

Physiological and biochemical characteristics of overcoming fatigue in elite cyclists during work at different power

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Abstract

The purpose of this study was to examine the dynamics of developing the overcoming fatigue during a strenuous muscular activity of submaximal and moderate power. **Material & methods:** The study involved 64 elite cyclists examined in laboratory conditions. Activities of moderate and submaximal power were modeled. The bioelectrical activity of cyclists' lower extremity muscles and the dynamics of kinematic and dynamic characteristics were examined, as well as the peculiarities of manifesting balance and mobility of nervous processes. The parameters of gas exchange, external respiration, indices of diffuse conductivity, systolic volume, pulse, arterial blood pressure, etc. were determined. **Results:** Studies have confirmed the existence of a period of overcoming fatigue during intense muscular activity and the heterogeneity of this state course. Conditionally overcoming fatigue is divided into three phases: initial, intermediate, and final. The specific character of overcoming fatigue during intense muscular activity is due to a change in the interaction of central nervous impacts and peripheral factors. They determine the quality of regulating the body somatic and autonomic functions, the aspiration of the regulatory systems to maintain high work capacity at the expense of volitional efforts at increasing levels of physiological system functioning. This is accompanied by the inclusion of intramuscular, intrasystem, and intersystem mechanisms for work capacity maintenance, various mechanisms of intracellular metabolism. The peculiarities of the period of overcoming fatigue are determined by the functional stability of the nerve centers, their ability to rebuild regulatory mechanisms and propel the body systems to the next level of functioning. Active inclusion of compensatory intra- and intersystem mechanisms during the period of overcoming fatigue occurs in the face of a progressive decrease in the efficiency and economy of the system functioning. The sharp decrease of the functional economy is not the only cause of the apparent fatigue that induces the decrease of work capacity. It reflects the sum of accumulated overcoming functional and metabolic difficulties, the state of the vegetative centers. **Conclusions:** Compensatory responses to overcome fatigue are aimed at activating mechanisms that provide increased excitation in the motor cortical centers while maintaining a high tone of the cortical structures. In addition, they contribute to maintaining the maximum level of the respiratory system functioning, circulation, and other mechanisms that ensure the maximum possible oxygen supply to working tissues, the maximum level of oxygen utilization from the blood, respiratory compensation for metabolic acidosis, and the maximum mobilization of anaerobic energy supply sources.

Keywords: cyclists, fatigue, testing, gas exchange, electromyography, biochemistry

Introduction

The study of athletes' activities under conditions of training sessions and competitions, experimental material of the laboratory investigations of the dynamics of changes in the body somatic and vegetative systems during strenuous muscular activity allowed to identify in the process of fatigue a period of compensated (latent or overcoming) fatigue and a period of uncompensated (apparent) fatigue. The existence of such periods was confirmed by V.M.Zatsiorsky (1966), A.A.Viru (1974), V.D.Monogarov & V.K.Bratkovsky (1979). These periods are also given in textbooks on sports physiology. Recent studies on athletes allowed to obtain the important data on morphophysiological mechanisms of fatigue development staging (Hebisz et al., 2019; Wangerin et al., 2017).

It has been experimentally proved that after a relatively short period after the onset of strenuous muscular activity, when a subjective sensation and objective signs of fatigue appear, the compensatory mechanisms are activated (Bini & Rossato, 2014; Fudin et al., 2015). Their activity is focused on overcoming the developed fatigue and maintaining work capacity at a given level (Ajiboe & Weir, 2009; Hug et al., 2008).

The success of the competitive activity, especially in cyclic sports events during covering the distances in zones of different power, is associated with the ability to overcome (compensate) the growing fatigue. The athlete's state during covering each subsequent segment of the distance can be characterized by a set of physiological parameters (Orlov et al., 2017; Turpin et al., 2011).

Functional transformations in the athlete's body occurring in the process of competitive activity and especially in the state of overcoming fatigue should be taken into account and modeled for different pedagogical impacts during the training process (Camara et al., 2012; Mornieux et al., 2006; Vardar et al., 2007). In modern theory and practice of sports, it is fundamentally important to develop quantitative criteria for changes that occur in the body functional systems including overcoming fatigue during the performance of work of different power.

The hypothesis was to identify the factors limiting work capacity during activities of submaximal and moderate power, specific regularities of compensatory responses of the neuromuscular apparatus, higher nervous activity, respiratory systems, circulation, blood, reflecting the functional state of the oxygen transport system, which would have contributed to work capacity maintenance under fatigue.

The purpose of this study was to examine the dynamics of developing the overcoming fatigue during a strenuous muscular activity of submaximal and moderate power.

Material & methods

Participants. The study involved 64 elite cyclists.

