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Unusual Pattern of Cerebral Electrical Activity in the Mongolian Hamster (*Allocricetulus curtatus*) During Heterothermia

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Abstract—Electroencephalogram (EEG), brain and abdominal temperature, and motor activity were recorded for the first time in 18 adult males of facultative hibernator, the Mongolian hamster, during hibernation under controlled laboratory conditions in winter. At room temperature, clear synchronous circadian rhythms of motor activity and body temperature were observed. In most animals, a gradual decrease in external temperature (from 24 to 4°C) led to a significant increase in motor activity, combined with an increase in the amplitude of circadian oscillations of body temperature. Six hamsters demonstrated torpor bouts and hibernation with radical changes in the EEG up to reaching the isoelectric line, as well as the disappearance of oscillations of brain temperature. It has been found that Mongolian hamsters can easily enter and exit both a state of torpor and a fairly deep hibernation with a decrease in body temperature down to 10°C during normal sleep periods.

Keywords: hibernation, EEG, body temperature, brain temperature, motor activity, Mongolian hamster

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INTRODUCTION

Hibernation and torpor are physiological states that have attracted the attention of researchers for many decades. Despite the huge number of experimental studies, the nature of these states remains essentially unknown. One of the reasons for the insufficient understanding of the mechanisms of deep hibernation and shallow torpor is the very limited number of species on which electrophysiological studies have been conducted. These are mainly several species of ground squirrels (Citellus, Urocitellus, Spermophilus and Callospermophilus). An interesting group for studying hypothermia is representatives of the subfamily Cricetinae. This rather compact phylogenetic group includes obligate hibernators (Mesocricetus raddei), facultative hibernators (most representatives of the genera Cricetus, Allocricetulus), species that fall into shallow torpor only (Phodopus), and species that do not fall into torpor at all (representatives of the genus Cricetulus) [1, 2]. This allows for interspecific and intergeneric comparisons, tracing the evolution of heterothermia and the mechanisms that ensure the transition from normothermia to hypothermia and back. However, electrophysiological studies have only been conducted on the Syrian hamster (Mesocricetus auratus) [3] and the Djungarian hamster (Phodopus sungorus) [4–7]. At the same time, the phenomena of hibernation and torpor are very widely represented in the animal kingdom, and there is reason to believe that in different species, these phenomena, similar in external features, could have formed on the basis of various molecular-genetic, biochemical and physiological mechanisms during the course of evolution [8, 9]. The objective of the present study was an electroencephalographic (EEG) study of the hibernation/torpor phenomenon in a facultative hibernator, the Mongolian hamster Allocricetulus curtatus [10], on which such studies had never been conducted before.

MATERIALS AND METHODS

The animals selected for the experiments belonged to the 6th–7th generation from individuals captured in 2009–2011 in Tuva. The hamsters were kept in the Institute's vivarium in pairs in standard cages under natural light conditions. A week before the start of the experiment, the animals were placed individually. The experiments took place in winter. They involved 18 adult males weighing about 50 g each. The technique

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of implanting epidural electrodes and an intraperitoneal thermosensors under general anesthesia (avertin), as well as recording and analyzing the EEG in freely moving animals, was described by us earlier [11, 12]. A miniature thermistor was additionally implanted in the frontal cortex of two animals. After the operation, the hamsters were placed in individual plexiglass boxes measuring 20 × 20 × 50 cm. The boxes contained pieces of cotton wool and paper, from which the hamsters could form a nest. Each animal was constantly connected via a flexible cable to the input of a miniature 2-channel autonomous biopotential amplifier, equipped with a 3D accelerometer and transmitting signals to a computer via a Bluetooth channel in standard EDF codes. The applied technique allows continuous recording of the EEG, accelerometer data and brain temperature of the animals in real time for many days without limiting their free moving in the chamber. EEG was recorded with a sampling frequency of 250 Hz, motor activity – 50 Hz, and brain temperature – 2 Hz. Brain and body temperature were measured in °C, and motor activity was measured in fractions of G (δG, the deviation of the sensor acceleration at the moment of measurement from the gravity acceleration). Intraperitoneal thermosensors fixed, body temperature every minute, and averaged over data each 10-minute. At the end of the experiment, each thermosensor was removed from the animal's body, and the data stored in internal memory were downloading off-line using a special device.

