

Predominance of clockwise swimming during rest in Southern Hemisphere dolphins

Guinevere M. Stafne, Paul R. Manger*

School of Anatomical Sciences, Faculty of Health Sciences, University of the Witwatersrand, 7 York Road, Parktown 2193, Johannesburg, Republic of South Africa

Received 27 February 2004; received in revised form 31 May 2004; accepted 2 August 2004

Abstract

Observations on eight bottlenose dolphins located in the Southern Hemisphere during rest indicated that they spent the majority of the time (85%) engaged in behaviors that can be considered clockwise. This is in contrast with many observations of sleeping/resting dolphins in the Northern Hemisphere that spend the majority of their time involved in counterclockwise activity. This observation leads to the possibility that the reason for preferential swimming biases in dolphins is the result of global forces rather than the result of the anatomy of the individual dolphins. Our observations also indicate that dolphins change overt behavior every 40 s, coincident with the respiration rate. The possibility is suggested that the salience of neural activity controlling respiration in the reticular system may effect/disrupt reticular attentional mechanisms, thus leading to the changes in overt behavior. It is hypothesized that this 40-s period may represent the possible attention span of the sleeping bottlenose dolphin.

© 2004 Elsevier Inc. All rights reserved.

Keywords: Clockwise swimming; Rest; Southern Hemisphere dolphins

1. Introduction

Many previous studies have noted a distinct bias in the direction that captive dolphins and other cetaceans swim. All these studies have been conducted in the Northern Hemisphere, with the vast majority concluding that captive cetaceans spend the majority of their time swimming in a counterclockwise direction. This directionally biased swimming was first reported by Lilly [1], where he noted that both of the observed captive dolphins would swim mostly counterclockwise. A review of earlier studies [2] found that studies conducted in both the United States and Russia had described the counterclockwise directional swimming bias. More recently [3], it was again reported that there was a counterclockwise bias during sleep in Pacific white-sided dolphins in the United States.

A comprehensive analysis of sleep behavior in the bottlenose dolphin was undertaken in Japan [4]. These authors report that of two observed dolphin pairs in captivity in Japan, the first, a mother and calf, spent approximately equal times swimming in each direction (52.9% clockwise, 47.1% counterclockwise), while the second, an adult male and young female, always swam in a counterclockwise direction. This report of the mother and calf spending approximately equal times in swimming in each direction is the only case of this occurrence [4]. Other observations of mother and calf pairs in the Northern Hemisphere have reported a predominance of counterclockwise swimming [2]. Other studies [5–7] have also noted the counterclockwise predominance of swimming directions; however, one study of 2 dolphins [8] showed a predominant clockwise swimming direction, while 3 of 13 dolphins [5] and 1 of 4 dolphins [6] were observed to swim predominantly clockwise in other studies. Despite the few exceptions, the predominance of counterclockwise swimming by cetaceans in the Northern Hemisphere is clear.

* Corresponding author. Tel.: +27 11 717 2497; fax: +27 11 717 2422.
E-mail address: mangerpr@anatomy.wits.ac.za (P.R. Manger).

Some suggestions as to why the cetaceans show a preferential swimming direction have been forwarded. These include the distinct asymmetry of the brain of cetaceans [9], suggesting that this will mean that one half of the brain will be dominant and thus cause counterclockwise swimming. Others have suggested that the unihemispheric nature of cetacean sleep associated with different levels of hemispheric neural activity will cause biases in the direction of swimming; however, physiological studies report that changes in the level of hemispheric activity do not correlate to changes or biases in the direction of swimming [10]. Social factors have also been implicated in directional swimming preference [5]. Despite these suggestions, the causal factors underlying the counterclockwise directional bias of swimming in captive cetaceans in the Northern Hemisphere are not understood.

No studies examining the preferential direction of swimming of captive dolphins in the Southern Hemisphere have been undertaken. The present study reports the results of several nights of observation of eight dolphins held at Seaworld in Durban, South Africa. This is the first study of rest behavior of dolphins in the Southern Hemisphere. The results are discussed in terms of the causal factors underlying directional swimming in captive cetaceans.

2. Materials and methods

Eight adult bottlenose dolphins (*Tursiops truncatus*, *T. aduncus*, and hybrids; four of each gender) that were well adapted to captivity at Seaworld, Durban, South Africa (latitude 29°53' S, longitude 31°00' E), were observed in the present study. The dolphins weighed between 150 and 350 kg and were 2.1 to 3.39 m in length. All were in good condition during the observation period and were performing daily shows. The observations took place during the night in May 2003 and did not disrupt the daily activities of the animals. No invasive procedures were undertaken, thus, no specific ethical clearance was required.