Organization of study. A complex method was used to conduct biochemical studies. Athletes were examined in a laboratory experiment on a bicycle ergometer (loads of submaximal and moderate power). The dynamics of the kinematic and dynamic characteristics of the horizontal and vertical components of the efforts applied by the cyclist, the peculiarities of the bioelectric activity of the quadriceps and biceps muscles of the thigh, gastrocnemius, and anterior tibial muscle of the right leg were studied. The amplitude and frequency of oscillations of biopotentials, the rhythmic structure of bioelectric activity, and integrated bioelectric activity of muscles were determined. The indices of motor activity efficiency and economy were calculated. The variability of the studied motion characteristics was determined (Kolumbet et al., 2019).

EMR-01 electromyoreflexometer was used to investigate the manifestation peculiarities of balance and mobility of cortical nervous processes according to indices of changes in the latent period of motor response to light signal applying the method of C.W.Telford modified by N.M.Peysahov.

The interrelated parameters of gas exchange, external respiration - frequency, depth, respiratory minute volume, alveolar ventilation, O₂ and CO₂ content in exhaled and alveolar air, basic lung volumes; indices of diffusion conductivity - respiratory and circulatory components; circulation - minute blood volume (according to Defar as modified by V.S.Mishchenko), systolic volume, pulse, arterial blood pressure, the proportion of venous blood admixture; blood respiratory function - blood oxygen capacity, hemoglobin content, blood O₂ and CO₂ tension, O₂ tension in arterialized blood according to Astrup, arterial blood oxygen saturation by oxyhemometry using a special calibration method; athlete's body temperature; indices of arterial blood acid-base balance, its lactic acid and glucose content.

The study of the body oxygen-transport system during physical loads envisaged the analysis of oxygen and carbon dioxide parameters alongside that of the activity of the main functional systems that determine them. We investigated the quantitative and qualitative assessment of the ratio between indices of work capacity and O₂ uptake - CO₂ release, other oxygen, and carbon dioxide parameters and functional indices.

Statistical analysis. During experimental data processing, we determined the average values of indices and their errors (M±m), the degree of difference of averages and the significance of differences (t, p).

While conducting complex pedagogical, biomechanical and biological surveys with the participation of athletes, the legislation of Ukraine on health care, the 2000 Helsinki Declaration, Directive No. 86/609 of the European Society regarding people's participation in biomedical research were adhered to.

Results

Three phases of overcoming fatigue (*initial, intermediate, and final*) during the work of submaximal power have been established experimentally. The initial phase begins sometime after the onset of muscular activity and constitutes 45-50% of the total load duration. At this time, that is, 2-3 minutes into the work, the pedaling speed temporarily decreases, and the effectiveness of the cyclists' pedaling efforts changes. These data were obtained on the basis of the analysis of subjective sensations of fatigue, parameters of work capacity (Table 1), and the dynamics of indices of the body respiration, blood circulation, oxygen regimes (Table 3) while working at submaximal power. The most pronounced were changes in the pedaling speed and effort efficiency in the first half of the work performance. 45-50% of the time after the onset of work (which corresponds to 2.0-2.5 minutes), the most pronounced decrease of the above indices is observed. 2.0-2.5 minutes after the beginning of work, the pedaling speed and the effectiveness of the pedaling efforts increase. At this moment, these indices reach the highest level. Then the values of these indices, which make up 17-20% of the total time of work of the submaximal power, stabilize. Such changes in pedaling speed and effort efficiency are characteristic features of the so-called intermediate phase of overcoming fatigue. During the final stage of work (the last 10-12% of the work time), a secondary increase in the effectiveness of pedaling efforts was noted. During the initial period of submaximal work, changes in the oscillation amplitude of the biopotentials of various muscles are of a multidirectional nature. The oscillation amplitude of the biopotentials of the biceps femoris and anterior tibial muscles increases (highest values) during the first 1.5 minutes of work. Later on, the oscillation amplitude of the

biopotentials of the latter decreases by more than 25% of the maximum value). In the gastrocnemius and quadriceps muscle of the thigh, the highest values of biopotential amplitude oscillations were observed 70-75% of the time from the onset of work (Table 2). 30-40% of the time after the onset of work, the frequency characteristics of muscle electromyograms significantly decrease (compared to the beginning of work). Then, the oscillation frequency of the biopotentials of the quadriceps and tibialis anterior muscles begins to increase and reaches maximum values in 2.5-3.0 min. A slight increase in the oscillation frequency of biopotentials followed by stabilization in the biceps of the thigh was noted. The oscillation frequency of biopotentials in the gastrocnemius muscle remains unchanged from the second minute of work until its completion. The period of overcoming fatigue, especially its final part is characterized by an increase in the oscillation amplitude of the biopotentials of the quadriceps muscle of thigh and gastrocnemius muscle. At the same time, the oscillation frequency of biopotentials in the gastrocnemius muscle remains unchanged, whereas in the quadriceps muscle of the thigh it decreases. The amplitude-frequency characteristics of the electromyogram of the anterior tibial muscle during the period of overcoming fatigue remain without significant changes. At the same time, the oscillation frequency of the biceps femoris potentials demonstrates a significant increase in the final phase of overcoming fatigue.

