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COMPARATIVE AND ONTOGENIC  
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## States of Rest and Activity in the Commerson's Dolphin *Cephalorhynchus commersonii*

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**Abstract**—The unihemispheric slow-wave sleep, the ability to sleep during swimming with one open eye and the absence of paradoxical sleep in its form observed in all terrestrial mammals are unique features of sleep in cetaceans. Visual observation supplement electrophysiological studies and allow obtaining novel data about sleep of cetaceans. In the present study we examined behavior of 3 adult Commerson's dolphins *Cephalorhynchus commersonii* kept in the oceanarium Sea World (San Diego, CA, USA). The behavior of the dolphins can be subdivided into 5 swimming types: (1) active swimming marked by variable and irregular trajectory of movement (for 3 dolphins, on average,  $35.1 \pm 2.7\%$  of the 24-h period) was the active wakefulness; (2) circular swimming was divided into the slow and fast swimming and occupied, on average,  $44.4 \pm 3.8$  and  $9.7 \pm 0.8\%$  of the 24-h period, respectively; during the circular swimming, dolphins performed from 1 to 6 circular swimming during one respiration pause; (3) quiet chaotic swimming ( $3.9 \pm 1.2\%$ ) that occurred at the bottom and was not accompanied by signs of activity; (4) hanging, and (5) slow swimming at the surface ( $4.1 \pm 0.5$  and  $2.8 \pm 0.4\%$ ) respectively; the latter two swimming types were accompanied by frequent respiration (hyperventilation). We suggest that the sleep state in Commerson's dolphins occurs predominantly during the circular and quiet swimming. From time to time the dolphins decreased the speed, up to complete stop. Such episodes appeared to be the deepest sleep episodes. In all dolphins, muscle jerks as well erection in male are observed. Most jerks and erections occurred during the circular and quiet chaotic swimming. Thus, Commerson's dolphins, like other studied small cetaceans, are swimming for 24 h per day and they sleep during the swimming. Some muscle jerks that were observed in the dolphins in this study might have been brief episodes of paradoxical sleep.

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**Key words:** unihemispheric sleep, paradoxical sleep, muscle jerks, rest, Commerson's dolphin, cetaceans.

### INTRODUCTION

Immobility (a behavioral rest) and circadian regulation are two important characteristics of sleep of the terrestrial mammals [1]. Unlike terrestrial animals, many cetaceans are in the state of con-

stant movement. The electrophysiological studies have demonstrated that dolphins can sleep during swimming and have lead to discovery of three no less important peculiarities of the cetacean sleep. First, the main form of the cetacean sleep is the so-called slow-wave "unihemispheric sleep" [2–

8]. Second, the paradoxical sleep in the cetaceans is absent in the form recorded in all terrestrial animals and birds [4]. Third, the cetaceans can sleep with only one eye closed. The other eye can be open or semi-open at this time [8]. It was suggested that the main adaptive functions of the unihemispheric sleep consist in combination of sleep and movement as well as of sleep and sensory control of the environment state [4, 8].

Further studies have found that the constant swimming is characteristic first of all of small cetaceans, for example, the common porpoise *Phocoena phocoena* [3] as well as of mothers with newborn calves [9, 10]. Obviously, in all these cases the animals should sleep during swimming. On the other hand, the state of rest in the captivity often occurs in cetaceans of middle and great size, for example, in the beluga, sword fish, grey whale, during the stay near the surface and in the deep water. Besides, representatives of these species have a rest by laying on the pool bottom [11–16].

The paradoxical sleep is absent in dolphins in its form recorded in the overwhelming majority of the studied terrestrial mammals. In the terrestrial mammals the signs of this sleep form are jerks of extremities, head, and eyes in the background of decreased tone of skeletal muscle and desynchronized electroencephalogram [1]. The head and trunk jerks, the eye fast movements, and erection were recorded in several cetacean species: the bottlenose dolphin [17], the white whale [13], the killer whale [14], the Amazon river dolphin [15], and in the gray whale [12]. It was suggested that some of these phasic components might be a behavioral manifestation of a modified paradoxical sleep in cetaceans [4, 13].

