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INVESTIGATION OF THE LONG-WAVELENGTH THRESHOLD OF SPECTRAL SENSITIVITY IN THE GRAY SEAL *HALICHOERUS GRYPUS* (FABRICIUS, 1791)

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In marine mammals, the absorption maxima of photopigments have a shift to the shorter-wavelength spectrum area compared to terrestrial mammals; this leads to a shift in the long-wavelength threshold of spectral sensitivity as well. In most publications focused on the investigation of long-wavelength sensitivity of marine mammals, only the absorption maxima of "red-sensitive" photopigments are given, but no data on maximum wavelengths of light emission that animals are able to perceive are provided. Therefore, this work was aimed at studying the long-wavelength thresholds of spectral sensitivity in a typical representative of earless seals – the gray seal *Halichoerus grypus* (Fabricius, 1791). During the experiment, a group of four gray seals was trained to press one of two buttons if a LED lamp located above it is switched on. In the lamp, there were groups of LEDs emitting monochromatic light in the wavelength range from 600 to 700 nm with a step of 10 nm and a luminous intensity of 0.5 cd. As shown, the lower perception threshold of light emission for the studied gray seals is light emission with a wavelength of 660 nm, and this confirms the data on the short-wavelength shift of the sensitivity peaks of photopigments in marine mammals. During prolonged exposure to extremely low-light conditions typical for the polar night, the long-wavelength perception threshold in the gray seals can increase from 660 to 670–680 nm.

Keywords: gray seal, vision, spectral sensitivity

The gray seals have a well-developed visual system which includes relatively large eyeballs and a developed visual area of the brain. Such anatomical peculiarities of the eye structure, as the tapetum and developed musculature of the iris, indicate the adaptation of the visual system to low-light conditions (Hanke et al., 2009). Most of the gray seals inhabit the Holarctic realm beyond the Arctic Circle, which is characterized by the midnight sun with its round-the-clock high illuminance and polar night with illuminance above 500 lux for only a few hours a day.

In marine mammals, the absorption maxima of photopigments have a shift to the shorter-wavelength spectrum area compared to terrestrial mammals, with a correlation found between feeding diving depth and spectral sensitivity of visual pigments (McFarland, 1971). Out of cetaceans, shallow-diving species have rhodopsin (Rh1) with an absorption maximum of about 500 nm; in deep-sea species, the absorption maximum shifts to 479 nm (Bischoff et al., 2012 ; Fasick & Robinson, 2000). Out of pinnipeds, deep-diving species, such as northern elephant seals *Mirounga angustirostris* (Gill, 1866) and Weddell seals *Leptonychotes weddellii* (Lesson, 1826), have an Rh1 absorption maximum of about 480 nm; shallow-diving species have an Rh1 absorption maximum close to that of terrestrial mammals. Many species of marine mammals lack the "red-sensitive" pigment (long-wavelength sensitive opsin, LWS), but if present, it has a short-wavelength shift to 530 nm; in terrestrial mammals, maximum absorption of the LWS pigment is about 560 nm (Levenson et al., 2006). All marine mammals lack the SWS1 photopigment (short-wavelength sensitive opsin 1) responsible for sensitivity to short-wavelength ("blue") photoactive emission (Peichl et al., 2001).

For most mammals, including humans, the long-wavelength threshold of visible light is emission with a wavelength of 760–780 nm (Sliney, 2016). Light in this range is perceived by long-wavelength (LWS) cone opsins, with their maximum sensitivity about 560–580 nm. When moving away from the maximum point, the sensitivity gradually decreases to zero; it is impossible to specify the exact spectral range threshold of visible emission. When perceiving reflective objects, the threshold strongly depends on the illuminance level, optical properties of a perceived object, the dark adaptation of the eye, and the state of the nervous system. When light sources are perceived at borderline wavelengths, the minimum brightness increases exponentially with wavelength; at extreme wavelengths, even under high brightness, those are perceived by humans as a very dim orange-red glow (Palczewska et al., 2014). The following effect was recorded as well: with continuous stimulation of retina with a laser at wavelengths of 1,060–1,064 nm, a feeling of red color arose; with pulsed exposure, it was a feeling of green color (Sliney et al., 1976). Nevertheless, researchers attribute it to the direct effect on retinal nerve cells rather than photopigments (Sliney, 2005).

