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Dolphins maintain cognitive performance during 72 to 120 hours of continuous auditory vigilance

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SUMMARY

The present study reports the first use of a choice visual–vocal response time cognitive task, during 72 or 120 h of continuous auditory vigilance. Two adult bottlenose dolphins (*Tursiops truncatus*), NAY (male) and SAY (female), maintained a very high detection rate (91.1–98.7%) of random 1.5 s goal tones infrequently substituted in a background of frequent 0.5 s equal-amplitude tones over continuous 72 or 120 h sessions. In addition, a choice visual–vocal response time task (CVVRT) tested cognitive performance during night time sessions, when the dolphins would have ordinarily been resting or asleep as we had observed in previous studies. NAY and SAY detected a single-bar, posterior, vertical, green (S1g) or 3-bar, anterior, horizontal, red (S2r) LED light stimulus presented randomly to each eye. They responded with a different vocalization (whistle or pulse burst) to each stimulus (S1g or S2r) presented randomly to left and right eyes. The animals maintained high levels of goal tone detection without signs of sleep deprivation as indicated by behavior, blood indices or marked sleep rebound during 24 h of continuous post-experiment observation. Acoustic goal tone response time (AGTRT) overall did not change during the 72 h (F=0.528, P=0.655) or 120 h (F=0.384, P=0.816) sessions. Nor did CVVRT slow or degrade over the 72 h (F=4.188, P=0.104) or 120 h (F=2.298, P=0.119) AGTRT sessions.

Key words: dolphin, *Tursiops*, vigilance, diurnal rhythm, brain, uni-hemispheric sleep, hemisphere autonomy, choice response time, callosum transfer time.

INTRODUCTION

A previous study (Ridgway et al., 2006), reported for the first time that bottlenose dolphins (*Tursiops truncatus*) could maintain auditory vigilance for 120 continuous hours. These animals showed no evidence of sleep rebound or health effects of sleep deprivation as indicated by behavior, blood indices or marked sleep rebound during 24 h of continuous post-experiment observation. The two dolphins maintained a very high detection rate (87–99%). They detected randomly presented, infrequent 1.5 s goal tones in a background of frequent 0.5 s equal-amplitude tones over five continuous 120 h sessions. Auditory goal tone response time (AGTRT) did not slow between day one and day five whereas AGTRT was slower during night time (21:00–04:00 h) compared with daytime (09:00–16:00 h). However, the dolphins were able to maintain levels of vigilance as indicated by reliable goal tone detection even during night time periods of slowed AGTRT when the animals appeared to be resting or sleeping (Ridgway et al., 2006).

The dolphins had to detect the infrequent, randomly presented 1.5 s goal tone every 4–24 min against a background of equal amplitude, equal frequency 0.5 s tone presented every 30 s. The animal responded to the goal tone by swimming to and pressing a response paddle at the side of its enclosure. This AGTRT task was sufficient to show that the dolphins could maintain auditory vigilance for a continuous 120 h without signs of sleep deprivation or health effects (Ridgway et al., 2006). However, the task did not test the dolphins' cognitive ability with the progression of continuous vigilance.

Human cognitive ability, as measured by choice response time, degrades more rapidly than physical performance during periods of continuous vigilance (Dinges et al., 1997; Liberman, 2006; Liberman et al., 2006). To test whether this is also true in dolphins, we introduced a dolphin night time cognitive task superimposed on the AGTRT. This would be a repetition of the same auditory vigilance task (Ridgway et al., 2006) with the addition of a night time choice visual–vocal response time (CVVRT) task. We hypothesized that during 72–120 h of continuous auditory vigilance, cognitive performance might degrade. This study included CVVRT probes with three night time sessions of about 100 visual stimuli per session delivered randomly to each eye under computer control. Cognitive degradation may be indicated by an increase in CVVRT, an increase in missed stimuli or perhaps by the dolphin occasionally failing to detect stimuli with one eye while continuing to detect with the other eye. Failure to detect with one eye might indicate uni-hemispheric sleep or drowsiness.

In the current study, we tested the same female dolphin (SAY) from our previous study with a male dolphin (NAY) not in our previous study to determine the effect of continuous vigilance on the dolphin's cognitive ability. We added a night time CVVRT to determine if: (1) continuous auditory vigilance had an impact on the speed and accuracy of CVVRT; (2) the CVVRT had an impact on continuous AGTRT accuracy or speed; or (3) the dolphins, among all placental mammals having a small corpus callosum relative to brain size (Tarpley and Ridgway, 1994) and completely crossed optic

chiasm (McCormick, 1969; Tarpley et al., 1994), could transfer learned behavior between their laterally positioned eyes.

MATERIALS AND METHODS

Auditory goal tone response time (AGTRT)

All experiments were conducted in accordance with a protocol approved by the Institutional Animal Care and Use Committee of the Navy Marine Mammal Program, Space and Naval Warfare Systems Center, Pacific, San Diego, CA, USA.

As in our previous study (Ridgway et al., 2006), we tested two adult bottlenose dolphins (*Tursiops truncatus* Montagu 1821). Dolphin NAY (male, age 22, mass 256 kg, length 302 cm) was not in our previous study. Dolphin SAY (female, age 26, mass 246 kg, length 274 cm) did participate in the previous study. The current study includes seven AGTRT sessions with concurrent CVVRT tasks including four 120 h sessions (3 SAY, 1 NAY) and three 72 h sessions (2 SAY, 1 NAY). The 120 h sessions occurred in May (S05), December (S12), March (S03) and November (N11) while the 72 h sessions occurred in May (S0504), October (S10) and February (N02). All sessions occurred within an eight month period.

Both animals were exposed to a 0.5 s tone presented every 30 s. The dolphins' task was to detect a 1.5 s tone of equal amplitude and frequency, which was infrequently substituted for one of the 0.5 s tones. If the 1.5 s tone was detected, the dolphin pressed a paddle for food reinforcement. All tones were the same intensity and projected every 30 s as the dolphins swam freely in their 9×9 m open air, open water enclosures under ambient light conditions in San Diego Bay (Fig. 1A).

The dependent variables for vigilance were the time to respond to the signal and the number of missed or ignored goal tones. Under computer control, the 1.5 s goal tone stimulus randomly replaced the 0.5 s tone at intervals between 4 and 24 min. The dolphin was required to press a paddle on one side of its enclosure within 20.5 s of a goal tone. When the paddle was pressed within 20.5 s of the goal tone, the computer sounded a buzzer both as a bridging stimulus (secondary reinforcer) to the dolphin and to signal the trainer to come out of the equipment hut (Fig. 1A) and give the dolphin a fish reward. The rewards were dispensed on a side of the enclosure away from the goal tone response paddle. If the dolphin pressed the paddle in response to a 0.5 s tone – a false alarm – the wait period for the next tone was extended for 30 s.