The recording of dolphin rest took place between 20.00 and 24.00 h for four consecutive nights. The sleeping dolphins were recorded in a dimly lit, sheltered pool that measured 12×5×3 m depth. A CCD infrared-sensitive video camera with a fish eye lens was placed 3 m above the pool. This afforded a full view of the pool, but the edges of the image were somewhat distorted. The output of the camera was recorded onto a VHS videotape and monitored visually at the same time. On the first and second nights, the four males were recorded, the females being recorded on the third and fourth nights. The tapes from the first and third nights were not analyzed, as the dolphins were not settled on these nights and did not show typical signs of sleep behavior (such as swim–rest, surface–rest, and hang–rest [4]). However, these behaviors were evident on the second and fourth nights; thus, these nights were used for analysis.

Four different behaviors were classified and quantified. These are swimming counterclockwise, swimming clockwise, hanging counterclockwise, and hanging clockwise. Swimming counterclockwise was defined as the forward motion of the animal in a counterclockwise direction. Due to the weak clockwise current in the pool, the dolphins would often remain in the same place, pointed in a counterclockwise direction, with the tail beating. This type of behavior was also considered to be swimming counterclockwise. Swimming clockwise was defined as forward motion in a clockwise direction, or with the tail beating if the dolphin did not move. Hanging counterclockwise was defined as the times when the dolphin was motionless, i.e., no beating of the tail, with the rostrum facing a counterclockwise direction. Hanging clockwise was defined as the times that the dolphin was motionless with the rostrum facing a clockwise direction.

The time spent in each of these four behaviors was quantified from direct observation of the video record. The minimum interval for scoring of a behavior was 1 s. These times were entered into a Microsoft Excel spreadsheet for each individual dolphin. Total times spent in each behavior, both individually and collectively, were calculated. The relationship between changes in behavior and respiratory rate (noted during behavioral analysis) was also explored.

3. Results

3.1. Time spent in directional behaviors

The time spent in each behavior was calculated as a percentage of total time for each dolphin, as well as for all the dolphins collectively. The results are shown in graphic form in Fig. 1. The most frequently observed of the four behaviors analyzed was clockwise swimming. For all dolphins, collectively, clockwise swimming occupied 49% of the time analyzed. The total time spent swimming clockwise varied among the individual dolphins, ranging from 32% to 58%. Hanging clockwise was the second most frequently observed behavior, occupying 37% of the total time analyzed for all the dolphins. This time varied among the individual dolphins, with a range of 20–68%. Swimming and hanging counterclockwise both occupied 7% of the total time analyzed for all dolphins. The ranges again varied, with both behaviors occupying between 0.1% and 11% of the time analyzed for the individual dolphins.

The total times spent in clockwise or counterclockwise activity was also calculated. Collectively, the dolphins spent 86% of the time analyzed involved in clockwise behaviors (14% in counterclockwise activity). Individually, the time spent in clockwise activity ranged from 78% to 99.9% of the time analyzed. Thus, clockwise activity was clearly the dominant form of behavior in all dolphins.

