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Tissue and subcellular activities of superoxide dismutase in skeletal muscles during physical exercises

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Activity of the enzyme superoxide dismutase (SOD) in the skeletal muscles was studied on the tissue and subcellular levels in the rats exposed to physical exercise. The specific differences in response to acute and regular training exercises were revealed in superoxide dismutase activities measured in tissue homogenate, mitochondrial and cytosolic fractions of white and red gastrocnemius muscles in the rats. These differences depended on exercise character (acute or chronic), fiber composition (glycolytic and oxidative) and subcellular localization of the enzyme. In the studied muscles, adaptive increase of SOD tissue activity was not shown in response to regular training exercise. In white muscles, preferentially composed of glycolytic fibers, adaptive induction of mitochondrial SOD (mitSOD) activity by regular training was more obvious than in red muscles, composed preferentially of oxidative fibers. However, induction of mitSOD activity by acute exercise in red muscles was displayed more strongly, than in white muscles. In red muscles of trained animals, the increase in SOD activity in the cytoplasm (cytSOD) becomes more moderate in response to testing exercise. In white muscles, cytSOD activity does not undergo adaptive changes and is not induced by testing exercise. Analysis of SOD activity in mitochondrial and cytoplasmic fractions of fast and slow muscles will be useful for elucidation of their adaptive peculiarities.

Keywords: *Skeletal muscles, physical exercise, superoxide dismutase, subcellular fractions*

INTRODUCTION

Aerobic organisms or their individual organs and tissues are able to adapt to the conditions of energy consumption. Physical exercise leads to a multiple increase in the demand of skeletal muscles for energy, which, in turn, is accompanied by increased pulmonary oxygen uptake. Here, however, muscle cells face a dangerous phenomenon for their structural and functional integrity - oxidative stress (Devies et al., 1982; Ji, 1999; Керимова и др., 2004; Powers et al., 2008; Steinbacher et al., 2015). Oxidative stress can occur when equilibrium between oxidants and antioxidants is disturbed. Oxidative stress occurs under conditions, when local antioxidant defenses are exhausted, because of oxidants or when the rate constants of the radical reactions are greater than the rate constants of the antioxidant defense mechanisms (Buettner, 1993; Vollaard et al., 2005). This could occur in skeletal muscles during acute exercise under conditions when oxidant/antioxidant balance shifts toward the pro-oxidant state.

It is well known that oxygen, which is the final electron acceptor in the respiratory chain of mitochondrias, plays a dual role in the life of cells; most of the oxygen entering the mitochondria, being completely reduced, turns into water, and a small part, according to various estimates, up to 5% of the total consumption, goes as a superoxide anion (O_2^-), which is a free radical (Halliwell et al., 1989; Halliwell, 2014; Скулачев, 1996). Aerobic cells, including muscle fibers, use superoxide dismutase (SOD) to fight O_2^- radicals, which promotes their dismutation and forms hydrogen peroxide (H_2O_2) and oxygen. Many

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works concern SOD as an important component of antioxidant protection of cells and tissues, among which the works, related to physical activity, occupy a significant place (Ji, 1999; Banerjee et al., 2003; Leeuwenburgh et al., 2011; Gomes et al., 2012).

In mammals, two isoforms of SOD exist in skeletal muscle; they vary in both cellular locations as well as in a metal ion bound to its active site. The Cu-Zn SOD is primarily located in the cytosol, whereas the Mn-SOD is principally found in the mitochondrial matrix (Ohno et al., 1994; Halliwell, 2014). Both enzymes catalyze the dismutation of superoxide anions with similar efficiency (Ohno et al., 1994). The Cu-Zn SOD is a dimer with a molecular weight of ~32,000 kDa, whereas the Mn SOD is a tetramer (MW = ~88,000 kDa) (Ohno et al., 1994).