Visual observations supplemented electrophysiological studies and allow obtaining new data about the cetacean state of rest and sleep. The main goal of the present work was to characterize behavioral signs of rest and sleep in Commerson's dolphins *Cephalorhynchus commersonii*. Dolphins of this species are among the smallest. They are present in cold waters along the southern coasts of Argentina and Chile, in the Magellan Strait, at Falkland Islands and the Kerbela Island. Their sizes do not exceed 174 cm, and their weight—86 kg [19]. Very little is known about the behavior of Commerson's dolphins.

## MATERIALS AND METHODS

For three consecutive days, we performed continuing 24-h visual observations and videoshooting of behavior of 3 adult Commerson's dolphins (two females—Betsy and Oreo and one male—Juan) in the oceanarium “Sea World” in San Diego, CA (USA). The animals were kept in a wide closed reservoir,  $1.3 \times 1.3 \times 4$  m in size, and by the moment of experiment they lived in the oceanarium for more than 14 years. The two lateral walls of the reservoir were of glass. The dolphins were fed three times a day: at 7:30, 12:00 and 16:00. The visitors of the oceanarium went to the reservoir only from one side from 10:00 to 18:00. The natural light was in the reservoir at day period (from 7:00 to 20:00). A minimal artificial light was in the reservoir at night period, which was necessary for observations and videorecording. The dolphin behavior was videorecorded by using four telecameras (Panasonic and Samsung, 300–400 lines, sensitivity 0.03 Lx) located near the reservoir glass walls. The telecameras were connected through a multiplexor (Panasonic WJ-PS20) to videotape (Panasonic AG-673OE).

In the dolphin behavior, 5 main swimming types were identified. Criteria for their identification and their peculiarities are described in Results. The swimming speed was calculated using the videorecording, from measurements period of swimming of the same distance along the glass wall (about 8 m). All episodes whose duration was 5 s and more were considered at the behavior analysis. Simultaneously with the swimming types, we recorded respiratory acts, body jerks, and stops as well as erections. The data were processed statistically by using the pair test, correlative and dispersion analyses.

## RESULTS

*Characteristics of dolphin behavior.* The dolphin behavior was classified according to 5 categories or swimming types.

The active chaotic swimming (AS) was characterized by variable speed and trajectory as well as by the following evident signs of activity: contact with other dolphins, vocalization, expressed reaction to external stimuli (the staff, the light switch-on, etc.). A variant of this type of this swimming

**Table 1.** Duration of the main swimming types (% of the 24-h period) in Commerson's dolphins (Oreo, Betsy, and Juan)

Type of swimming	Oreo			Betsy			Juan			Oreo	Betsy	Juan
	1st day	2nd day	3rd day	1st day	2nd day	3rd day	1st day	2nd day	3rd day	the mean		
AS	28.7	34.3	28.3	31.3	39.1	34.1	38.4	43.0	38.4	30.5 ± 1.9	34.8 ± 2.3	39.9 ± 1.5
CS fast	50.5	53.1	51.3	47.5	38.4	43.0	41.5	37.0	37.8	51.6 ± 0.8	43.0 ± 2.6	38.7 ± 1.4
CS slow	15.6	6.3	11.6	12.7	8.9	7.0	10.5	6.2	8.6	11.1 ± 2.7	9.5 ± 1.7	8.4 ± 1.3
QS	0.7	2.4	1.5	0.9	6.2	7.3	1.4	6.9	7.4	1.6 ± 0.5	4.8 ± 2.0	5.2 ± 1.9
SS	2.5	2.3	4.4	3.4	3.9	5.5	4.5	4.8	5.4	3.1 ± 0.7	4.3 ± 0.6	4.9 ± 0.3
Hanging	2.0	1.5	2.9	4.1	3.6	3.0	3.8	2.2	2.3	2.1 ± 0.4	3.6 ± 0.3	2.8 ± 0.5

Note: The data are presented for each dolphin for 3 consecutive days and as the mean ± standard error. AS—Active chaotic swimming, CS—circular swimming, QS—quiet chaotic swimming, SS—slow swimming at the water surface (the same for Table 3).

was considered short episodes of the accelerated (“explosive”) swimming with duration up to 90 s as well as the animal behavior during feeding.