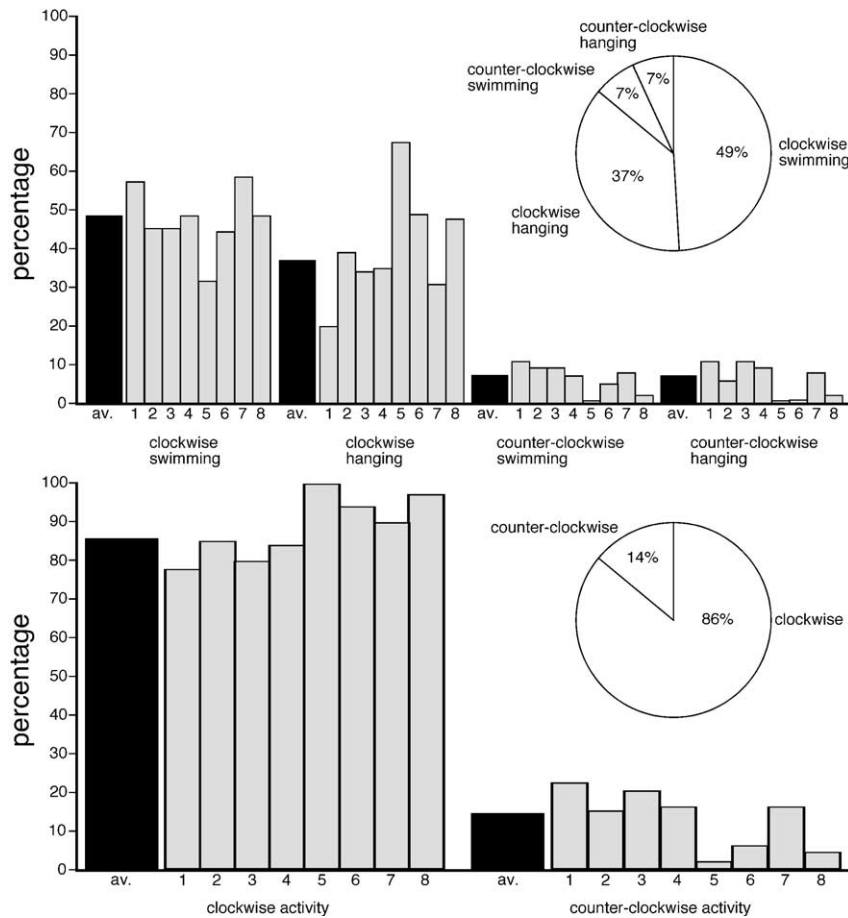


Fig. 1. The upper bar graph depicts the time (expressed as a percentage) that each dolphin (gray bars numbered 1–8) and the dolphins collectively (black bars) spent in each of the four behaviors described in the present study. Note the far longer time spent in the two clockwise activities as compared with the counterclockwise activities. The pie chart to the right of the upper panel depicts the percentages spent in each behavior in a more visual fashion. The lower bar and pie charts represent the same conventions as in the upper and depicts the total time spent in clockwise and counterclockwise activities. Again, note the excessive time spent in clockwise as opposed to counterclockwise activities.

3.2. Behavioral ordering

During the analysis of the videotapes, it became evident that certain behaviors followed others more frequently; thus, we calculated the percentage of time that one behavior led to another for all dolphins (Fig. 2). The behavior observed most often following a bout of clockwise swimming was clockwise hanging (79%). Counterclockwise swimming (17%) and counterclockwise hanging (4%) occurred less frequently following clockwise swimming. The behavior observed most often following a bout of clockwise hanging was clockwise swimming (86%). Again, counterclockwise swimming (8%) and counterclockwise hanging (6%) occurred less frequently following clockwise hanging. The behavior observed most often following counterclockwise swimming was clockwise hanging (41%), while clockwise swimming (38%) and counterclockwise hanging (21%) occurred only slightly less frequently. Following a bout of counterclockwise hanging, the most often observed behavior was clockwise swimming (45%). Counterclockwise swimming (36%) and clockwise hanging (19%) were observed less often following counterclockwise hanging.

The main bias in the observed behaviors was the tendency to enter a form of clockwise behavior after any given behavior, while entering a counterclockwise behavior

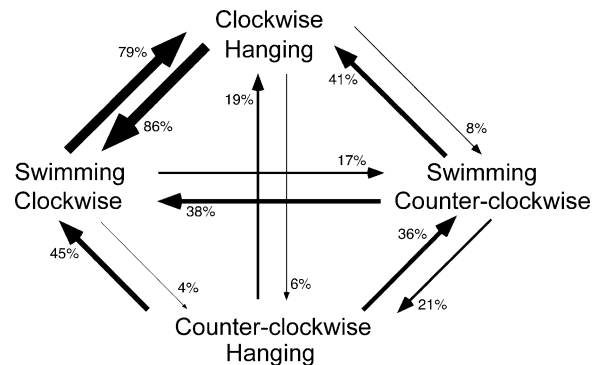


Fig. 2. This figure graphically depicts the relationships between the four quantified behaviors. The percentages written on the scaled arrowed lines give the amount that one behavior was seen to follow the other. The exchange between clockwise swimming and hanging was most predominant. Even when animals were engaged in a counterclockwise behavior, they were more likely to follow this with a clockwise behavior than a counterclockwise one. This diagram reinforces the dominance of clockwise activity in the Southern Hemisphere dolphins.

occurred far less often. Even during bouts of counterclockwise behavior, the probability that a dolphin would exhibit an ensuing clockwise behavior (0.64–0.79) was greater than exhibiting a counterclockwise behavior (0.21–0.36). These observations underpin the dominance of clockwise activity exhibited by the dolphins.

