

Features of hemodynamics of pulmonary circulation during the diving reflex in men and women

Tatyana Zemlyanukhina¹, Maria Karpova², Anna Vankova², Anastasia Bozhedomova², Dmitriy Anisimov¹, and Tatyana Baranova²

¹Faculty of Biology, Saint Petersburg State University, Universitetskaya nab., 7–9, Saint Petersburg, 199034, Russian Federation

²Department of Physical Culture and Sports, Saint Petersburg State University, Universitetskaya nab., 7–9, Saint Petersburg, 199034, Russian Federation

Address correspondence and requests for materials to Tatyana Baranova, tatyana.baranova@spbu.ru

Abstract

Diving reflex is a mechanism of protection against hypoxia. This effect is achieved through a complex of cardiovascular reactions. The adaptive cardiovascular reactions of the diving reflex in women and men were studied. The diving reflex was activated by submerging a face in cold water under laboratory conditions. Men (n = 50) and women (n = 49) untrained in diving aged 18 to 25 were recruited into the study. The vascular reactions and blood flow were examined by integrated rheography and rheography of the pulmonary artery. Peripheral blood circulation was registered by plethysmography. A statistically significant decrease in heart rate (HR), cardiac minute output (CO), an increase in blood pressure (BP), peripheral vascular tone, and dilatation of pulmonary vessels were detected in all subjects during the diving response. It has been established that when simulating diving, women experience a greater increase in blood flow to the lungs than men and a more pronounced decrease in diastolic index (DCI), which reflects a decrease in resistive vascular tone, as well as diastolic index (DSI), which characterizes lung perfusion. Probably, this provides the female organism with greater protection in extreme conditions of diving.

Keywords: diving reflex, systemic circulation, pulmonary circulation, sex differences in adaptive responses, impedance rheography, photoplethysmography.

Introduction

Knowing natural mechanisms of protection against extreme environmental factors is the key to the human organism control. For example, in secondary aquatic Amniotes, the most important universal form of adaptation to diving is the diving reflex, which is accompanied by reflexes of apnea, bradycardia, peripheral vasoconstriction and selective redistribution of blood flow. The blood supply is stopped to the organs that can withstand temporary hypoxia and redistributed to the brain and heart (Galantsev, 1977; Galantsev, 1982; Galantsev, 1986; Elsner, 1970; Thompson and Fedak, 1993; Butler and Jones, 2007). Humans demonstrate the reaction like diving mammals. Currently, the fact of increasing blood flow to the lungs when diving has been proven. This occurs due to a decreased air volume in the lungs and, as a consequence, an increased hyperbaric factor that affects the body during submersion. It is assumed that increased blood flow into the lung vessels has a protective effect and helps to maximize the chest volume diving reflex. We recently reported pulmonary vessel dilation during imitation of the diving reflex with a latent period of 2–4 s, which indicated that the autonomic nervous system (ANS) acted prior to the hyperbaric factor (Podyacheva, Zemlyanukhina, Shadrin, and Baranova, 2020). However, the indicators characteristic of

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Authors' information: Tatyana Zemlyanukhina, Doctoral Student, orcid.org/0000-0003-2651-8521; Maria Karpova, Master's Student, orcid.org/0009-0006-5105-2830; Anna Vankova, Master's Student, orcid.org/0009-0007-1250-5435; Anastasia Bozhedomova, Graduated Student; Dmitriy Anisimov, Master's Student, orcid.org/0009-0006-2342-7172; Tatyana Baranova, PhD in Biology, orcid.org/0000-0003-0524-2933

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reflective dilation of the pulmonary vessels had a large dispersion. We decided to check whether the sex factor can influence the mechanisms of the diving response.

Sex specific features of organism adaptation to extreme environmental factors remain insufficiently studied at present. Analyzing divers of different ethnic groups associated with pearl or food extraction makes an important observation that the majority of divers are women (Brilsky, 2012). But whether this is due to tradition, culture or physiological characteristics of men and women that favor diving remains to be seen.

Within this study, we aimed to investigate the adaptive cardiovascular reactions in response to imitation of the diving reflex and their variations in men and women.

Materials and methods

Subject recruitment and data collection

99 healthy volunteers (49 women and 50 men) without special physical training were included in the study. All the subjects (students at the Saint Petersburg State University, Russia) were informed about the study purposes, objectives and methods, and gave their voluntary consent by signing the Informed Consent Form. All the subjects participated in the study voluntarily and had no direct benefit from the test (financial rewards, educational requirements, or credits). Information about the general results of the research or personal data (such as genetic variants) was provided for individuals who were interested in. At the time of the experiment, none of the volunteers had arteriosclerosis or diabetes or were taking any drugs. The subjects were asked to skip smoking or use coffee at least two hours prior the study. A short list of the groups' characteristics is presented in Table 1. The study was approved by the Saint Petersburg State University Ethics Review Committee for human studies (no. 40 dated March 7, 2012).

