baltzopoulos 1995). In comparison, the strength gains that occur following relatively slow concentric training protocols (e.g. 0.5 rad·s^{-1}) are more likely to be confined to a narrow range at or about the training velocity (Coyle et al. 1981; Ryan et al. 1991; Kellis and Baltzopoulos 1995).

A small number of studies have attempted to describe the velocity-specific nature of chronic eccentric contractions by subjecting individuals to a single velocity, isokinetic, training programme (typically 2.1 rad·s^{-1}) and then examining muscle torque during faster and slower eccentric contraction velocities (Kellis and Baltzopoulos 1995; Seger et al. 1998). Studies targeting the quadriceps (Duncan et al. 1989) and hamstring (Ryan et al. 1991) muscle groups demonstrated that 6 weeks of eccentric training performed at 2.10 rad·s^{-1} was not velocity-specific, producing similar increases in eccentric torque at 1.05, 2.10 and 3.14 rad·s^{-1}. In contrast, a more recent study examined eccentric knee extension torque at 0.52, 1.57, and 4.71 rad·s^{-1} following 10 weeks of eccentric quadriceps training at an intermediate velocity (1.57 rad·s^{-1}) (Seger et al. 1998). The authors reported no change in muscle fibre composition, but did observe an increase in eccentric torque at the training velocity. Interestingly, this improvement was velocity-specific, with no improvement observed when eccentric torque was measured at 4.71 rad·s^{-1}.

With few exceptions (Hortobágyi et al. 1996; Seger et al. 1998), most eccentric training studies have relied almost exclusively on torque production as the criterion of muscle adaptation and many have employed similar experiment protocols. As a consequence, it is not known if the contraction velocity used in an eccentric training programme differentially affects the structural or functional properties of human skeletal muscle. For example, if eccentric training induces adaptations in functional capacity that are most prominent at the training velocity (Seger et al. 1998), it follows that a direct comparison of fast and slow eccentric training velocities should be made to identify the training velocity that produces the largest, most specific and most generalisable neuromuscular adaptations.

The purpose of this study was to compare changes in elbow flexor muscle fibre composition and muscle strength indices following a 10 week unilateral, isokinetic training programme consisting exclusively of fast (i.e. 3.14 rad·s^{-1}) or slow (i.e. 0.52 rad·s^{-1}) velocity eccentric muscle contractions. We hypothesised that slow eccentric training would produce velocity-specific strength improvement while fast eccentric training would produce a more generalised training adaptation.

Methods

Subjects

A group of 20 non-resistance trained male and female volunteers completed this study which complied with the requirements of The University of Queensland Medical Research Ethics Committee and with current Australian laws and regulations. Written consent was obtained from all participants. Mean (SD) age, height and mass were 24.2 (7.0) years, 176.6 (5.9) cm and 76.2 (15.8) kg, respectively. Subjects were counterbalanced on pre-test eccentric torque values and randomly assigned to a FAST (3.14 rad·s^{-1}, $n=7$, 5 men, 2 women), SLOW (0.52 rad·s^{-1}, $n=6$, 5 men, 1 woman) or a non-training control group (CONTROL, $n=7$, 5 men, 2 women). All subjects refrained from extraneous strenuous exercise throughout the training period.

Testing and training equipment

The eccentric training programme targeted the elbow flexors of the non-dominant arm and were performed on a preacher curl bench (Force Fitness Systems: 42SBP-U, Brisbane, Queensland) located alongside an isokinetic dynamometer (Cybex 6000, Lumex Inc., Ronkonkoma, N.Y.). With the subject in a stable seated position, the non-dominant arm was placed on the sloping front incline (0.78 rad) of the preacher curl bench with the forearm supinated, hand grasping the lever arm and the elbow adjacent to the axis of rotation of the dynamometer. Mechanical stops on the dynamometer were engaged to prevent excessive elbow flexion or extension and to standardise the range of motion of the elbow at 2.27 rad.

Eccentric training

Pre-test data were obtained 10 days prior to the start of the training period. During the week following the pre-tests subjects also completed 2–3 eccentric familiarisation sessions. These sessions included several submaximal (e.g. 50%–60%maximal) and 3–4 maximal eccentric contractions and were designed to reduce the severity of muscle damage and soreness experienced during the initial stages of the training programme.