Table 1. Changes of muscular activity indices in cyclists during work of submaximal power (M)

Indices	Duration of work, %										
	0	10	20	30	40	50	60	70	80	90	100
Fatigue subjective evaluation, points	0.5	2.5	2.4	2.6	3.0	4.3	5.0	6.5	8.3	9.0	8.5
Work capacity, km.h ⁻¹	-	46.0	46.5	47.3	46.7	46.2	46.8	47.6	47.5	47.7	47.4
Time of light-motor response, ms	175	193	205	200	192	186	178	174	173	172	170
Effort efficiency, %	-	82	80	79	77	76	77	80	79	78	81

Oscillation amplitude and frequency of the potentials of all examined muscles increase simultaneously, however, to a different degree.

Table 2. Dynamics of oscillation amplitude and frequency of muscle biopotentials of the cyclist N.M-v during work of submaximal power (M)

Muscles	Duration of work, %										
	0	10	20	30	40	50	60	70	80	90	100
	Oscillation amplitude of biopotentials, μ V										
Quadriceps femoris	-	1205	1130	1170	1230	1250	1200	1160	1130	1150	1200
Biceps femoris	-	620	680	700	650	645	670	6950	660	650	680
Gastrocnemius	-	1130	1180	1200	1250	1280	1220	1180	1200	1300	1350
Anterior tibial	-	500	630	620	550	450	390	405	410	410	405
	Oscillation frequency of biopotentials, hz										
Quadriceps femoris	-	135	120	104	108	125	135	138	130	126	135
Biceps femoris	-	120	116	113	108	108	114	117	118	123	138
Gastrocnemius	-	-	185	168	155	150	148	145	147	152	155
Anterior tibial	-	146	135	130	135	143	140	135	130	134	140

Spatiotemporal structure of muscle electrical activity does not change significantly in elite cyclists during the period of overcoming fatigue.

Increased excitability of the nerve centers in the final phase before refusal to work in elite athletes (under submaximal power load) is also confirmed by studies of the function of higher nervous activity. A decrease in the time of the light-motor response was revealed during the period of overcoming fatigue. In the final phase, the value of the light-motor response in elite cyclists progressively decreased. Before the refusal to work, it was less than in the initial state before the load.

The onset of overcoming fatigue coincides with the appearance of the first signs of a discrepancy between the oxygen uptake rate and the body oxygen demand for work and an increase in the anaerobic reaction contribution to the work energy supply. This is evidenced by increased lactic acid content in arterial blood. Its content reaches 120-160 mg% (and higher in some athletes) at the end of the load.

Table 3. Dynamics of gas exchange indices in cyclists during work of submaximal power (M)

Indices	Duration of work, min					
	0	1	2	3	4	5
VO ₂ , l.min ⁻¹	0.5	2.9	4.0	4.6	4.9	5.2
V _{CO2} , l.min ⁻¹	0.4	2.5	3.8	4.5	5.1	5.5
RQ	0.82	0.86	0.92	0.98	1.02	1.06

Explanation of symbols: VO₂ – oxygen uptake rate; V_{CO2} – carbon dioxide evolution rate; RQ – gas exchange ratio

In the first minutes of work of submaximal power, the excess of acids increases sharply reaching the values of 20.2 ± 0.3 mmol/l by the end of the load. This is accompanied by a significant decrease in the number of alkaline equivalents, which may be traced according to the decrease in the capacity of common buffer bases. The pride of place in the neutralization of strong acids goes to the bicarbonate buffer. The decrease of its capacity is reflected in the changes in standard bicarbonate to 8.3 ± 0.7 mmol/l.

In the examined cyclists, the oxygen uptake rate was in the range of 93-97% of the maximum during the final phase of work of submaximal power (duration 5 minutes). This indicates a close to the maximum mobilization of energy supply aerobic mechanisms. Such work is ensured by a significant increase in the level of functioning of the external respiration and circulatory systems. If at the beginning of work (Table 4) a rapid increase in ventilation (V_E) is provided by an increase in both the respiratory frequency (f) and tidal volume (V_T), then beginning from the second minute of work, the intensity of V_E increment slows down and the elevation of V_E occurs exclusively due to breathing acceleration. A significant decrease in V_T is observed immediately prior to refusal to work. Multidirectional changes in the parameters of external respiration characterize the state of overcoming fatigue during work of submaximal intensity.