Behavioral thresholds measured at 1 m from the source (Ridgway and Carder, 1997; Schlundt et al., 2000) showed that dolphin SAY could hear the 70 kHz tones well. She reliably responded to tones at a level about 20 dB above her audiometric threshold in the bay. Behavioral tests showed that the male dolphin NAY had a high-frequency hearing loss. His goal tones were presented at 15 kHz at about 20 dB above his hearing threshold at that frequency.

The dolphin's approach to the underwater paddle was illuminated at about 850 nm wavelength by infrared (IR) light sources mounted to illuminate both dolphin eyes and video recorded by IR cameras (Fig. 1B) on each side of the dolphin's head throughout all AGTRT sessions (Ridgway et al., 2006). Much of the time, the state of both dolphin eyes (open or closed) could be observed on the recorded video. As in the previous study, the dolphin's behavior was recorded for a 24 h period before and after one AGTRT session for each dolphin (S03, N11). Behavior on video during the 24 h periods before was compared with the 24 h periods after the 120 h session and was analyzed for each dolphin as an indicator of sleep rebound. The video record was scored for behavioral indices of sleep (Flanigan, 1974; Goley, 1999; Lima et al., 2005; McCormick, 1969; McCormick, 2007) at 30 s intervals. Two types of behavior were scored as sleep: slow stereotyped circular swimming (Flanigan, 1974; Goley, 1999), and floating at the surface with only an occasional beat of the tail to bring the blowhole above the surface to breathe (McCormick, 1969; McCormick, 2007; Flanigan, 1974).

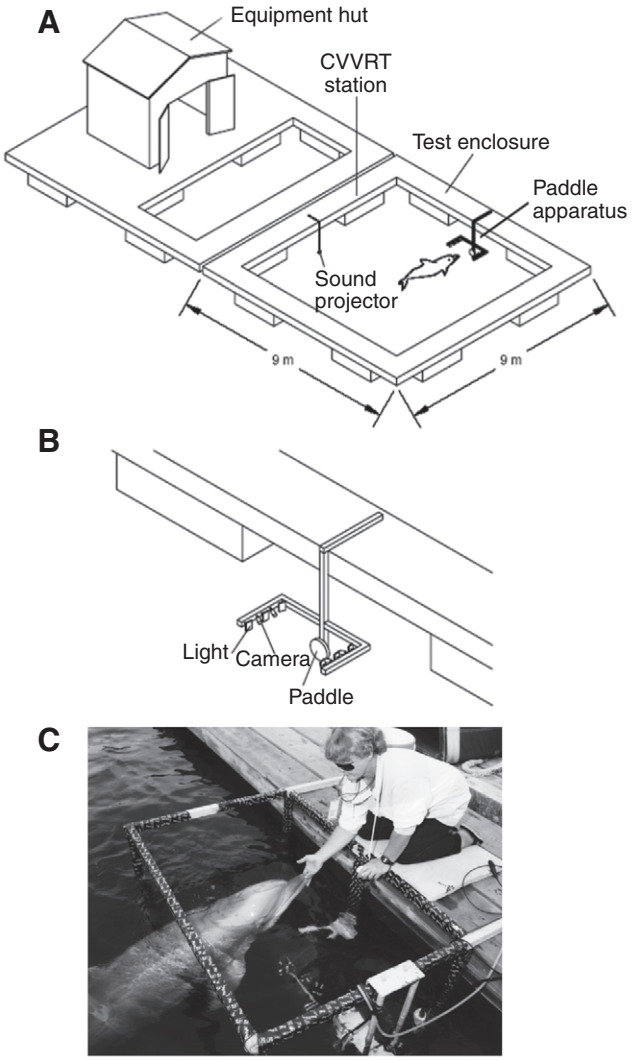

Fig. 1. Experimental setup for the dolphin vigilance sessions. (A) Equipment hut and test enclosure showing the location of the response paddle and the sound projector on the adjacent side of the pen where the dolphin was rewarded. (B) Close-up drawing showing the response paddle apparatus, the underwater infrared cameras at equal distance on each side and infrared light sources that allowed for visualization of the dolphin's eyes on goal paddle approaches for the auditory goal tone response time (AGTRT). The choice visual–vocal response time (CVVRT) station was put in only at night for the visual–vocal response time task. (C) Trainer signals the dolphin to go down to position for CVVRT testing.

Prior to the vigilance sessions, the dolphins were fed a standard amount of fish each day during the daylight hours – 15 kg for NAY, 12 kg for SAY. During the vigilance sessions the total daily food consumption was maintained and spread out over a 24 h period. The animals were fed around-the-clock with small amounts being given for each correct goal tone response. The trainers randomized the amount of reward, giving 1–4 small fish for each correct response so that the day's standard ration (in kilocalories) was delivered by the end of each 24 h period of the vigilance session. No food was given to the animals outside of experimental task rewards.

Table 1. Sixteen blood parameters from blood samples collected before and after three 120 h vigilance sessions for dolphin SAY

Blood variables	S03 before task	S03 after task
WBC ($\times10^{-3}$ µl)	9.20	7.80
Seg. neutrophils (%)	51	50
Lymphocytes (%)	16	19
Monocytes (%)	1	4
Eosinophils (%)	32	27
Hemoglobin (g dl^{-1})	13.9	14.7
Hematocrit (%)	40.3	42.7
Sed. rate (60 min)	4	6
Glucose (mg dl^{-1})	97	100
Albumin (g dl^{-1})	4.2	4.4
Globulins (g dl^{-1})	2.4	2.3
A/G ratio	1.8	1.9
Calcium (mg dl^{-1})	8.9	8.7
Iron (µg dL^{-1})	228	259
Cortisol (µg dl^{-1})	1.2	2.0
ACTH (pg ml^{-1})	25	24
Dopamine (pg ml^{-1})	27	<20
Norepinepherine (pg ml^{-1})	611	400
Epinepherine (pg ml^{-1})	70	65
Total T3 (ng dl^{-1})	80	94
Total T4 (ug dl^{-1})	10.0	10.7

ACTH, adrenocorticotropic hormone; Sed. rate, sedimentation rate; Seg. neutrophils, segmented neutrophils.