The necessary identification of the circular swimming (CS) was accepted, when the dolphin performed at least one complete circle. All dolphins were swimming predominantly clockwise (on average, from 98.4 to 98.9% from the time of CS). CS was divided to 2 subtypes by the swimming speed—fast and slow. The mean speed during the slow swimming was 1.5 (Betsy)—2.2 (Juan) times lower than that during the fast swimming. In 20 randomly chosen cases of swimming along the viewing window, the swimming speed during two CS subtypes differed statistically significant in all 3 dolphins (the pair *t*-test,  $p < 0.001$  in all animals). On average in 3 dolphins, the swimming speed during the fast and slow CS amounted to  $1.3 \pm 0.1$  and  $0.8 \pm 0.2$  m/s, respectively, and also was differenced statistically significant (the pair *t*-test,  $p < 0.02$ ). At the slow swimming the dolphins often stopped the work of tail and chest fins for several seconds by continuing swimming by inertia. At the end of the CS episodes, before ascending, the dolphins increased speed and floated to the surface for inspiration. During one respiratory pause the dolphins were swimming from 1 to 6 circles.

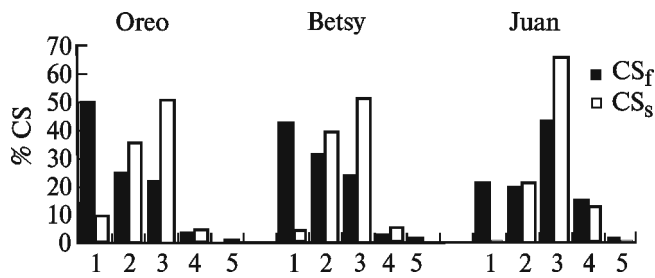
The quiet chaotic swimming (QS) was a slow swimming in the reservoir along an uncertain trajectory, as a rule near the reservoir bottom, without signs of activity.

The slow swimming at the water surface (SS) always occurred at the depth not exceeding 2 m, without any behavioral signs of activity. This behavior was always accompanied by series of inspirations (from 2 to 6) with short intervals.

Hanging also was always accompanied by hyper-ventilation, the dolphins stopping at the surface or drifted slowly.

*Duration of various types of swimming.* Active chaotic and circular types of swimming dominated in all 3 dolphins (Table 1). In various animals, these two swimming types occupied in total from 84 to 95% time of day. The mean AS episode in 3 animals lasted for  $89 \pm 2$  s. The longer AS periods were noted during the animal feeding and could be 2-h long. The QS in dolphins accounted, on average, for 4% of the time of day. The mean duration of these episodes was  $72 \pm 6$  s, although occasional episodes lasted up to 17 min. The sum of the episodes of hanging and SS was from 4 to 9% (on average,  $7 \pm 1\%$ ) of time of day. More than 80% of SS episodes and 91–97% of hanging episodes (in different animals) were shorter than 20 s (the mean durations were  $15 \pm 1$  and  $13 \pm 1$  s, respectively).

Thus, Commerson's dolphins were swimming the greatest part of day in circles (from 43 to 66% of time of day). The slow CS in all animals accounted, on average, for 10% of time of day (or 18% of the whole CS). The episodes of CS two subtypes were differenced not only to the swimming speed, but also to circle number, which the dolphins swam



**Fig. 1.** The total duration of episodes of the fast and slow circular swimming in Commerson’s dolphins. *Abscissa*: the number of circles performed by the dolphins per one respiration pause; *ordinate*: duration of the circular swimming for 2 days (%). CS<sub>f</sub>—the fast circular swimming, CS<sub>s</sub>—the slow circular swimming.

**Table 2.** The mean duration (s) of episodes of the fast and slow circular swimming in Commerson’s dolphin depending on the number of circles per one respiration pause

The number of circles	Circular swimming		<i>p</i>
	fast	slow	
1	19.3 ± 0.3	25.6 ± 0.6	0.005
2	38.9 ± 1.2	48.5 ± 1.4	0.002
3	56.4 ± 0.9	64.3 ± 1.1	0.001
4	70.4 ± 0.9	77.5 ± 2.5	0.170

Note: The data are presented as the mean ± standard error for 3 dolphins, *p*—statistical significance of differences between the mean values (the paired *t*-test).

for one respiratory diapause (RD). In both females, episodes with one circle during one RD accounted for 42 and 50% of the fast CS, whereas the slow CS was represented mostly by episodes with 2–4 circles per RD (Fig. 1). In Juan, the part of slow CS episodes, during which the male swam 3 circles during one RD, was by 20% higher than the part of fast CS episodes with the same number of circles. The mean duration of the slow CS episode was higher than that of fast CS (Table 2) with the same number of circles per one RD. A decrease of differences in the mean duration of the fast and slow CS episodes at passing 4 circles for one respiratory pause was due to that the animals (in particular, Oreo) decreased gradually the diameter of each next circle by beginning to swim by spiral.

