A 108-h total sleep deprivation did not impair fur seal performance in delayed matching to sample task

Oleg I. Lyamin[1,2], **Vasilisa D. Borshchenko**[3], **Jerome M. Siegel**[1]

[1]Department of Psychiatry, University of California Los Angeles, Center for Sleep Research, 16111 Plummer St, North Hills, Los Angeles, CA 91343, USA

[2]A.N. Severtsov Institute of Ecology and Evolution, Moscow, Russia

[3]I.M. Sechenov Institute of Evolutionary Physiology and Biochemistry, St Petersburg, Russia

Abstract

While the majority of studies have concluded that sleep deprivation causes detrimental effects on various cognitive processes, some studies reported conflicting results. We examined the effects of a 108-h total sleep deprivation (TSD) on working memory in the northern fur seal, an animal with unusual sleep phenomenology and long-range annual migrations. The performance of fur seals was evaluated in a two-choice visual delayed matching to sample (DMTS) task, which is commonly used to evaluate working memory. In baseline conditions, the performance of fur seals in a DMTS task based on the percentage of errors was somewhat comparable with that in nonhuman primates at similar delays. We have determined that a 108-h TSD did not affect fur seals' performance in a visual DMTS task as measured by overall percentage of errors and response latencies. On the contrary, all fur seals improved task performance over the study, including the baseline, TSD and recovery conditions. In addition, TSD did not change the direction and strength of the pattern of behavioral lateralization in fur seals. We conclude that a 108-h TSD did not interfere with working memory in a DMTS test in northern fur seals.

Keywords

Cognitive functions; Working memory; Delayed matching to sample task; Learning; Total sleep deprivation; Northern fur seal

Introduction

A substantial amount of research has been conducted in an effort to understand the impact of sleep on various cognitive processes, such as attention, sensory perception, discrimination, decision-making, learning, and memory. The majority of studies have been performed either in human subjects, primates or in a small number of animal species in laboratory

conditions using methods of total sleep deprivation (TSD) or sleep restriction (Rechtschaffen et al. 1983; Banks and Dinges 2007). These studies usually reported a link between sleep intervention and evidence of the impaired performance, and the results were presented as supporting the idea that sleep deprivation has a detrimental effect on most cognitive domains (e.g., for human studies: Walker and Stickgold 2004; Banks and Dinges 2007; Alhola and Polo-Kantola 2007; Wickens et al. 2015; Leong and Chee 2023; for animal studies: Rattenborg et al. 2004; Porrino et al. 2005; Hagewoud et al. 2010; Brawn et al. 2010; Havekes et al. 2015; Pinheiro-da-Silva et al. 2018; Johnsson et al. 2022). The limitations of this approach have been reviewed (Siegel 2001, 2021).

There is another group of data which suggests that wild animals can substantially reduce their sleep in different periods of their lives (e.g., in northern elephant seals, African elephants, pectoral sandpipers, great frigate birds; Kendall-Bar et al. 2023; Gravett et al. 2017; Lesku et al. 2012; Rattenborg et al. 2016). It is during such periods that these animals display the most complex forms of behavior, such as navigation, feeding, reproduction, and escaping predators. There is no evidence to suggest that sleep restriction was detrimental to cognitive processes of different levels of complexity and performance under these circumstances. One approach to reducing the gap between the two groups of data is to use the same methodology of sleep deprivation and testing of cognitive processes, as were employed in laboratory animals and in human subjects while conducting experiments in wild animals which display extraordinary examples of variation in the amounts of their sleep.

The delayed matching to sample (DMTS) task is one of the most commonly used tasks to examine working memory in humans in normal, pharmacologically altered or pathological conditions (Adamson et al. 2000; Daniel et al. 2016; Hahn and Rose 2020). In general, the complexity of the memory task is determined by the delay between the presentation of the sample and comparison stimuli among which the object to match needs to be found, as well as the number of comparison objects and their novelty to the subject. Test performance is characterized primarily by the percentage of correct choices (or errors) and reaction time. It is acknowledged that performance in DMTS task is not only affected by the state of memory, but also by other cognitive processes of varying complexity, such as attention, discrimination and learning. In additional tests, the state of these functions can be assessed and their roles can be separated. By changing the delay phase, one can characterize and measure the subject's ability to retain the image over a particular interval of time. The DMTS task has been also used as a tool to evaluate the impact of sleep deprivation or restriction on cognition, including memory (e.g., Lieberman et al. 2002; Habeck et al. 2004; Drummond et al. 2012; Wee et al. 2013; Cousins and Fernández 2019).

The semiaquatic northern fur seal (Callorhinus ursinus) is unique in having both bilateral slow wave sleep (SWS) when sleeping on land as recorded in most land mammals, and unihemispheric sleep when sleeping in water as reported in cetaceans (Lyamin et al. 2017, 2018). Moreover, when fur seals stay in water (up to 10 months each year), these animals substantially reduce or eliminate REM sleep for days, or even weeks at a time (Lyamin et al. 2018). In prior studies we have determined that performance of fur seals in a visual discrimination task did not deteriorate in the conditions of a 108-h TSD compared with the baseline conditions (Lyamin et al. 2015). The aim of this study was to examine the effect

of a 108 h of TSD on the performance in northern fur seals in a visual DMTS task and to evaluate the effect of TSD on working memory.

