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Physiological adaptations of motor units to endurance and strength training

WŁODZIMIERZ MRÓWCZYŃSKI[1], DAWID ŁOCHYŃSKI[2]

The motor units consisting of motoneuron and muscle fibers, is the smallest functional unit of the neuromuscular system, which has ability to adopt plastically to acting stimuli. The increase of the physical activity, evoked by various type of trainings is one of the most important factors which induces morphological, biochemical and physiological changes in motor units. Endurance and strength training are two forms of physical activity leading to differential modifications in physiological features of motor units. Endurance training improves ability of muscle to sustain contractile activity for a long time, while strength training improves muscle strength and power. This manuscript summarizes the knowledge on the essential physiological adaptations in the both components of motor units – motoneuron and muscle fibers to endurance and strength training. The main aim of this paper is to enhance understanding on the strategy by which the neuromuscular system optimizes its activity in order to improve capabilities of the skeletal muscles to both forms of physiological activity.

KEYWORDS: endurance training, strength training, motoneuron, motor units.

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Corresponding author: mrowczynski@awf.poznan.pl

[1] *University School of Physical Education, Department of Neurobiology, Poznań, Poland*
[2] *University School of Physical Education, Department of Motor Rehabilitation, Poznań, Poland*

What is already known on this topic?
Endurance and strength training represent the most common and extremely different forms of physical activity resulting in specific conditioning of the neuromuscular system. Endurance training improves the muscular ability to sustain contractile activity for prolonged periods, while strength training enhances muscle strength and power. Generally, both types of training are responsible for an improvement in the ability to perform physical exercise, and they considerably enhance cardio-respiratory and muscular fitness. However, endurance and strength training lead to different adaptive modifications in the physiological characteristics of motor units, i.e. in the basic functional units of the neuromuscular system. This review focuses on physiological adaptations of motor units to endurance and strength training interventions.

Introduction

Both endurance and strength training serve rehabilitation, prophylactic, and sports purposes to restore, maintain, develop or enhance cardio-respiratory and muscular fitness. Yet, they represent extremely different types of human physical activity. Endurance training is based on repeated activation of muscles (running, cycling, swimming) and improves the ability to sustain rhythmic movements for long periods of time [1]. On the other hand, strength training utilizes high-intensity exercises of particular muscle groups, which are performed repeatedly in series composed of short-term contractions (2-12) against incremental external loads, and improves muscle strength [2].

The mechanical force of mammalian skeletal muscles is produced during contractions of muscle fibers of active motor units (MUs). In humans and other mammals the muscle fibers of MUs are normally controlled by specialized nerve cells within the brain and spinal cord called motoneurons (MNs). These neurons relay signals from various brain centers to striated muscles, bringing about motor functions such as pushing, pulling, lifting, walking, running or maintaining a posture. Hence, motoneurons become control elements with an ability to translate synaptic input into a sequence of motor commands (action potentials) which are then executed by muscle fibers during contractions of MUs. Therefore, a motor unit constitutes the simplest functional link between the neural and contractile components of the neuromuscular system resulting in movement or posture [3].

The MNs of motor units are usually classified into two major types in terms of their morphology (size) and distribution of synaptic input and excitability: (1) small, slow with high excitability; and (2) large, fast with low excitability. The physiological division of motor units is based on the metabolic activity of muscle fibers contained in single MUs [4]. In the majority of mammalian skeletal muscles MUs are principally classified on the basis of contractile characteristics of their muscle fibers into the three types: (1) slow-contracting, resistant to fatigue (slow, S), with low force generating capacity, composed of slow oxidative (SO, I) muscle fibers; (2) fast-contracting, resistant to fatigue (fast resistant, FR, IIA) with medium force generating capacity, composed of fast oxidative-glycolytic (FOG, IIB) muscle fibers; and (3) fast-contracting, fatigable (fast fatigable, FF), with high force generating capacity, composed of fast glycolytic (FG) muscle fibers [5, 6, 7, 8].

Physical training evokes changes in both ultrastructural and functional levels of the neuromuscular system [9] and leads to alterations in MU physiology [10, 11, 12, 13, 14]. Data from human studies indicate that alternations in the neuromuscular system depend on the type of used training [1], and that the extent of training effects depends on the frequency, intensity and duration of employed training [15]. It has been well known that the functional properties of MNs, the phenotype and contractile properties of muscle fibers contained in MUs, and their distribution within a muscle strictly depend on muscular function and activity pattern [3]. Various morphological, biochemical and physiological alterations can be noticed in MU properties in response to different forms of physical exercise [16]. Therefore, changes in MUs properties evoked by altered muscle activity constitute the basis of neuromuscular plasticity [13, 17, 18].