Thus, the CS speed in the Commerson’s dolphins was not constant. The slow stereotypic CS was characterized by longer swimming near the reservoir bottom and longer (as compared with the fast CS) respiration delays.

*Representation of different forms of behavior during the day.* Behavior of all Commerson’s dolphins was synchronized. Correlation of each-hour amount of AS, fast and slow CS as well as QS was statistically significant at the pair comparison of all animals (Oreo—Betsy, Oreo—Juan, Betsy—Juan) for the entire period of observations (the correlation coefficients varied from 0.57 to 0.85; *p* << 0.001).

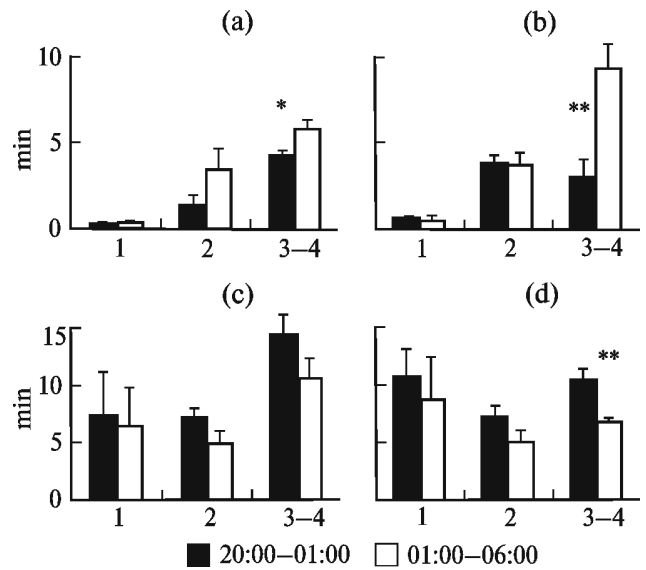
The highest AS amount corresponded to the day period between 06:00 and 14:00. At this period the animals were fed twice. The each-hour number of the remaining swimming types at this time, on the contrary, decreased. The each-hour number of fast CS depended little on the time of day, except for periods of animal feeding. The slow CS was practically absent at the morning and day hours (06:00–17:00; on average, for 3 animals the total was 2 ± 1% of the entire duration of the slow CS per day). During the night second part (01:00–06:00), the total duration of the slow CS episodes with 3–4 circles per RD was statistically significantly higher (the pair *t*-test, *p* < 0.05) than at the evening time and at the beginning of night (20:00–01:00; Fig. 2). The fast CS amount decreased regardless of the circle number for one RD, although the differences between two compared periods did not reach the level of statistical significance. Thus, the swimming types (behavior forms) identified in Commerson’s dolphins had differently representation during the day, and the highest amount of the slow CS corresponded to the night second part.

*Respiration peculiarities.* We analyzed respiration parameters in Commerson’s dolphins at different swimming types during one day (the third by the order) of observation. The durations of respiratory pauses depended on the swimming type (one-factor ANOVA:  $F_{3,8} = 37.93, p < 0.001$ ). The mean respiratory pauses differed statistically significantly for different swimming types (post-hoc-test for minimal differences, *p* < 0.05) by the pair comparison of all types, except for the pair AS—QS. The majority of RD were shorter than 30 s during AS, QS, and CS (on average, 90, 80, and 75% of all

respiratory pauses, respectively). The respiratory pauses at SS were even shorter: more than 80% were shorter than 10 s and all RD without exception were shorter than 20 s. The maximal detected respiratory pause was similar in two females during AS and was 97 s. In the male the maximal RD was longer than 10 s; it was recorded during the slow CS episode with 4 circles at the respiratory pause. Since from duration of the CS episodes it can also be judged about duration of the respiratory pause, the maximal RD actually was even longer. Thus, the maximal duration of the slow CS episode in the male amounted to 126 s. In Table 3, RD during the hanging are not represented. The disposition of videocameras below the water level did not allow record reliably all respiratory acts during the dolphin hanging at the water surface. Based on visual observations from the pool board, we found that at hanging the dolphins performed from 1 to 5 respiratory acts in succession with intervals from 2 to 10 s.