On-line recording of EEG (frontal-parietal leads), data of the accelerometer built into the amplifier and brain temperature began one week after the operation simultaneously in 4 animals and continued uninterruptedly until the end of the experiment lasted 6–8 weeks. Visual EEG scorings in 20-sec epochs was performed using a special semi-automated program created on the basis of the open-source EDF browser. According to generally accepted criteria for rodents, states of wakefulness, NREM and REM sleep were distinguished. Periods of hypothermia with altered EEG were designated as a special state Q (quite state). The compressed data were subjected to further processing using the Excel packet.

Individual boxes with Mongolian hamsters were placed (4 boxes each) in a special isolated and ventilated refrigeration unit, where the animals were adapted for a week at a temperature 24.0 ± 1.0°C, 12L/12D (light from 9 a.m. to 9 p.m.) and free access to food and water. Then feeding was reduced to a minimum, and the temperature in the chamber was gradually reduced to 4.0 ± 1.0°C, by 1°C per day. The light period was also gradually reduced, from 12 hrs (from 9 a.m. to 9 p.m.) to 2 hrs (from 2 to 4 p.m.), half an hour per day.

After completion of the experiments, the thermosensors were removed through a small incision in the abdominal skin under light anesthesia, the wound was sutured, the cables were cut, the animals were given antibiotics, and they were returned to their home cages. The electrodes were spontaneously discarded by the animals over the next month. Animals returned to vivarium conditions were subsequently used in other experiments, including reproduction.

RESULTS AND DISCUSSION

As noted above, Mongolian hamsters are facultative hibernators, and most of the experimental animals did not enter hibernation. Only 6 of 18 males demonstrated bouts of shallow torpor and/or hibernation in laboratory conditions. At room temperature, all hamsters showed clear circadian rhythms: a high level of motor activity in the dark, "night" period of the nychthemeron and its low level in the light, "day" period. The body temperature rhythm was synchronous and in phase with the activity-rest rhythm: increases in the "night" time and decreases in the "day" (Fig. 1).

As can be seen from the figure, in those animals that did not go into torpor or hibernation, a gradual decrease in external temperature, from 24 to 4°C, led to a significant increase in motor activity within the hours that corresponded to the "night" during the adaptation period. The increase in motor activity was combined with an increase in the amplitude of circadian temperature fluctuations, with its growth during the "night" period. In other words, the lower the external temperature, the more the hamster moved during the nighttime activity period (despite the fact that the light period was constantly shortening, and food was practically absent) and warmed up more, which allowed it to retain heat during the daytime rest period [11].

Figure 2 shows a typical pattern of hibernation in one of the six experimental hamsters. Hibernation began with a series of successively deepening bouts of torpor with a passive decrease in intraperitoneal temperature to 11°C and radical changes in the EEG until the isoelectric line was reached. As can be seen from the figure, in this case, during the 2-month cold test, the hamster demonstrated the last, 21st bout of hibernation 42 days after the beginning of the experiment, on February 24. After that, it spontaneously switched to the above-described type of cold adaptation by increasing motor activity during the usual dark hours. In other individuals, in addition to bouts of hibernation, single and burst shallow torpor bouts were also observed, which did not turn into deep hibernation. In these bouts, the body temperature dropped only to 17–25°C.

As can be seen from Fig. 3a, just over an hour after the start of the bout, when the animal's body temperature decreased to 30°C, the EEG pattern did not resemble any of the known physiological states (active wakefulness, quiet wakefulness, NREM sleep, REM sleep). Here, the EEG is dominated by a low-amplitude high-frequency rhythm of 12–14 Hz against the