Under natural conditions, animals do not actually encounter objects that emit light; in rare cases, it can be bioluminescence or open sources of fire. Mostly, eyes perceive objects reflecting light, the source of which is the Sun. Its maximum emission is about 500–550 nm; a short-wavelength spectrum area, from 350 nm, is actively absorbed by upper atmospheric layers, while the long-wavelength area, from 600 nm, is absorbed by its lower layer saturated with water vapor. Meanwhile, with an increase in emission wavelength, the degree of its absorption by the atmosphere rises as well (Kirk, 2015).

In the gray seal *Halichoerus grypus* (Fabricius, 1791), the LWS pigment–containing cones are present in the retina; those are distributed in the central fovea of the retina in a ratio of 1 : 200 in relation to the rods and have an absorption maximum about 530 nm (Braekevelt, 1986). Based on a calculation of a spectral sensitivity curve for long-wavelength photopigments (Lamb, 1995 ; Lewis, 1955), it is assumed that the long-wavelength threshold of spectral sensitivity for the gray seals varies within 650–700 nm.

The aim of the work was to reveal the long-wavelength threshold of spectral sensitivity of the visual system in the gray seal. In addition to theoretical significance, this information has practical importance since night video recording of seals using infrared light is of great interest.

MATERIAL AND METHODS

Four female gray seals were involved in the experiment: seals No. 1 and 2, at the age of 15; seals No. 3 and 4, at the age of 5. All of them represented one population and were caught on the Bolshoy Kiy Island (the eastern Varanger Fjord, the Barents Sea). At the beginning of the experiment, all the animals were healthy, and no deviations in behavior were observed. All these seals have already participated in several experimental studies of hearing (Litvinov & Pakhomov, 2019) and vision (Pakhomov, 2020) and were trained to work according to paradigms "stimulus–response", "choice of two", and “choice by pattern.” In the present study, the animals had to designate the switched-on lamp by pressing the corresponding button; they worked according to a scheme of free choice from two stimuli – reinforced and stimulus-noise.

For the study, an experimental setup was developed (Fig. 1). On a platform (3), two lamps (4) and two buttons (5) were located at a distance of 1 m. In the identical lamps, there were groups of LEDs emitting light with different wavelengths. In each experiment, either the right or left lamp worked; the seal had to press the button located under the working lamp (this was considered as a correct choice). Correct choices were reinforced by food rewards with a preliminary bridge signal (one long whistle at a frequency of 3,200 Hz, with a duration of 1 s); mistakes were punished through a work termination for 15 “penalty” seconds with a preliminary bridge signal (two short whistles at a frequency of 3,200 Hz, with a duration of 0.25 s and a break of 0.5 s). Fish cut into 20-g pieces and placed in containers (2) served as a food reward.