*Stops, overturns, jerks, erections.* The dolphins stopped the fin movements from time to time during CS. They continued to swim by inertia and sometimes fell on side or made overturn through head (Fig. 3). The fin function was resumed after some seconds. In other cases the dolphins stopped completely for some seconds, then began to emerge. No rowing movements were observed. We recorded only 29, 47, and 51 such stops and overturns in Oreo, Betsy, and Juan, respectively. The stops and overturns occurred mostly during CS (on average, in  $74 \pm 6\%$  of all cases in three dolphins) and more seldom during QS ( $24 \pm 6\%$ ). On average,  $83 \pm 2\%$  of all stops were observed at evening and night periods (between 18:00 and 07:00), about 80% of them being recorded on the background of slow CS.

The head and body jerks were observed in all three Commerson's dolphins. The jerks in male were the most frequent, intensive, and long. As a whole, for 3 days, 35 jerks were recorded in Juan, 31 in Oreo, and 13 in Betsy. The jerks were observed both at night time during CS and QS (89% of all jerks in Juan, 52% in Oreo, and 31% in Betsy), when the dolphins could sleep, and at day hours, when they most likely were wakeful. On average, 23% of all jerks occurred with intervals less than 20 s, i.e., they represented series.



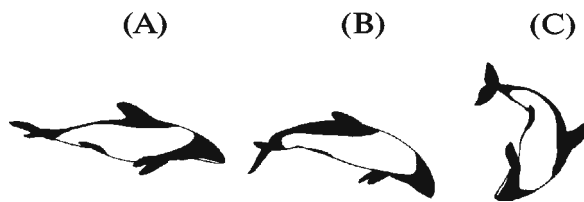
**Fig. 2.** The total duration of episodes of the fast and slow circular swimming with different numbers of circles per one respiration pause during two night periods (20:00–01:00 and 01:00–06:00). *Abscissa*: the number of circles performed by the dolphins per one respiration pause; *ordinate*: the total duration of the swimming (in min for 1 h). Circular swimming: (a) slow, the 2nd day; (b) slow, the 3rd day; (c) fast, the 2nd day; (d) fast, the 3rd day. Statistical significance of differences: \*— $p < 0.05$ , \*\*— $p < 0.01$  (the paired  $t$ -test).

**Table 3.** The mean duration of respiration pauses (s) in different swimming types in Commerson's dolphin at the third day of observations

Type of swimming	Oreo	Betsy	Juan
AS	18.2 ± 0.4 (97; 709)	17.2 ± 0.3 (97; 1017)	18.8 ± 0.5 (81; 694)
QS	16.6 ± 3.2 (71; 25)	24.1 ± 1.5 (96; 179)	19.0 ± 2.3 (96; 75)
CS	25.0 ± 0.4 (95; 1194)	24.9 ± 0.4 (77; 769)	25.3 ± 0.9 (107; 464)
SS	8.1 ± 0.2 (16; 143)	9.0 ± 0.3 (18; 169)	6.9 ± 0.2 (29; 249)

Note: The data are presented as the mean ± standard error. In parentheses—the maximal value of the respiration pause and the sample volume.

We observed in the male 5 erections for 3 days. Once the erection occurred during QS, three



**Fig. 3.** Postures of Commerson's dolphins during the slow circular swimming (A), hanging (B), and overturns (C).

times—during slow, and one time—during fast CS. Twice the erections coincided in time with jerks, once the erection was observed at the 4-s intervals between jerks, in other case—68 s after the jerk.

### DISCUSSION

Our observations have shown the Commerson's dolphins to move uninterruptedly for 98% of time of day. Hanging at the water surface was the only swimming type characterized by the absence of the rowing activity and was always accompanied to polypnea. Such behavior accounted for not more than 4% of time of day. As demonstrated in other studies, the virtually uninterrupted motor activity is also characteristic of other species of small cetaceans, for example, common porpoises [3], Dall's porpoises [15], and Pacific white-sided dolphins [20]. The size of these animal species seldom exceeds 2 m, and weight usually is less than 150 kg [19]. On the contrary, the cetaceans of middle (for example, the bottlenose dolphin—weight 200–350 kg, body length to 2.8 m; white whale—weight up to 1500 kg, length up to 5.5 m) and great sizes (for example, killer whale—weight up to 6000 kg, length up to 9 m; gray whale—weight 16 000–45 000 kg, length up to 15 m [19]) can have rest either by hanging at the surface in the water depth [11, 17] or by laying on the pool bottom [12–14, 16]. By comparing these data, we can conclude that only in the smallest cetaceans, all sleep forms occur on the background of movement, whereas in cetaceans of middle and great sizes the sleep can occur both on the background of movement and on the background of immobility.