It is well-established that the antioxidant defense systems of many mammalian tissues are capable of adaptation in response to chronic exposure to oxidants. Because prolonged physical exercise results in an increased production of oxidants in skeletal muscle, regular physical exercise training should bring to upregulation of muscle antioxidant enzyme systems. There is some evidence that endurance exercise training results in an increase in skeletal muscle antioxidant enzyme activity. Nonetheless, a few studies have failed to find augmented muscle antioxidant activity after physical exercise training. It can be assumed that these differences may be the result of differences in methodological approaches at choosing the types of muscles, fibers as well as the type of exercise training protocols (Powers et al., 1999). On the other hand, the existence of different isoforms of enzymes can also be the cause of conflicting statements concerning the role of an enzyme in the antioxidant response of muscles to physical activity (Laughlin et al., 1990; Tonkonogi et al., 2000; Hacıyev və b., 2013).

In this article, we present the results of the experiments on animals (albino rats) in studying the superoxide dismutase activity of skeletal muscles on the tissue and subcellular levels during acute exercise and regular physical training. The study was performed simultaneously over fast (white) and slow twitch (red) fiber type muscles of the same organism. Such approach makes it possible to analyze the activity of SOD in relation to the presence of various isoforms of the enzyme and their fiber affiliation to find out the antioxidant adaptive properties of skeletal muscles.

MATERIALS AND METHODS

Experiments were conducted on male Wistar albino rats of 250-300 g body mass kept in normal vivarium conditions. During the experiments, we followed the bioethical standards for the treatment of experimental animals in accordance with the European Convention for the protection of the rights of vertebrates used for experimental and scientific purposes (March 18, 1986, Strasbourg).

Rats were randomly pooled into four groups: untrained, non-exercised (*before removing the muscles*) (UN, n=6), untrained and exercised (UE; n=6), trained, non-exercised (TN n=6) and trained and exercised (TE, n=6).

The training process for the TN and the TE groups was carried out in a wheel with a diameter of 44 cm via running exercise. The load was given daily in the wheel rotation mode at a speed of 15-25 m/min, in the first days for 10-20 min, starting from the 3rd week the load duration was set to 30 min (~75% O_{2max}). Training process continued for 4 weeks, 5 days a week. Acute exercise (single physical load) was given by running in a wheel at a speed of 25 m/min for 30 min. Groups of sedentary animals that did not receive physical training loads (UN and UE) were subjected to running in a wheel for 10 minutes once a week for training in running under experimental conditions. A day after the end of physical training process, one group of the untrained (UE) and one group of the trained (TE) rats were subjected to an acute exercise, and immediately after that all animals were sacrificed and muscles were removed.

The calf muscle (*m.gastrocnemius*), its white and red components were studied. Red m. gastrocnemius (Type IIa fibers) is composed of highly oxidative fibers, but the white m. gastrocnemius (Type IIb fibers) is composed of highly glycolytic fibers. Mitochondria were obtained by centrifugation from 10% tissue homogenate in a sucrose medium (0.3M sucrose, 10 mM EDTA; pH 7.5). The activity of cytoplasmic SOD (cyt-SOD) was determined in the supernatant. The mitochondrial sediment was transferred to a phosphate buffer to

determine the activity of mitochondrial SOD (mit-SOD). The method for mitochondria isolation is described in (Прохорова, 1982).

The activity of SOD was determined by a method based on the competition of SOD with nitroblue tetrazolium in the reduction of superoxide radicals generated in the reaction of phenazine methosulphate (Дубинина, 1984).

The statistical reliability of differences between indicators of different groups was evaluated by the Student's t-criterion and the differences between average values were accepted as reliable at $p<0.05$.

RESULTS AND DISCUSSION

The results of study of SOD activity in skeletal muscle homogenate under the influence of regular training loads and acute single load are shown below (Table 1).

Table 1. Superoxide dismutase activity in the homogenate of skeletal muscle tissue in rats during exercise (arbitrary units/mg protein), $M \pm m$, $n=6$

Status / Muscles	Untrained		Trained	
	Rest (UN)	Exercise (UE)	Rest (TN)	Exercise (TE)
White	7.86±1.19	3.08±0.44*	8.17±1.22	6.18±0.93
Red	6.26±0.88	10.21±1.53*	6.96±0.90	9.98±1.35*

* $p<0.05$ compared the exercised groups with the termed "rest" groups;
# $p<0.05$ compared trained rest groups with untrained rest groups.