Methods

Animals, permits and approvals

Data were collected from 3 northern fur seals (*Callorhinus ursinus*). The animals (two adult females 20–23 kg, were 3–4 and 4–10 years, with one subadult male, 25 kg, that was 4–5 years) were captured on the Commander Islands (the Western Pacific, Russia) 1–2 years before the study. The capture permits were issued by the Russian Federation Federal Agency for Fishery. All procedures were approved by the Committee for Bioethics of A.E. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences. The experiments were performed at the Utrish Marine Station of the A.N. Severtsov Institute Ecology and Evolution (the Black Sea, Russia). The fur seals were well-adapted to captivity based on their appearance, behavior, amount of fish eaten, body weight, regular examination by a staff veterinarian and blood test results. They were housed in outdoor pools with seawater (4 m in diameter and 1.8 m deep), containing a platform next to each pool. Usually, 2 animals were housed in one pool. At night, the fur seals usually slept on the platform, but spent most of the daytime in the water. The fur seals were maintained at the Utrish marine station for 2–3 years. During this period, they participated in several experiments. After that they were transferred to a commercial dolphinarium.

Experimental design

The fur seals were trained in a visual alternative DMTS task. During the training and study period, which lasted 1–2.5 months, each seal was housed individually in the same type of pool. The training of seals 1 and 2 began in early July, and the experiments were conducted in the first 2 weeks of August. In the male, training was performed in September–October, and the experiments were conducted between November 5 and 15th. Daily ranges of air and water temperature during the experiments in seals 1 and 2 was 20–35 °C and 22–25 °C, and in fur seal 3—from 8 to 14 °C and 16 to 18 °C, respectively.

First, each fur seal was trained to stay at the surface touching the start target with the tip of its muzzle for at least 30 s and wait for the sample object (Fig. 1). To initiate the trial, the sample object was presented above the water in the center of a 0.8×0.7 m dark background screen at a distance of 1 m from the start position. After the 3-s display, the trainer released a cover screen that obscured the background screen. During the next 5 s (a delay phase or delay), the trainer installed the previously shown (matched) object and the second (non-matched) object on the background screen. The fur seal could not see behind the covering screen. After the delay phase had expired, the screen cover was lifted and two objects were presented to the animal. The animal had 10 s to indicate the matched object by touching its muzzle one of two targets (left or right) located under the objects. The fur seal was rewarded with fish for the correct choice. The animal was not rewarded if its choice was incorrect, or if it did not make a selection or left the start position. Either of these events terminated the trial. The trainer released the screen which covered the objects, removed them, and installed the next sample object behind the cover screen.

In each fur seal, the same 2 objects were used over the entire experimental period: two squares of different sizes in female 1, a triangle and square in female 2, and a circle and cross in the male (Fig. 1). The diameter of the circle, the height of the triangle, the width and height of the cross were 18 cm. The sides of the squares were 18 and 11 cm. The distance between the centers of the two objects was 40 cm. They were 20 cm to the left and to the right from the center, where the sample object was presented. At the initial stage of training, it became clear that two animals had a preference to select or to not select one of the figures in the pair. Therefore, pairs of figures were chosen for each seal taking into account the speed of learning and the absence of clear preference for one of two figures at the training stage. While the maximum linear length of five figures (the side of the largest square, diameter of a circle, height and side of a triangle) was the same, the ratio of the areas of the paired figures was different: in fur seal 1—1:0.37 (two squares), in seal 2—1:0.50 (square and triangle) and in fur seal 3—1:0.80 (circle and cross).

Training and experimental sessions were conducted 2 times a day: in the morning (from 07 to 08 h) and in the evening (from 18 to 19 h). The usual session consisted of 72 trials and lasted 40–50 min. The average interval between trials was 40 s. The position of two objects on the right and left side was switched randomly but the total number of presentations of each object from the right and left side were equal during each session. Starting from the first day of training and ending with the last day of the recovery period, the fur seals received fish only during trials as a reward for the correct choices (from 1 to 3 small capelin, *Mallotus villosus*). The amount of fish eaten during the experiment was controlled by the trainer, so that the animal ate the same amount per experiment, regardless of the number of errors. The behavior of animals was monitored and videorecorder continuously throughout the study.

The stage 1 learning criteria for all seals was 70% correct choices in the first block of 24 out of 72 trials with a minimum delay of 5 s. On the next experimental day, the two additional delays were introduced: 10 or 15, and 15, 20 or 25 s. The third delay was selected and if necessary adjusted within the first 2–3 training sessions aiming for the percentage of errors for the delay to be at the 40–50% level per session. Each training session was divided into 3 blocks of 24 trials at the same delay in each block: minimal, intermediate and the longest. Blocks took place in order of increasing delay, which made the task more challenging. The stage 2 learning criterion was selection of the appropriate (matched) object at a minimum delay (5 s) with no more than 7 errors per 24 trials (29.2%) in 5 out of 6 consecutive experiments. This was the threshold for random selection of one of two events in a block of 24 trials as projected by the binomial criterion ($p < 0.05$). The percentage of correct selections (or errors) and the latency of the reaction were calculated based on frame-by-frame viewing of video recordings (measurement accuracy was 35 ms).