It was also noted that the observed dolphins tended to switch between behaviors simultaneously, as there were four dolphins in the pool together and they exhibited schooling behavior. This has been noted in a previous study [5]. This observation was not quantified; however, this correlated behavior is depicted using cryptograms (Fig. 3). These cryptograms also provide a timeline for the behaviors and reflect the dominance of clockwise activity.

3.3. Duration of behaviors

The time spent in bouts of each of the four behaviors was analyzed for each dolphin and for all dolphins collectively. For all dolphins, collectively, each bout of clockwise swimming lasted an average of 44.7 s (Figs. 4 and 5). The average time spent in a bout of clockwise swimming varied for the individual dolphins, ranging from 32.9 to 52.1 s. Collectively, dolphins spent an average of 41.4 s exhibiting clockwise hanging before changing behavior. The average time spent hanging clockwise varied from 34.6 to 62.9 s

among individual dolphins. The average time spent during a bout of counterclockwise swimming for all dolphins collectively was 29.4 s, with a range of 24.3 to 75.2 s for the individual dolphins. Counterclockwise hanging was observed to last for an average of 34.8 s for all dolphins and ranged from 6 to 89.7 s for the individual dolphins.

The times for all behaviors, and all dolphins, were grouped, and an average time spent in any given behavior was calculated (Figs. 4 and 5). This average time was found to be 41.1 s. For all behaviors for each dolphin, the average time ranged from 33.9 to 57.2 s. Interestingly, the average time spent in any one behavior was slightly higher for the females studied than for the males (Fig. 4). Moreover, these results suggest that, on average, the dolphins change overt behavior approximately every 40 s. This correlates closely to the time determined for the average interbreath interval for all dolphins, which was 39.2 s (Fig. 5). This interbreath interval corresponds closely to the results found previously [4].

4. Discussion

Two results of significance arose from the present series of observations. The first is that the dolphins observed in captivity in the Southern Hemisphere spend the majority of

