Adaptative changes and contractile properties of skeletal muscle: Significance and problems of tension measurement

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Abstract The contractile function of skeletal muscles is comprised of 3 major elements: strength (maximum muscle strength), speed (contractile velocity), and endurance. In sport science, the muscle contractile function facilitating exercise is a notable muscle function, and many studies have investigated training effects on skeletal muscle. In the sport science field, various training effects on skeletal muscle have been examined. For example, the level of protein forming the muscular microstructure and composition of muscle fiber type change. Recently, in skeletal muscle training experiments, correlation between changes in molecular and gene control systems in response to training have been attracting attention; however, few studies have simultaneously measured the contractile properties. In this review, the experimental significance of measuring the muscle contractile function has been outlined with reference to previous studies.

Keywords: skeletal muscle, contractile function, adaptation

Introduction

Skeletal muscles account for about 40% of body weight, and play many roles in the body, such as water storage, energy production, and thermogenesis, in addition to mechanical contraction. The contractile function of skeletal muscles is comprised of maximum muscle strength, contractile velocity, and endurance. In the sport science field, many studies on muscular physiology have investigated the training effects on skeletal muscle. An enhancement of the muscle contractile function, e.g. maximum muscle force and fatigue resistance, is important to validate the effectiveness of training methods used in experiments. On the other hand, the level of protein forming the muscular microstructure and composition of muscle fiber type both change according to the manner of training. Elucidation of the low-molecular-weight protein-mediated signal transmission system has progressed in recent studies, and the mechanism of adaptative changes of skeletal muscles has been clarified; however, it is surprising that few studies have simultaneously measured the contractile properties.

In studies conducted 25 years ago, the biochemical and histochemical characteristics of skeletal muscle were compared with the characteristics of skeletal muscle contraction. The dependence of exerted muscle strength on the contractile protein level, determination of the contractile velocity by ATPase activity, and the close relationship between muscle fiber composition and contraction characteristics were investigated. The achievements of these studies led to conclusions currently considered as common sense. Skeletal muscle fibers are capable of exerting stable muscle strength through their microstructure with high regularity excitation-contraction coupling (EC coupling), and the molecular system of force generation has been elucidated. These systems are unlikely to be changed by exercise training, and this may be a reason for not attaching greater importance to measurement of muscular contractile properties in animal experiments. Do muscular contractile properties change as expected in skeletal muscle in which hypertrophy has already been induced, or are the biochemical characteristics or molecular control systems changed by exercise training?

Force exerted with muscular hypertrophy

Muscular hypertrophic changes are investigated by measuring the muscle weight or muscle cross-sectional area, and these measurements may be based on the view that muscle strength is proportional to muscle weight and cross-sectional area. Moreover, contractile protein is considered to increase in a muscle cross-sectional area-dependent manner. Skeletal muscle tissue is formed by the assembly of muscle fibers (muscle cells), and the main components are muscle fibers and intercellular fluid. Muscle fibers are comprised of contractile and regulatory proteins, organelles, and intracellular fluid. Do these components change in the same ratio in training-induced
hypertrophic muscle fibers? Surprisingly, few studies have investigated whether or not muscle fibers and the fluid between them change at the same rate in hypertrophied skeletal muscle (due to proliferation or enlargement of muscle fibers).

In a compensatory muscular hypertrophy model prepared by synergist resection, marked muscle fiber hypertrophy is observed within a short time (about 1-2 weeks) in muscle to which a marked load is rapidly applied; but this hypertrophy is not accompanied by the development of muscle strength. It may be an edema-like state due to an increase in interstitium between cells, swelling, or increased blood flow in muscle fibers in response to marked stress - similar to that observed after exercise. Changes in satellite cells were investigated in studies using a compensatory muscular hypertrophy model, and changes in the mechanism of signal transmission controlling protein anabolism were investigated in the period within 2 weeks after muscle resection when muscle strength had not increased. Measurement was performed within a short time because various marked changes occur in the early phase after applying a weight load on the muscle, and these changes decrease and become difficult to detect in the period in which strength increases in proportion to the thickness. Therefore, stress responses are observed only within a short period; and no muscular hypertrophy-related findings leading to functional development have been investigated.

Even though signal transmission occurs at the molecular level, it does not necessarily result in improvement of muscular function. It only presents the possibility of exercise exhibiting a training effect in the future, and it does not serve as a means to predict the exercise effect or evaluate the training effect. The discovery of a new molecular system may only clarify that the molecular system sensitively responds to changes in the internal environment accompanying muscle contraction. However, it is known that an increase in muscle weight with long-term training using a treadmill is accompanied by an increase in muscle strength.

Muscle contractile velocity

The second functional element of skeletal muscle, contractile velocity, is dependent on the ATP hydrolysis rate. Differences in ATPase activity are related to the muscle fiber type classification.

Muscle fiber types have been classified, such as slow and fast muscle fibers and subgroups of fast muscle fibers. In the muscle fiber classification based on differences in the contractile velocity, differences in the number of mitochondria, oxidative enzyme activity, and the extent of capillary blood vessels on histochemical staining are described. It is also known that there are several isoforms of the myosin heavy chain, which is the contractile protein of muscle fibers, and they act as a contractile velocity-determining factor in combination with the myosin light chain. In addition to these studies on muscle fiber type classification using enzymatic histochemical staining, classification using antibodies according to the individual myosin heavy chain isoform appeared in the 1980s, which clarified the presence of differences among the muscle fiber types at the gene expression level.