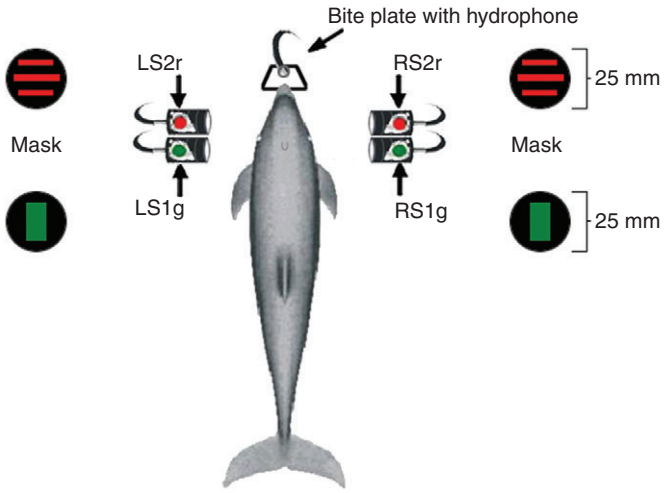

Fig. 2. Schematic showing the choice visual–vocal response time (CVVRT) station with positions of the different light stimuli to which the dolphin responded with a whistle or burst of pulses. To each side are shown the masks for the red (S1r, S2r) and green (S1g, S2g) that allowed for a different appearance of each stimulus when the light came on (L, left; R, right).

With the female dolphin SAY, we replicated the measures of blood indices for comparison with the previous results (Ridgway et al., 2006) in one of the 120 h AGTRT session (S05). Using voluntary fluke presentation, non-fasting blood samples were collected for complete blood cell count (CBC), serum chemistry, catecholamines and selected hormone analyses (Table 1). Blood was collected at the same time of the day both immediately prior to the start and at the end of the 120 h AGTRT session. Samples were analyzed by two laboratories with experience in performing these specific analyses on dolphin blood (Quest Diagnostics, San Diego, CA, USA; and ARUP Laboratories, Salt Lake City, UT, USA). Handling of blood was in accordance with previously established protocols by Romano et al. (Romano et al., 2004).

Data were analyzed with Systat 10 (Systat Software Inc., Point Richmond, CA, USA). Repeated-measures analysis of variance (ANOVA) was used to evaluate the response time to the goal tone between 24 h periods within the 72 h or 120 h vigilance sessions and between daytime (09:00–16:00 h) and night time (21:00–04:00 h). Goal tone response time was used as the dependent variable, and 24 h periods of the vigilance session (1–24 h; 25–48 h; 49–72 h; 73–96 h; 97–120 h), time of day (daytime *vs* night time) and animal as the independent variables. Logistic regressions were used to evaluate changes in the accuracy (correct *vs* missed goal tones) by 24 h periods and by time of day (daytime *vs* night time) within each session. Probabilities less than 0.05 were considered significant.

Choice visual–vocal response time (CVVRT)

Both animals learned a choice auditory–vocal response time task for a previous study (Ridgway et al., 1991). For the CVVRT task we selected two different stimuli that appeared in different colors to our human eye – blue/green and red. We designated blue/green as S1g and red as S2r. Work on color vision in bottlenose dolphins has been reviewed by Griebel and Schmidt (Griebel and Schmidt, 2002). This was not a test of dolphin color vision. The colors were useful for the trainers and investigators to quickly discriminate the lights and identify equipment faults that might occur.

Dot matrices of blue/green or red LEDs (Lite-on, Milpitas, CA, USA) were set up as stimuli for the dolphins to discriminate. A black opaque mask 25 mm in diameter was placed over each LED matrix so that the presentation of blue/green (S1g) was a 10×20 mm blue/green bar through the center of the mask (Fig. 2). Stimulus 2 (S2r) was a 50×70 mm LED matrix that appeared red to the human eye. S2r had three equally spaced horizontal bars of red light. The center bar was 4×20 mm with side bars of 4×13 mm above and below the center bar (Fig. 2).

Bottlenose dolphin light spectral sensitivity has previously been measured in the range of 397–636 nm with a sensitivity peak of 490 nm (Griebel and Schmidt, 2002). A recent review (Peichl et al., 2001) noted that *T. truncatus* and many other marine mammals have L-cones but not S-cones. At least two types of cones are required for color vision and dolphins were found to be ‘essentially color blind’. Therefore, we were determined not to attempt a test of color vision but to design stimuli for our CVVRT task that the dolphin could readily discriminate based on any one of several characteristics.

With the light stimuli configured as shown in Fig. 2, a monochromator was used to measure spectra and luminous flux at a distance of 25 cm from each stimulus. This was the distance of each stimulus from each dolphin eye. S1g in the blue/green region had a peak of about 480 nm with a range of roughly 440–550 nm (Fig. 3A) whereas S2r had spectral peak of 630 nm and a range of roughly 580–670 nm (Fig. 3B). The luminous flux of S1g was 0.5 mlu nm^{-1} and S2r was 2.5 mlu nm^{-1}. In this configuration, the dolphin had clues other than color for discrimination. These included the different stripes through the mask aperture, the difference in brightness, the slightly different positions of the two stimuli (Fig. 2) and possibly the different spectral characteristics (Fig. 3A,B). Each dolphin retina has two areas of ganglion cell density (Mass and Supin, 1995). This feature may aid in differentiating stimulus position.

Dolphin SAY was first trained to respond to S1g with the right eye while the left eye was covered with a rubber suction cup.

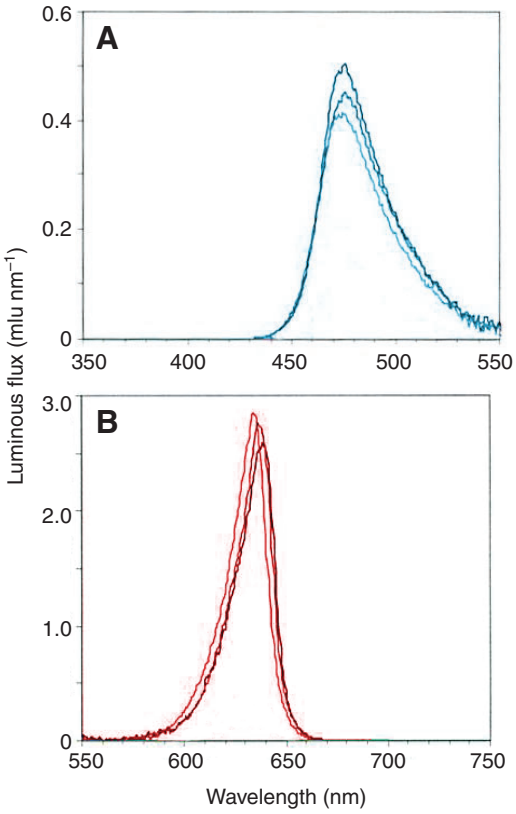

Fig. 3. (A) Plots of monochromator readings of luminous flux in millilumens per nm (mlu nm^{-1}) *vs* wavelength (nm) for three of the units used as S1g stimuli and (B) S2r stimuli. Note that the peak of luminous flux for S1g was less than one–fifth of that of S2r.