Table 4. Changes of external respiration indices in cyclists during work of submaximal power (M)

Indices	Duration, min					
	0	1	2	3	4	5
$V_E, l \cdot \text{min}^{-1}$	12	55	90	117	120	134
V_T, l	0.6	2.5	2.9	2.8	2.7	2.5
$f, \text{breaths} \cdot \text{min}^{-1}$	10	21	30	37	43	53
$VE,$	27.8	26.5	22.6	24.3	25.5	27.1
$OE, \text{ml} \cdot \text{breaths}^{-1}$	85	113	120	117	107	95
Ratio of alveolar ventilation to respiratory minute volume, $AV/V_E, \%$	68.1	72.6	78.9	76.9	73.3	65.2

Explanation of symbols: V_E – minute volume; V_T – tidal volume; f – respiratory frequency; VE – ventilation equivalent; OE – oxygen effect; AV/V_E – ratio of alveolar ventilation to respiratory minute volume

A significant increase in pulmonary ventilation is associated with tidal volume decrease. Increased respiratory frequency and reduced tidal volume lead to elevation of a relative volume of physiologically dead respiratory space, decrease of alveolar ventilation portion in respiratory minute volume, lung oxygen utilization coefficient. Besides, ventilation equivalent begins to increase and the oxygen effect of the respiratory cycle decreases. The economy of external respiration starts to decline (Table 4). This state characterizes the initial phase of overcoming fatigue.

The efficiency of blood flow in supplying O_2 to tissues becomes almost maximal in the initial phase of overcoming fatigue. Later on (under the load of submaximal power), the efficiency of circulation does not decrease and continues to remain high in the final phase of overcoming fatigue. This is evidenced by the change in the hemodynamic equivalent, which is at the lowest level since the second minute of work. Meanwhile, the oxygen effect of heart contraction reaches its maximum values (Table 5).

Compensatory reinforcement of the respiratory and cardiovascular system function provides the body with a maximum increase in the rate of oxygen supply to the lungs, alveoli, and its transport by arterial blood. That is, it provides a maximum increase in the rate of O_2 delivery to working muscles. The maximum indices of these autonomic functions are practically achieved already at the initial phase of overcoming fatigue. A further increase in ventilation turns out to be less effective with regard to O_2 delivery because it hardly satisfies the increased oxygen demand of the respiratory muscles. Beginning from the second minute of muscular activity of submaximal power, fatigue develops in the apparatus of external respiration. This is evidenced by decreased tidal volume, efficiency and economy of respiration. The most important factor limiting work capacity during the performance of work at submaximal power is the mismatch between oxygen delivery to the working tissues and their oxygen demand. This is due to the limited capabilities of the respiratory and circulatory system functioning.

Table 5. Circulation indices changes in cyclists during work of submaximal power (M)

Indices	Duration of work, min					
	0	1	2	3	4	5
$Q, l \cdot \text{min}^{-1}$	-	22.1	27.5	31.8	33.7	34.5
Q, ml	77	128	146	160	167	168
$HR, \text{beats} \cdot \text{min}^{-1}$	144	165	185	191	194	197
$POE, \text{ml} \cdot \text{beats}^{-1}$	6	15	22	23	24	24
$C_{(a-v)}O_2,$	6.3	12.2	14.1	14.6	14.7	14.9
$HE, \text{c.u.}$	10.4	7.8	7.3	7.3	7.3	7.2

Explanation of symbols: Q – systolic volume; Q – minute volume; HR – pulse; $C_{(a-v)}O_2$ – oxygen arteriovenous difference; C_vO_2 – venous blood oxygen content; HE – hemodynamic equivalent for oxygen; POE – pulse oxygen effect

The factors limiting work capacity include the restricted ability to reinforce the activity of O₂ utilization mechanisms in tissues and cells. Among these mechanisms are an increase in blood microcirculation, opening of capillaries, decreased resistance in the microcirculation, an increase in the surface for the diffusion of gases in tissues, enhanced activity and concentration of respiratory enzymes, the content and distribution of myoglobin. The reinforced activity of these mechanisms during submaximal muscular load results in a significant increase of arteriovenous oxygen difference and the coefficient of oxygen utilization from the blood (Table 5). A second minute into the work, the arteriovenous O₂ difference, as well as the coefficient of O₂ utilization from the blood, reach their maximum. Their further increase is impossible due to the fact that pV_{O₂} decreases to a level below the critical one. This is a factor that limits the increase in oxygen uptake rate by the tissues, and thus the work capacity. This leads to the development of tissue hypoxia, accumulation of insufficiently oxidized products, metabolic acidosis development, and ultimately a decrease in the contractile properties of muscle fibers.

More visual characteristic of overcoming fatigue was obtained in the study of higher nervous activity, neuromuscular activity, subjective sensations of fatigue, vegetative indices, body oxygen regimes during a muscular activity of mild power.