Subjects in the FAST and SLOW groups trained on 3 non-consecutive days each week for 10 weeks. During each session the subjects performed 24 maximal eccentric contractions (4×6 repetitions) at an angular velocity of 0.52 rad·s^{-1} (SLOW) or 3.14 rad·s^{-1} (FAST). The CONTROL group did not train. A 60 s rest was taken between sets. During each eccentric repetition, subjects maximally resisted the dynamometer from the very beginning of the movement, as it forced their forearm from full flexion (0.70 rad) to near full elbow extension (2.97 rad). Verbal and visual feedback was provided to encourage maximal effort. To avoid activating the stretch-shorten cycle, the dynamometer slowly and passively returned the arm of the subject to full flexion at 0.26 rad·s^{-1} on completion of each eccentric repetition.

Strength variables

All strength variables were assessed using the same equipment and positioning as during training. Concentric, eccentric and isometric torque values were obtained at an elbow angle of 1.57 rad. During pre, mid and post-test assessments, peak torque values were recorded as subjects completed three maximal isometric contractions and three maximal eccentric and concentric contractions at 0.52 and 3.14 rad·s^{-1}. The order of contractions was randomised and a 2 min rest was taken between modes. To monitor training progress, total eccentric work performed during the first training session (i.e. 24 repetitions) of each week was recorded during weeks 2–10.

Muscle biopsy and histochemistry

Muscle biopsy samples (approximately 50 mg) were obtained under local anaesthetic from a depth of approximately 3 cm in the belly of the biceps brachii using a 6 mm biopsy needle (Bergström 1962). Samples were blotted dry, orientated for transverse sectioning, mounted in an optimal cutting temperature embedding medium, frozen in isopentane cooled by liquid nitrogen and stored at –80°C until analysis. Serial 8 μm transverse sections were obtained at –20°C using a Cryostat (Leica CM 1800) on 3-aminopropyltriethoxysilane coated slides. Fibre typing was performed using a metachromatic dye-adenosine triphosphatase (ATPase) method for the simultaneous identification of skeletal muscle fibre types I, IIa, and IIb. Toluidine blue (Chroma) was used to stain muscle sections following routine ATPase histochemistry to permit muscle fibre differentiation. Fibres with low ATPase activity stained metachromatically while fibres with high ATPase activity stained orthochromatically with the intensity of the colour proportional to the content of insoluble phosphate (Ogilvie and Feeback 1990). Using light microscopy, approximately 300 fibres from each subject (pre- and post-test) were counted by three investigators working independently.

Data analysis

Data were assessed for normality using a D'Agostino-Pearson omnibus test. A logarithmic transformation (Log_{10}) was applied to non-normally distributed torque data prior to analysis. One-way analysis of variance (ANOVA) and planned comparisons of group means were made to investigate differences within and between FAST, SLOW, and CONTROL groups at 0, 5 and 10 weeks. An intraclass correlation was performed to assess the reliability of calculations of muscle fibre percentage. Significance was accepted at an α of $P < 0.05$.

Results

Subjects

The pre- and post-test torque-velocity relationships are presented in Fig. 1. Pre-test mean torque values in the FAST group were uniformly lower than SLOW group values, however this difference was not statistically significant ($P > 0.05$). Following the initial familiarisation period, volunteers subjectively reported little or no muscle soreness despite the intensity of the 10 week training programme.

Total eccentric work

Total eccentric work values obtained during weeks 2–10 were similar, with both FAST and SLOW groups experiencing a 40% improvement in eccentric work capacity as a result of the training programme ($P < 0.05$). A projection of work values over all 30 training sessions indicated that SLOW and FAST groups performed approximately 73 kJ and 77 kJ of eccentric work, respectively. Over the 10 week period, 4 kJ would be equivalent to approximately 36 repetitions.