Training the vocal responses has been previously described (Ridgway and Carder, 1988; Ridgway et al., 1991; Ridgway et al., 2001; Schlundt et al., 2000). Briefly, S1g presentation to the right eye was paired with a tap on the left margin of the nasal plug eliciting a whistle from the animal. The S1g presentation was put under computer control with custom software. The program output a stimulus with a uniform duration of 109 ms so that S1g onset time and hydrophone reception of the whistle onset could be recorded and response time (CVVRT) calculated and stored (Fig. 4A,B). After SAY performance exceeded 90% correct responses, the suction cup was removed from the left eye and placed on the right so that S1g could now be presented only to the left eye. Yaman et al. have presented data and reviewed literature suggesting right eye dominance in bottlenose dolphins (Yaman et al., 2003).

The vocal response to S2r was a burst pulse sound first elicited with a tap on the right side of the blowhole. The burst pulse was paired with S2r. The same procedure was used for the 109 ms S2r presentation first training the right eye with the left eye covered and then training the left eye with the right eye covered. Dolphin NAY was trained in the same manner except that his responses were reversed from those of dolphin SAY; S1g elicited a burst pulse and S2r a whistle.

We conducted CVVRT trials only during dark hours between approximately 20:00–03:00 h. Each CVVRT session lasted about 20 min and consisted of several brief sittings during which the dolphin stationed (Fig. 1C; Fig. 2) to receive a series of light stimuli. Three of these 20 min sessions were conducted each night. A sitting began with the trainer pausing the AGTRT program, then signaling the dolphin down to a station 1 m underwater (Fig. 1C). When the dolphin was positioned correctly (Fig. 2), the trainer pushed a switch beginning the CVVRT computer program that presented the S1g and S2r stimuli to each eye with an inter-stimulus interval of 4.1–8.2 s randomized in 0.1 s increments. The dolphin had to remain on station for about one minute and attend to four different light sources, two on the right and two on the left (Fig. 2). The computer program established a 2 s window following the onset of each 109 ms light stimulus to record dolphin vocal responses from the hydrophone (Fig. 4A,B). The computer program controlled stimulus presentation in a random order and the trainer was not aware of stimulus order. After a series of several responses, an operator in the computer hut switched on an underwater buzzer immediately following a correct response in the series near the one minute stationing period. The buzzer was a signal to the dolphin to surface and a signal to the trainer to reward the animal with fish. No responses and responses outside the 2 s window

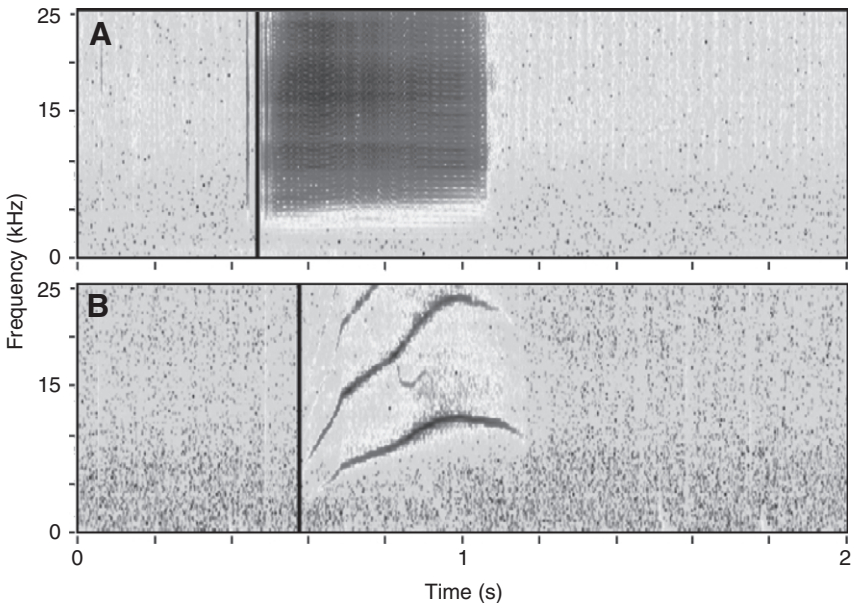

Fig. 4. Examples of the 2 s window provided for dolphin SAY to respond to a S2r stimulus with a correct burst pulse vocalization above and an S1g stimulus with a correct whistle response below. NAY responded to S2r with a whistle and to S1g with a burst pulse sound.

were counted as misses. Response time for correct trials to the visual stimulus within each AGTRT session was used as the dependent variable with the night and stimulus (S1g, S2g, S1r, S2r) or stimulus side (left *vs* right) as the independent variable in repeated-measures ANOVA. There was no attempt to train the animal to respond as fast as possible to the light stimuli.

The impact of the night CVVRT trials on the dolphin's ability to maintain continuous auditory vigilance was also assessed by comparing the AGTRT accuracy and response time with the goal tone during the four hours prior to and the four hours following the CVVRT trials. Logistic regressions were used to evaluate changes in accuracy by time of trial (before *vs* after the visual task) and night. For these analyses, accuracy (correct *vs* missed) was used as the dependent variable with night and time of trial as the independent variables.

RESULTS

The training procedure with one eye covered with an opaque suction cup allowed us to determine if the response learned with right eye stimulus correct response transferred to the left eye and *vice versa*. For both stimuli (S1g and S2r), transfer was almost immediate requiring only one to three trials.

Results of blood measures taken before and after one 120 h AGTRT session for SAY are presented in Table 1 and did not differ from previously reported blood values during AGTRT (Ridgway et al., 2006).