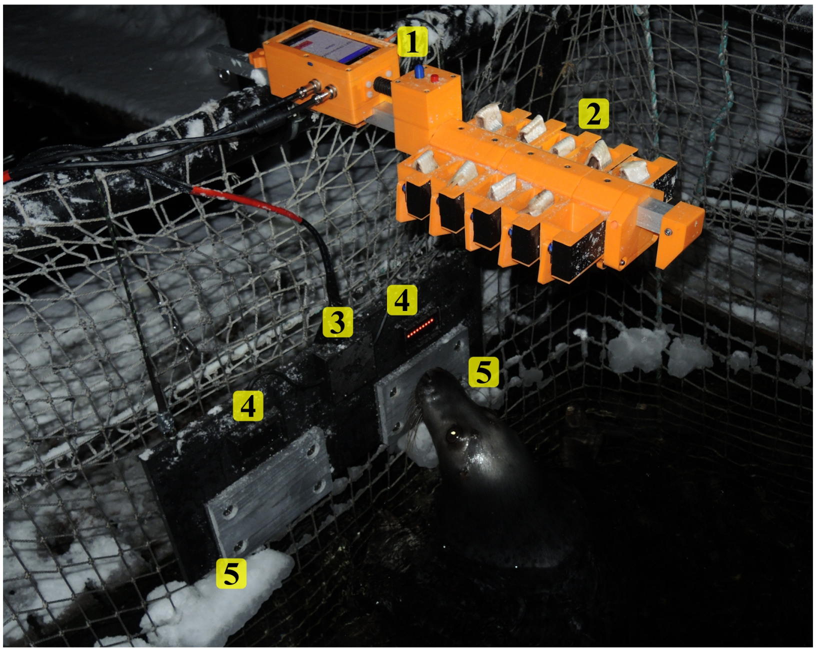

Fig. 1. Scheme of the experimental setup for determining the long-wavelength threshold of spectral sensitivity of the visual system of the gray seal: 1, control unit; 2, block of containers for fish feed; 3, distribution unit; 4, lamps; 5, buttons for interacting with the seal

The studies were carried out in September–February, when the gray seals first have a pupping season (November–December) and then a mating season (December–January). Accordingly, food motivation of the animals was significantly reduced. Therefore, firstly, the studied animals were on a special diet before, during, and after the experimental work; secondly, special attention was paid to the bridge signals. For the animals involved in the experiments, the bridge signals were associated during the initial adaptation to cage keeping and were maintained in a course of various researches. Immediately *prior* to the experiment, the work on consolidating the association was carried out with the gray seals: one long whistle was followed by a food reward; two short whistles were followed by a punishment through a work termination.

The source of the light stimulus were LEDs placed in a plastic case with a neutral filter cutting out 25 % of the light; this filter is designed for protecting LEDs from splashes, eliminating a halo around the working group of LEDs, and filtering out glare from the non-working groups. We used gallium-arsenide-phosphide LEDs with a narrow monochrome emission spectrum in the wavelength range of 600–700 nm with a step of 10 nm (for wavelengths of 600, 630, and 690 nm, produced by TZT; for all other wavelengths, produced by FSXSEMI). To check the LEDs for compliance with the declared characteristics, a Zolix Omni-λ300 spectroradiometer was applied. The luminous intensity of all LEDs did not change during the study and was calibrated for each "color" group by a value of 0.5 cd – with the light filter taken into account. Calibration and final measurements of the assembled lamps were carried out with a CEM DT-1308 luxmeter applied to determine the luminous intensity and with a two-tube spectroscope applied to determine the wavelength of the groups of LEDs.

To avoid glare and to increase the contrast of the emitted light, the platform (3) and the lamp cases (4) (see Fig. 1) were coated with anthracite-black matt waterproof paint.

For a human, the light of these LEDs is perceived in a range from amber (600 nm) to crimson (700 nm), and the threshold of perception is about 740–760 nm. Considering that and aiming to avoid the possibility of hints from the researcher, the system worked in a standalone mode. The researcher filled the containers with fish pieces, launched the system, and moved out of the seal visibility range. The general scheme of work was as follows. At the beginning of each cycle, the microcontroller-based control system paused for 5–30 s. If the gray seal pressed any button during this interval, there was a punishment through adding 5 "penalty" seconds to the waiting time. Then, the system pseudo-randomly, according to the Hellman sequence (Gerard et al., 2014) (no more than two identical combinations in a row and an equal number of right and left positions), switched on either the right or left lamp for 5 s. If the gray seal made a correct choice and pressed the button corresponding to the working lamp, he received a food reward. If the animal chose a non-working lamp, there was a punishment through a work termination for 15 s. Skipping a cycle was neither reinforced nor punished, but it was considered as an incorrect choice. After 10 cycles (emptying of the containers), the system terminated its work and signaled to the researcher. They came back to the cage, assessed whether the seal is ready to continue the experiment, filled the containers with fish pieces, and launched the continuation of the work. The system automatically ended the experiment in two cases: 1) if the gray seal missed five cycles in a row; 2) if the animal began to randomly press the buttons during a delay and gained more than two minutes of "penalty" time.