We have also identified three phases of overcoming fatigue: initial, intermediate, and final. These phases are longer in time. The initial phase of overcoming fatigue occurs after 45-55% of the work onset and takes 15-22% of the time. The intermediate phase takes 10-20%, whereas the final one - 10-12% of the total duration of the work.

The initial phase is characterized by a slow decline of work capacity. It is manifested in the appearance of a feeling of fatigue, small fluctuations in the pedaling speed, a slight decrease in the efficiency of efforts (Table 6).

Table 6. Changes of muscular activity indices in cyclists during work of submaximal power (M)

Indices	Duration of work, %											
	0	10	20	30	40	50	60	70	80	90	100	
Fatigue subjective evaluation, points	-	0	1.5	1.5	3.0	4.5	5.0	6.5	8.0	9.2	9.5	
Work capacity, km.h ⁻¹	-	39.5	39.4	39.3	39.0	38.6	38.5	38.4	38.6	39.0	39.2	
Time of light-motor response, ms	175	196	180	175	175	175	173	172	173	176	200	
Effort efficiency, %	-	72	74	75	74	72	72	74	77	79	79	

At the beginning of the work of moderate power, in most of the examined muscles, a multidirectional change in the amplitude of the electromyogram and the oscillation frequency of biopotentials (Table 7) occurs. At the initial phase of overcoming fatigue, the oscillation amplitude of the biopotentials of the quadriceps femoris muscle increases, whereas in the biceps femoris muscle and the tibialis anterior muscle, the value of electrical activity decreases. During this period of work in the gastrocnemius muscle, both the amplitude and the oscillation frequency of biopotentials decrease.

Decreased respiration efficiency with a reorganization of its regimes is observed at the initial phase of overcoming fatigue. The frequency of respiratory movements increases more sharply, a decrease in the tidal volume begins. The continued V_E elevation is provided by a significant increase in frequency and less deep respiration. At the same time, an increase in the ventilation equivalent occurs (Table 8). Pronounced changes in cardiac activity are noted. The modes of cardiac function change: the heart rate increases, the stroke volume begins to decrease, but the cardiac output is maintained at a high level.

Table 7. Dynamics of oscillation amplitude and frequency of muscle biopotentials of the cyclist V.K-y during work of moderate power (M)

Muscles	Duration of work, %											
	0	10	20	30	40	50	60	70	80	90	100	
	Oscillation amplitude of biopotentials, μV											
Quadriceps femoris	-	710	760	800	860	930	940	880	850	920	950	
Biceps femoris	-	800	670	480	440	450	470	550	730	760	780	
Gastrocnemius	-	840	850	840	850	870	760	760	900	880	830	
Anterior tibial	-	420	410	360	330	290	350	400	410	410	380	
	Oscillation frequency of biopotentials, hz											
Quadriceps femoris	-	170	160	138	140	155	155	155	155	145	140	
Biceps femoris	-	160	160	160	145	120	107	100	94	87	75	
Gastrocnemius	-	185	150	142	148	160	155	165	200	195	180	
Anterior tibial	-	134	139	152	147	127	125	115	105	108	120	

Changes in the cardiac function modes occur somewhat later - 40-50 minutes after the work onset (35-40% of the total duration of work). Respiration changes begin 30-40 minutes into the work (25-35% of the total duration of work). A decrease in the efficiency of external respiration is associated with a slight decline of the efficiency of the blood O₂ supply (between the 20th and 30th minutes of work) (Table 8).

Table 8. Changes of external respiration indices in cyclists during work of moderate power (M)

Indices	Duration of work, min												
	0	10	20	30	40	50	60	70	80	90	100	110	120
V _E , l.min ⁻¹	14	81	93	100	108	114	117	125	123	124	123	127	140
f, breaths.min ⁻¹	8	28	29	29	33	36	37	38	40	41	43	48	63
V _T , l	1.10	2.72	3.15	3.33	3.23	3.21	3.15	3.09	3.05	2.95	2.87	2.71	2.31
OER, ml.breaths ⁻¹	39	88	125	126	124	123	121	120	117	115	113	110	85
VE	25.8	21.8	21.0	22.5	24.4	24.6	24.8	25.1	25.2	25.5	25.5	26.0	27.0
Ratio of alveolar ventilation to respiratory minute volume, %	79.2	84.5	86.5	86.6	86.7	86.5	86.4	86.1	85.9	85.3	85.1	83.7	80.2

Explanation of symbols: V_E – minute volume; V_T – tidal volume; f – respiratory frequency; VE – ventilation equivalent; OER – oxygen effect of respiration; AV/V_E - ratio of alveolar ventilation to respiratory minute volume

At the intermediate phase of overcoming fatigue, the work capacity is maintained at a given level while the efficiency of efforts increases. In this phase, the oscillation amplitude of the biopotentials of the anterior tibial and biceps femoris muscles increases, whereas in other muscles it decreases slightly (quadriceps femoris muscle). The oscillation frequency of the biceps and tibialis anterior muscles decreases, whereas that of the gastrocnemius increases.