Experimental model of the diving reflex in humans

Activation of the diving reflex was performed using face submersion in cold water under laboratory conditions. As it is well known (Galantsev, 1988) that 10°C gradient between air temperature and water temperature is optimal for the manifestation of the diving reflex, in our experiments water temperature was $13.9 \pm 2.5^\circ\text{C}$ and air temperature was $20.1 \pm 3.4^\circ\text{C}$. Prior to the start of the experiment, all subjects stayed in the laboratory for at least 30–40 min and were adapted to the local temperature. The procedure was performed on a subject who lay in a ventricumbent position on a coach with arms along the body, as published previously in (Baranova et al., 2017). During an experimental procedure, all subjects kept their hands at the heart line, did not change this position and did not move

their fingers with a finger sensor. Three face submersions on a normal exhale were performed in cold water. Duration of the first submersion was limited by the feeling of the first discomfort. After the first face submersion, which we considered as an orienting one, a full recovery of cardiovascular parameters was conducted within 10 minutes. A pause between submersions was 2–3 min.

Measurements of the physiological parameters

Before the experimental procedure, an electrocardiogram (ECG) was recorded in I standard lead and checked for abnormalities. During the whole experiment (rest, imitation of the diving reflex and recovery) ECG, blood pressure (BP) and the central blood flow were constantly recorded. The rheography was recorded by Tishchenko's integrated body rheography method (Tishchenko's impedance cardiographic method of total systemic blood flow assessment) (Tishchenko, 1973) using RGPA-6/12 "Rean-Poly" (Medicom-MTD, Russia). A relative index of skin capillary blood flow in the left index finger was recorded by photoplethysmogram (PPG). The pulmonary artery reogram was recorded by impedance method for investigation of right pulmonary artery blood flow (RPABF) (Zenkov and Ronkin, 1991; Palko, 2007; Hammoud et al., 2022), and the next physiological parameters were used for the evaluation: stroke output (SO, ml), rheographic index (RI, Ohm) reflects the lung tissue blood filling, dicrotic index (DCI, %; reflects the vascular tone of resistant vessels of the pulmonary artery system), and diastolic index (DSI, %; reflects the ratio of venous drainage to arterial blood supply).

The pulse wave amplitude (PWA, pm) and the pulse transit time (PTT, ms), were calculated based on the photoplethysmogram records using "Rean-Poly" software (Elite version). It previously has been reported that PWA indirectly reflects vascular perfusion of the distal phalanx of the hand and essentially depends on the sympathetic influences of the autonomic nervous system (Alian and Shelley, 2014). Heart rate (HR), systolic and diastolic BP were registered by the oscilloscopic method (AND UA-797, Japan). To determine BP latency period, the noninvasive method with Finometer (FMS, Netherlands) was used.

Respiratory flow and volume, as well as expiratory O_2 and CO_2 fractions ($p\text{O}_2$ and $p\text{CO}_2$) for determination of alveolar gas exchanges were recorded with the microprocessor analyzer (MF01, Research and Production Center for Environment and Health — CEZ, Russia).

Statistical analysis. The values are expressed as means and SDs. The statistical analysis was performed using the statistical package for Windows 7 (MS Excel 2010, Origin Pro 2015 version b9.2). A T-test was calculated to assess the significance of differences in samples with normal distribution. P values < 0.05 were considered to be statistically significant.

Results

Characteristics of the studied groups of men and women

All subjects completed the protocol, had no special physical training, and had never practiced free diving. In accordance with instructions, subjects did not hyperventilate before face immersion. Mean values in groups of women and men were: weight, kg — 58.6 ± 8.5 and 73.4 ± 10.7 ; height, cm — 165.7 ± 6.2 and 178.9 ± 6.2 ; BMI — 21.4 ± 3.1 and 22.8 ± 2.5 ; age, yr — 21.9 ± 2.9 and 24.2 ± 4.7 .

The average duration of apnea during the imitation of the diving reflex in the study group was 34.5 ± 13.3 sec. In all subjects, the alveolar PO_2 was significantly reduced, while the alveolar PCO_2 was significantly increased in the exhaled air after breath holding with the face immersion in water compared with the control level ($P < 0.05$). In ambient air was as follows: $PO_2 = 159.0$, $PCO_2 = 0.28$ mm Hg, before apnea — $PO_2 = 123.0 \pm 6.4$ mm Hg, $PCO_2 = 39.1 \pm 7.1$ mm Hg, at end of the diving reflex imitation — $PO_2 = 95.1 \pm 7.1^*$ mm Hg, $PCO_2 = 48.9 \pm 6.5^*$ mm Hg.