Each animal was usually subjected to 20–50 experiments *per* training – depending on its state and weather conditions. The ratio of correct choices to the total number of experiments was considered, as well as the reaction time of the gray seal. At the beginning of each training, the readings of illuminance, air temperature, humidity, and presence of precipitation or any other distractions were recorded. To reveal the randomness of correct choices, a binomial distribution for each sample of the corresponding wavelength was used. The resulting samples were subjected to multivariate analysis of variance – to determine correlations with weather conditions, date of the experiment, and stimulus position and order. Calculations and statistical data processing were carried out in Microsoft Excel 2019.

The work was carried out under conditions of the Murmansk Marine Biological Institute aquatic complex in the Polyarny town (the Kola Bay water area, the Tonya Cape vicinity). There, the studied gray seals are kept in individual cages under conditions as close to natural as possible. The experiment was conducted from September 2020 to February 2021 in two stages. At the preparatory stage (September–November), the animals were taught to choose the working lamp ignoring the non-working one. At the investigation stage (December–February), the seals were involved in the experimental work. Preparatory work was carried out twice a day – in the morning (before dawn) and in the evening (at dusk, with a total illuminance of not more than 15 lux). Experimental work was conducted twice a day as well – in the morning (at 7:00) and in the evening (in an hour after dark). For the experiment, the animals were chosen whose cages were the most darkened and where the level of illuminance at the platform location did not exceed 5 lux.

RESULTS

In total, 100 experiments were carried out with each gray seal for each group of LEDs during morning trainings, and 100 experiments were carried out during evening trainings. Fig. 2 shows the ratio of correct choices (touching the button under the switched-on lamp) by the gray seals depending on a wavelength of the given light stimulus.