Four-week training loads do not lead to significant changes in SOD activity in the skeletal muscles at rest. However the decrease in SOD activity in the white muscle (white m. gastrocnemius), observed after the acute exercise in the untrained rats (UE), becomes less abrupt in the trained rats group (TE); that is, if the decrease in activity in the group UE relative to the group UN was 61% ($p<0.05$), then in the group TE relative to the group TU it became only 24% at $p>0.05$. In the red muscle (red m. gastrocnemius), the enzyme activity increases after the acute exercise by ~35% ($p<0.05$), both for the untrained and trained groups (UE vs.UN and TE vs. TN).

The results of studies of the effect of physical activity on superoxide dismutase activity in the subcellular fractions of skeletal muscles in the rats are presented in Table 2.

Under the influence of physical training, the changes in activity of SOD are observed, depending on both the fiber type of muscle and the subcellular affiliation of the enzyme. In the rats, that are not subjected to physical training (UN and UE groups), the activity of mit-SOD in the white muscle increases almost twice after acute physical exercise. However, in the red muscle, the activity of mit-SOD in the rats of these groups does not show significant changes in response to the same acute exercise, moreover, some statistically unreliable decrease ($p>0.05$) of activity is noted.

The baseline level (at rest) of mit-SOD activity in the white muscle increases by more than 2 times as a result of 4 weeks of physical training (the UN and the TN groups are compared). However, the reaction of mit-SOD activity in the trained rats to acute exercise (the TE vs. the TN) becomes different from the reaction of the untrained animals (the UE vs. the UN): the increase in activity under acute physical exercise in the trained rats disappears. There is only a tendency to decrease from rest activity of enzyme, resembling the situation with red muscle in the untrained rats.

In red muscle, the activity of mit-SOD does not change significantly under 4-week physical training. The 19% increase in activity (TN) compared to the untrained group (UN) of animals is statistically unreliable ($p>0.05$). As for the reaction of red muscle mit-SOD activity to acute exercise in the trained rats, here we observe a tendency to increase in contrast to the white muscle. Although the activity of mit-SOD of the red muscle in the trained rats after exercise (TE group) exceeds the baseline level for the TN group by 34% and the reliability of the difference is characterized by a low level of confidence ($p=0.06$), but it is noteworthy that there is a significant increase in the activity of mit-SOD in relation to the baseline activity of the untrained rats (UN, 0.205±0.025 arb.unit) ($p<0.05$).

Table 2. Superoxide dismutase activity in subcellular fractions of skeletal muscles in the rats during exercise (arbitrary units/mg protein). *M*±*m*, *n*=6

Status / Muscles	Untrained		Trained	
	Rest (UN)	Exercise(UE)	Rest (TN)	Exercise (TE)
Mitochondrial SOD				
White gastrocnemius	0.112±0.015	0.234±0.022*	0.307±0.031$^{\#}$	0.267±0.027$^{!}$
Red gastrocnemius	0.205±0.025	0.175±0.019	0.243±0.032	0.325±0.045$^{!}$
Cytoplasmic SOD				
White gastrocnemius	0.051±0.006	0.052±0.005	0.045±0.006	0.056±0.006
Red gastrocnemius	0.046±0.005	0.182±0.015**	0.043±0.005	0.102±0.012*$^{!}$

*, ** - $p<0.05$ and $p<0.01$ compared exercised groups with termed "rest" groups;
$^{\#}$ - $p<0.05$ compared trained rest groups with untrained rest groups;
$^{!}$ - $p<0.05$ compared trained exercised groups with untrained rest groups.

The changes in the activity of cyt-SOD in white and red muscles in response to acute exercise are different from the changes in the activity of the mitochondrial isoform. It should be noted that the rest levels of cys-SOD activity in the white and red muscle in the untrained rats (UN group) are almost equal, in contrast to mit-SOD, whose activity in the red muscle significantly exceeds the white muscle level.

After regular physical training for 4 weeks, the rest activity of cys-SOD of both muscles in the TN group rats remains at the level of activity for the rats in the UN group. Acute physical exercise does not lead to changes in the activity of cys-SOD in the white muscle in both the untrained (the UN and the UE groups) and the trained rats (the TN & the TE groups).