The aim of this paper is to summarize the most essential knowledge on alterations in the MU physiology after increasing physical activity. Data obtained from human and animal experiments are presented to describe adaptive strategies of MUs to endurance and strength training.

Methodological considerations

The limited knowledge concerning modifications in the physiological properties of MUs after various types of training results mainly from difficulties to apply specific electrophysiological techniques in humans, due to their strong invasive character. For this reason numerous data concerning MUs plasticity resulting from physical training come from animal studies, e.g. on rats [2].

It should be stressed that changes in both components of rodent MUs (i.e. MNs and muscle fibers) induced by endurance training have been well described in literature [11, 14, 19]. It is due to the fact that endurance training can be applied relatively easily in laboratory rats, e.g. on a spinning wheel or a treadmill [14, 19].

Application of voluntary exercises aimed at strengthening limb muscles in animals is much more complicated. So far only three models of strength training have been used in rats. In the first model, rats with overloaded shoulders are provoked to perform squat like exercises in response to electrical pulses [2]. In the second model, rats are made to climb a ladder while carrying loads attached to the tail [16]. The third training model was proposed by Klitgaard [20]. In this model, rats are nutritionally conditioned in order to perform squat-like exercises with progressively increasing loads. This type of voluntary resistance exercise program imitates training that utilizes similar exercises in humans. It also enables exercise intensity control in a very similar manner to human training. Therefore, this last model of strength training resembles most closely exercises performed by athletes, and it seems to be the best option to study changes in properties of both essential elements of MUs in response to strength training. However, there are many difficulties with planning, application and management of proper training programs in animals. Moreover, training procedures used on animal models are often different from these used on humans. Hence, the detailed information on changes in electrophysiological properties, e.g. rhythmic discharges of spinal MNs, as well as contractile properties evoked by endurance and strength training is still lacking.

Physiological adaptations in the neural component of motor units

Endurance training

It is known that the training-induced increase in physical activity affects the basic membrane parameters of MNs which are responsible for setting the discharge rates of MUs. It is accepted that endurance training induces changes in the electrophysiological properties of MNs. A considerable decrease in motoneuronal resting potential and spike threshold, increase in the afterhyperpolarization (AHP) amplitude and faster antidromic action potential rising time have been demonstrated in rats subjected to increased spontaneous activity as well as endurance running [11, 19, 21]. Moreover, a gradual reduction in the MU discharge rate following endurance training was noted in humans [1]. These findings suggest that adaptive endurance training-induced changes in the basic biophysical properties of MNs can influence their excitability and functional properties [19] resulting in decreasing MU firing rates.

Strength training

The essential adaptive changes in MUs after strength training have been described in humans. At the beginning of a strength training period (2-3 weeks), the increase in maximal force developed during voluntary contractions of overloaded skeletal muscles as well as the lack of changes in the muscle mass were observed. Such results obtained in the initial period of strength training were explained by a functional reorganization of the nervous system [22], which can lead to changes in the manner of activation of the spinal motoneurons innervating the skeletal muscles. Strength training causes an increase in the maximal discharge rate of MUs during voluntary contractions of the skeletal muscles [23]. Due to the strong stimulation delivered from motoneurones to muscle fibers, their potential to generate forceful contractions increases significantly. Some studies performed on humans showed that changes in the recruitment of MUs (i.e. reduced threshold of activation of strong MUs at the early stage of muscle force development) and increase in rate of discharges of MNs were the initial effect of intensive strength training [1, 24, 25]. Moreover, a significant increase in the MU discharge rate was found in humans as a result of a 6-week strength training [1]. A considerable increase in the number of initial doublets (two-action potentials discharged at the interval less than 10 ms) at the beginning of the motoneuronal firing pattern was also noticed in human muscles after strength training [24, 26].

Physiological adaptations in the muscular component of motor units

Endurance training

Studies on humans have shown that endurance training increases the ability to sustain repetitive high-intensity physical efforts (cycling, running, and swimming) performed with low-resistance loads, for minutes to hours [1]. This is accomplished through an increase in maximal oxygen uptake and the enhanced ability of skeletal muscle to generate energy via oxidative metabolism [27]. Moreover, endurance training results in an increase in muscle capillary density. It also induces intracellular changes in muscle fibers, which are manifested by an increase in mitochondrial protein content, appearance of more metabolically efficient forms of contractile and regulatory proteins and an increase in the activity of fatty acid–oxidation enzymes [28].