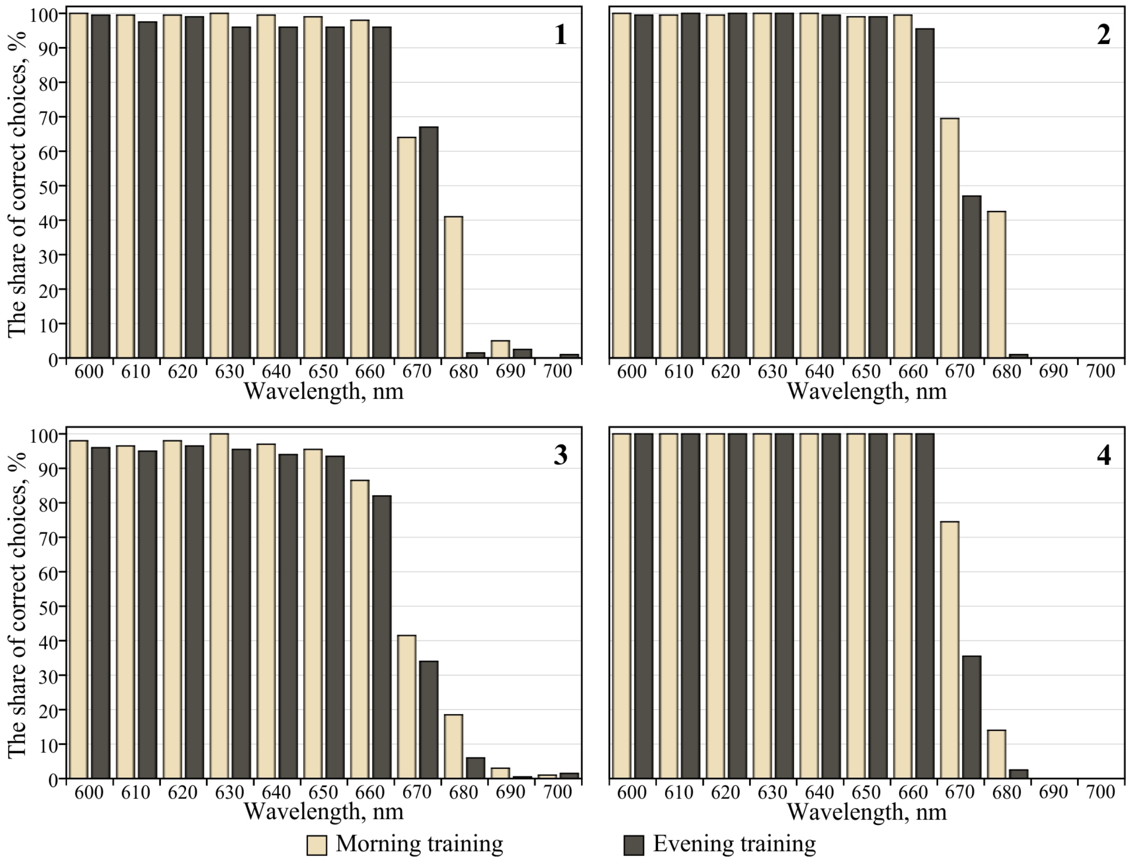

Fig. 2. Ratio of correct choices (touching the button under the switched-on lamp) of the gray seals No. 1–4 during morning and evening trainings

For all the gray seals, the ratio of correct choices (the choices of the switched-on lamp) at wavelengths of 600–660 nm was significantly higher than 75 %; for these samples ($n = 100$; $p < 0.05$), it indicates the non-randomness of the animal actions. Moreover, in this range, for all the seals, except for the seal No. 3, the ratio of correct choices was above 95 %; for the seal No. 4, the value was 100 %. The results of the binomial distribution were as close as possible to 1; for the seal No. 4, those were 1. This shows that the seals made their choices based on feelings rather than random guessing.

In this range, the ratios of correct choices during morning and evening trainings differed little. However, the gray seals made more mistakes during evening trainings. Mainly, those were mistakes when the animals pressed the buttons during the waiting time; to a lesser extent, those were mistakes when they ignored the given stimulus. The seal No. 1 often chose the non-working lamp instead of the nearby switched-on one. The ratio of this mistake made by the seal No. 1 was 2–3 %, while the ratio for other seals was less than 0.1 % of all the choices.

At 670 nm, the ratio of correct choices for all the gray seals decreased sharply and dropped significantly below 75 %, with the exception of the ratio for the seal No. 4: its ratio of correct choices was 74 % during morning trainings. During evening trainings, for all the seals, except for the seal No. 1, the ratio of correct choices decreased to the values below 50 %. For the seal No. 1, the ratio of correct choices during evening trainings was 67 % and was higher than during morning trainings (64 %).

At the same time, out of mistakes made by all the gray seals, the omission of the given stimulus prevailed. By the methods of multivariate analysis of variance, no significant correlations were revealed between the occurrence of the above mistake and weather conditions, date of the experiment, and stimulus position and order.

At 680 nm, the seals showed a reaction only during morning trainings. The ratios of correct choices of 15-year-old animals were 41 and 43 % for the seals No. 1 and 2, respectively, and were significantly higher than for younger ones (18 and 14 % for the seals No. 3 and 4, respectively).

When light stimuli with wavelengths of 690 and 700 nm were given, the gray seals showed no reaction and skipped these stimuli.

Data on the reaction time of the seals with a correct choice made are shown in Fig. 3 as a box plot. The mean, standard deviation of the mean, and extreme values for each wavelength are given.

At visible wavelengths, 600–650 nm, individual characteristics of the gray seals were revealed, such as mean reaction time and scatter of values. During morning trainings, the animals reacted faster than during evening ones. Starting from 660 nm, the mean reaction time and scatter of values began to increase.