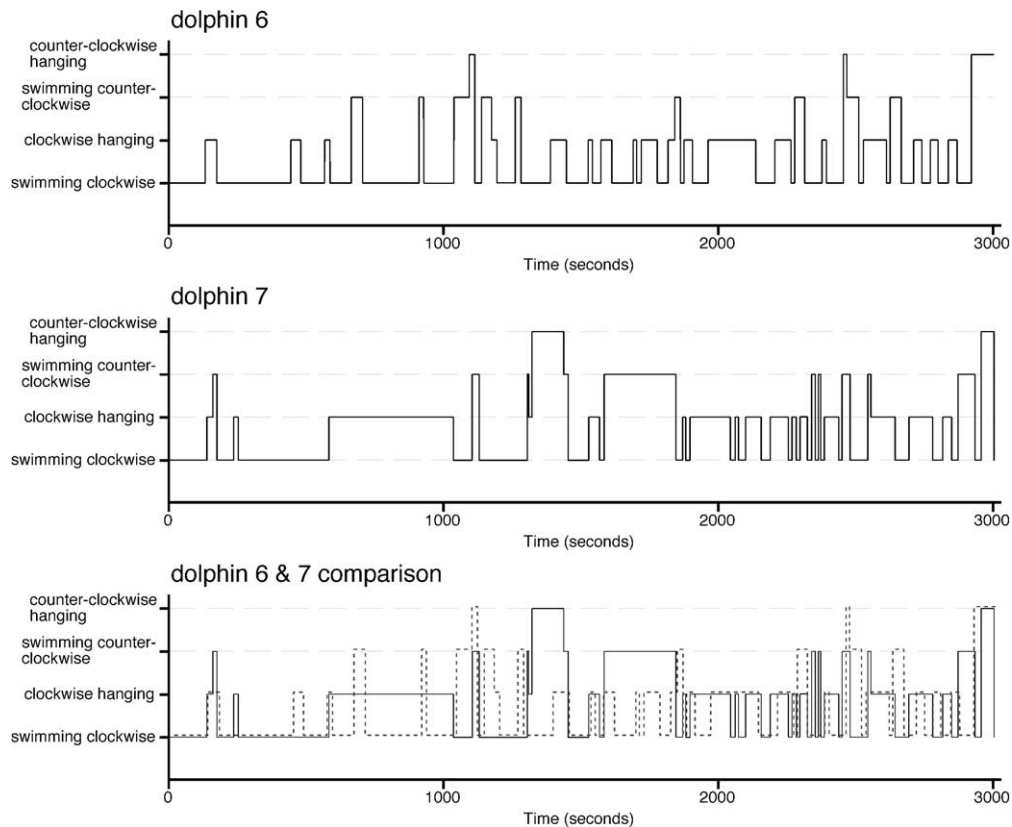


Fig. 3. These figures are cryptograms of the behavior observed (*y* axis) plotted against time (*x* axis). These diagrams provide a pictorial account of the alterations in behavior and which behaviors were seen more often. Again, it is clear that clockwise activities prevailed. The lower cryptogram plots both dolphins 6 and 7 together to demonstrate that the changes in behaviors often occurred simultaneously among the dolphins under observation.

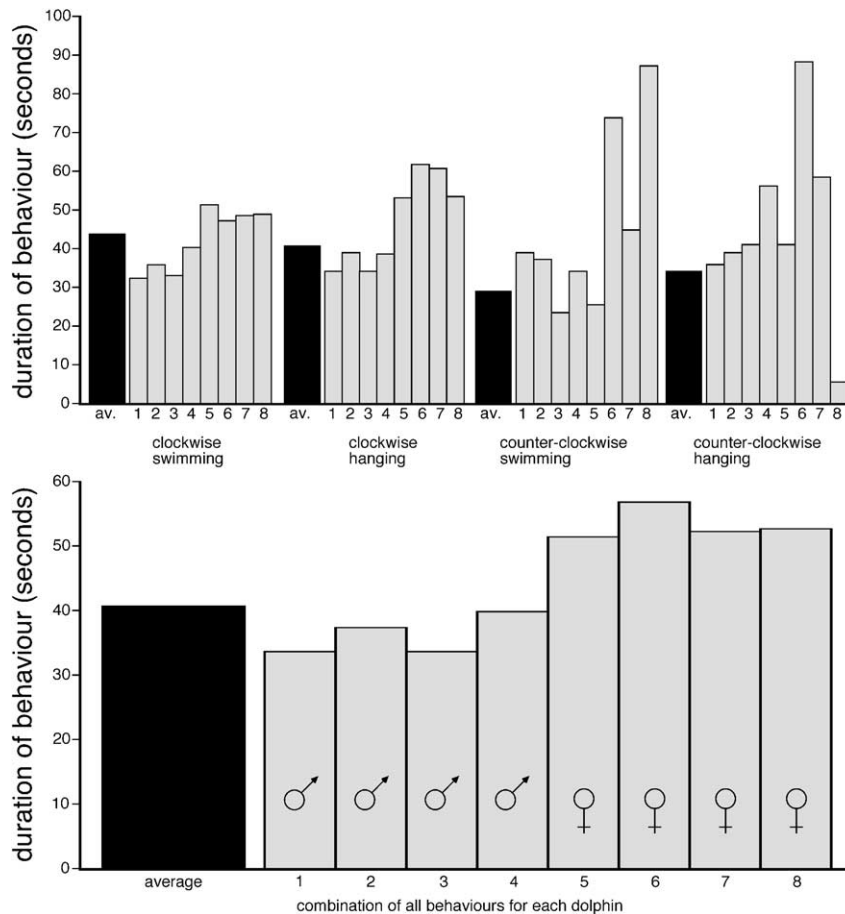


Fig. 4. The upper bar graph follows the same convention as that in Fig. 1. This bar graph depicts the average time spent in a particular behavior for the individual dolphins (gray bars numbered 1–8) and for all dolphins collectively (black bars). The lower bar graph depicts the average time spent in any behavior for all dolphins collectively (black bar) and individually (gray bars). Note that the females (the four gray bars to the right) spent significantly longer, on average, in any given behaviors than the males did.

their time during rest exhibiting behaviors that can be classified as clockwise. The second result of interest is that the dolphins change overt behavior, on average, approximately every 40 s, this correlating closely with the time between breaths.