Indicators of the systemic circulation during the implementation of the diving response

The analysis of cardiac performance parameters at resting state did not reveal any differences between men and women in heart rate (HR, bpm) but statistically significant differences were revealed in the stroke output (SO, mL) and cardiac minute output (CO, L) (Table 1). Men had significantly higher CO and SO than women. During the diving reflex imitation, HR decreased statistically significantly in both men and women. No statistical differences

were found between men and women. SO in both groups changes insignificantly. CO during the diving reflex imitation decreases in both groups. But for men this indicator remains statistically significantly higher than for women.

Changes in vascular reactions when simulating diving

Blood supply to peripheral vessels was measured indirectly using the pulse wave amplitude (PWA, per mille (pm)). Peripheral vascular tonus was indirectly determined by pulse transit time (PPT, ms). At resting state, during diving simulation and during recovery, the peripheral vascular blood supply parameter (PWA) in women is lower than in men. PPT in women was statistically significantly lower than in men at resting state and during recovery. No differences were found in diving simulation (Table 2).

Statistically significant increases in systolic and diastolic blood pressure were found in both groups during imitation of the diving reflex (Fig. 1). SBP were significantly higher in men before, during, and after imitation of the diving reflex. No differences between men and women were found in DBP index.

Indicators of pulmonary blood flow during the implementation of the diving response

The comparison of parameters by sexual characteristics revealed statistically significant differences in RI, DCI, DSI. Thus, the RI parameter is higher in women in all states: at the background, during the submersion and in recovery (Fig. 2).

Vascular tone of the right pulmonary artery was determined by DCI. Perfusion index (inflow to outflow

Table 1. Sex-related differences in the blood flow parameters before, during, and after diving reflex imitation

Parameter	CO, L/min			HR, bpm			SO, mL		
	Control level	Diving simulation	Recovery	Control level	Diving simulation	Recovery	Control level	Diving simulation	Recovery
Female (n = 49)	5.70 ± 0.09	$4.98 \pm 0.12^{\circ\circ\circ}$	$5.52 \pm 0.09^{\cdot\cdot}$	73.9 ± 1.0	$63.6 \pm 1.2^{\circ\circ\circ}$	$68.3 \pm 0.9^{\cdot\cdot\cdot}$	77.6 ± 1	78.7 ± 1.2	$81 \pm 1^{\cdot}$
Male (n = 50)	$8.06 \pm 0.16^{***}$	$7.31 \pm 0.16^{\circ\circ\circ\circ}$	$7.69 \pm 0.17^{***}$	74.8 ± 1.1	$66 \pm 1.1^{\circ\circ\circ}$	$69.5 \pm 1.1^{\cdot\cdot\cdot}$	$107.8 \pm 1.4^{***}$	$110.1 \pm 1.5^{***}$	$110.3 \pm 1.5^{***}$

Note: HR — heart rate; SO — stroke output; CO — cardiac minute output. The significance of differences was estimated using t-test: female/male: * — $p < 0.05$, ** — $p < 0.01$, *** — $p < 0.001$; control level/diving simulation: $^{\circ}$ — $p < 0.05$, $^{\circ\circ}$ — $p < 0.01$, $^{\circ\circ\circ}$ — $p < 0.001$; diving simulation/recovery: $^{\cdot}$ — $p < 0.05$, $^{\cdot\cdot}$ — $p < 0.01$, $^{\cdot\cdot\cdot}$ — $p < 0.001$; control level/recovery: $^{\cdot}$ — $p < 0.05$, $^{\cdot\cdot}$ — $p < 0.01$, $^{\cdot\cdot\cdot}$ — $p < 0.001$.