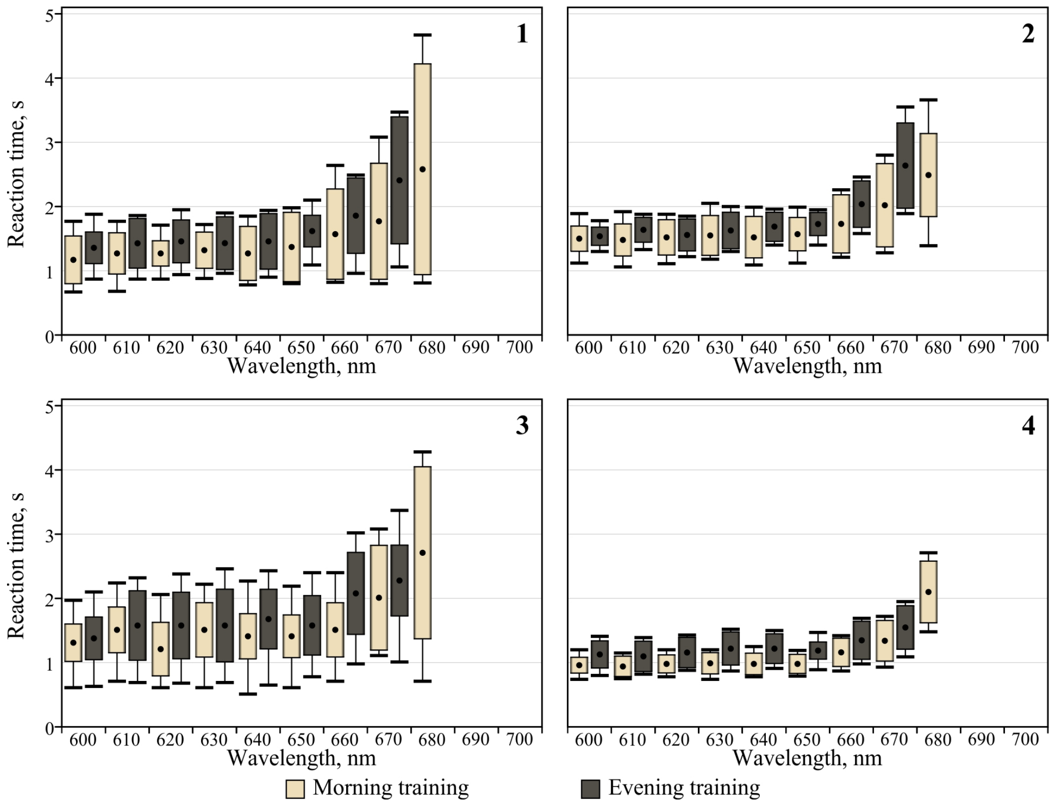

Fig. 3. Reaction time of the gray seals No. 1–4 to switching on the lamps during morning and evening trainings

Analyzing the relationship between the reaction time and external factors, we could establish the correlation with time of the day only; a weak correlation with weather conditions was revealed as well. With wind and sea waves of more 2 points on the Beaufort scale during the night before the experiment, the mean reaction time increased by 5–7.5 %, but the scatter of values did not change.

DISCUSSION

The results of the experiment show that the studied gray seals reliably perceive light with wavelengths up to 660 nm; the mean reaction time of the animals to a given stimulus and its scatter of values generally correspond to individual characteristics of these seals obtained in previous experiments with them (Litvinov & Pakhomov, 2019 ; Pakhomov, 2020). At a wavelength of 660 nm, for all the animals, the mean reaction time to the switched-on lamp and its scatter began to rise; this may result from the fact that the brain spends extra time processing the borderline signal.