However, in the red muscles from the untrained and trained animals, SOD activity is greatly increased in the cytoplasm in response to exercise; the increase above baseline in the untrained rats is about 300% ($p<0.01$, compare UN and UE groups), and the trained somewhat lower, around 140% ($p<0.05$, compare TN and TE groups). We can say that in the red muscle, the reaction of superoxide dismutase activity in the cytoplasm, i.e., a sharp increase in the activity of the cyt-SOD in response to acute exercise becomes less abrupt as a result of regular physical training.

There are discrepant data on adaptive changes in SOD activity in skeletal muscles under the influence of physical training loads. Some studies indicate an increase in the activity of the enzyme after training (Higuchi et al., 1985; Leuwenburgh et al., 2001; Azizbeigi et al., 2014), while other studies show no significant changes in the activity of SOD (Alessio et al., 1988; Laughlin et al., 1990; Ji, 1993; Tonkonogi et al., 2000; White et al., 2017). These discrepancies could be explained by the fact that different authors' studies used different muscle types and fiber compositions, applied different exercise techniques, and, that is more important, measured the activity of different SOD isoforms. When our own data on measuring SOD activities at the tissue and subcellular levels are compared, there are also differences in responses to exercise.

If SOD activities of both types of muscles do not show significant changes at the tissue level with 4-week regular training loads, then subcellular activities, namely the activity of mit-SOD shows some adaptive growth, which is more significant in the white muscle. This result is consistent with the data of studies where it was concluded that cytosolic CuZn-SOD is passive in adapting to physical exertion in comparison with Mn-SOD (Higuchi et al., 1985; Ji, 1993; Lambertucci et al., 2007; Ristow et al., 2009).

A significant decrease in SOD tissue activity in white muscle after an acute exercise, which becomes moderate in the trained rats, seems paradoxical. However, if we pay attention to the changes in subcellular activity in response to an acute exercise, we can assume that the cytoplasmic component of SOD activity makes a greater contribution to the measured tissue activity. This assumption can be supported by the data from the work (Oh-Ishi et al., 1997), which shows an exercise-induced decrease in the level of m-RNA for CuZn-SOD in the untrained rats and the leveling of changes with regular training.

An increase in the red muscle tissue activity of SOD (both in the untrained and the trained rats) after a single acute exercise also indicates the pre-

valence of the proportion of cytoplasmic activity of the enzyme, which undergoes a 4-fold increase after acute exercise in the untrained rats and more than 2-fold increase in the trained ones. In particular, this is confirmed by the study in which it was shown that the activity of CuZn-SOD isoform of the enzyme in muscles increases significantly in response to acute exercise than the activity of the Mn-SOD isoform (Hollander et al., 1999; 2001; Lawler et al., 2009).

These results and a number of literature data on the content of protein and m-RNA of the SOD enzyme suggest that changes in the activity of mitochondrial and cytosolic isoenzymes in skeletal muscles may occur due to both post-transcriptional and post-translational effects of physical exercise (Hollander et al., 1999; 2001; Ji, 1999). In other words, the increased activity of SOD isoenzymes in skeletal muscles during exercise may be due to both the synthesis of a new protein and post-translational modification of a previously synthesized protein.

Our results indicate that the induction of SOD isoforms' activity by physical training is specific to the type of muscle fiber (see also, Hollander et al., 1999; 2001; Lawler et al., 1993). In white muscle, which consists primarily of a fast (glycolytic) type of fibers, adaptive upregulation of mit-SOD activity by training exercise is clearly visible. In the red muscle, which consists mainly of slow fibers, adaptive induction of mit-SOD activity by training exercise is weaker, however, the induction of activity by acute physical exercise is stronger than in the white muscle.

Differences of changes in SOD activity under the influence of regular training and acute physical exertion can probably be explained by differences in post-transcriptional and post-translational peculiarities of Mn-SOD and CuZn-SOD expression stimulated by physical exercise (Ji, 1999; Hollander et al., 1999; 2001). Taking into account the results of work (Oh-Ishi et al., 1997), which studied the activity of SOD isoforms, corresponding protein and m-RNA contents under the influence of physical exercise, we can assume that in fast type muscles, training loads lead to the induction of mitochondrial SOD activity by a post-transcriptional mechanism, and in slow type muscles - post-translational modulation of activity takes place. For cytoplasmic SOD, the effect of training loads is only seen in the slow-type muscles, and it is associated with the induction of activity due to post-translational changes in the protein.