Total sleep deprivation

TSD started after the morning training in which the stage 2 learning criteria had been met. The last 6 sessions became the baseline experiment. TSD lasted for 108 h (4.5 days) and ended at 20:00. TSD followed by a recovery period which lasted 3 days in the females and 2 days in the male (the 3rd recovery day was interrupted due to adverse weather conditions).

During the baseline and recovery periods, the animals had access to the platform and could sleep both on land and in water. Only one experiment was conducted at a time. During TSD, the fur seals were not allowed to rest on the platform and their attempts to assume a characteristic sleep position in the water (Fig. 2A, B) were interrupted by laboratory personnel as we did in our prior work (Lyamin et al. 2015). During the entire period of TSD, several people with prior experience with fur seals took turns watching the behavior of the study animal continuously for 24 h on the monitor screen from the laboratory, which was located 3 m from the pool. The personnel were instructed to disturb the fur seal if it assumed a sleep posture in the water longer than 10 s or to make the fur seal to return to the water if it stayed on the platform longer than 30 s. As a rule, it was sufficient for someone to approach the pool to make the animals to engage in active behavior (swimming or grooming) or return to the water. On the third and fourth deprivation days the personnel sometimes had to slap the water to interrupt the sleep posture and to make the seals swim. Our analysis of video recordings revealed that in the majority of cases it took no longer than 30 s to react and approach the pool. Thus, in this study we did not interrupt sleep itself in fur seals but their attempts to rest in a characteristic posture which may (or may not) be followed by sleep. The number of attempts to assume a sleep posture in water and "trips" to the platform during TSD were considered as a measure of sleep pressure.

Statistical analysis

Data were assessed for statistical significance using a one-way ANOVA followed by Tukey's post hoc multiple-comparison tests, T test, Fisher's exact test or Pearson product moment correlation test using Sigma Plot 11 software. The threshold for random selection was calculated by the binomial criterion ($p < 0.05$). Values are given as mean ± S.E.M.

Results

Behavior of fur seals during TSD

During the period of TSD, all 3 fur seals repeatedly went to the platform and assumed a characteristic sleep posture in the water (Fig. 2A, B). The number of trips to the platform varied over 4 days (Fig. 2C). When on the platform, the seals were grooming intensively. Within 1 min, the animals returned to the water (by themselves or after they were disturbed by the personnel). We completely exclude the possibility that during TSD fur seals had sleep while on the platform. Over the period of TSD all fur seals also progressively increased the number of attempts to assume a sleep posture in the water (Fig. 2D). In the females, the increase was almost tenfold (from 0 and 4 attempts on the first day to 31 and 36 on the fourth day). In the male, the increase was threefold: from 4 to 12 per day, respectively. While adjusting in a sleep posture, fur seals continued grooming, and their eyes were open most of the time. In almost all cases, such episodes were interrupted within 30 s, but in a few cases on days 3 and 4, within 40–50 s. Motor activity decreased as such episodes progressed.

Over 3 baseline days, fur seals rested on average 26.6 ± 1.2% of 24 h (in different seals on different days 16.9–34.9%). The majority of rest occurred on the platform. Over the period of TSD, the greatest amounts of time fur seals spent in the water in a sleep posture were recorded on day 4: on average 0.9 ± 0.3% of 24 h or 3.5 ± 1.1% of the total rest time in

the baseline conditions (maximum was 5.2% in female 2; Fig. 2E). On the first recovery day, all fur seals rested longer than in the baseline conditions. In female 1 the amount of rest increased up to 175% of the average baseline value, while in female 2 and in the male, the increase was less—up to 132% and 125%, respectively. All rest episodes on recovery day 1 occurred on the platform and the majority within the night period. On the second recovery day, only female 2 rested more than on average in the baseline conditions. Female 1 rested less than 10% of the time it did in the baseline conditions, while the male was active continuously for 24 h (largely swimming around the pool).

In conclusion, during TSD the fur seals displayed repeated attempts to assume a characteristic sleep posture in the water and the number of such attempts progressively increased. The total rest time did not exceed 5% of the baseline values. After TSD all fur seals had a rebound of resting behavior on the 1st recovery day.

Overall percentage of errors in a DMTS task

Baseline conditions—After preliminary training, all 3 fur seals were able to select the matched object at a delay from 5 to 15 s (based on the formal criteria percentage of errors less than 29.2% per experiment of 24 trials) (Fig. 3A, B). Differences among the fur seals were substantial. Female 1 made very few mistakes at a minimum delay of 5 s (overall average percentage of errors was 6.3%). All 6 experiments of the baseline series were successful. The male had 4 times as many errors (on average 24.3%) at a delay of 5 s and 5 out of 6 experiments in the baseline series were successful. In female 2 the percentage of errors at the same delay was intermediate (on average 15.3%). Female 1 and the male also completed the task at intermediate delays (15 and 10 s) with the average percentage of errors 22% and 25% and 5 and 4 out of 6 successful experiments, respectively. Female 2 did not perform the task at a delay of 10 s based on the formal criteria: the average percent of errors was 31.3% and only 3 out of 6 experiments were successful. No animals completed the task at the maximal delays (15, 20 and 25 s) in the baseline conditions.