Gradual reduction of respiration efficiency is observed during the intermediate phase. Its slow increase, heart rate elevation, and smooth decrease of the stroke volume are noted. During this period, the arteriovenous O₂ difference increases and the O₂ content and its tension in the mixed venous blood significantly decrease (Table 9).

The work capacity does not decrease during the final phase (Table 6), although a subjective feeling of great fatigue is noted. In this phase, an increase in the oscillation amplitude of the biopotentials of the biceps femoris and tibialis anterior muscles is observed. The economy of using efforts in the pedaling cycle continues to improve. The gastrocnemius and quadriceps femoris showed a tendency to decrease in electrical activity. The oscillation frequency of muscle biopotentials showed multidirectional changes in the final phase (Table 7).

Redistribution of the activity of examined muscles was the most peculiar feature of the overcoming fatigue period during the activity of mild intensity. It was expressed in electrical activity increase in some muscles and decrease in the other.

A slight decrease in the duration of visual-motor response was observed in elite cyclists at the end of the final phase directly before the refusal to continue the work (Table 6).

In the final phase, the vegetative responses and especially the body oxygen regimes undergo significant changes: the respiratory frequency increases, the tidal volume, and the respiration efficiency decrease, the ventilation equivalent becomes higher (than at rest), the oxygen effect of the respiratory cycle decreases sharply, the proportion of alveolar ventilation in the pulmonary minute volume drops (Table 8).

Cardiac activity modes undergo significant changes – the heart rate increases and stroke volume output decreases. The cardiac output cannot be maintained at the level providing adequate oxygen delivery. This is associated with a decrease in hemodynamics efficiency with respect to O₂ supply to the tissues. Arteriovenous O₂ difference (the coefficient of its utilization from blood decreases), hemodynamic equivalent are increased, whereas the oxygen effect of heart contraction drops (Table 9).

Table 9. Circulation indices changes in cyclists during work of moderate power (M)

Indices	Duration of work, min												
	0	10	20	30	40	50	60	70	80	90	100	110	120
Q, ml	100	150	195	200	210	200	195	185	180	172	168	165	145
Q, l.min ⁻¹	8	26	32	33	34	34	34	33	33	32	33	32	31
HR, beats.min ⁻¹	75	158	166	167	165	172	177	180	180	185	190	200	220
C(a-v)O ₂ , ob/%	7	12.5	13.0	13.1	13.3	13.5	13.6	13.9	14.3	14.5	14.7	14.5	13.7
C _V O ₂	10.1	7.3	8.1	8.3	8.4	8.3	7.7	7.4	7.3	7.3	7.4	7.4	7.6
HE	14.1	7.8	7.3	8.0	7.7	7.5	7.3	7.1	6.9	6.8	6.7	6.6	7.5
POE, ml.beats ⁻¹	8	22	26	27	26	27	27	27	28	27	26	24	22

Explanation of symbols: Q – systolic volume; Q – minute volume; HR – pulse; C(a-v)O₂ – oxygen arteriovenous difference; C_VO₂ – venous blood oxygen content; HE – hemodynamic equivalent for oxygen; POE – pulse oxygen effect

An increase in hemoconcentration and blood oxygen content maintaining the rate of O₂ transport by arterial blood for some time. Due to increased blood viscosity, this creates additional difficulties for the heart pumping function and the efficiency of microcirculatory processes. At this time, the reserves for adequate perfusion of intensively working organs are significantly limited due to an increase in the thermoregulatory function of blood flow.

Body temperature elevation represents a typical sign of the onset of overcoming fatigue period during the intense muscular activity of moderate power. A pronounced elevation of body temperature is observed within the entire period of overcoming fatigue.

Table 10. Dynamics of gas exchange indices in cyclists during work of moderate power (M)

Indices	Duration of work, min												
	0	10	20	30	40	50	60	70	80	90	100	110	120
VO ₂ , l.min ⁻¹	1.4	4.4	4.6	4.5	4.5	4.5	4.5	4.6	4.7	4.7	4.8	4.7	3.5
RQ, %	0.83	0.87	0.88	0.89	0.90	0.89	0.88	0.87	0.86	0.86	0.85	0.84	0.83
La, mg/%	33	39	36	33	32	31	30	30	32	33	32	30	29
t°, degrees	37	37.9	38.2	38.3	38.5	38.6	38.7	39.1	39.3	39.2	39.1	39.2	39.4
V _{CO₂} , l.min ⁻¹	1.1	3.8	4.1	4.0	4.1	4.2	4.1	4.2	4.1	4.2	4.2	4.0	3.2
GC, mg/%	5.5	5.0	4.9	4.7	4.8	4.9	4.9	4.9	4.8	4.9	4.8	4.8	4.7
C _{max} O ₂	20.3	20.7	20.9	21.0	21.2	21.3	21.4	21.3	21.2	21.3	21.2	21.5	21.8