Endurance training evokes changes in MUs. It was reported that following endurance training the diameter of muscle fibers remains unchanged or slightly decreased [29]. An increase in FOG and parallel reduction in FG muscle fiber number were also observed [30, 31]. Moreover, an increase in FR MUs (consisting of FOG muscle fibers) in parallel to the reduction of FF MUs (consisting of FG fibers) numbers were demonstrated in relation to rat MUs after treadmill training [14]. Changes in the number of muscle fibers as well as in the MU proportion indicates a transformation of MUs towards FR units with relatively high resistance to fatigue. This may be a principal physiological mechanism responsible for improvement of skeletal muscle fatigue resistance following endurance training.

Strength training

Strength training increases muscle mass [27] and the capacity to generate force [28]. This stage of adaptations in response to strength training starts approximately 3-4 weeks after the beginning of training when a progressive increase in muscle mass [32, 33] as well as in crosssection of muscles [34] are observed either in humans or rodents. After that the increase in muscle contractile force is predominantly caused by the growth of contractile protein volumes (hypertrophy) due to the increase in muscle fiber cross-sectional area and myofibrilar RNA and protein content [2]. The increase in the proportion of type IIa muscle fiber as well as the decrease in proportion of type IIx fibers with an unchanged proportion of type I fibers [32, 35] are observed in muscles as training is continued. It has also been shown in humans that short-term involuntary muscle training increases maximum force of S and FR MUs, decreases force, and increases fatigue resistance in FF MUs [36].

Neurophysiological studies demonstrate two separate stages of strength training. In the first stage (the first 2-3 weeks after the training onset), training initially affects the excitability and rate of discharges generated by motoneurones, which influence the manner of activation of muscle fibers [1, 24, 25]. In the second stage (starting 4-5 weeks after the training onset), gradual morphological, histochemical and biochemical changes start to significantly influence muscle fiber force generating capacity [32, 33, 34].

Unresolved aspects of endurance and strength training

There has been no information regarding numerous questions about changes in the motoneuronal excitability and connections between MNs membrane properties and alternations in the MUs activity, which can explain changes in the properties of muscle fibers in humans subjected to endurance and strength training. Therefore, electrophysiological studies performed on animals should be undertaken in order to: (1) determine changes in the electrical parameters of slow and fast MNs; (2) indicate modifications in rhythmic discharges generated by different types of motoneurones; (3) recognize changes in the contractile properties of muscle fibers in various types of MUs. Such complex investigations would enable a better understanding of training-evoked associations between changes in motoneuronal excitability, motoneuronal firing rate and contractility of muscle fibers in MUs.

Conclusions

The presented data show that endurance and strength training is responsible for many plastic changes in the MU physiology. Endurance training evokes mainly a reduction in the MU discharge rate and causes an increase in the number of oxidative-glicolytic muscle fibers; while it rather does not affect the muscle fiber diameter. Strength training evokes an increase in the MUs discharge rate, causes hypertrophy and an increase in the proportion of fast-twitch muscle fibers with relatively high resistance to fatigue within a muscle. Therefore, these two forms of training induce different alterations in the physiological properties of both components of MUs. Changes in the recruitment and firing rate seem to constitute a basic physiological adaptation of MNs to different types of training which influence the contractile properties of MU muscle fibers. Nevertheless, little is still known about factors involved in modulation of spinal MNs properties, directly responsible for their functional adaptations. It seems likely that changes observed in MNs are manifested by numerous alternations in the supraspinal (corticospinal and subcorticospinal) and spinal (excitatory and inhibitory interneurones) neuronal networks of the central nervous system. These alternations probably modulate the intensity of descending drive to MNs, and in turn, determine their excitability and firing rate [23]. These aspects of endurance and strength training have been almost unknown. Therefore, future investigations should recognize: (1) changes emerging in the cortical and subcortical structures of the brain after endurance and strength training; (2) sources of supraspinal and spinal inputs to MNs in relation to a given type of training; and (3) molecular changes in the membrane of spinal MNs evoked by endurance and strength training. Such studies are necessary to obtain a more complex understanding of the adaptive processes taking place in the neuromuscular system in response to different types of physical activity.

What this paper adds?

This paper demonstrates that endurance and strength training induces numerous functional changes in the neural and muscular components of motor units. It is shown that alterations in the physiological properties of motoneurones and their muscle fibers are different in response to both types of training, and thus strictly depend on the type of physical activity. Moreover, it is proposed that alterations in the recruitment and firing rate of motoneurons induce a specific adaptive response in the mechanical properties of muscle fibers. Therefore, training-evoked changes in physiological properties of motoneurons seem to be a key factor responsible for modifications of the contractile properties of motor units.

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