The relationship between muscle fiber type and contractile velocity was investigated by comparing the rates of fast and slow muscle fibers and contraction characteristics and performing experiments with single muscle fibers. The contractile velocity of fast muscle fibers is about 5-10 times faster than that of slow muscle fibers, and about 1.3-2 times differences are observed among the fast muscle fiber subtypes. It has been reported that muscular ATPase activity increases with training, in which the contractile velocity rises and the muscle fiber composition also changes. But, does the contractile function significantly change in type-transformed muscle fibers? There are several problems with the muscle fiber type classification using histochemical staining. On histological staining, muscle fibers are compared based on the staining intensity. The myosin heavy chain related to the contractile velocity is classified into muscle fiber types, such as types 1 and 2, utilizing differences in stainability among the isoforms. Normally, a single type of myosin heavy chain is preferentially expressed in a muscle fiber. However, a muscle fiber is not necessarily composed of a single type of myosin isoform, in spite of it being a small amount; other myosin heavy chain isoforms are contained in muscle fibers. Moreover, the ratios of several myosin heavy chain isoforms are changed by exercise training and by reversing the ratios, which is considered a type transformation. When exercise stimulation is applied, several molecular species of myosin heavy chain, such as fast and slow muscle types, are observed within a muscle fiber in a specific period. When muscle fibers are individually investigated, mixed myosin heavy chain types are observed in many fibers even in control muscles without exercise stimulation. If a mixture of several molecular species of myosin heavy chain is normal, muscle fibers cannot simply be classified into fast and slow muscle fibers, but should be regarded as one type with various mixed ratios, i.e., muscle fibers are classified into slow and fast muscle fibers and subgroups based on the most abundantly contained myosin heavy chain isoform. Training-induced changes in the muscle fiber composition ratio do not directly correspond to changes in the contractile velocity; but it is also known that the mixture ratio of myosin heavy chain isoforms influences the contractile velocity. When myosin with various rotation speeds is present in single muscle fibers connected in series, the contractile velocity is not determined by the simple ratio of the molecular species, although changes in this ratio may markedly influence the contractile velocity.
Studies on muscle fiber type transformation have recently progressed through studies on the molecular system, and the relationship between calcineurin and the expression of the genetic phenotype of the slow muscle type has been clarified\(^5\). Differences in signal transmission system proteins, considered present between slow and fast muscle fiber types, may also parallel the mixture ratio of the myosin heavy chain isoforms.

Considering the above comprehensively, it is questionable whether the contractile properties acquired by fiber type transformation have been similar to that of the native type fibers. For example, are contractile properties of fast type fibers transformed into slow type fibers by training similar to that of native slow type fibers? It is difficult to identify muscle fibers with exercise stimulation-induced type transformation, and there has been no study on the contractile function of type-transformed muscle fibers.

**Muscle endurance**

Oxidative system enzyme activity serves as an endurance index of muscle fibers which may have transformed from type IIa to type IIb with an exercise load; and it has been reported that the enzyme activity level after type transformation is lower than that of the original type IIa fibers\(^7\). This report also suggests that the ratio of type transformation is not directly associated with muscle endurance of the contractile function. Regarding changes in the oxidative system enzyme activity level, transformation from fibers with a poor oxidation system to those with a superior system may progress in stages with training because the mitochondrial size and enzyme activity level show proportional changes.

Muscle endurance capacity has been investigated with regard to the system supplying oxygen to muscle and the energy resynthesis system utilizing this oxygen by biochemical or histochemical measurement of the number of mitochondria, oxidative system enzyme activity, capillaryization in the muscle and the occupancy of oxidative system-dominant muscle fibers\(^10\). Recently, the promotion of endurance through several signal transmission pathways has been confirmed, such as factors increasing mitochondrial function, oxidative system enzyme activity, and PGC-1α which increases capillary blood vessels\(^10\). Endurance capacity results from the summation of numerous factors, e.g. the transport of oxygen incorporated through the lungs by the circulatory system and the supply of oxygen to muscle, the speed of muscular energy resynthesis, and the lactate removal ability in the resynthesis process. However, these processes are rarely discussed with respect to the rate-limiting element in endurance capacity. Moreover, it is difficult to investigate muscle endurance based on measurements of tension and its related parameters\(^17\). As shown by studies on human muscle endurance\(^9\), muscle endurance markedly varies depending on the relative load intensity and frequency of force exertion. In previous studies in which skeletal muscle endurance was investigated in animals, electric stimulation intermittently caused incomplete contraction, and endurance was measured based on the tension reduction rate\(^9,11\), but it is unlikely that it was measured as accurately as the maximum muscle strength and contractile velocity.

Skeletal muscle is the core of dynamic sporting activities, and it shows marked adaptability. The physiques of athletes, that are specific to their respective sporting events\(^41\), result from daily training, and are due to hyper trophy of the event-specific muscles. The muscle fiber composition of the legs of top athletes reflects the speed and endurance required for each type of sporting event; and these are markedly influenced by adaptive changes, although there may be hereditary factors. The essential condition to acquire superior skeletal muscle functions (strength, speed, and endurance) is training involving long-term repeated muscle contraction activity. It is of concern that studies focusing only on the results of short-term exercise loading on skeletal muscle only investigate the possibility of muscular hypertrophy, changes in the contractile velocity, or an increase in endurance.

**Conflict of Interests**

The author declare that there is no conflict of interests regarding the publication of this article.

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