Effect of night time CVVRT tasks on AGTRT

Mean AGTRT for each 24 h period of the three 72 h and four 120 h AGTRT sessions are presented in Table 2. Mean response time increased slightly for each of the first three 24 h periods and then declined slightly for the last two 24 h periods of each the 120 h session (Fig. 5A). A similar trend was found in the 72 h AGTRT sessions, with a slight increase in the mean response time during each of the three 24 h periods (Fig. 5B). However, the slight changes observed over the course of the AGTRT sessions were not significant for the 120 h (F=3.503, P=0.062) or 72 h (F=0.528, P=0.655) sessions. Numerical data and percentage of correct responses for each 24 h period for all seven AGTRT sessions are shown in Table 2. There was no change in accuracy over the course of any of the 72 h or 120 h (logit<1.389, P>0.185) AGTRT sessions when compared by 24 h period.

The significant diurnal pattern of AGTRT observed in the previous 120 h continuous auditory vigilance sessions (Ridgway et al., 2006) was not as obvious in the AGTRT of the two dolphins in the present study. There was no significant difference between goal response time between the night time (21:00–04:00 h) compared with daytime (09:00–16:00 h) for the 120 h (F=2.800, P=0.236) or 72 h (F=5.044, P=0.267) sessions. Nor was there a difference in accuracy between the night time (21:00–04:00 h) compared with daytime (09:00–16:00 h) during any of the 72 h or 120 h (logit<1.288, P>0.280) AGTRT sessions.

The AGTRT for correct responses did not significantly change during the four hours following the CVVRT trials compared with the four hours before the CVVRT during the 120 h session (F=2.627, P=0.352) nor did it change over the course of the AGTRT session (F=1.480, P=0.357; nights 1–5). Further, there was no change in accuracy of the AGTRT session during the four hours following CVVRT (logit>3.979, P>0.313).

In the 72 h sessions, AGTRT during the four hours following the CVVRT trials did not significantly change compared with the four hours prior (F=2.978, P=0.334) nor was there an increase in missed trials (logit>0.00, P>0.348). However, the AGTRT during the four hours after the CVVRT trial did significantly slow over the course of the session (F=27.619, P=0.035; nights 1–3).

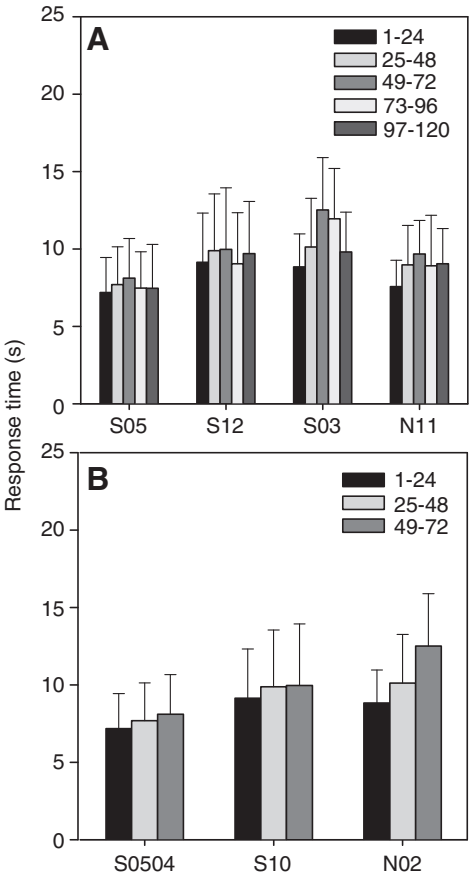

Fig. 5. (A) Response latency for 120 h auditory goal tone response time (AGTRT) vigilance sessions (S05 May, S12 December, S03 March, N11 November) for both animals. (B) Response latency for 72 h vigilance sessions (S0504 May, S10 October, N02 February) for AGTRT trials. Shaded boxes refer to the number of hours.

When the 24 h before the start of the AGTRT session was compared with the 24 h following the AGTRT sessions (Fig. 6) there was not a substantial increase in sleep behaviors (Flanigan, 1974; Goley, 1999; McCormick, 1969) or signs of sleep deprivation (Dinges et al., 1994; Dukas and Clark, 1995; Oleksenko et al., 1992); however, dolphin SAY did show a slight increase in 'sleep' time after one of the 120 h vigilance sessions (S03). In contrast to NAY's night time behavior, SAY floated less and usually continued to circle the enclosure. Especially at night this circling became very slow and stereotyped as has been previously described by Flanigan (Flanigan, 1974) and Goley (Goley, 1999).

Eye closure could not always be determined from our IR illuminators and underwater camera system. Video records from cameras on each side of the head with views of both eyes never clearly indicated simultaneous closure of both eyes (Fig. 7). The dolphin might approach the goal paddle at any angle, thus recognition of eye state (open or closed) was especially difficult at night.

Effect of continuous AGTRT on the cognitive (CVVRT) task

Of the 29 different 24 h periods during which CVVRT trials were conducted, there did not appear to be a difference in accuracy of response between the two dolphins. Mean accuracy (% correct

Table 2. Descriptive statistics for each 24 h period of each 72 h and 120 h AGTRT trial

	Time period	Range	Min.	Max.	Mean	s.d.	Accuracy (%)
S05	1–24	13.46	2.63	16.09	7.18	2.27	100
	25–48	14.28	3.90	18.18	7.69	2.44	94.1
	49–72	13.85	3.02	16.87	8.11	2.56	90.8
	73–96	12.24	2.64	14.88	7.47	2.35	87.1
	97–120	12.91	3.13	16.04	7.46	2.83	97.9
S12	1–24	14.82	4.07	18.89	9.14	3.18	100.0
	25–48	14.55	3.85	18.4	9.88	3.67	92.1
	49–72	15.27	3.73	19.00	9.97	3.97	84.9
	73–96	14.17	3.57	17.74	9.04	3.30	87.8
	97–120	14.01	3.95	17.96	9.69	3.37	98.8
S03	1–24	10.00	4.28	14.28	8.84	2.13	96.7
	25–48	15.82	4.34	20.16	10.12	3.15	95.3
	49–72	14.28	5.27	19.55	12.51	3.39	94.7
	73–96	15.05	4.62	19.67	11.95	3.25	96.8
	97–120	13.07	4.56	17.63	9.80	2.57	95.5
N11	1–24	7.64	4.39	12.03	7.57	1.70	100
	25–48	13.23	4.23	17.46	8.97	2.55	98.9
	49–72	11.26	6.04	17.30	9.68	2.16	97.8
	73–96	16.64	2.42	19.06	8.91	3.26	100
	97–120	12.35	5.11	17.46	9.04	2.27	96.6
S0504	1–24	10.39	3.24	13.63	6.55	2.12	94.0
	25–48	7.86	3.13	10.99	6.90	1.81	94.6
	49–72	14.55	3.74	18.29	8.61	2.91	92.7
S10	1–24	13.46	5.00	18.46	9.74	2.88	97.7
	25–48	14.02	4.44	18.46	10.23	2.91	100
	49–72	15.27	4.34	19.61	10.48	3.06	91.5
N02	1–24	6.25	4.07	10.32	6.61	1.22	88.5
	25–48	7.41	4.83	12.24	7.70	1.49	93.6
	49–72	8.13	4.40	12.53	8.16	1.53	91.3

Statistics included accuracy (%), range, minimum goal paddle response time (min.), maximum goal paddle response time (max.), mean goal paddle response time and standard deviation (s.d.).

responses) are shown for each 24 h period in Table 3. Overall, mean CVVRT accuracy for all 24 h periods for SAY were: left S1g, 95.6%; left S2r, 94.1%; right S1g, 87.8%; and right S2r, 95.9%. For NAY, CVVRT accuracy means were: left S1g, 92.4%; left S2r, 90.3%; right S1g, 92.2%; and right S2r, 89.2%.