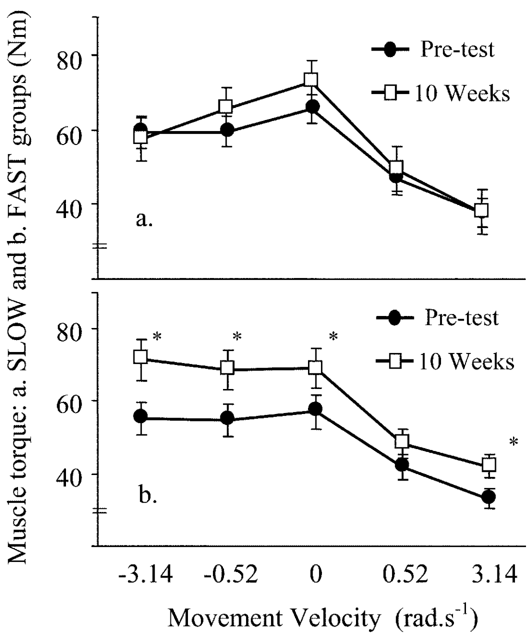

Fig. 1 The torque-velocity relationship for **a** *SLOW* and **b** *FAST* groups prior to and following 10 weeks of eccentric training. *Significant ($P < 0.05$) difference from pre-test

Isometric torque

Isometric torque data are presented in Fig. 2. Isometric torque values in the SLOW group did not improve significantly over the 10 week period ($P > 0.05$). In contrast, the FAST group experienced a significant post-training increase in isometric torque ($P < 0.05$).

Concentric torque

Neither the FAST nor SLOW group demonstrated any improvement when concentric torque was measured at 0.52 rad·s^{-1} ($P > 0.05$) (Fig. 3a). In contrast, after 5 weeks both SLOW and FAST groups had improved in their ability to produce concentric torque at 3.14 rad·s^{-1} ($P < 0.05$). Continued concentric torque improvement at 3.14 rad·s^{-1} was observed during the final 5 weeks of

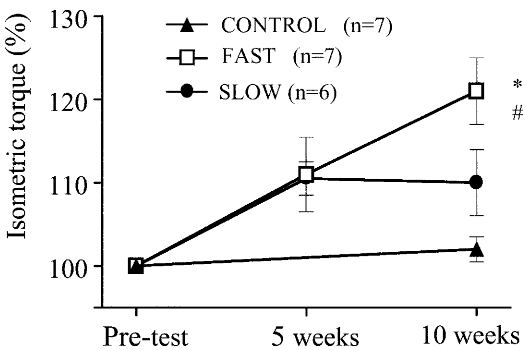

Fig. 2 Relative change in isometric torque (%). *Significant ($P < 0.05$) difference from *pre-test*. #Significant ($P < 0.05$) difference from *CONTROL* at week 10

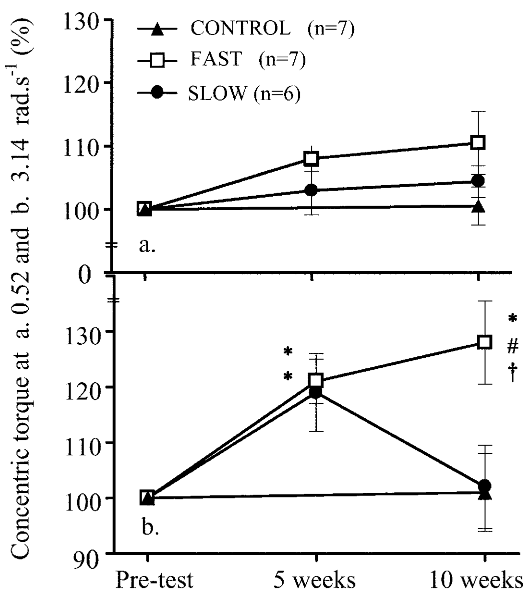

Fig. 3 Relative change in concentric torque at **a** 0.52 rad·s^{-1} and **b** 3.14 rad·s^{-1}. *Significant ($P < 0.05$) difference from pre-test. #Significant ($P < 0.05$) difference from *CONTROL* at week 10. † Significant ($P < 0.05$) difference from *SLOW* at week 10

training in the FAST group. However, during weeks 5–10, the training adaptation in the SLOW group was lost with fast concentric torque values (3.14 rad·s^{-1}) returning to near pre-test levels by week 10 (Fig. 3b).