A one-way repeated measures ANOVA revealed a delay-dependent increase in the percentage of errors in all fur seals (female 1, $F_{2,5} = 48.40$, $p < 0.001$; female 2, $F_{2,5} = 19.78$, $p < 0.001$, and the male, $F_{2,5} = 6.405$, $p = 0.013$; Fig. 3B). In the females the differences were significant for all paired comparisons (Tukey's post hoc test, $p < 0.05$). In the male, the average percentage of errors was similar at delays of 5 and 10 s but almost doubled at a delay of 20 s (5 s versus 20 s, and 10 versus 20 s delays; $p < 0.05$).

Female 2 continued to improve her performance in the task at a 10 s delay during the baseline series. In the last four experiments the percentage of errors consistently decreased (Fig. 3A). At the same time, this was not a significant trend throughout the 6 experiments (Pearson's linear coefficient of correlation, $R^2 < 0.36$, $p > 0.21$).

In conclusion, in the baseline conditions northern fur seals were able to perform in a visual DMTS task at delays ranging between 5 and 15 s. The percentage of errors increased as the delay phase lengthened.

Sleep deprivation and recovery—One-way ANOVA revealed a significant effect of experimental conditions on the overall percentage of errors in the task in all fur seals at least at one delay: in female 1 at an intermediate and the longest delays (15 s, $F_{2,18} = 5.023$, $p = 0.018$; 25 s, $F_{2,18} = 6.254$, $p = 0.009$), in female 2 at the longest delay (15 s, $F_{2,18} = 8.462$, p = 0.003), and in the male at a minimum delay (5 s, $F_{2,16} = 5.568$, $p = 0.015$).

During TSD in both females the average percentage of errors substantially decreased at the longest delays (Fig. 3A, B). It dropped below the formal criteria for random selection in female 1 (21.3% during TSD and 36.8% in baseline; $p < 0.05$, Tukey's paired test), and the number of successful experiments during TSD was greater than in the baseline conditions: 7 out of 9 (78%) versus 1 out of 6 experiments (17%), respectively ($p < 0.041$, Fisher's test). In female 2 the average percentage of errors at the longest delay over the period of TSD approached the threshold of random selection (32.9% and 45.1%, respectively; $p < 0.02$). In addition, female 1 substantially improved at an intermediate delay (15 s): on average 23% of errors during the first 4 experiments, and 8% during the last five experiments ($R^2 = 0.554$, $p = 0.021$; Pearson's linear correlation coefficient, experiment number versus percentage of errors; Fig. 3A). In the male, the overall average percentage of errors and the number of successful experiments during TSD and in the baseline conditions did not differ significantly regardless of the delay.

During the recovery periods, in the females the overall average percentage of errors in the task was less than during TSD (for the same delays). In both animals the differences were significant between the recovery and baseline conditions for the longest delays ($p < 0.01$) and in female 1 also for an intermediate delay ($p < 0.05$). In female 2 the percentage of errors at an intermediate delay (10 s) decreased in 6 consecutive recovery days ($R^2 = 0.698$, $p = 0.039$; Fig. 3A). As a result, during the recovery period both females completed the task at all delays based on the formal criteria. The male substantially improved his performance only for the minimum delay (recovery versus TSD and baseline; $p < 0.05$).

Both during TSD and recovery periods a repeated measures ANOVA detected a delay-dependent increase in the percentage of errors in all fur seals (female 1: TSD, $F_{2,8} = 14.941$, $p < 0.001$ and recovery, $F_{2,5} = 6.335$, $p = 0.017$; female 2: TSD, $F_{2,8} = 14.643$, $p < 0.001$, and recovery, $F_{2,5} = 7.842$, $p < 0.01$; the male: TSD, $F_{2,8} = 5.003$, $p = 0.021$ and recovery, $F_{2,3} = 59.727$, $p < 0.001$; Fig. 3B).

In conclusion, our data indicate that a 108-h TSD did not impair the fur seals' performance in a visual DMTS task. On the contrary, over the TSD and recovery period the animals improved their performance compared to the baseline (non-deprived) conditions.

Behavioral lateralization: number of errors

Baseline conditions—In the baseline conditions the percentage of errors in the task at some delays depended on the matched object, its position (from the right or left side) relative to the animal, or both. Similar behaviors are referred to as behavioral lateralization or asymmetry. The effect of delay and experimental conditions on the number of errors was analyzed separately for each of the 3 delays and different positions of two matched objects:

3 delays × 2 objects × 2 sides of presentation, i.e., a total of 12 "object-side combinations" or cases (Fig. 4A).

Thus, female 1 made more errors at the longest delay of 25 s when a small square as the object to match was located to the right of the animal, i.e., female 1 displayed a "dislike" for the small square (O2) from the right side of the animal, while the position of the large square (O1) did not make a difference in this task (O2R > O1R, O2R > O1L, O2R > O2L, $p < 0.05$, the paired comparison, after a repeated measures ANOVA, $F_{3,5} = 12.52$, $p = 0.001$). Female 2 at the longest delay of 15 s made more errors if the matched object was a triangle (O1) compared to a square (O2) regardless of the side of presentation, i.e., this female displayed a "preference" for the square as the object to match (O1R > O2R, O1R > O2L, $p < 0.05$, the paired comparison, after ANOVA, $F_{3,5} = 4.38$, $p = 0.03$). In both females the overall percentage of errors at the longest delays was greater than the formal threshold for random selection. In each animal lateralization was also noted at intermediate delays and the direction of laterality was same as at the longest delays. However, the effects of the matched object and its position was not significant at intermediate delays ($p > 0.05$), as for the maximum delays. No preference for either one of two matched objects (cross and circle) or its position was detected in the male fur seal ($p > 0.05$ at all delays).