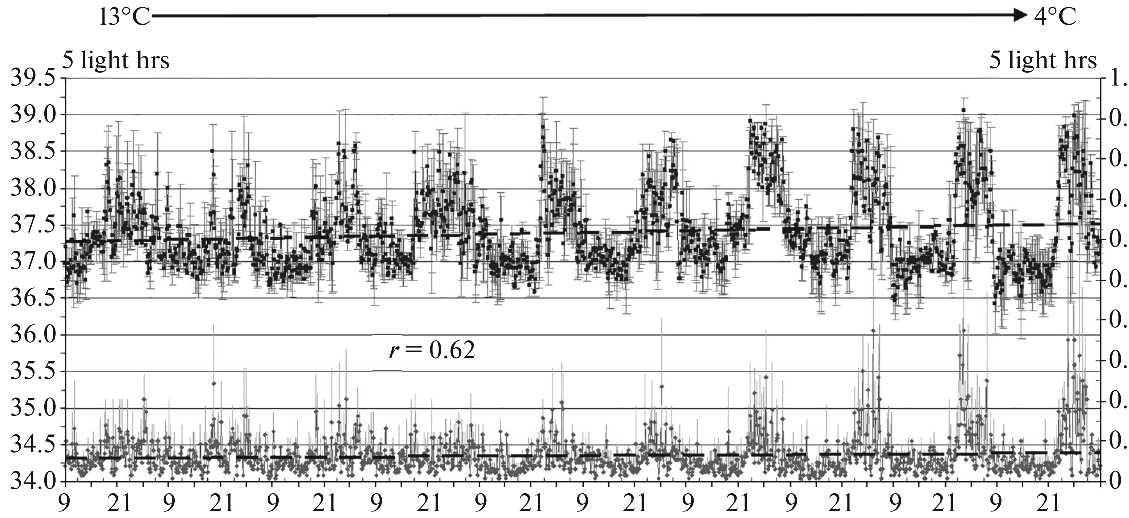


Fig. 1. Averaged 10-day fragment of a two-month record of body temperature (upper trace, left ordinate, °C) and motor activity (lower trace, right ordinate, δG) in two hamsters that did not enter a hypothermia while the chamber temperature was reduced from 24°C (from 13°C, in this fragment) to 4°C. Accordingly, the light period was reduced from 12 h (from 5 hr, in this fragment) to 2 h per day. The abscissa axis shows the time of day in hours. The dotted line marks the trend line; $r = 0.62$ is the correlation coefficient between the two curves ($p < 0.05$).