4.1. The predominance of clockwise activity

The present study is the first to fully quantify the directional swimming behavior of dolphins and the first to examine if there is a bias in the direction of swimming in dolphins in the Southern Hemisphere. Many previous studies, all conducted in the Northern Hemisphere [1–7], have concluded that dolphins swim predominately in the counterclockwise direction. The present study demonstrates that dolphins in the Southern Hemisphere swim predominately in the opposite, clockwise direction. This result is interesting, as it bears upon the explanations forwarded for the reasons that dolphins swim in a particular direction. Suggestions such as cerebral hemispheric dominance have been previously discounted by direct physiological examination [10]. The fact that dolphins swim in opposite

directions in the different global hemispheres shifts the focus of explanation from the anatomy of individual dolphins to possibilities that forces acting on a more global scale induce the bias in swimming direction.

At the global scale, there are two possibilities for explanation of directional bias in the swimming of dolphins. The first is the potential magnetic sensibility; the second is the induction of a preferential swimming direction by the action of the Coriolis force. With regard to specific studies of the magnetic sense in cetaceans, only three original scientific articles could be found addressing this issue. The first reports the existence of magnetic material in the left falx cerebri of a common Pacific dolphin (*Delphinus delphis*) that appears to be associated with nerve fibers, suggesting a sensory function [11]. The second report associates the migrational movements of Fin whales to gradients in geomagnetic intensities over different seasons [12]. The third report [13] measured changes in the vegetative physiological parameters of dolphins in response to changes in the permanent magnetic field, these measurements suggesting a magnetic sensibility in the dolphins. Despite these observations, a magnetic sense in dolphins is