Explanation of symbols: VO₂ – oxygen uptake rate; V_{CO₂} – carbon dioxide evolution rate; RQ – gas exchange ratio; La – lactic acid concentration; t° – body temperature; GC – glucose concentration; C_{max}O₂ – blood oxygen capacity

Oxygen uptake rate reaches the level of oxygen demand almost immediately after the work onset (Table 10). In the examined cyclists in the period of a relatively steady state, the oxygen uptake rate during 60-minute work was in the range of 78-86%, whereas during a 120-minute load - 72-85% of the maximum. In the most trained road cyclists, these values reached 85-90%. Well-prepared athletes are able to maintain oxygen uptake rate in the range of 84-87% VO_{2max} for 1.0-1.5 hours. A relatively steady state of O₂ uptake rate and CO₂ release rate is established from 10 to 110 minutes of work (Table 10).

An increase of insufficiently oxidized product concentration is noticeable in the first 10-15 minutes of the work. The onset of the overcoming fatigue period is accompanied by some decrease of pH. The acidosis that has arisen at this stage is of a mixed nature. This is evidenced by an increase in the excess of acids, a rather noticeable elevation in the level of blood carbon dioxide tension (from 39 to 46 mm Hg). Then a smoothing of the impairments occurs through respiratory compensation (pCO₂ is reduced to 34 mm Hg). The metabolic component is also involved and the pH levels off to 7.330 despite the increasing content of insufficiently oxidized products (BE=6.7 mmol/l). The work continues already in the face of compensated metabolic acidosis. The action of compensation mechanisms is effective enough to keep the pH at 7.370 until the end of the load.

A specific feature of strenuous muscular activity of moderate power is a pronounced decrease in blood glucose concentration during the development of overcoming fatigue and a decrease in the gas exchange ratio.

Discussion

The multidirectional changes in oscillation amplitude and frequency of biopotentials in the initial and intermediate phases of overcoming fatigue during the work of submaximal power is a consequence of the replaceability manifestation in the activity of the motor units of the examined muscles. Unidirectional changes in the above indices attest to an elevating central impulsation in connection with an increasing volitional effort (Ambrosini et al., 2012). This leads to the increased number of functioning motor units and the rhythm of their contractile activity (Emanuele et al., 2012; Hug & Dorel, 2009).

The stability of the spatio-temporal structure of muscle electrical activity is explained by the sustainable activity of the motor centers in highly skilled athletes in the period of overcoming fatigue during work of submaximal power (Degallier & Ijsper, 2010).

An increase of nerve center excitation during the final phase before refusal to work in elite athletes (at submaximal power of load) indicates the enhancement of the excitation process in the nerve centers under the influence of increasing volitional stimulation (Ericson, 1988).

The accumulation of insufficiently oxidized products results in the changes of blood acid-base state, metabolic acidosis development. Lactic acid contributes to a weakening of the connection of catecholamines with plasma proteins, an increase of biologically active catecholamine concentration, a more intensive mobilization of energy supply anaerobic mechanisms (Dahmen, 2012).

The release of insufficiently oxidized products in blood impairs well-coordinated work of a number of body functional systems, thus exacerbating the degree of acidotic disorders (Barratt et al., 2016).

Under conditions of cyclists' competitive activity (4 km pursuit), where the intensity of work is in the zone of submaximal power, the acid-base balance shifts are more pronounced than in studies under laboratory

conditions. Quite often, the pH of elite athletes drops to 7.00-7.02, and the excess acid exceeds 25.0 mmol/l. The compensatory mechanisms on the part of the external respiration system are extremely tense (Boyles et al., 2012). This is evidenced by a significant decrease in the tension of carbon dioxide in the arterial blood.

Lactic acid accumulation, shifts in blood acid-base balance by the end of work of submaximal power are also the factors limiting the work capacity and leading to fatigue (Antonov et al., 2017; Miller et al., 2019). The biochemical changes in tissues are reflected in the state of receptors, which is accompanied by pain sensations due to which the athlete may stop working.

An increase in oscillation amplitude of biopotentials during work of moderate power indicates the involvement of a larger number of motor units in the active state, compensating for the decreased activity of fast motor units at the expense of the inclusion of new slow motor units with a lower threshold of excitation (Mornieux et al., 2010).

An increase in the duration of the visual-motor response of cyclists at the end of the final phase immediately before refusal to work is indicative of a reduction in the excitability of the nerve centers (De Oliveira, 2002; Theurel et al., 2011).

A decreased stroke volume is one of the most important factors limiting work capacity under a load of moderate power (Thakur et al., 2008).