There was a difference in CVVRT between the two animals, and between the different AGTRT sessions with the same animal (Table 3). However, the CVVRT did not significantly slow or degrade over the course of the 72 h (F=4.188, P=0.104; nights 1–3) or the 120 h (F=2.298, P=0.119; nights 1–5) AGTRT sessions. Nor was there a difference in CVVRT between stimulus sides (left *vs* right eye) over the course of the 72 h (F=2.319, P=0,267) or 120 h (F=4.566, P=0.122) AGTRT sessions. Accuracy of the CVVRT did not significantly change over the course of any of the AGTRT sessions (logit>1.131, P>0.191).

Correct vocal response to light stimulus S1g was faster than to S2r for both animals (Table 3.). Overall, mean CVVRT for all 24 h periods for SAY were: left S1g, 0.311 s; left S2r, 0.444 s; right S1g, 0.388 s; and right S2r 0.399 s. For NAY, CVVRT means were: left S1g, 0.594 s; left S2r 0.800 s; right S1g, 0.628 s; and right S2r, 0.790 s (Table 3).

DISCUSSION

Dolphins exhibited rapid inter-ocular transfer of learned discrimination

This was the first test of inter-ocular transfer of learned behavior in dolphins or any cetacean. The position of the dolphin eyes on the side of the head suggested the need for a test of inter-ocular transfer. Dolphins only have a small binocular field of view (McCormick, 1969; McCormick, 2007). Furthermore, with similar lateral eye positions, rabbits and pigeons sometimes fail to transfer information learned in one eye to the other (de Vos-Korthals and Van Hof, 1983; Graves and Goodale, 1977; Jimanez Ortega et al., 2008). Although dolphin pupils respond consensually to bright light presented unilaterally (Lyamin et al., 2008), dolphin eyes may move independently, one orienting backward while the other orients forward (McCormick, 1969), and measured eye movements are slow (Dawson et al., 1981). Author Herman Melville spent many hours observing and thinking about cetacean behavior aboard the whaling vessel *Acushnet*. In *Moby Dick* he wrote about the sperm whale's laterally spaced eyes. Melville noted:

> *The whale, therefore, must see one distinct picture on this side, and another distinct picture on that side; while all between must be profound darkness and nothingness to him. Nevertheless, any one's experience will teach him, that though he can take in an indiscriminating sweep of things at one glance, it is quite impossible for him, attentively, and completely, to examine any two things – however large or however small – at one and the same instant of time; never mind if they lie side by side and touch each other. But if you now come to separate these two objects, and surround each by a circle of profound darkness; then, in order to see one of them, in such a manner as to bring your mind to bear on it, the other will be utterly excluded from your contemporary consciousness. How is it, then, with the whale?... is his brain so much more comprehensive, combining, and subtle than man's, that he can at the same moment of time attentively examine two distinct prospects, one on one side of him, and the other in an exactly opposite direction.*
>
> Chapter 74, p. 329 in *Moby-Dick* (Melville, 1851)

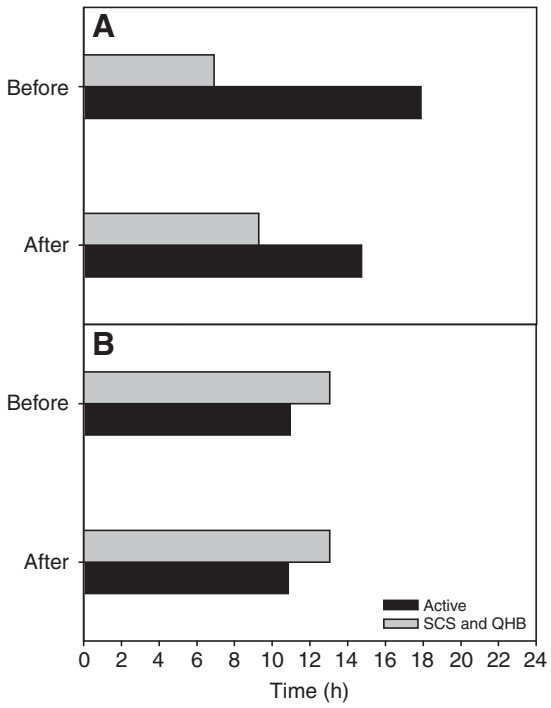

Fig. 6. Behavior recorded in the 24 h before and the 24 h after two of the 120 h continuous vigilance auditory goal tone response time (AGTRT) trials for SAY (A) and NAY (B). Slow circular swimming (SCS) and quiescent hanging behavior (QHB) are associated with sleep or resting.

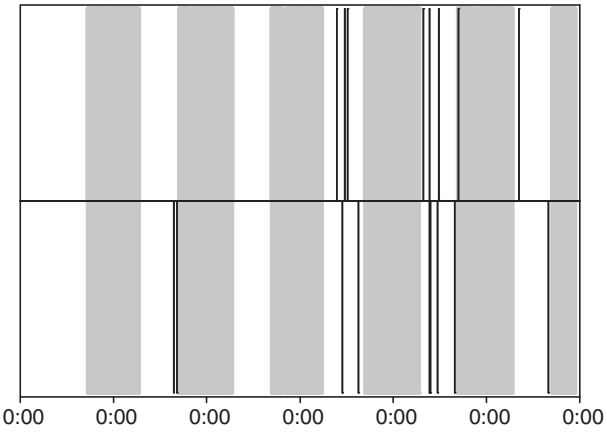

Fig. 7. Eye closures observed on video as dolphin SAY approached the target response paddle. All closures (save 1) involved only one eye and all were during daytime hours. Gray areas denote time between sunset and sunrise.