Eccentric torque

Changes in eccentric torque are presented in Fig. 4. In both the SLOW and CONTROL groups, eccentric torque at 0.52 and 3.14 rad·s^{-1} did not change over the 10 week period ($P>0.05$). However, after 10 weeks, the FAST group had significantly improved their ability to generate eccentric torque at both 0.52 and 3.14 rad·s^{-1} ($P<0.05$).

Histochemical muscle fibre type

Changes in histochemical muscle fibre type percentage are presented in Table 1. A significant decrease in the percentage of type I fibres and an increase in type IIb fibres was observed in the FAST group. No significant fibre type changes were observed in the SLOW group although trends suggesting a decrease in the percentage of type I fibres and increase in type IIa fibre percentage were noted. No fibre type changes were evident in the CONTROL group ($P>0.05$). An intraclass correlation suggested the reliability of fibre counting was good ($r=0.82$).

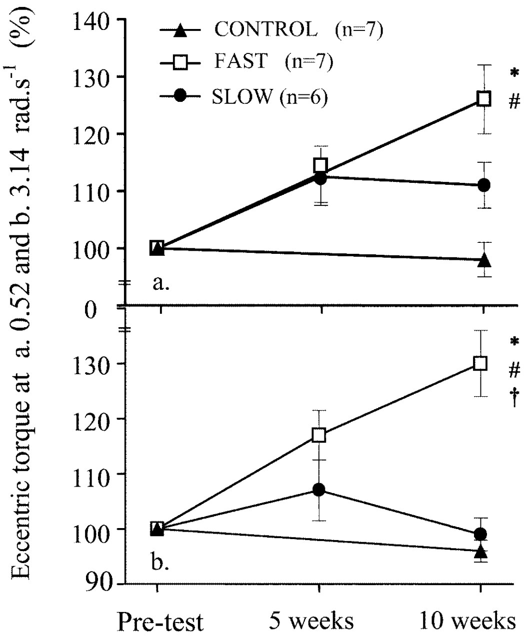

Fig. 4 Relative change in eccentric torque at **a** 0.52 rad·s^{-1} and **b** 3.14 rad·s^{-1}. *Significant ($P<0.05$) difference from pre-test. #Significant ($P<0.05$) difference from *CONTROL* at week 10. † Significant ($P<0.05$) difference from *SLOW* at week 10

Discussion

The type of muscle contraction required to perform an athletic task is usually dictated by the nature of the event. Nevertheless, the ability to generate concentric and eccentric torque over a range of contraction velocities is often a critical determinant of athletic success. To the best of our knowledge, this was the first study to examine velocity-specificity by directly comparing changes in muscle fibre type and strength indices following eccentric training at relatively slow (0.52 rad·s^{-1}) or fast (3.14 rad·s^{-1}) contraction velocities.

Several studies have examined training adaptations following isokinetic training at a single eccentric contraction velocity (Duncan et al. 1989; Ryan et al. 1991; Higbie et al. 1996; Seger et al. 1998). In these studies, post-training improvements in eccentric torque were shown to occur at eccentric contraction velocities both faster and slower than the training velocity in some (Duncan et al. 1989; Ryan et al. 1991), but not all (Seger et al. 1998) cases. However, methodological differences such as choice of muscle group, exercise equipment, subject positioning and training status make it difficult to compare directly the results of different studies. For example, Seger et al. (1998) used a training velocity of 1.57 rad·s^{-1}, whereas Duncan et al. (1989) and Ryan et al. (1991) trained their subjects at a slightly faster 2.10 rad·s^{-1}. In the present study, if we had only examined post-training changes in eccentric torque in the FAST group of subjects, we may have concluded that 10 weeks of eccentric elbow flexor training at 3.14 rad·s^{-1} does not produce velocity-specific adaptations (Duncan et al. 1989; Higbie et al. 1996). Alternatively, if we had only measured isometric, concentric and eccentric torque at 3.14 rad·s^{-1} in the FAST group we would have noted that 10 weeks of eccentric elbow flexor training