Table 2. Sex-related differences in the blood flow parameters before, during, and after diving reflex imitation

Parameter	PWA, pm			PTT, ms		
	Control level	Diving simulation	Recovery	Control level	Diving simulation	Recovery
Female (n = 49)	0.57 ± 0.05	$0.29 \pm 0.02^{\circ\circ\circ}$	$0.69 \pm 0.06^{\cdot\cdot}$	200.81 ± 1.47	$194.90 \pm 1.74^{\circ\circ}$	195.37 ± 1.52
Male (n = 50)	$1.15 \pm 0.08^{***}$	$0.47 \pm 0.03^{\circ\circ\circ\circ}$	$1.35 \pm 0.08^{\cdot\cdot\cdot}$	$209.78 \pm 1.73^{***}$	$198.56 \pm 1.94^{\circ\circ}$	$203.04 \pm 1.74^{**}$

Note: PWA — pulse wave amplitude; PTT — pulse transit time. The significance of differences was estimated using t-test: female/male: * — $p < 0.05$, ** — $p < 0.01$, *** — $p < 0.001$, control level/diving simulation: $^{\circ}$ — $p < 0.05$, $^{\circ\circ}$ — $p < 0.01$, $^{\circ\circ\circ}$ — $p < 0.001$; diving simulation/recovery: $^{\cdot}$ — $p < 0.05$, $^{\cdot\cdot}$ — $p < 0.01$, $^{\cdot\cdot\cdot}$ — $p < 0.001$.

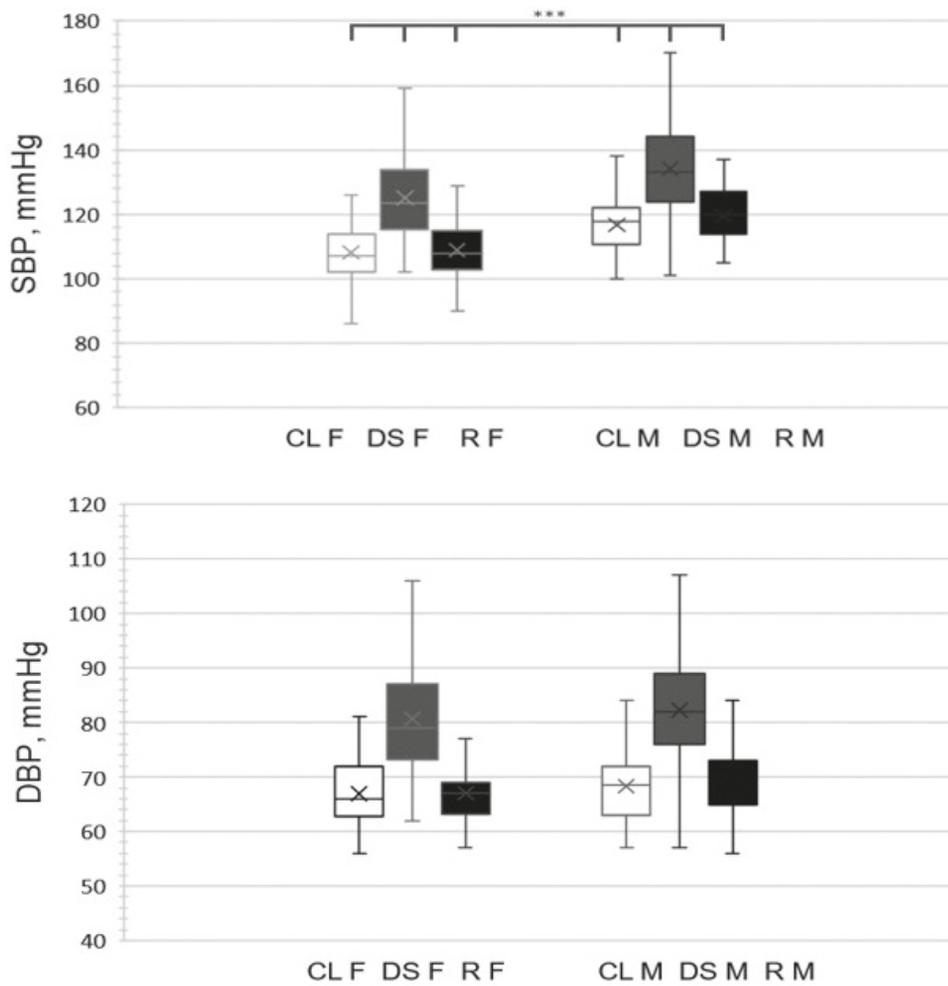


Fig. 1. Dynamics of blood pressure in the diving reflex manifestation in men and women. A — SBP, systolic blood pressure; B — DBP, diastolic blood pressure. CL — control level; DS — diving simulation; R — recovery after face submersion. The significance of differences was estimated using t-test: female/male: *** — $p < 0.001$. The significance of differences was estimated using t-test.