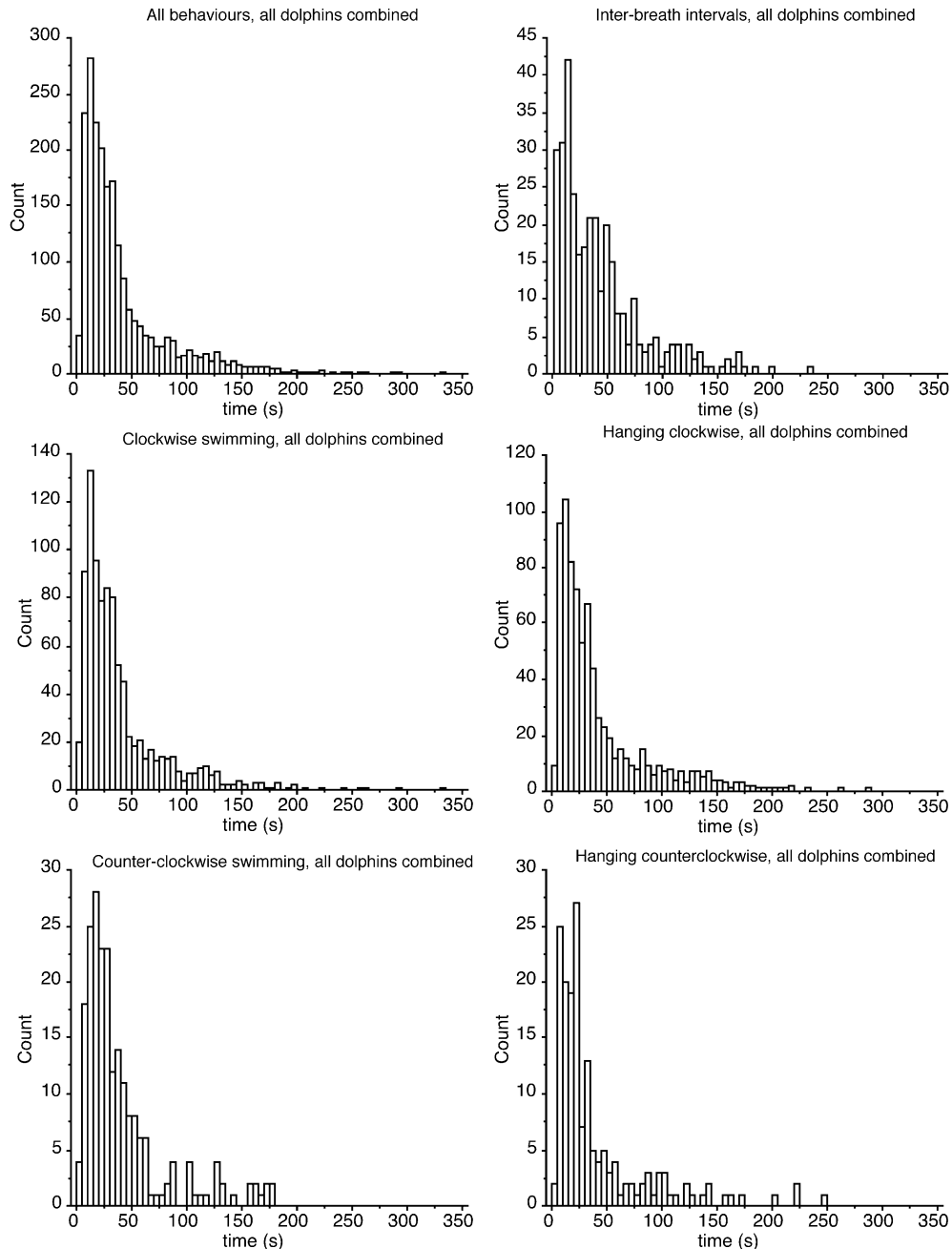


Fig. 5. Frequency histograms depicting the spread of times spent in particular behavior for all dolphins. The upper left histogram is for all behaviors, with all dolphins. The upper right histogram represents the interbreath interval. The lower four histograms represent the four different behaviors quantified in the present study. Note, in all the histograms, the high count around the average of 40 s.

not yet conclusively proven. Moreover, due to the apparent manner in which the magnetic sense appears to work in animals, where it has been studied in more detail [14,15], it appears unlikely that the Earth's magnetic field could be the cause of the directional swimming bias in cetaceans.

The Coriolis force is initiated by the rotation of the Earth and acts upon objects moving within the fluid regions of the Earth, such as the atmosphere and the oceans. The Coriolis force is responsible for both the major atmospheric and oceanic currents [16]. In the Northern Hemisphere, the major ocean currents course in a clockwise direction; those

in the Southern Hemisphere course in a counterclockwise direction. This induction of the direction of ocean currents by the Coriolis force is diametrically opposed to the results found for the bias in swimming direction of dolphins in either hemisphere. Thus, it cannot simply be that the dolphins are "hitching a ride" with the effects of the Coriolis force, rather, they are swimming into the current in both hemispheres. Thus, the possibility that the bias in swimming direction being a product of a weak or simple effect of the Coriolis force also faces problems. We can only conclude that the reason that dolphins in the different hemispheres

swim in different directions is presently unclear. It would be of interest to examine the swimming patterns of dolphins or other cetaceans that have been relocated from one hemisphere to the other. We could only find one report of this [17], where two Amazonian dolphins were moved from Peru to Russia and were observed to swim solely in a clockwise direction.

4.2. The 40-s duration of dolphin behaviors

The second observation of interest derived from the present study is that, on average, the dolphins observed changed behavior every 40 s. Such a quantification of changes of overt behavior in the dolphin, or any other cetacean, has not been previously reported. This observation raises several questions of interest. It should first be noted that these changes in behavior occur with the same frequency as the rate of respiration; that is, there appears to be a causal link between taking a breath and changing behavior. The rate of respiration in the present study correlates closely with that of another study [4]. The neural control of respiration is centered in the reticular formation of the brainstem, and anatomical observations of the brainstem in cetaceans do not present any specific difference that might indicate that respiration is controlled differently in cetaceans as compared with other vertebrates [2,18–21]. Breathing is clearly a salient matter for cetaceans; thus, one might expect that the neural impulses leading to respiration might have rather widespread effects on the reticular system, more so than might be seen in other mammals. The mechanisms for attention are also found in the reticular formation. It is possible that the neural activity created by the respiratory control centers has such salience as to effect/disrupt the attentional systems located within the reticular formation. This might then be the underlying reason for the change in overt behavior with every breath. The following question can then be raised: Do the cetaceans have an attention span that is limited by the need to breathe? This interesting correlation between changing behaviors and respiratory rate needs to be examined in more detail, as does the hypothesis that the effect of breathing limits the potential attention span of, at least, sleeping cetaceans. Breath holding, as seen in cetaceans, has been observed to both inhibit behavior [22] and have deleterious effects on cognitive tasks [23], while respiratory-related sleep disorders, such as sleep apnea, which may be likened to the respiratory action of a sleeping cetacean, have been shown to have deleterious effects on waking cognitive performance in tasks requiring short-term memory and long attention spans [24,25].

Acknowledgements

The authors wish to thank Seaworld in Durban, South Africa, for allowing us to make the presented observations on the dolphins housed at this facility. We extend a special thank you to Hayley McClellan of Seaworld for her part in

facilitating the present study and to the rest of the staff for their enthusiastic and patient help. We also thank Mr. Sean Gordon for his invaluable help with the processing of data in Excel. The research reported herein was supported by a University of the Witwatersrand Faculty Research Grant to P.M.