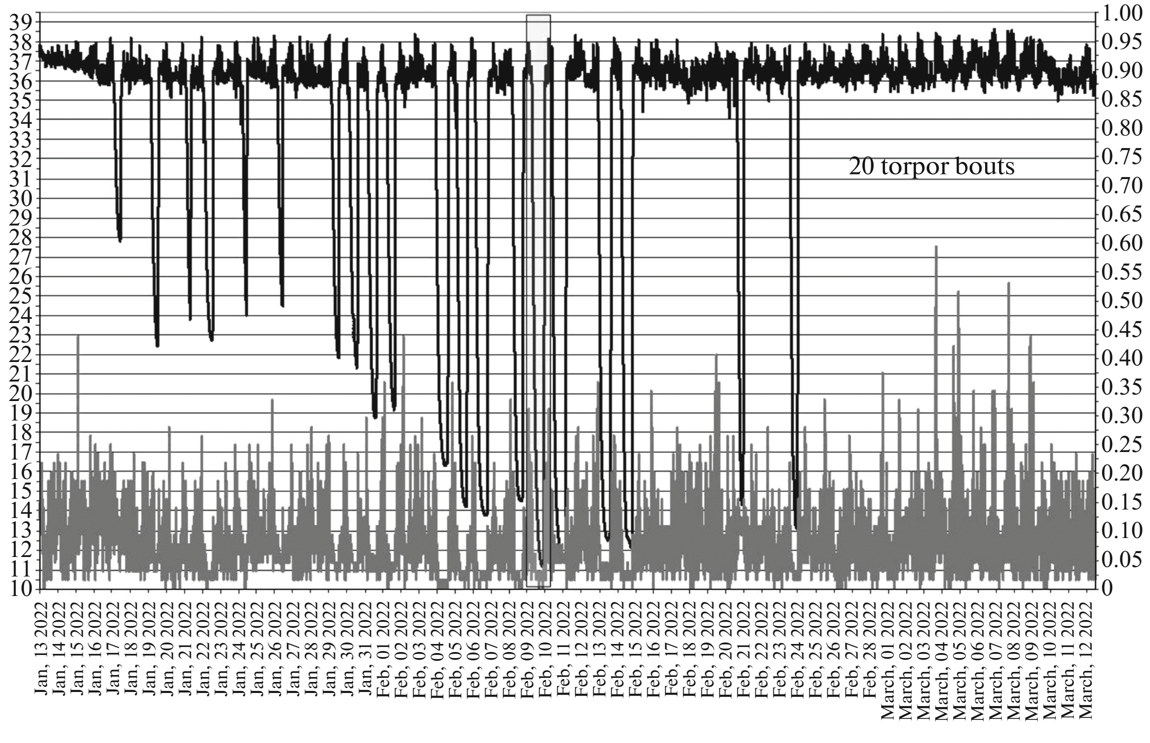
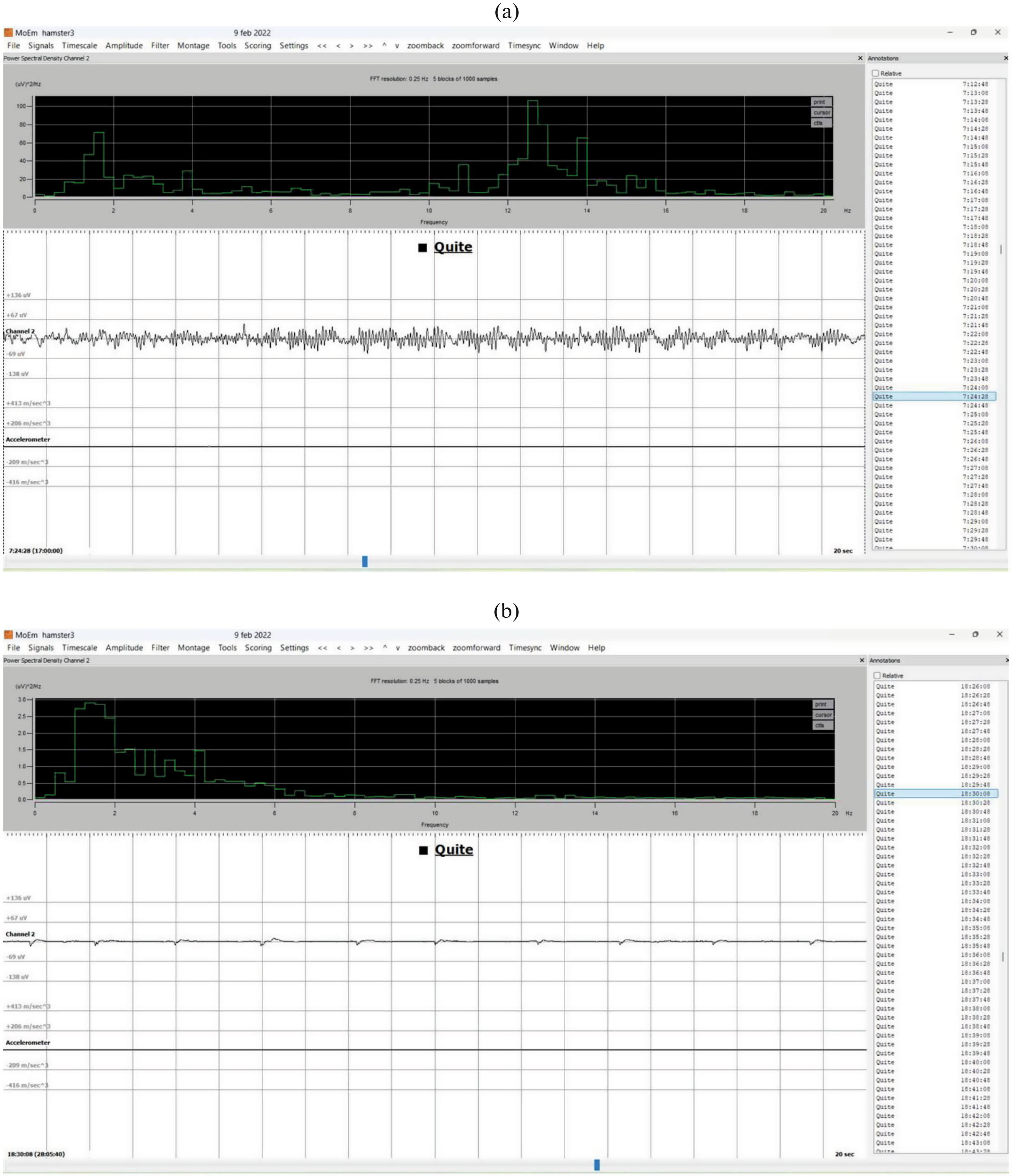


Fig. 2. Typical hibernation in a Mongolian hamster in the laboratory for two months during the winter is presented. The top trace, body temperature (°C, left ordinate); the bottom trace, motor activity (δG, right ordinate). The temperature in the experimental chamber was lowered from 24°C (January, 13, beginning of the experiment) to 4°C (February, 4) and maintained at this level until the end of the experiment. The photoperiod was also reduced from 12 h (January 13) to 2 h (February 4). The fragment shown in detail in Fig. 5 is framed and shadowed.

background of complete immobility of the animal. Such an EEG pattern has not been previously described in other hibernating species [13]. Five hrs 30 min after the start of the bout, the body temperature of the experimental animal dropped to 20°C and the brain completely “switched off”: the EEG demonstrates an