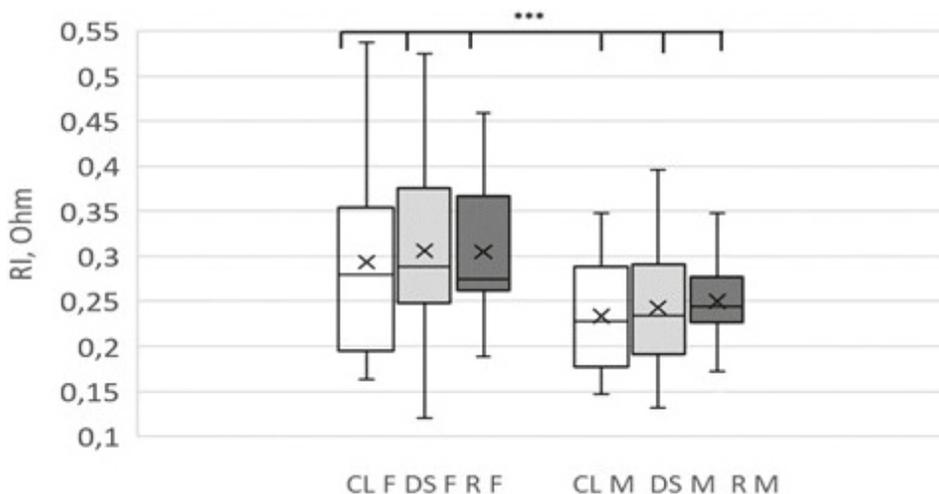


Fig. 2. Difference in the rheographic index of the pulmonary artery in men (M) and women (F). CL — control level; DS — Diving simulation; R — recovery after face submersion. * — $p < 0.05$ — DS F — DS M. The significance of the differences was assessed using the Mann — Whitney test.

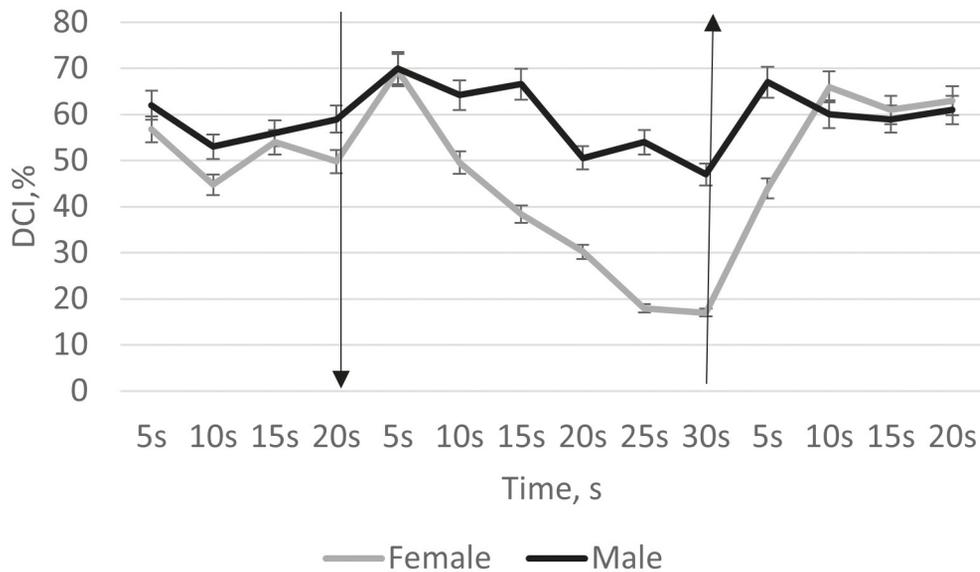


Fig. 3. Representative dynamic of diastolic index (DCI, %) during diving simulation. Arrow pointing down indicates the beginning of face submersion, arrow pointing up indicates the end of face submersion.

Table 3. Sex-related differences in the blood flow parameters before, during, and after diving reflex imitation. DSI — diastolic index of the right pulmonary arterial system; DCI — diastolic index

Parameter	DSI, %			DCI, %		
	Control level	Diving simulation	Recovery	Control level	Diving simulation	Recovery
Female (n = 49)	55.3 ± 0.8	50.5 ± 1.1 ^{ooo}	55.8 ± 0.7	52.9 ± 0.8	47.3 ± 1 ^{ooo}	51.0 ± 0.7 ^{..}
Male (n = 50)	58.0 ± 0.8	56.32 ± 1.2 ^{***}	58.8 ± 0.8	55.3 ± 0.8	54.1 ± 1.2 ^{***}	53.9 ± 0.8

Note: The significance of differences was estimated using t-test: female/male: * — $p < 0.05$, ** — $p < 0.01$, *** — $p < 0.001$; control level/diving simulation, ^{ooo} — $p < 0.001$; diving simulation/recovery: ^{..} — $p < 0.01$. The significance of the differences was assessed using the Mann — Whitney test.

ratio) was determined by DSI. Statistically significant differences in DSI and DCI were found in diving simulation (Table 3).