It cannot be ruled out that the uninterrupted swimming of small cetaceans as well as of cetaceans calves [9–10] is connected with the greater heat loss in all small species due to an increase of the

relative body surface area (and accordingly the heat loss) with decrease of the animal size. In the case of Commerson's dolphin, this factor becomes even more essential. The animals of this species inhabit cold waters (the temperature of 10–12°C) near the South America coasts [19]. It has been shown that frequency of the rowing movements during the slow swimming or in rest at the surface of water is higher in dolphins with the greater relative body surface [21]. Therefore, the uninterrupted swimming of the small cetaceans has to be accompanied by the more intensive muscle thermogenesis than that during hanging at the surface of water by compensating thereby the heat loss in the cold water. Both the uninterrupted swimming [6, 18] and the immobile hanging [22, 23] were observed under conditions of capture in the river dolphins that inhabit in nature the relatively warm water. The uninterrupted swimming in river dolphins can be due to that in rivers the water stream is always present. The constant motor activity might possibly prevent the unwanted translocation of animal with the water flow. Another explanation of the small cetacean uninterrupted swimming can be the necessity of stabilization of the animal disposition in water, as even the minimal roughness prevents their quiet hanging at the surface or in the depth of water.

An important result of this work is that the intensity of the Commerson's dolphin motor activity was not constant. The circular swimming was clearly divided by speed into 2 subtypes. The slow CS had the lower speed, the longer swimming in the water depth and at the bottom, and, as a consequence, the longer respiratory pauses. The slow CS was also recorded at the evening–night period when the animals were not disturbed. Another “low active” swimming type in Commerson's dolphins was the quiet chaotic swimming that in many aspects was similar with the slow CS. The electrophysiological studies have shown that the sleep in the bottlenose dolphins, Amazon river dolphins, and common porpoises can occur on the background of the uninterrupted swimming that often is slower as compared with the swimming during wakefulness [2–4, 6]. Thus, a significant part of sleep in Commerson's dolphins occurred most likely on the background of the slow swimming, both circular and chaotic. In total, these two be-



havior forms accounted, on average, for 14% of time of day. This is about 2.5 times less than the total sleep duration in bottlenose dolphins (on average, 33% of time of day [4]) and 3–3.5 times less than that in other studied cetacean species (46% of time of day in one common porpoise [3], 57% in the Amazon river dolphin [6], and 43% in the white whale [8]). Therefore, it cannot be ruled out that the sleep in Commerson's dolphins could also occur during the fast CS. In total, both subtypes of CS and QS account for 55% of time of day. It is not possible to evaluate more correctly the sleep duration in Commerson's dolphins, like in other cetaceans, based on only visual observations. It is also to be noted that practically each ascending after a CS episode with 2–4 circles at the respiratory pause was accompanied by an enhancement of the rowing activity and acceleration; subsequent episodes of SS and hanging seemed to be accompanied by at least brief awakening or a decrease of the sleep depth.

The main sleep form in all studied cetaceans is known to be the unihemispheric slow-wave sleep. At present there are no data that could connect the level of the dolphin motor activity during the sleep with depth or contrast of the unihemispheric sleep. However, such data have been obtained in study of sleep in the sea bears, in which, like in dolphins, the unihemispheric sleep was recorded during their sleep in water. It was detected that the rowing intensity of the anterior flapper in sea bear in water decreased with the sleep becoming deeper (an increase of the EEG slow wave amplitude) and with the level of the EEG interhemispheric asymmetry becoming lower [24]. As mentioned above, the swimming speed in Commerson's dolphins was not constant. The stops, falls to the side, and overturns occurred predominantly during the slow circular and restful chaotic swimings and mostly at the night period. This behavior most likely was a consequence of a decrease of the motor activity and of the short-term loss of coordination. We suggest that such episodes were the episodes of the deepest sleep in Commerson's dolphins and, specifically, of the asymmetric high-amplitude or bilateral-symmetrical low-amplitude slow-wave sleep.