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Quite    7:12:48
Quite    7:13:08
Quite    7:13:28
Quite    7:13:48
Quite    7:14:08
Quite    7:14:28
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Quite    7:15:08
Quite    7:15:28
Quite    7:15:48
Quite    7:16:08
Quite    7:16:28
Quite    7:16:48
Quite    7:17:08
Quite    7:17:28
Quite    7:17:48
Quite    7:18:08
Quite    7:18:28
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Quite    7:27:08
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Quite    7:27:48
Quite    7:28:08
Quite    7:28:28
Quite    7:28:48
Quite    7:29:08
Quite    7:29:28
Quite    7:29:48
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Quite    18:26:08
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Quite    18:26:48
Quite    18:27:08
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Quite    18:28:08
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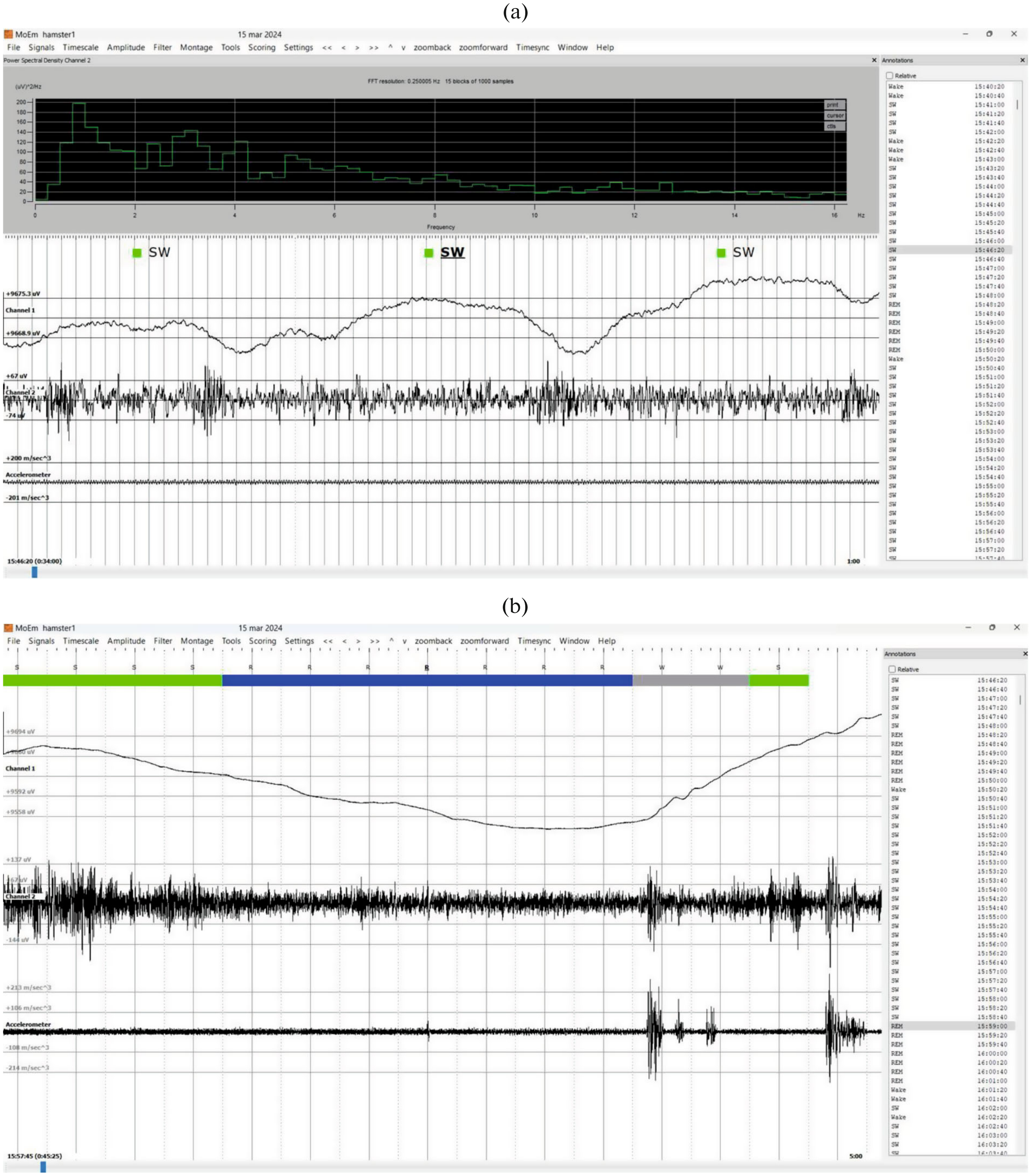
Quite    18:40:48
Quite    18:41:08
Quite    18:41:28
Quite    18:41:48
Quite    18:42:08
Quite    18:42:28
Quite    18:42:48
Quite    18:43:08
```

Fig. 3. Radical changes in EEG during hibernation at a chamber temperature of 4°C are presented. Twenty sec epochs of native recording are shown. On a white background, EEG (Channel 2) is at the top, motor activity (Accelerometer) is at the bottom. On a black background are spectral characteristics of the EEG. The column on the right is the result of the EEG scoring. (a) 1 hr 15 min after the start of the bout. Body temperature is 30.6°C. (b) 12 hr 30 min after the start of the bout. The lowest point of the bout, body temperature is 11.2°C.

isoelectric line; only tiny artifacts from weak twitching of the heart are visible (Fig. 3b). This state persisted for another 7 h, until the beginning of the arousal from hibernation. It took about 14 hrs to reach the temperature "bottom" (11°C). Radical changes were observed not only in the EEG: small fluctuations in brain temperature characteristic of NREM (Fig. 4a) and REM (Fig. 4b) sleep disappeared during the transition to hibernation bout, and brain temperature passively followed body temperature.



(a)

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Annotations
☐ Relative
Wake      15:40:20
Wake      15:40:40
SW        15:41:00
SW        15:41:20
SW        15:41:40
SW        15:42:00
Wake      15:42:20
Wake      15:42:40
Wake      15:43:00
SW        15:43:20
SW        15:43:40
SW        15:44:00
SW        15:44:20
SW        15:44:40
SW        15:45:00
SW        15:45:20
SW        15:45:40
SW        15:46:00
SW        15:46:20
SW        15:46:40
SW        15:47:00
SW        15:47:20
SW        15:47:40
SW        15:48:00
REM       15:48:20
REM       15:48:40
REM       15:49:00
REM       15:49:20
REM       15:49:40
REM       15:50:00
Wake      15:50:20
SW        15:50:40
SW        15:51:00
SW        15:51:20
SW        15:51:40
SW        15:52:00
SW        15:52:20
SW        15:52:40
SW        15:53:00
SW        15:53:20
SW        15:53:40
SW        15:54:00
SW        15:54:20
SW        15:54:40
SW        15:55:00
SW        15:55:20
SW        15:55:40
SW        15:56:00
SW        15:56:20
SW        15:56:40
SW        15:57:00
SW        15:57:20
SW        15:57:40
```