Statistically significant differences between men and women were found for both parameters — DCI and DSI. This index is lower in women. At the same time, the highest level of differences is observed in the diving simulation. This is due to the fact that in women during diving simulation the DCI index significantly decreases, while in men the decrease of this index is insignificant (Fig. 3).

Discussion

The human diving reflex can be triggered by simulating diving, i. e. by immersing the face in water and holding the breath (Gooden, 1994). Then, signals from cold and tactile sensors of the facial skin, baro- and chemoreceptors in the circulatory system, and mechanoreceptors in the respiratory system come to the n. vagus nucleus and then, via cholinergic fibers, to the heart sinoatrial node, thus causing bradycardia. Long-term conative ap-

nea makes adrenergic effects on the heart increase. The total effect on the heart sinoatrial node from n. vagus and sympathetic postganglionic neurons depends also on the background state of the sinoatrial node cells; this state is in turn dependent on various neuropeptides released by cardiomyocytes and endothelial tissue in the blood vessels. They can affect the sinoatrial node directly or indirectly, together with classical neurotransmitters. We have established high individual variability in adaptive reactions of the diving response. This observation can be explained by the current hormonal status of a body (i. e., sex hormones).

The analysis of cardiovascular responses in men and women revealed statistically significant higher values of stroke output and cardiac minute output, systolic blood pressure in women compared to men. These data are consistent with many results obtained by other researchers. The differences are explained by smaller heart size, myocardial thickness, and hence lower functional capacity (SO and CO) in women than in men (De Simone et al., 1991; Hammond, Devereux, Alderman, and Laragh, 1988; Huxley, 2007; Bassareo and Crisafulli, 2020).

Arterial pressure directly corresponds to the cardiac output, arterial elasticity, and peripheral vascular resistance. According to the literature, two factors contribute to higher blood pressure levels in men: higher cardiac output and higher peripheral resistance. The higher level of peripheral resistance in men is associated with the potential of testosterone for adrenergic sympathetic influences on peripheral vascular walls, while high estrogen levels in women, on the contrary, limit the strength of these influences. Our studies show that systolic blood pressure is indeed higher in men than in women in all states: at rest, during diving simulation and during recovery. But there were no differences between the sexes in diastolic blood pressure. There were also no differences in the index reflecting the tone of peripheral vessels — PTT. Blood filling of peripheral vessels in men is higher than in women. When realizing the diving response, a decrease in PWA and PTT was observed in all subjects. This indicates reflex narrowing of peripheral vessels. At the same time, blood flow in this state is higher in men than in women, which can be explained by their higher SO.

Currently, the fact of the increased blood flow into the lungs during imitation of the diving reflex (when immersing the face into cold water) is well established (Tetzlaff et al., 2021). This is a protective mechanism to prevent the lungs from collapsing when diving. In our previous works, we established that the expansion of the blood vessels of the lungs occurs reflexively (Podyacheva, Zemlyanukhina, Shadrin, and Baranova, 2020).

However, in the previous study, we found that DCI and DSI parameters, which characterize pulmonary vascular tone, had a large group mean dispersion during the diving response. This suggests that pulmonary vessels may respond differently in the subjects during the formation of the diving response. In this study we compared the diving response in men and women and found that in women reflex dilatation of pulmonary vessels during the diving response is better expressed. How can this be explained?

Pulmonary vessels are innervated by autonomic sympathetic and parasympathetic nerve fibers. According to numerous observations, parasympathetic activity is higher in women than in men. This is attributed to the modulating influence of autonomic regulation by female sex hormones. It was shown that intravenous or intracerebral injection of estrogen increased the vagus nerve tone and suppressed sympathetic efferent activity in female and male rats with ovariectomy (Saleh and Connell, 1999; Saleh, Connell, and Saleh, 2000).

There is some data that estrogens increased density (Rainbow, Degroff, Luine, and McEwen, 1980; Olsen, Edwards, Schechter, and Whalen, 1988; Ciriello and Caverson, 2016) and excitability of vagus nerve afferent endings in the nucleus of the solitary pathway (NTS) (Qiao et al., 2009).

Estrogen also increases nitric oxide production, which is known to presynaptically inhibit norepinephrine release (Huang, Sun, Koller, and Kaley, 1997).

These differences are formed by sex hormones both at the level of the central nervous system and at the level of peripheral effectors (Du, Riemersma, and Dart, 1995). Possibly, during realization of diving response in women due to hormonal status against the background of limiting influence of adrenergic influences by estrogens, parasympathetic cholinergic influences on pulmonary vessels are more pronounced. As a consequence, they expand and fill with blood to a greater extent.