Table 1 Muscle fibre type percentage. Values are means (SEM). FAST $n=7$, SLOW $n=6$, CONTROL $n=7$

Group	Fibre type	Pre-test (week 0)			Post-test (week 10)		
		I	IIa	IIb	I	IIa	IIb
FAST	mean	53.82	40.39	5.79	39.12	47.97	12.91
		(6.60)	(7.35)	(1.91)	(4.43)[a]	(6.19)	(3.34)[a]
SLOW	mean	56.99	34.26	8.76	49.94	41.38	8.68
		(3.32)	(5.33)	(2.30)	(3.18)	(4.72)	(2.31)
CONTROL	mean	46.83	42.59	10.58	50.12	39.17	10.71
		(3.80)	(4.89)	(2.03)	(4.81)	(6.28)	(2.08)

[a]Significant difference from pre-test

was not mode-specific and produces adaptations during all contraction modes (Ryan et al. 1991). Examination of these fragments of data clearly demonstrate how the selection of dependent variables and eccentric training velocity may dramatically alter the interpretation of results. Further, these data highlight the need for caution when examining velocity-specificity using experiment designs that are limited to a single training velocity.

Several mechanisms may have contributed to the positive training adaptation observed in the FAST group in the present study. In addition to changes in muscle fibre type, these mechanisms include improvements in muscle fibre recruitment perhaps mediated by better neural control. In untrained individuals the ability to generate eccentric torque in the knee extensors is initially limited by an inhibitory/protective neural mechanism which may be more prevalent during faster eccentric contractions (Westing et al. 1988, 1990; Stauber 1989; Tesch et al. 1990; Hortobágyi et al. 1996). If such inhibition occurred in the elbow flexors and was more prevalent during the pre-tests and the early stages of the FAST groups eccentric training programme, it may have resulted in the FAST group experiencing a less initially severe yet more progressive overload stimulus than the SLOW group. This gradual resolution of inhibition may have contributed to the greater proportional strength gains conferred by the fast ($3.14\ \mathrm{rad \cdot s^{-1}}$) eccentric training stimulus (Fig. 1).

Unlike the FAST group, torque values in the SLOW group reached a plateau or fell during the final 5 weeks of training. This trend was consistent in all SLOW group subjects. The failure of the SLOW group to demonstrate significant post-training improvements in muscle torque occurred despite both FAST and SLOW groups performing a similar amount of total work during the 10 week training period. This lack of functional improvement in the SLOW group was unexpected and certainly inconsistent with previous research demonstrating 116%, 36%, 18% and 34% increases in eccentric quadriceps torque following 6–12 week eccentric training protocols performed at $1.04\ \mathrm{rad \cdot s^{-1}}$ (Higbie et al. 1996; Hortobágyi et al. 1996), $1.57\ \mathrm{rad \cdot s^{-1}}$ (Seger et al. 1998) and $2.09\ \mathrm{rad \cdot s^{-1}}$ (Duncan et al. 1989).

While the mechanisms responsible for this anomaly are unclear, data from our laboratory suggests that an acute damaging bout of slow velocity eccentric exercise ($0.52\ \mathrm{rad \cdot s^{-1}}$) may cause greater muscle injury and loss of muscle function compared to a similar eccentric bout performed at $3.14\ \mathrm{rad \cdot s^{-1}}$ (Paddon-Jones 1999). Furthermore, the eccentric training velocity in the SLOW group ($0.52\ \mathrm{rad \cdot s^{-1}}$) was six times slower than the FAST group ($3.14\ \mathrm{rad \cdot s^{-1}}$) and therefore during the entire study, maximal eccentric contractions were performed for 17.4 min in the SLOW group, but only 2.9 min in the FAST group. Consequently, while it may seem plausible or intuitive that a training stimulus of greater duration would confer a greater training adaptation, it is perhaps more likely that the cumulative effects of muscle damage and the increased amount of time that the elbow flexor muscles in the SLOW group were engaged in maximal effort eccentric contractions may have contributed to an overtraining-like response which inhibited strength development during the final 5 weeks of training. Further research is clearly required to determine if chronic eccentric exercise and contraction velocity elicits a functionally and symptomatically distinct overtraining response.