References

- [1] Lilly JC. Man and dolphin. New York: Victor Gollancz; 1962.
- [2] Ridgway SH. The central nervous system of the bottlenose dolphin. In: Leatherwood S, Reeves RR, editors. The bottlenose dolphin. New York: Academic Press; 1990. p. 69–97.
- [3] Goley PD. Behavioral aspects of sleep in Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). Mar Mamm Sci 1999;15:1054–64.
- [4] Sekiguchi Y, Kohshima S. Resting behaviors of captive bottlenose dolphins (*Tursiops truncatus*). Physiol Behav 2003;79:643–53.
- [5] Sobel N, Supin AY, Myslobodsky MS. Rotational swimming tendencies in the dolphin (*Tursiops truncatus*). Behav Brain Res 1994;65:41–5.
- [6] Mukhametov LM, Lyamin OI. The Black Sea bottlenose dolphin: the conditions of rest and activity. In: Sokolov VE, Romanenko EV, editors. The Black Sea bottlenose dolphin. Moscow: Nauka; 1997. p. 650–68.
- [7] Caldwell MC, Caldwell DK, Siebenaler JB. Observations on captive and wild Atlantic bottlenosed dolphins, *Tursiops truncatus*, in the northeastern gulf of Mexico. Contrib Sci 1965;91:3–10 [Los Angeles County Museum].
- [8] Marino L, Stowe J. Lateralized behavior in two captive bottlenose dolphins (*Tursiops truncatus*). Zoo Biol 1997;16:173–7.
- [9] Balanov L, Deglin V, Kaufman D, Nikolaenko N. Functional asymmetry of the animal brain. J Evol Biochem Physiol 1988; 17:163–70 [article in Russian].
- [10] Mukhametov LM, Supin AY, Polyakova IG. Interhemispheric asymmetry of the electroencephalographic sleep patterns in dolphins. Brain Res 1977;134:581–4.
- [11] Zoeger J, Dunn JR, Fuller M. Magnetic material in the head of the common Pacific dolphin. Science 1981;213:892–4.
- [12] Walker MM, Kirschvink JL, Ahmed G, Dizon AE. Evidence that fin whale respond to the geomagnetic field during migration. J Exp Biol 1992;171:67–78.
- [13] Kuznetsov VB. Vegetative reactions of dolphins to a change in the permanent magnetic field. Biofizika 1999;44:496–502 [article in Russian].
- [14] Kirschvink JL, Walker MM, Diebel CE. Magnetite-based magnetoreception. Curr Opin Neurobiol 2001;11:462–7.
- [15] Walker MM, Dennis TE, Kirschvink JL. The magnetic sense and its use in long-distance navigation by animals. Curr Opin Neurobiol 2002;12:735–44.
- [16] Briggs D, Smithson P, Addison K, Atkinson K. The global ocean, the atmosphere in motion. Fundamentals of the Physical Environment. 2nd edition. London: Routledge; 1997.
- [17] Oleksenko AI, Mukhametov LM. Rest and activity states in Amazonian dolphins. J Sleep Res 1994;3(suppl. 1):185.
- [18] Breathnach AS. The cetacean central nervous system. Biol Rev 1960;35:187–230.
- [19] Kesarev VS. The inferior brain of the dolphin. Sov Sci Rev 1971;1:52–8.
- [20] Langworthy OR. A description of the central nervous system of the porpoise (*Tursiops truncatus*). J Comp Neurol 1932;54:437–99.
- [21] Pilleri G, Gihir M. The central nervous system of the Mysticete and Odontocete whales. Investig Cetacea 1970;2:89–135.
- [22] Alpher VS, Blanton RL. Motivational processes and behavioral inhibition in breath holding. J Psychol 1991;125:71–81.

- [23] Alpher VS, Nelson RB, Blanton RL. Effects of cognitive and psychomotor tasks on breath-holding span. *J Appl Physiol* 1986; 61:1149–52.
- [24] Fulda S, Schulz H. Cognitive dysfunction in sleep disorders. *Sleep Med Rev* 2001;5:423–45.
- [25] Naegele B, Pepin JL, Levy P, Bonnet C, Pellat J, Feuerstein C. Cognitive executive dysfunction in patients with obstructive sleep apnea syndrome (OSAS) after CPAP treatment. *Sleep* 1998;21: 392–7.