Although the dolphin corpus callosum is small relative to brain size, the posterior commissure is large relative to that seen in most mammals (Lyamin et al., 2008). Also the inter-collicular commissures are present. This anatomy could at least partially explain why the inter-ocular transfer of the unilaterally learned behavior of the visual–vocal response was almost immediate despite the complete decussation of the optic nerve at the chiasm and the lateral position of the eyes.

Since the dolphin optic nerve is completely crossed at the optic chiasm (McCormick, 1969; Tarpley et al., 1994) visual input to the left eye is transmitted directly to the right brain hemisphere and *vice versa*. In addition, the dolphin has, among placental mammals, a relatively small corpus callosum relative to brain size connecting the two brain hemispheres (Keogh and Ridgway, 2008; Tarpley and Ridgway, 1994). These anatomical arrangements influenced our choice of a CVVRT task presenting two different stimuli in a random order to the dolphins' left and right eyes. Dolphins in uni-hemispheric sleep have been shown to have uni-hemispheric slow waves from electrodes over the cerebral cortex, including visual cortex, as well as in the thalamus (Mukhametov, 1984; Lyamin et al., 2008). If a dolphin had been in uni-hemispheric sleep mode during these visual trials of the CVVRT task, there should have been a marked asymmetry in the speed or accuracy of the CVVRT task between the two eyes. Our results did not show any such asymmetry during the CVVRT task (Table 3).

Dolphins showed no vigilance decrement in auditory–physical or visual–vocal cognitive performance

The dolphins showed no indications of a vigilance decrement during the 72 h or 120 h continuous vigilance sessions. This was shown by the: (1) accuracy of AGTRT during each session; (2) AGTRT latency over the course of trial; (3) correct response accuracy to the CVVRT trials each night; and (4) maintenance of response speed in the CVVRT cognitive task. In human vigilance trials, degradation in both physical and cognitive performance have been consistently observed. Human cognitive ability, as measured by choice response time, degrades more rapidly than physical performance during periods of continuous vigilance (Dinges et al., 1997; Liberman et al., 2006). A reduced amount of sleep resulted in a degradation of human response time (Lim and Dinges, 2008) and performance on a response time task. The dolphins' lack of a significant decrement in auditory vigilance or in a cognitive task over 72 h or 120 h sharply contrasted with both field observations and laboratory studies of other species (Dinges et al., 1997; Dukas and Clark, 1995; Liberman et al., 2006; Siegel, 2005). It is an almost universal finding that prolonged periods of continuous vigilance or sleep deprivation of even shorter periods than our dolphin trials cause a reduction in vigilance performance (Beaumont et al., 2001; Davies and Parasuraman, 1982; Gilberg and Akerstedt, 1998; Horne and Pettitt, 1985). Cognitive performance degrades even more rapidly (Dinges et al., 1997; Liberman et al., 2006).

Sleep deprivation changes result from many human clinical blood measurements (Dinges et al., 1994; Heiser et al., 2000; Suchecki et al., 1998). Using the same measurements as had been used for humans, we quantified 57 parameters from whole blood, serum and plasma samples taken at the start and at the end of one 120 h continuous vigilance session for dolphin SAY. For example, leukocyte measurements, cortisol, epinephrine, norepinephrine and dopamine showed no drastic changes before and after the vigilance session and all parameters of interest remained within normal ranges (St Aubin et al., 1996; Venn-Watson et al., 2007). These results (Table 1) are consistent with the previously reported 120 h continuous vigilance sessions (Ridgway et al., 2006).

Sleep rebound is a universal finding in sleep deprivation in humans and other mammals (Benington and Heller, 1999; Tobler, 1985). Neither dolphin showed marked sleep rebound after any of the 120 h vigilance sessions as indicated by our observations of behavior and posture (Flanigan, 1974; McCormick, 1969; McCormick, 2007) comparing the 24 h before and after the 120 h vigilance session (Fig. 6). Although dolphin SAY did demonstrate more 'sleep behaviors' after the 120 h vigilance session for which these behaviors were quantified, the amount of such post-vigilance behavior was within the range of

Table 3. Descriptive statistic for onset of vocal response (s) by stimulus for each 24 hour period

		Left						Right					
		S1g			S2r			S1g			S2r		
	Time period	Mean RT (s)	s.d.	Accuracy (%)	Mean RT (s)	s.d.	Accuracy (%)	Mean RT (s)	s.d.	Accuracy (%)	Mean RT (s)	s.d.	Accuracy (%)
S05	1–24	0.360	0.024	92.0	0.618	0.035	100.0	0.562	0.025	75.0	0.526	0.075	100.0
	25–48	0.375	0.036	91.7	0.633	0.029	91.7	0.562	0.029	88.0	0.492	0.029	91.6
	49–72	0.364	0.025	100.0	0.658	0.082	100.0	0.542	0.040	72.0	0.508	0.032	100.0
	73–96	0.380	0.036	100.0	0.646	0.035	100.0	0.553	0.036	70.8	0.515	0.029	100.0
	97–120	0.368	0.029	80.8	0.681	0.064	100.0	0.596	0.039	86.9	0.526	0.073	100.0
S12	1–24	0.280	0.031	96.1	0.324	0.022	78.4	0.275	0.025	92.2	0.324	0.031	96.2
	25–48	0.271	0.025	96.1	0.316	0.024	90.8	0.274	0.030	93.5	0.318	0.023	91.0
	49–72	0.282	0.028	97.3	0.316	0.028	96.0	0.281	0.031	90.7	0.316	0.024	100.0
	73–96	0.284	0.023	100.0	0.327	0.020	87.0	0.288	0.032	93.4	0.328	0.022	96.2
	97–120	0.279	0.027	93.3	0.317	0.033	92.1	0.282	0.030	88.2	0.318	0.023	98.7
S03	1–24	0.277	0.027	93.2	0.322	0.027	98.6	0.293	0.026	84.2	0.326	0.052	93.4
	25–48	0.278	0.060	100.0	0.339	0.037	93.3	0.284	0.027	85.1	0.339	0.038	93.5
	49–72	0.276	0.023	93.5	0.327	0.029	98.7	0.287	0.043	89.0	0.329	0.033	97.3
	73–96	0.273	0.028	100.0	0.328	0.029	92.0	0.275	0.019	86.7	0.326	0.024	97.3
	97–120	0.277	0.026	100.0	0.332	0.035	86.7	0.288	0.042	89.3	0.339	0.040	78.4
S0504	1–24	0.369	0.022	97.3	0.579	0.031	100.0	0.551	0.054	90.8	0.518	0.068	98.7
	25–48	0.357	0.018	91.7	0.608	0.035	80.3	0.558	0.051	90.8	0.516	0.038	98.7
	49–72	0.373	0.021	90.9	0.667	0.057	98.7	0.568	0.030	93.4	0.551	0.078	98.7
S10	1–24	0.270	0.022	97.4	0.326	0.026	96.0	0.287	0.058	98.6	0.336	0.048	93.2
	25–48	0.271	0.033	98.7	0.324	0.030	98.7	0.264	0.022	93.3	0.324	0.027	92.1
	49–72	0.274	0.026	98.7	0.338	0.053	96.0	0.274	0.024	92.1	0.320	0.029	100.0
		0.311		**95.6**	**0.444**		**94.1**	**0.388**		**87.8**	**0.399**		**95.9**
N11	1–24	0.539	0.063	93.5	0.657	0.073	93.8	0.552	0.090	90.6	0.685	0.075	74.2
	25–48	0.548	0.075	94.2	0.680	0.105	84.9	0.555	0.065	100.0	0.704	0.083	84.3
	49–72	0.582	0.080	88.0	0.656	0.112	90.2	0.584	0.064	91.8	0.659	0.091	86.0
	73–96	0.586	0.081	96.0	0.691	0.097	89.6	0.592	0.068	94.8	0.722	0.088	89.3
	97–120	0.586	0.093	87.8	0.751	0.101	85.3	0.585	0.068	85.5	0.753	0.095	82.7
N02	1–24	0.637	0.084	97.3	0.930	0.073	100.0	0.730	0.087	90.8	0.913	0.135	98.7
	25–48	0.626	0.080	91.7	1.019	0.095	80.2	0.702	0.080	90.8	0.899	0.079	98.7
	49–72	0.645	0.083	90.9	1.019	0.096	98.7	0.727	0.083	93.4	0.984	0.120	100.0
		0.594		**92.4**	**0.800**		**90.3**	**0.628**		**92.2**	**0.790**		**89.2**