In conclusion, in the baseline conditions two female fur seals exhibited a preference for selecting one of the two objects and the side of its presentation at the longest delays.

Sleep deprivation and recovery—During TSD behavioral lateralization in the percentage of errors was recorded in female 2 and in the male (Fig. 4B). In female 2, the preference was significant for the same delay as in the baseline conditions (for 15 s; $F_{3,8} = 5.04$, $p < 0.01$); however, the "disliked" object appeared to be different (square versus triangle regardless of the side; $p < 0.05$, the paired comparison, O2R > O1R, O2R > O1L). This female still made selections largely randomly.

During TSD there was also some evidence for a preference for the matched object in the male (a circle versus cross, O2 and O1). This preference reached significance at a 5 s (minimum) delay ($p < 0.05$, the paired comparison, O1R > O2R; $F_{3,8} = 3.18$, $p = 0.045$), while there was no indication for this in the baseline conditions. It appears that the male had a "dislike" for a cross when presented from the right side to the animal.

During TSD in female 1 the average number of errors was similar at all delays, regardless of the matched object and its position. In this female, the overall percentages of errors at each of the 3 delays were significantly lower than in the baseline conditions, and all met the criterion for non-random selection. During the recovery period, in all seals the average number of errors at all delays did not differ regardless of the objects and their position (Fig. 4C).

In conclusion, the directions of changes for this lateralization pattern (a preference for an object or the size of presentation as measured by the percentage of errors) in fur seals during TSD were not consistent.

Behavioral lateralization: response time

Baseline conditions—The effect of delay and experimental conditions on the match response latency (MRL) was also analyzed separately for 3 delays and two different positions of two matched objects (Fig. 5A).

In the baseline conditions in female 1 at all 3 delays, the MRLs were shorter if both matched objects (large and small squares, O1 and O2) were presented to the right side of the animal. At a 5 s (minimum) delay the differences between MRLs were close to the level of significance (a repeated measures ANOVA, $F_{3,5} = 2.294$, $p = 0.12$). At a 15 s (intermediate) delay, the differences were highly significant for 4 cross side comparisons (each of the objects from one side versus each object from the other side; or O1R < O1L, O2R < O1L, O1R < O2L, O2R < O2L; p ranged between 0.035 and 0.009; after a repeated measures ANOVA, 7.631, $p = 0.003$) and at a 25 s (maximum) delay for 2 cross side comparisons (one of the objects from the right side versus each of the two objects on the left side; or O1R < O1L and O1R < O2L; p < 0.05; $F_{3,5} = 6.240$, $p = 0.006$, after ANOVA). At all 3 delays the differences between the MRLs were not significant for 2 matched objects presented on the same side (O1R and O2R, O1L and O2L).

In female 2, the MRLs were shorter at all 3 delays if the matched objects (a triangle and square, O1 and O2) were presented to the left side of the animal (for 5 s delay, $F_{3,5} = 5.091$, $p = 0.017$; 10 s delay, $F_{3,6} = 5.432$, $p = 0.014$; 15 s delay, $F_{3,4} = 6.020$, $p = 0.008$). At delays of 5 and 10 s (minimum and intermediate), the differences were significant only for 2 paired cross side comparisons (O1R > O1L and O1R > O2L; $p < 0.05$) suggesting that the female had a preference for the matched object on the left side. At a 15 s (maximum) delay, the MRL was also significantly longer if the square was presented on the right side compared to the triangle on the same side (O1R > O2R, $p < 0.05$). Thus, the direction of the laterality or side preference in female 2 was opposite to that in female 1.

In the male, the MRLs did not significantly depend on the object or its position relative to the animal, regardless of the delay or its duration ($p > 0.05$, for all 4 object x cross side combinations).

In conclusion, both female fur seals displayed behavioral lateralization in the MRLs for the preferred side of the matched object: the MRL was shorted if the object was presented from one side compared to the opposite side, while the direction in two animals was opposite.

Sleep deprivation and recovery—During TSD both females retained the same directions of laterality in respect to the MRL at all delays: female 1 responded faster to the matched object from the right side, and female 2-to the object from the left side (Fig. 5B). In female 1, the behavioral lateralization reached the level of significance for the minimum delay of 5 s ($F_{3,8} = 4.051$, $p = 0.018$), and it was significant for all 3 delays (15 s, $F_{3,8} = 14,560$, $p < 0.001$ and for 25 s, $F_{3,8} = 7.440$, p < 0.001) versus 2 delays in baseline. During TSD in female 2, the paired differences between the MRLs were highly significant for all 4 paired cross side comparisons at all 3 delays (each of 2 objects from the left side versus each of 2 objects from the other side; or O1L < O1R, O1L < O2R, and O2L < O1R, O2L < O2R; p ranged between 0.030 and 0.001; after ANOVA, for 5 s, $F_{3,6} = 14.300$, p

< 0.001; for 10 s, $F_{3,6} = 16.26$, $p < 0.001$; for 15 s, $F_{3,6} = 16.18$, $p < 0.001$) versus 1–2 pairs of significant comparison in baseline (see above). Similar to the baseline conditions, regardless of the delay the differences between the MRLs were not significant for 2 matched objects presented from the same side (O1L and O2L, O1R and O2R). There was no evidence that behavioral lateralization as described in the male as was not present in the baseline conditions (Fig. 5A, B).