(b)

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Annotations
☐ Relative
SW        15:46:20
SW        15:46:40
SW        15:47:00
SW        15:47:20
SW        15:47:40
SW        15:48:00
REM       15:48:20
REM       15:48:40
REM       15:49:00
REM       15:49:20
REM       15:49:40
REM       15:50:00
Wake      15:50:20
SW        15:50:40
SW        15:51:00
SW        15:51:20
SW        15:51:40
SW        15:52:00
SW        15:52:20
SW        15:52:40
SW        15:53:00
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SW        15:55:20
SW        15:55:40
SW        15:56:00
SW        15:56:20
SW        15:56:40
SW        15:57:00
SW        15:57:20
SW        15:57:40
SW        15:58:00
SW        15:58:20
SW        15:58:40
REM       15:59:00
REM       15:59:20
REM       15:59:40
REM       16:00:00
REM       16:00:20
REM       16:00:40
REM       16:01:00
Wake      16:01:20
Wake      16:01:40
SW        16:02:00
Wake      16:02:20
SW        16:02:40
SW        16:03:00
SW        16:03:20
SW        16:03:40
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Fig. 4. Time-course of EEG, brain temperature and motor activity at the chamber temperature of 22°C and the brain temperature of 36.2°C is presented. Native recording. (a) 1-minute episode of NREM sleep (SW). On a white background, from top to bottom: brain temperature (Channel 1, a downward deviation means an increase in temperature, and vice versa), EEG (Channel 2), motor activity (Accelerometer). Temperature calibration is 0.01°C. The upper trace on a black background is the spectral characteristic of the EEG. The column on the right is the result of scoring the EEG in 20-sec epochs. (b) 5-minute episode of NREM sleep (S), turning into REM sleep (R) and ending with a short awakening (W). The upper trace is brain temperature (Channel 1, a downward deviation means an increase in temperature and vice versa). Temperature calibration is 0.25°C. The middle trace is EEG (Channel 2), the lower one is motor activity (Accelerometer). The column on the right is the result of scoring EEG in 20-second epochs.