Body temperature elevation within the entire period of overcoming fatigue during work of moderate power indicates a significant increase in thermoregulatory difficulties and an additional load on the central circulation system in the process of overcoming fatigue development. This precludes the possibility of increasing (or even maintaining) high O₂ utilization from arterial blood (Castronovo et al., 2012). Besides, it prevents efficient transport of oxidation substrates (which are characteristic of a steady-state during such work).

Well-trained athletes can maintain oxygen uptake in the range of 84-87% of VO_{2max} for up to two hours. In the literature on this issue, we have not come across any information about the possibility of maintaining the main indices of gas exchange at such a high level for 120 minutes.

The acid-base balance maintenance (an insignificant degree of metabolic acidosis, its compensated form) is, probably one of the special mechanisms for supporting the work capacity under conditions of moderate loads.

Less pronounced changes in regulatory compensation (pH) during longer and, thus, less intense loads compared to shorter-time work can be associated with a lower amount of insufficiently oxidized products of muscle metabolism entering the blood (Dedieu et al., 2020; Zameziati et al., 2006). Under conditions of prolonged loading, the intensification of oxidative phosphorylation becomes of key importance. Due to the more efficient regulation of the potassium-sodium balance, one of the important mechanisms for maintaining acid-base balance is provided - the retention of Na for the body in the form of NaHCO₂. That is, the blood bicarbonate level is stabilized in the process of performing work. The ability to maintain the blood buffer system capacity during prolonged loads creates, probably, optimal conditions for a trained body during which the shift in homeostatic parameters is less pronounced (Gorkovenko et al., 2012).

A decrease of blood glucose content in the process of overcoming fatigue development and gas exchange ratio indicates certain depletion of body carbohydrate stores. It is a key factor limiting work capacity during the performance of moderate power work (Fudin et al., 2015; Ya-weng Tseng et al., 2006).

During moderate power of work, compensatory mechanisms provide improved functioning of the respiratory and circulatory systems. They also ensure the rate of oxygen delivery, which is necessary to satisfy the body oxygen demand for a long period of work (Pryimakov, 2012). One of the mechanisms for overcoming the growing fatigue in elite athletes is the redistribution of the relative activity of the muscles involved in movement (Hug et al., 2010).

During the muscular activity of moderate power in the period of overcoming fatigue, specific compensatory responses of the body are aimed at surmounting a complex of factors that restrain work capacity (Dorel et al., 2009; Takaishi et al., 1998). The main compensatory reactions include functional stability of the nerve centers, their ability to maintain for a long time the intensive activity of the body locomotor apparatus and oxygen supply systems under tense conditions of homeostasis; a significant degree of expenditure of oxidation substrates, and other factors of muscle metabolism; complication of thermoregulation.

Conclusions

Significant temporal and quantitative differences in compensatory mechanisms for maintaining work capacity were recorded during a strenuous muscular activity of different power. This indicates the specific character of compensatory mechanisms with respect to each load being studied.

Studies have confirmed the presence of overcoming fatigue period during strenuous muscular activity and the heterogeneity of this state course. Conditionally overcome fatigue is divided into three phases: initial, intermediate, and final.

The specific nature of overcoming fatigue during strenuous muscular activity is conditioned by altered interaction of central nervous influences and peripheral factors. They determine the quality of regulation of the body somatic and autonomic functions, the aspiration of the regulatory systems to maintain a high level of work capacity at the expense of volitional efforts at increasing levels of physiological system functioning. This is

accompanied by the involvement of intramuscular, intrasystem, and intersystem mechanisms for maintaining work capacity level by various mechanisms of intracellular metabolism. The peculiarities of overcoming fatigue period are determined by the functional stability of the nerve centers, their ability to rebuild regulatory mechanisms and bring the body systems to the next level of functioning.

Active inclusion of compensatory intra- and intersystem mechanisms during the period of overcoming fatigue occurs in the face of a progressive decrease in the functioning efficiency and economy of systems. A rapid decline of functional efficiency is not the only reason for the apparent fatigue during which the work capacity is decreased. It reflects the sum of the accumulated overcoming functional and metabolic difficulties, the state of the vegetative centers. It also reflects the state of the entire complex aggregate of regulatory processes to ensure a high level of work capacity. Obvious fatigue is observed even in case of a significant decrease in the efficiency of individual functional systems. In obvious fatigue, a decrease in the muscle contractile function and impaired coordination structure of movements are observed. These changes in the motor and vegetative spheres during the period of obvious fatigue indicate discoordination in the activity of the body functional systems.

The findings point to the good perspectives of the purposeful usage of the modeled states of overcoming fatigue in the training process to expand the body functional capacities of elite athletes in cyclic sports events.

Conflict of interest

The authors declare that there is no conflict of interests.

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