During the recovery period, the degree of lateralization in females decreased, although the preference (if significant) remained the same (Fig. 5C). In the male there was no indication of lateralization in the MLR during the recovery period (as there was not in the baseline conditions and during TSD).

In conclusion, in the conditions of a 108 h of TSD, both females retained the same direction of behavior lateralization in the MRLs as in the baseline conditions.

Match response latency

Baseline conditions—In all seals in the baseline conditions the MRLs generally increased in parallel with the delay length. The effect of the delay was variable among animals, and it was lateralized in regards of the position of the matched object (Fig. 6A).

Thus, in female 1 the task caused a delay-dependent increase in the MRLs if the matched objects were presented from the left (disliked) side, where the MRLs were longer (a repeated measures ANOVA, large square or O1, $F_{2,5} = 34.608$, $p < 0.001$; small square or O2, $F_{2,5} = 17.178$, $p < 0.001$). The differences between MRLs were highly significant at 5 and 25 s delays (for both squares), 15 and 25 s delays (for the large square), and at 5 and 25 s delays (for the small square; $p < 0.001$). When presented from the right side, the MRLs to the matched objects were not affected by the delay phase (large square, $F_{2,5} = 0.123$, $p = 0.086$; small square, $F_{2,5} = 2.481$, 0.137). In female 2 the task caused a delay-dependent increase in the MRLs only for one matched object, which was a triangle (O1), when presented from the right (disliked) side to the animal ($F_{2,5} = 3.88$, $p < 0.05$).

The male's MRLs increased as the delay duration became longer for all 4 combinations. A delay-dependent effect on the MRL reached the level of significance for one of the matched objects (the circle, O1) regardless of the side of presentation (circle from the right side, $F_{2,5} = 7.511$, $p < 0.01$; circle from the left side, $F_{2,5} = 7.937$, $p < 0.009$), but not for the other (cross from the right side or left side, $p > 0.05$).

In conclusion, in both females, the delay-dependent effect on the MRLs was significant (3 of 4 cases) if the sample was presented from the disliked side, where the MRLs were longer. In the male, the effect was significant only for one matched object.

Sleep deprivation and recovery—During TSD in female 1 the average MRLs were shorter than in the baseline conditions in all cases (4 object-position and 3 delay combinations, Fig. 7). In a half of these cases the decrease was significant ($p < 0.05$, the paired comparisons; after ANOVA; both objects from the right side at a delay of 5 s and both objects from the left side at delays of 15 and 25 s; baseline versus TSD and recovery).

During the recovery period, the MRL did not differ from that during TSD except for one case. The average MRL was significantly less than during TSD ($p < 0.05$).

In female 2 during the period of TSD, the average MRLs in the majority of the cases were less than in the baseline conditions (8 out of 12; Fig. 7). However, only in one of these cases was the effect of experimental conditions significant ($p < 0.05$). Only for one object–side–delay combination (1 out of 12, O2 from the right side at a delay of 15 s) was the average MRL during TSD greater than in the baseline conditions but the effect of experimental conditions on MRL was not significant ($p = 0.270$). In the remaining cases (3 out of 12) the MRLs during baseline and TSD were similar. In the male, the average MRL during TSD, as well as in the recovery period, could be either more or less than the average values in the baseline conditions at the same delays, matched objects and the presentation sides, but the differences were not significant (Fig. 7).

In all fur seals under conditions of TSD and during the recovery period, the MRLs increased with increases in the delay phase, as it did in control conditions (Fig. 6B, C). One-way ANOVA revealed that in female 1 during TSD and recovery periods the delay-dependent effect on the MRL was less expressed than during baseline (based on the number of significant combinations). In female 2 and in the male this was opposite.

In conclusion, during the period of TSD, the average MRLs in a visual DMTS task in two of the 3 fur seals studied were not significantly different from that in the baseline conditions. In the third fur seal, in half of the cases, the MRLs were significantly less than in control conditions for the same delays and the positions of the matched objects. In all animals under conditions of deprivation and the recovery period, the MRLs increased with increasing the delay phase, as it did in control conditions.

Discussion

DMTS test as a tool to study working memory

A DMTS task is one of the most commonly used tools to evaluate working memory (e.g., Adamson et al. 2000; Daniel et al. 2016; Hahn and Rose 2020). In our study, we used a simple form of the task with a minimum number of objects. This is a visual alternative or two-image test. Working memory span can be measured by changing the difficulty of the task through changing only one parameter, the delay. In primates and humans, studies of working memory often implies more complex tasks, including multi-image, a series of "matching" and "dismatching" tasks, etc. (Adamson et al. 2000; Porrino et al. 2005; Hoffman et al. 2009; Lind et al. 2015; Peng et al. 2020). Such modifications affect workloads on different cognitive functions (such as memory, spatial visual discrimination, attention). Several different tests based on a delayed-matching paradigm have been also used to measure working memory in the rodent models (e.g., the T-maze, 5-choice-based operant, or radial arm water maze task). They measure the ability of animals to retain visual–spatial information (Piérard et al. 2007; Alhaider et al. 2010; Teutsch and Kätzel 2019).