A typical hibernation bout is shown in Figs. 5a, 5b. The entry into torpor occurred against the background of a normal sleep period, so it was impossible to predict in advance how a given sleep cycle would end with: arousal, transition to a new cycle, or spontaneous transition to torpor/hibernation. In the latter

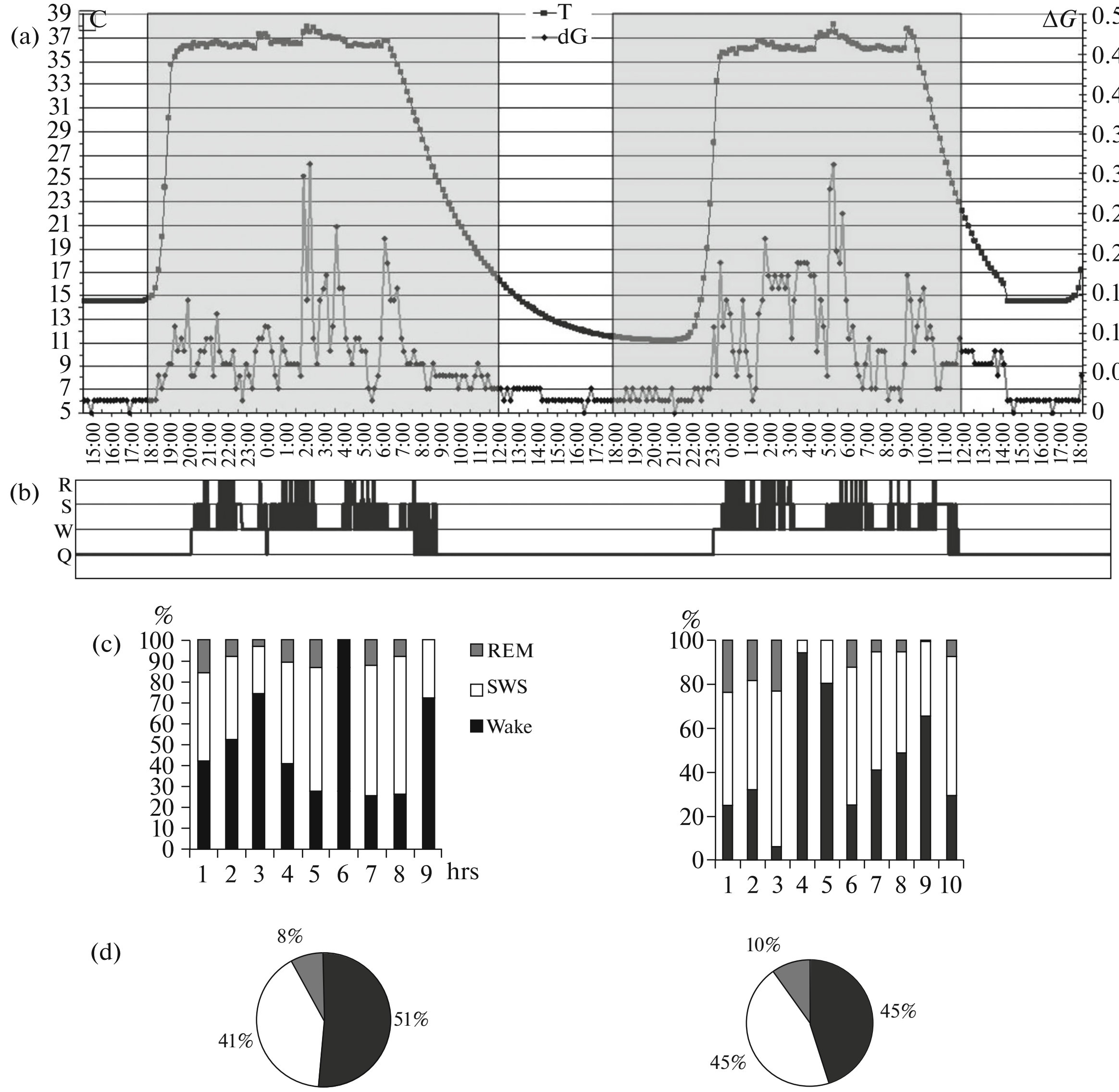

Fig. 5. Representative hibernation bout is demonstrated. (a) body temperature (upper trace, °C, left ordinate) and motor activity (lower curve, δG, right ordinate). Abscissa—time of day. (b) Compressed result of EEG scoring: Q—immobile state, different from sleep and wakefulness; W—wakefulness; S—NREM sleep; R—REM sleep. (c) Hourly representation of Wake, NREM sleep (SWS) and REM sleep during two inter-bout periods. (d) Percentage of the three states for the entire inter-bout period. Shaded part is a dark period in the chamber.