Conclusions

However, our data require deeper theoretical understanding and confirmation by other methods of studying the pulmonary blood flow.

Reflex dilatation of pulmonary vessels, as well as reflex bradycardia and reflex vasoconstriction during diving (or its imitation) are protective reactions of the organism in humans and animals. Reflex bradycardia slows down the blood flow and provides slower consumption of oxygen in conditions of its cessation in the body. Reflex constriction of peripheral vessels allows redistribution of the blood flow to the organs least resistant to hypoxia — the brain and heart. Reflex dilatation of pulmonary vessels triggers blood flow to the lungs, which is enhanced by hyperbaric factor during diving. Blood filling of pulmonary vessels prevents the lungs from collapsing under hyperbaric conditions when the body is submerged at depth during diving. According to the data obtained in women, reflex constriction of peripheral vessels and dilatation of pulmonary vessels during realization of the diving response are expressed to a greater extent. Perhaps, this provides the female organism with greater protection in the extreme conditions of diving. Perhaps Brilsky's (2012) observation that the majority of divers are women is not only due to tradition, but also to the advantages of the female organism.

The knowledge of these sex differences is important for understanding adaptive defense mechanisms, as well as for assessing the risk of adaptation failure and the formation of pathological abnormalities on this basis (e. g., pulmonary edema under hyper- and hypobaric conditions).

References

- Alian, A. A. and Shelley, K. H. 2014. Photoplethysmography. *Best Practice & Research Clinical Anaesthesiology* 28(4):395–406. <https://doi.org/10.1016/j.bpa.2014.08.006>
- Baranova, T. I., Berlov, D. N., Glotov, O. S., Korf, E. A., Minigalin, A. D., Mitrofanova, A. V., Ahmetov, I. I., and Glotov, A. S. 2017. Genetic determination of the vascular reactions in humans in response to the diving reflex. *American Journal of Physiology-Heart & Circulatory Physi-*