Differences among species in memory spans

Lind and colleagues (Lind et al. 2015) compared performance in a DMTS task in 25 species from the honey bee to chimpanzee and dolphin based on the rate of performance decline with delay increase. The list of top 10 performing species included the dog, dolphin, sea lion, rat, primates and even one corvid, but the order was different depending on how the performance was measured: the average values for different species for all independent studies (from 1 to 18/species) or the best performance reported for each species. The authors were not able to reach a conclusion about species differences. Overall, the data suggested working memory spans in animals ranged from a few seconds to several minutes, and the spans in mammals were generally greater than in other species. As suggested among the reasons which could explain the differences between the animals were "extensive training", the biological significance of the stimuli, and the experimental conditions. In other words, the lack of a standard methodology for conducting such comparative studies. The effect of sleep deprivation on performance in DMTS task was not the subject of any of these studies.

Performance of fur seals in a DMTS task: overall percentage errors

Taking into account the above considerations, we selected 3 studies in which a visual DMTS task was used in mammals in similar conditions and compared their performance in the two-object trials with that in fur seals. Those species are the baboon, rhesus monkey and Californian sea lion. As follows from the published data, juvenile baboons in a two-object DMTS task maintained 80% correct responses for delays of 4 s, and between 65% and 75% for delays of 8 and 16 s (Rodriguez et al. 2011). This was comparable with performance of fur seals in the baseline conditions in our study: for 3 seals on average 84% of correct responses (or 16% of errors) for a delay of 5 s and 76% correct responses (24% of errors) for delays of 10–15 s. In rhesus monkeys, the average percentage of correct reactions at delays from 1 to 15 s was above 90% (Porrino et al. 2005). This was close to that of the best of our fur seals for a delay of 5 s (94%). For delays from 20 to 25 s, the average percentage of correct responses in the monkeys was below 80%. Only one of our fur seals showed this high a performance at a delay of 15 s. However, at the end of experiments, the performances of fur seal 1 at delays from 5 to 25 s, were as high as the average for monkeys. Based on the available data, the rate of decline in accuracy with delay increase (or the delay response dependency) was comparable: 15% per 10 s delay increase (from 4 to 8–16 s) in the baboons, 10–15% per 15 s (from 5 to 20–25 s) in the rhesus monkeys, and 8% per 10 s (from 5 to 15 s) in fur seals as determined in our study.

Matching visual performance for a pair of sample objects was measured in a juvenile California sea lion (Pack et al. 1991), which belongs to the Otariidae family as the fur seal does. The sea lion maintained performance in a DMTS task at a level of 78% correct responses or better for delays of up to 45 s. The performance of the baboons and rhesus monkey at longer (> 15 s) delays appeared to be less accurate than that in the sea lion. Only one of our fur seals was tested at delay of 25 s. While in the baseline conditions, this animal at this delay made random selections, during the recovery period (that is after about additional 5 days of training) it performed on average at a level of 85%. This was less accurate than in the sea lion. However, we did not perform "extensive training" and started

TSD when the fur seals performed at the overall level of 70%, while in the sea lion, the training was continued until the 90% correct response level.

Thus, we conclude that performance of northern fur seals, baboons, rhesus monkeys and one California sea lion in a DMTS task as measured by the percentage of correct responses can be considered quite comparable in similar delays, although the rate of degradation in accuracy with delay increase (or the delay response dependency) was not exactly the same in all species.

Performance of fur seals in a DMTS task: behavioral lateralization

Behavioral lateralization may result from functional asymmetry of the cerebral hemispheres with one hemisphere specializing in particular tasks more than the other. Functional asymmetry increases cognitive capacity allowing different functions that are executed simultaneously on the left and right sides of the brain and avoiding duplication (Rogers 2021). Both acute and chronic stress and emotional state can affect different forms of lateralization most often enhancing behavioral lateralities which are linked specifically to the right hemisphere, such an emotional image recognition task, left-sided head turning in response to a loud stressful auditory sound or earlier life separation (Ocklenburg et al. 2016; Mundorf et al. 2020; Berretz et al. 2020). However, other studies reported a shift toward ambilaterality after an acute stress and a lower laterality index in the chronically stressed animals (Boulinguez-Ambroise et al. 2020; Salgirli et al. 2023).

In our study behavioral lateralization was observed clearly in 2 out of 3 fur seals, while they performed on a DMTS task. The asymmetry was measured by the percentage of errors and MRLs which could depend on the object or the side of its presentation to the animal. The lateralization of both parameters was most pronounced at the longest delays (during the most difficult tasks) when the females made many mistakes. The bias in two females was opposite and the pattern of lateralization of two parameters was not exactly the same particularly in female 1 (namely, it made more errors when one of two objects was presented as the object to match from the right side but it reacted slowly to both objects on the left side).

Both lateralizations in fur seals could be a sensory asymmetry. Thus, human subjects and animals were shown to display an ocular preference for the left eye when looking at emotionally significant and novel objects and for the right eye when looking at familiar objects, implying content-related differences between the cortical hemispheres in analysis of the visual images (Austin and Rogers 2007; Farmer et al. 2010; Braccini et al. 2012; Yeater et al. 2014; Ocklenburg et al. 2016). This type of lateralization usually has a population-based nature. However, the degree of laterality may decrease when the animals became more familiar with the environment or more trained on a task, which imply a role of learning and emotionality on the expressions of laterality (Sankey et al 2011; Rogers 2021).