It is known that dolphins can sleep with only one eye closed, whereas the second eye at this time can be open or semi-opened. The hemisphere con-

tralateral to the open eye most often is in the wakefulness or a superficial sleep state, while the hemisphere contralateral to the closed eye is in the state of the deeper sleep [8]. The asymmetric eye state during the quiet swimming or rest on the surface and in the dept of water was also noted in other cetacean species [12, 13, 20, 25] as well as in bottlenose dolphin mothers and their calves [10]. In the present work, we could not observe the eye state in Commerson's dolphins. The black color of head and small sizes of eyes did not allow distinguishing reliably the eye state. However, as shown by our observations, both AS and slow CS were synchronous in all 3 animals. Such behavior is not possible without the visual control of each animal both of its disposition in the pool and disposition of other animals. This allows us to suggest that the Commerson's dolphins, like other cetaceans, maintain visual contact with other individuals of the group not only during wakefulness, but in the sleep.

The muscle jerks as well as erections are phasic components of the paradoxical sleep in terrestrial mammals. The jerks were observed in the rest state in many cetacean species in capture [11–14, 17, 18]. In Commerson's dolphins, the jerks were not numerous as compared with bottlenose dolphins (from 15 to 98 per day [17]) and with one studied white whale (on average, 144 per day [13]). On the other hand, the jerks were also sufficiently rare in the Amazon river dolphins (25 for 3 days [18]) and in the gray whale (45 for 6 days [12]). We have also observed some periodicity of the jerks in Commerson's dolphins, a grouping of the jerks in sequences or series. Unfortunately, the small total number of the recorded jerks does not allow evaluating their periodicity by statistical methods. The erections—one more component of the paradoxical sleep—were recorded in the male during the slow CS and QS. It is not to be ruled out that the overturns also can be a manifestation of the paradoxical sleep. We also observed similar episodes in bottlenose dolphins [17]. Thus, our obtained data do not contradict our hypothesis [13, 17] that some jerks in cetaceans might be manifestations of a modified paradoxical sleep.

Thus, this work has allowed us to find out that Commerson's dolphins are in movement practically 24 h per day. Therefore, sleep in this species, like in other small dolphins, occurs on the back-

ground of the stereotypic, often slow swimming. Such events as stops, overturns, the posture “the tail up,” seem to be the behavioral signs of the deepest slow sleep in this species, while some muscle jerks, especially their series, as well as erections in the male, might possibly represent brief episodes of the modified paradoxical sleep.