Like contraction velocity, the ability to generate muscle torque following eccentric training may also be influenced by the contraction mode employed during the tests. In a number of previous studies, adaptation to eccentric training has been shown to be mode-specific (Duncan et al. 1989; Ryan et al. 1991; Higbie et al. 1996; Hortobágyi et al. 1996) while other studies have demonstrated increases in both eccentric and concentric torque following eccentric training (Komi and Buskirk 1972; Ryan et al. 1991). A recent study highlighted the potential magnitude of the mode-specific eccentric training effect demonstrating a large increase in eccentric (116%) but not concentric torque (5%) following 12 weeks of eccentric quadriceps training performed at $1.05\ \mathrm{rad \cdot s^{-1}}$ (Hortobágyi et al. 1996). Unfortunately, changes in concentric torque at 2.09 and $3.14\ \mathrm{rad \cdot s^{-1}}$ were not reported. Consequently, it is unclear if these previous data support the results of the present study which suggested that eccentric training at $3.14\ \mathrm{rad \cdot s^{-1}}$ improves the ability to generate isometric torque and concentric torque at a fast velocity ($3.14\ \mathrm{rad \cdot s^{-1}}$) but has no observable effect during strength tests at a slow ($0.52\ \mathrm{rad \cdot s^{-1}}$) concentric contraction velocity. In the present study, concentric torque at $0.52\ \mathrm{rad \cdot s^{-1}}$ was the least specific (mode and velocity) measure of dynamic muscle function in the FAST group and was the only strength variable not to improve following eccentric training at $3.14\ \mathrm{rad \cdot s^{-1}}$. These data suggest that eccentric training at relatively fast isokinetic velocities produces general non-mode specific improvements in the ability to generate torque. However, as described in the previous sections, it appears that changes in the ability to generate isometric, concentric and eccentric torque may be independently influenced by contraction velocity.

Changes in muscle fibre type distribution following an eccentric training programme may represent chronic adaptation to selective muscle fibre recruitment (Fridén et al. 1983; Hather et al. 1991; Hortobágyi et al. 1996). In the present study, subjects in the FAST group experienced a 13% decrease and a 7% increase in the proportion of type I and IIb fibres, respectively ($P < 0.05$). In comparison, Hortobágyi et al. (1996) reported a 5% decrease (type I), a 12% increase (type IIa) and a 7% decrease (type IIb) in muscle fibre percentages following a 12 week eccentric quadriceps training programme. However, Hortobágyi's subjects performed the eccentric training programme at an intermediate velocity ($1.05\ \mathrm{rad \cdot s^{-1}}$) and consequently differences between the studies may reflect a normal physiological response to two different eccentric training velocities or other methodological differences such as muscle group selection.

Reports of an increase in the percentage of type IIb fibres following resistance training are relatively uncommon, but have been shown to occur in both human (Prince et al. 1981; Anderson et al. 1994) and animal (Yarasheki et al. 1990) models. The majority of resistance training studies examining changes in histochemical muscle fibre type or myosin heavy chain isoforms have reported an increase in the percentage of type IIa fibres and/or a reduction in type IIb fibres (Nardone et al. 1989; Adams et al. 1993; Staron et al. 1994). To the best of our knowledge, this is the first study to demonstrate an increase in type IIb fibre percentage following relatively fast eccentric exercise. Further research examining different muscle groups and/or different training velocities is recommended.

In conclusion, a 10 week training programme performed using relatively fast eccentric contractions (3.14 rad·s^{-1}) resulted in a decrease in type I muscle fibre percentage, an increase type IIb muscle fibre percentage and significant improvements in almost all specific and non-specific measures of muscle torque. The SLOW group did not experience a significant change in type IIb muscle fibre type but did experience a trend towards similar functional improvements as the FAST group during the first 5 weeks of training. However, during the final 5 weeks of training the SLOW group failed to improve in any measure of muscle function. The mechanisms responsible for this differing responses to the eccentric training velocity are unclear but may be linked to an overtraining response, changes in motor unit recruitment patterns and/or the cumulative effects of velocity-specific muscle microdamage.

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