Statistics include accuracy (% correct responses), mean response time (RT) and standard deviation (s.d.) for correct responses. S1g=blue/green stimulus, S2r=red stimulus. Bold numbers are grand means for each animal.

that was observed previously (Ridgway et al., 2006) for the same animal before and after 120 h vigilance sessions.

Dolphin light sensitivity and complete crossing of the optic nerve

Some birds have adopted uni-hemispheric sleep to maintain visual vigilance (Lima et al., 2005; Rattenborg et al., 1999). The dolphin's ability to sleep with one hemisphere and to have each brain hemisphere sleeping alternately (Lyamin et al., 2008) seems the most likely explanation for the dolphin's ability to detect and respond to the acoustic goals randomly presented over the continuous three or five days of these sessions without signs of sleep deprivation.

Goley (Goley, 1999) observed night time eye closures by visible light; however, an animal with both eyes below the surface at night where visible light is minimal may have little need for eye closure to reduce illumination that might interfere with sleep. Based on multi-lead electroencephalographic (EEG) recordings from both hemispheres, Mukhametov (Mukhametov, 1984) suggested that the open dolphin eye could perform a sentinel function 'regardless of whether the contralateral hemisphere was asleep or awake'. When 'checkerboard' square stimuli were presented to an open eye of sleeping dolphins there was a rapid startle response or other behavioral reaction (Lyamin et al., 2008). However, during uni-hemispheric sleep the eye contralateral to the hemisphere exhibiting slow waves was usually closed (Lyamin et al., 2008).

When the dolphins in our study were slowly swimming around their enclosure at night we could not determine their eye state; however, video did record eye state during approaches to the goal paddle in response to the goal tones. During EEG recordings of dolphin uni-hemispheric sleep, as indicated by slow waves, the eye contralateral to the sleeping hemisphere was closed about 75% of the time in the studies of Lyamin et al. (Lyamin et al., 2004). In the current vigilance studies, we replicated the findings of our previous work (Ridgway et al., 2006). Closure of either eye was observed only during daytime goal paddle approaches (Fig. 7). Bright sunlight penetrating surface waters during daylight hours or visible light used for observation at night might influence the need for eye closure. We used IR illumination at 850 nm to illuminate the dolphin when at the surface and underwater approaching the goal paddles because these events were not visible to our trainers without the IR system.

The absence of eye closure during night time goal approaches observed during this study (Fig. 7) suggests that if the dolphin were asleep in either hemisphere with one or both eyes closed, the AGTRT tone aroused the animal. Whether the dolphin was asleep in both brain hemispheres (McCormick, 1969; McCormick, 2007; Ridgway, 2002; Lyamin et al., 2008) or in only one brain hemisphere (Mukhametov, 1984; Ridgway, 2002; Lyamin et al., 2008) it was probably aroused by the goal tone. This arousal lasted at least for the approach and paddle press followed by collection of the fish reward near the hydrophone station on the adjacent side of the enclosure (Fig. 1A,B).

During the night time periods, the dolphin's posture and behavior was often consistent with rest (Flanigan, 1974; Goley, 1999; Lima et al., 2005; McCormick, 1969) except during the brief periods of 25 s or so required for goal approach and taking of the food reward. Slowed AGTRT response times (Fig. 6A,B) could be viewed as an increased arousal threshold. If the slowed response time was an indication of increased arousal threshold, it suggests that the goal tone response involved an arousal even from uni-hemispheric sleep. The dolphin might have been able to process the auditory cue, awaken and initiate the behavioral response. The dolphin auditory system is well connected to brainstem alerting systems. Still, it seems remarkable that the dolphin was able to discriminate the goal tone from the non-salient background tones, swim to the goal tone response paddle, then swim to the adjacent side of the enclosure and eat the fish reward and repeat this 25 or 35 times during the night time period and show no signs of sleep deprivation or cognitive impairment.

It is apparent that dolphins were able to maintain cognitive ability as well as to detect goal tone stimuli at intervals during long vigilance trials to at least 120 continuous hours. The ability of the dolphin to obtain sufficient sleep by uni-hemispheric means during intervals when a behavioral or vocal response is not required, most probably explains the dolphin's vigilance capability.

From a cognitive standpoint, dolphins rapidly detected a visual stimulus and give a separate and distinct vocal response to two different lateral visual stimuli. The dolphins attended and responded correctly even though the stimuli alternated randomly between the laterally positioned eyes. How many distinct vocal responses can be made by a dolphin to a larger number of different visual stimuli is still to be determined.

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