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#### REFERENCES

1. Tabler, I., Phylogeny of Sleep Regulation, *Principles and Practice of Sleep Medicine*, Kryger, M.H., Roth, T., and Dement, W.C., Eds., W.B. Philadelphia: Saunders Company, 2005.
2. Mukhametov, L.M. and Supin, A.Ya., EEG-Study of Different Behavioral States of Free-Moving Dolphins, *Zh. Vyssh. Nervn. Deyat.*, 1975, vol. 25, pp. 386–401.
3. Mukhametov, L.M. and Polyakova, I.G., Electrophysiological Study of Sleep in Common Porpoises, *Zh. Vyssh. Nervn. Deyat.*, 1981, vol. 31, pp. 333–339.
4. Mukhametov, L.M., Oleksenko, A.I., and Polyakova, I.G., A Sleep Structure in Black Sea Bottlenose Dolphin, *Chernomorskaya afalina* (Black Sea Bottlenose Dolphin), Sokolova, V.E. and Romanenko, E.V., Eds., Moscow, 1997, pp. 492–512.
5. Mukhametov, L.M., Sleep in Marine Mammals, *Exp. Brain Res.*, 1984, vol. 8, pp. 227–238.
6. Mukhametov, L.M., Unihemispheric Slow-Wave Sleep in the Amazonian Dolphin, *Inia geoffrensis*, *Neurosci. Lett.*, 1987, vol. 79, pp. 128–132.
7. Mukhametov, L.M., Supin, A.Y., and Polyakova, I.G., Interhemispheric Asymmetry of the Electroencephalographic Sleep Patterns in Dolphins, *Brain Res.*, 1977, vol. 134, pp. 581–584.
8. Lyamin, O.I., Mukhametov, L.M., and Siegel, J., Relationship between Sleep and Eye State in Cetaceans and Pinnipeds, *Arch. Ital. Biol.*, 2004, vol. 142, pp. 557–568.
9. Lyamin, O., Pryaslova, J., Lancer, V., and Siegel, J., Animal Behavior: Continuous Activity in Cetaceans after Birth, *Nature*, 2005, vol. 435, no. 7046, p. 1177.
10. Lyamin, O., Pryaslova, J., Kosenko, P., and Siegel, J., Behavioral Aspects of Sleep in Bottlenose Dolphin Mothers and Their Calves, *Physiol. Behav.*, 2007, vol. 92, pp. 725–733.
11. Flanigan, W.F., Nocturnal Behavior of Small Cetaceans, II. The Beluga Whale, *Delphinapterus leucas*, *Sleep Res.*, 1974, vol. 3, p. 85.
12. Lyamin, O.I., Mukhametov, L.M., Siegel, J.M., Manger, P.R., and Shpak, O.V., Resting Behavior in a Rehabilitated Gray Whale Calf, *Aquatic Mammals*, 2001, vol. 27, pp. 256–266.
13. Lyamin, O., Shpak, O.V., Nazarenko, E.A., and Mukhametov, L.M., Muscle Jerks during Behavioral Sleep in a White Whale (*Delphinapterus leucas L.*), *Physiol. Behav.*, 2002, vol. 76, pp. 265–270.
14. Lyamin, O.I., Shpak, O.V., and Siegel, J.M., Ontogenesis of Rest Behavior in Killer Whales, *Sleep*, 2003, Suppl. no. 26, p. 116.
15. McCormick, J.G., Relationship of Sleep, Respiration and Anesthesia in the Porpoise: a Preliminary Report, *Proc. Natl. Acad. Sci.*, 1969, vol. 62, pp. 697–703.
16. Sekigushi, Y. and Kohshima, S., Resting Behaviors of Captive Bottlenose Dolphins (*Tursiops truncatus*), *Physiol. Behav.*, 2003, vol. 79, pp. 643–653.
17. Mukhametov, L.M. and Lyamin, O.I., State of Rest and Activity in Black Sea Bottlenose Dolphin, *Chernomorskaya afalina* (Black Sea Bottlenose Dolphin), Sokolova, V.E. and Romanenko, E.V., Eds., Moscow, 1997, pp. 650–668.
18. Oleksenko, A.I., Chetyrbok, I.S., Polyakova, I.G., and Mukhametov, L.M., State of Rest and Activity in Amazon Dolphin, *Amazonskii delfin* (Amazon Dolphin), Sokolova, V.E., Ed., Moscow, 1996, pp. 257–266.
19. *Encyclopedia of Marine Mammals*, Perrin, W.F., Wursig, B., and Thewissen, J.G.M., Eds., San Diego: Acad., 2002.
20. Goley, P.G., Behavioral Aspects of Sleep in Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*, Gill 1866), *Mar. Mamm. Sci.*, 1999, vol. 15, pp. 1054–1064.
21. Pillay, P. and Manger, P.R., Testing Thermogenesis as the Basis for the Evolution of Cetacean Sleep Phenomenology, *J. Sleep Res.*, 2004, vol. 13, pp. 353–358.
22. Klocek, R., Chico’s Story: A Special Dolphin, *Aquaticus*, 1981, vol. 13, no. 2, pp. 1–9.



23. Renjun, L., Comparative Studies on the Behaviour of *Inia geoffrensis* and *Lipotes vexillifer* in Artificial Environments, *Aquatic Mammals*, 1994, vol. 20, no. 1, pp. 39–45.
24. Lyamin, O.I. and Mukhametov, L.M., Sleep Organization in Nord Sea Bear, *Severnyi morskoi kotik. Sistematika, morfologiya, ekologiya, povedenie* (Nord Sea Bear. Classification, Morphology, Ecology, Behavior), Sokolov, B.E., Aristov, A.A., and Lisitsyna, T.Yu., Eds., Moscow, 1998, pp. 280–302.
25. Lilly, J.C., Animal in Aquatic Environments: Adaptation of Mammals to the Ocean, *Handbook Physiol. Section 4: Adaptation to the Environment*, Dill, D.B., Ed., Washington, D.C: Amer. Physiol. Society, 1964, pp. 741–747.