Thus, we observe the participation of antioxidant protection of skeletal muscles in adaptive processes, associated with regular exercise at the level of enzymatic protection against superoxide anion radicals.

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Fiziki yüklənmələr zamanı skelet əzələlərində superoksiddismutazanın toxuma və subhüceyrə aktivliyi

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Fiziki yükün təsiri altında ağ siçovulların skelet əzələlərində superoksiddismutaza (SOD) fermentinin aktivliyi toxuma və subhüceyrə səviyyələrində tədqiq edilmişdir. Ağ və qırmızı gastrocnemius əzələlərinin toxuma homogenatında, mitoxondri və sitozol subhüceyrə fraksiyalarında ölçülmüş SOD aktivliyinin kəskin və müntəzm məşq yüklərinə reaksiyalarında fərqlilik aşkar olunmuşdur. Bu fərqlər yükün xarakterindən (birdəfəlik, ya xroniki), əzələnin lif tərkibindən (qlikolitik, ya oksidativ) və fermentin subhüceyrə mənsubiyyətindən asılıdır. Tədqiq edilən əzələlərdə sakitlik halında SOD-un toxuma aktivliyində adaptiv yüksəlmə üzə çıxarılmayıb. Ağ əzələdə mitoxondrial SOD-un xroniki yüklə adaptiv induksiyası aşkar olunub. Qırmızı əzələdə mitoxondrial SOD-nın xroniki yüklə induksiyası zəifdir, ancaq onun kəskin yüklə induksiyası ağ əzələyə nisbətən özünü daha aydın göstərir. Məşqli heyvanlarda qırmızı əzələdə submaksimal fiziki yükə cavab olaraq SOD-un sitoplazma aktivliyinin yüksəlməsi mülayimləşir. Ağ əzələdə sitoplazma SOD aktivliyində məşq yükləri ilə adaptiv dəyişikliklər üzə çıxmır, testləşdirici fiziki yüklə induksiya da baş vermir. Müxtəlif əzələlərdə (sürət tipinə görə) superoksiddismutazanın subhüceyrə aktivliklərinin təhlili onların adaptasiya xüsusiyyətlərinin üzə çıxarılması üçün faydalı olacaq.

Açar sözlər: *Skelet əzələləri, fiziki yük, superoksiddismutaza, subhüceyrə fraksiyaları*

Тканевая и субклеточная активность супероксиддисмутазы скелетных мышц при физических нагрузках

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Изучалась активность супероксиддисмутазы в скелетных мышцах на тканевом и субклеточном уровнях под влиянием физических нагрузок у крыс. Обнаружены различия в изменениях активности СОД, измеренной в тканевом гомогенате, митохондриальной и цитоплазматической субфракциях белой и красной мышц *gastrocnemius,* в ответ на субмаксимальные и регулярные тренировочные нагрузки. Эти различия зависят от характера нагрузки (однократной или хронической), от волоконного состава (гликолитического или оксидативного) мышц, а также от субклеточной принадлежности фермента. В исследованных мышцах в состоянии покоя адаптивный рост активности СОД на тканевом уровне не обнаруживается. В результате регулярной тренировочной нагрузки имеет место адаптивная индукция активности митохондриальной СОД (мСОД) в белой (быстрой) мышце. В красной (медленной) мышце при хронической нагрузке адаптивная индукция активности м-СОД слабее, однако индукция активности острой физической нагрузкой (субмаксимальная нагрузка) проявляется сильнее, чем в белой мышце. В красной мышце тренированных животных увеличение активности СОД в цитоплазме (цСОД) в ответ на физическую нагрузку становится более умеренным. В белой мышце активность цСОД не обнаруживает адаптивных изменений и не индуцируется тестирующей физической нагрузкой. Анализ супероксиддисмутазной активности в субклеточных фракциях мышц различных типов может быть полезен для выявления их адаптационных свойств.

Ключевые слова: *Скелетные мышцы, физическая нагрузка, супероксиддисмутаза, субклеточные фракции*