At 670–680 nm, the ratio of correct choices significantly decreased but was not equal to zero, as was the case for wavelengths of 690 nm and higher. Considering that the choice is two-alternative, it can be concluded that such values indicate a high probability of random guessing of the switched-on lamp. Importantly, in case of guessing, the gray seals had to guess not only which of two lamps was switched on, but also when it would be switched on. Accordingly, with the lamp working time of 5 s and with taking into account the delay before switching on in a random range of 5–30 s, a probability of getting into a time interval when one of two lamps is working is about 17 %. Moreover, when pressing any button while the delay time had not yet expired, "penalty" 5 s were added to the delay time with the corresponding bridge signal. When gaining 120 s of "penalty" time, the system stopped the training. Thus, a probability of making a correct choice by chance was 8 %; according to the multiplication rule of probability, it was the product of a probability of guessing which of two lamps is switched on (50 %) and a probability of guessing when the lamp would be switched on (17 %). Therefore, the decrease in the ratio of correct choices when giving groups of LEDs with wavelengths of 670 and 680 nm can be explained by the fact that these emissions were the borderline for the gray seals: the animals pressed the correct button only when they were really able to distinguish a working lamp from a non-working one, preferring in case of doubts to wait for the next experiment. There, the effect could be explained by both short-term changes in weather conditions (drizzle fall, water evaporation, *etc.*) and physiological state of the seal, which primarily affects the degree of its focus on the task. This is also indicated by the difference between the results during morning and evening trainings: *prior* to morning trainings, the seals were under low-light conditions for a long time, and, due to dark adaptation, the sensitivity of photoreceptors was increased. The effect may result from own thermal noise of the retina as well: its intensity depends on many physiological peculiarities of the body and is taken into account by the brain when processing visual signals (Ala-Laurila et al., 2004).

Similar results were obtained in a number of behavioral response investigations with the South American sea lion [*Otaria byronia* (de Blainville, 1820)], the harbor seal [*Phoca vitulina* Linnaeus, 1758] (Griebel et al., 2006), and the harp seal [*Pagophilus groenlandicus* Erxleben, 1777] (Lavigne & Ronald, 1972). In all studied animals, the ratio of correct responses sharply decreased starting from 650–670 nm.

Conclusion:

1. For the gray seals studied, the long-wavelength threshold of the perception of light emission is light with a wavelength of 660 nm. This confirms the data on the short-wavelength shift of the sensitivity

peaks of photopigments in marine mammals. During prolonged exposure to extremely low-light conditions, the perception threshold in the gray seals increases from 660 to 670–680 nm.

2. According to the results obtained, the gray seals are unable to perceive light with a wavelength higher than 680 nm. Accordingly, the use of lamps operating in the near-infrared spectrum (750–1,000 nm) will be imperceptible to the seals, and this will allow using such lamps for night watching both domesticated and wild gray seals.

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ИССЛЕДОВАНИЕ ДЛИННОВОЛНОВОЙ ГРАНИЦЫ СПЕКТРАЛЬНОЙ ЧУВСТВИТЕЛЬНОСТИ У СЕРОГО ТЮЛЕНЯ *HALICHOERUS GRYPUS* (FABRICIUS, 1791)

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У морских млекопитающих максимумы поглощения фотопигментов имеют сдвиг в более коротковолновую часть спектра относительно наземных млекопитающих; это обусловливает также и смещение длинноволновой границы спектральной чувствительности. В большинстве публикаций, посвящённых изучению длинноволновой чувствительности морских млекопитающих, приведены только максимумы поглощения «красночувствительных» фотопигментов, но нет данных о максимальных длинах волн светового излучения, которое животные способны воспринимать. Именно поэтому целью настоящей работы было исследовать длинноволновую границу спектральной чувствительности у типичного представителя настоящих тюленей — серого тюленя *Halichoerus grypus* (Fabricius, 1791). В эксперименте группу из четырёх серых тюленей обучили нажимать на одну из двух кнопок, если находящийся над ней светодиодный фонарь включён. В фонаре были расположены группы светодиодов, излучающие монохроматический свет в диапазоне длин волн 600–700 нм с шагом 10 нм и силой света 0,5 кд. Изучение показало, что длинноволновым пределом восприятия светового излучения для исследованных серых тюленей является свет с длиной волны 660 нм, что подтверждает данные о коротковолновом сдвиге пиков чувствительности фотопигментов у морских млекопитающих. При длительном пребывании серых тюленей в условиях крайне низкой освещённости, что характерно для полярной ночи, длинноволновая граница восприятия у них может увеличиваться с 660 до 670–680 нм.

Ключевые слова: серый тюлень, зрение, спектральная чувствительность