- ology 312(3):H622–H631. <https://doi.org/10.1152/ajp-heart.00080.2016>
- Bassareo, P. P. and Crisafulli, A. 2020. Gender differences in hemodynamic regulation and cardiovascular adaptations to dynamic exercise. *Current Cardiology Reviews* 16(1):65–72. <https://doi.org/10.2174/1573403X15666190321141856>
- Brilsky, A. 2012. The complete diver: The history, science and practice of scuba diving. 352 p. Dive training LLC, Parkville.
- Butler, P. J. and Jones, D. R. 1997. Physiology of diving of birds and mammals. *Physiological Reviews* 77(3):837–899. <https://doi.org/10.1152/physrev.1997.77.3.837>
- Ciriello, J. and Caverson, M. M. 2016. Effect of estrogen on vagal afferent projections to the brainstem in the female. *Brain Research* 1636:21–42. <https://doi.org/10.1016/j.brainres.2016.01.041>
- De Simone, G., Devereux, R. B., Roman, M. J., Ganau, A., Chien, S., Alderman, M. H., Atlas, S., and Laragh, J. H. 1991. Sex differences in left ventricular anatomy, blood viscosity and volume regulatory hormones in normal adults. *American Journal of Cardiology* 68(17):1704–1708. [https://doi.org/10.1016/0002-9149\(91\)90333-G](https://doi.org/10.1016/0002-9149(91)90333-G)
- Du, X. J., Riemersma, R. A., and Dart, A. M. 1995. Cardiovascular protection by oestrogen is partly mediated through modulation of autonomic nervous function. *Cardiovascular Research* 30(2):161–165. [https://doi.org/10.1016/S0008-6363\(95\)00030-5](https://doi.org/10.1016/S0008-6363(95)00030-5)
- Elsner, R. W. 1970. Diving mammals. *Science Journal* 6(4):69–74.
- Galantsev, V. P. 1977. The evolution of adaptations of diving animals. 191 p. Nauka Publ., Leningrad. (In Russian)
- Galantsev, V. P. 1982. Physiological adaptations of diving mammals. Ecological physiology of animals. Nauka Publ., Leningrad. (In Russian)
- Galantsev, V. P. 1986. Adaptations of the cardiovascular system of secondary aquatic amniot. 202 p. Leningrad State University Press, Leningrad. (In Russian)
- Galantsev, V. P. 1988. Adaptation of the cardiovascular system of diving animals. Leningrad: 198 p. Leningrad State University Press, Leningrad. (In Russian)
- Gooden, B. A. 1994. Mechanism of the human diving response. *Integrative Psychological and Behavioral Science* 29(1):6–16. <https://doi.org/10.1007/BF02691277>
- Hammond, I. W., Devereux, R. B., Alderman, M. H., and Laragh, J. H. 1988. Relation of blood pressure and body build to left ventricular mass in normotensive and hypertensive employed adults. *Journal of the American College of Cardiology* 12(4):996–1004. [https://doi.org/10.1016/0735-1097\(88\)90467-6](https://doi.org/10.1016/0735-1097(88)90467-6)
- Hammoud, A., Tikhomirov, A., Myasishcheva, G., Shaheen, Z., Volkov, A., Briko, A., and Shchukin, S. 2022. Multi-channel bioimpedance system for detecting vascular tone in human limbs: An approach. *Sensors* 22(1):138. <https://doi.org/10.3390/s22010138>
- Huang, A., Sun, D., Koller, A., and Kaley, G. 1997. Gender difference in myogenic tone of rat arterioles is due to estrogen-induced, enhanced release of NO. *American Physiological Society Journal* 272(4):H1804–H1809. <https://doi.org/10.1152/ajpheart.1997.272.4.H1804>
- Huxley, V. H. 2007. Sex and the cardiovascular system: The intriguing tale of how women and men regulate cardiovascular function differently. *Advances in Physiology Education* 31(1):17–22. <https://doi.org/10.1152/advan.00099.2006>
- Olsen, K., Edwards, E., Schechter, N., and Whalen, R. 1988. Muscarinic receptors in preoptic area and hypothalamus: Effects of cyclicity, sex and estrogen treatment. *Brain Research* 448(2):223–229. [https://doi.org/10.1016/0006-8993\(88\)91259-0](https://doi.org/10.1016/0006-8993(88)91259-0)
- Palko, T. 2007. Impedance rheography for systemic and pulmonary circulation study and clinical application; pp. 608–611 in: *Proceedings of the 13th International Conference on Electrical Bioimpedance and the 8th Conference on Electrical Impedance Tomography, IFMBE. Graz, Austria, 29 August–2 September 2007*. Vol. 17. Eds H. Scharfetter, R. Merwa. Springer, Berlin; Heidelberg.
- Podyacheva, E., Zemlyanukhina, T., Shadrin, L., and Baranova, T. 2020. Features of hemodynamics of pulmonary circulation during the diving reflex. *Biological Communications* 65(3):244–251. <https://doi.org/10.21638/spbu03.2020.304>
- Qiao, G. F., Li, B. Y., Lu, Y. J., Fu, Y. L., and Schild, J. H. 2009. 17-Estradiol restores excitability of a sexually dimorphic subset of myelinated vagal afferents in ovariectomized rats. *American Journal of Physiology-Cell Physiology* 297(3):C654–C664. <https://doi.org/10.1152/ajpcell.00059.2009>
- Rainbow, T. C., Degroff, V., Luine, V. N., and McEwen, B. S. 1980. Estradiol 17 β increases the number of muscarinic receptors in hypothalamic nuclei. *Brain Research* 98(1):239–243. [https://doi.org/10.1016/0006-8993\(80\)90362-5](https://doi.org/10.1016/0006-8993(80)90362-5)
- Saleh, T. M. and Connell, B. J. 1999. Centrally mediated effect of 17beta-estradiol on parasympathetic tone in male rats. *American Physiological Society Journal* 276(2):R474–R481. <https://doi.org/10.1152/ajpregu.1999.276.2.R474>
- Saleh, M. C., Connell, B. J., and Saleh, T. M. 2000. Medullary and intrathecal injections of 17beta-estradiol in male rats. *Brain Research* 867(1-2):200–209. [https://doi.org/10.1016/s0006-8993\(00\)02313-1](https://doi.org/10.1016/s0006-8993(00)02313-1)
- Tetzlaff, K., Lemaitre, F., Burgstahler, C., Luetkens, J. A., and Eichhorn, L. 2021. Going to extremes of lung physiology-deep breath-hold diving. *Frontiers in Physiology* 9(12):e710429. <https://doi.org/10.3389/fphys.2021.710429>
- Thompson, D. and Fedak, M. A. 1993. Cardiac responses of grey seals during diving at sea. *Journal of Experimental Biology* 174(1):139–154. <https://doi.org/10.1242/jeb.174.1.139>
- Tishchenko, M. I. 1973. Stroke volume measurement by integral rheography of human body. *Fiziologicheskii zhurnal SSSR imeni I. M. Sechenova* 59(8):1216–1224. (In Russian)
- Zenkov, L. R. and Ronkin, M. A. 1991. Functional diagnostics of nervous diseases. 640 p. Meditsina Publ., Moscow. (In Russian)