case, the periods of REM sleep disappeared, the brain and body temperature began to drop rapidly, and the EEG pattern changed radically, as described above. Analysis of the interbout intervals shows, however, that long periods of particularly deep NREM sleep with unusually powerful delta waves (such periods are considered an indispensable sign of hibernation in the species studied so far) preceding the transition to bout are absent. There were also no pronounced periods of NREM sleep rebound, usually followed bouts in other species [8, 13]. As can be seen from Figs. 5c, 5d, 9-10-h inter-bout periods either showed no differences from the statistical norm (1st period), or a very slight predominance of NREM and REM sleep within the limits of intra-day variations. It is also evident that in the first 2 h since the hypothermia bout, when the sleep rebound should be most clearly observed, no increase in the percentage of NREM sleep occurred.

The arousal from hibernation occurred through active warming up for 2.5–3 h. In this case, the restoration of the EEG occurred in the order opposite to that observed during entering hypothermia, but much faster, as happens in other mammals [14].

Thus, our study has shown that the so-called “special connection” of NREM sleep with torpor and hibernation, repeatedly described in the literature [8, 9], is apparently not an obligatory feature of this process. In some hibernators, this connection is expressed in the form of unusually long periods of NREM sleep both at the onset of bout and at the arousal from it, with a predominance of strongly expressed delta waves of high amplitude and low frequency. This served as the basis for global conclusions about structural and functional rearrangements in the brain of hibernating rodents at the entry into each bout and at the arousal from it, as well as about sleep deprivation during bout and rebound following exit [15]. However, the present study of the Mongolian hamster does not confirm these observations. It has been shown for the first time that these facultative hibernators can easily enter not only a state of shallow torpor, but also a deep hibernation with a decrease in body temperature to 10°C (and even to 4°C [10]). They do not require special periods of sleep to enter and exit the torpor, and they do not experience an additional need for NREM sleep after hypothermia periods.

An unusual characteristic of the EEG of Mongolian hamsters during the transition to torpor, not described in other heterothermic rodents, is the rapid disappearance of slow waves and the dominance of the 13–14 Hz rhythm already when the temperature of the body "core" decreases to 30°C. The EEG completely disappears at a body temperature of 20°C and only an isoelectric line remains visible on the recording. In parallel with the disappearance of the EEG signs of NREM and REM sleep, small fluctuations in brain temperature characteristic of these states also disappear. Perhaps all these features are associated with the rapid entry and short duration of torpor bouts in this species.

The entry into the states of torpor and hibernation is associated with the ability of the animal's organism to switch off and on the hypothalamic thermoregulatory "center" [16–18]. This ability is quite widespread among small mammals and is observed in various ecological conditions. Thus, a non-hibernating mammal, a laboratory mouse (*Mus musculus*), can spontaneously enter torpor at room temperature in the absence of food [19]. We have recently discovered that naked mole rats (*Heterocephalus glaber*) switch off their thermoregulation in a state of behavioral activity and switch it on during periods of rest and sleep, demonstrating the phenomenon of heterothermia at an ambient temperature of 28°C [11]. Thus, these rodents apparently save themselves from overheating in the stuffy underground tunnels in North Africa, where they inhabit. The neural and neurochemical mechanisms of switching on and off thermoregulation have recently been studied in detail in laboratory mice [17]. However, the extent to which these mechanisms are universal for all mammals, hibernating and nonhibernating, remains unknown. Expanding the range of species studied will allow us to answer the questions posed and identify previously unknown mechanisms characteristic of mammals with different strategies for coping with adverse conditions. The study of these neuronal systems is of considerable interest from both scientific and applied points of view, including for application to humans [20].

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

All experimental procedures performed in this study complied with the ethical standards approved by the legal acts of the Russian Federation and the principles of the Basel Declaration, and were approved by the Bioethics Commission of the Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences (application no. 61 dated March 2, 2024).

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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