The lateralization of MRLs in fur seals could be also a motor asymmetry, such as a form of left–right paw preference (Austin and Rogers 2007; Salgirli et al. 2023). The motor laterality is most often individual-level asymmetry. At the population level, the ratio of left- and right-sided individuals may be equal or shifted to one direction (Rogers 2021). Lateralized motor behavior was described in marine mammals. In pinnipeds it is present in

Californian sea lions (Wells et al. 2006) and in northern fur seals (Pryaslova et al. 2009b) as a preference for swimming rotation in pools in a clockwise or counterclockwise direction. The bias was linked to the animals' sex but it seemed to be opposite in the two species: a counterclockwise direction in male fur seals and a clockwise direction in females, and vice versa in Californian sea lions. The strength of preference for the direction of circling in fur seals was so strong that two animals, when housed together in one small pool, continued to follow their preferred direction of swimming. In agreement with our prior data, both studied female fur seals displayed a preference for swimming in a clockwise direction and the male had a preference for swimming in a counterclockwise direction. Therefore, it appears that the behavioral lateralization in a DMTS task in the studied fur seals were not related to their preference of swimming in a clock or counterclockwise direction. In cetaceans, the direction of circular swimming may be a population level asymmetry, while the strength of laterality may depend on the environmental conditions (Sobel et al. 1994; Stafne and Manger 2004; Lyamin et al. 2007).

Performance in a DMTS task: match response latency

Performance in a DMTS task in primates as measured by the MRLs was evaluated regardless of the object's position relative to the animals. In rhesus monkeys, the task produced a delay dependent increase in MRLs irrespective of the number of comparison objects (Porrino et al. 2005). For 2 items, an increase of delay from 1–5 to 20–25 s resulted in an increase in average latency by about 15–20%. In baboons, the match response latency increased as the delay interval increased. However, the difference was significant only for delays between 1 and 16 s versus no delay task (Rodriguez et al. 2011). No data on the MRLs was reported in the studied Californian sea lion (Pack et al. 1971).

An evident lateralization in the MRLs for the side of presentation was recorded in both female fur seals, while no clear lateralization pattern was recorded the male. It is interesting that in the females, with delay increase the MRLs clearly increased only for the non-preferred side of the object to match. We are not familiar with such cases in cognitive tests in other animal studies. It is also difficult to know if this lateralization was linked to the sex of fur seals as it was the direction of swimming (Pryaslova et al. 2009b), because the number of animals was too small. Thus, in primates, sea lions and fur seals performance in DMTS test (as measure by MRL) degraded with delay increase but in fur seals the decrease could be limited to the "disliked" object and the sides of presentation.

TSD procedure and estimate the amount of residual sleep

In this study TSD in fur seals appeared to be effective. Regardless the differences among the animals (they will be discussed later), the progressive increase in the number of attempts to assume the characteristic sleep posture in the water, as well as a rebound of the resting behavior on the first recovery day suggest that sleep pressure increased in all fur seals (especially in seals 1–2, these were females), while sleep deficit was building up. According to our estimate, on day 4 of TSD, fur seals could spend no more than 12 min on average in a characteristic sleep position. This is somewhat more than our estimate for the prior study when we examined the effect of TSD on the fur seals performance in a visual discrimination task (Lyamin et al. 2015). However, we believe that in both cases, SWS

was almost completely excluded during TSD, and episodes of EEG slow waves could only be short and low-voltage. Based on the EEG studies, during the first minutes in the sleep position in the water, the seals were awake while continuing extensive grooming, although the intensity of movement progressively decreased. Slow waves in the EEG did not develop instantly in this position, but usually within 10–20 min (Fig. 2B). In this study, the sleep position was interrupted in almost all cases within 30 s. Even if we assume that under conditions of TSD the latency of slow waves was reduced, then such episodes of microsleep could not exceed 20–30 s per attempt, or on average less than 0.6% or 0.9% of 24 h. This approach is a large overestimate the maximum amounts of SWS in fur seals in this study. Even with this estimate these amounts would be less than 1/20th of the amount of SWS reported for captive fur seals of similar age in the prior EEG studies (e.g., 23.7 ± 3.0, $n = 7$, Lyamin and Mukhametov 1998; 21.0 ± 2.1, $n = 4$, Lyamin et al. 2008; 19.4 ± 0.8 of 24 h, $n = 4$, Lyamin et al. 2018). In addition, EEG slow waves were asymmetrical and the EEG power could only be low in comparison with the usual bilateral and unihemispheric SWS in this species. REM sleep was totally excluded during the period of TSD.

Effect of sleep deprivation on performance in working memory tests: human and animal studies

In prior human studies of visual working memory as evaluated by a DMTS task, it was often concluded that TSD generally decreased accuracy and increased reaction times (e.g., Lieberman et al. 2002; Habeck et al. 2004; Alhola and Polo-Kantola 2007). Later studies rather emphasized specific effects of TSD on different components of cognition, including attention, vigilance and visual working memory (e.g., no effect on working capacity and negative impact on filtering efficiency, Drummond et al. 2012; compromised retrieval, while the object information remained intact, Wee et al. 2013; impacted encoding new memories, while retrieval mechanisms remained unaffected, Cousins and Fernández 2019). Working memory may be affected by changes in mood, increased fatigue, stress and other altered brain conditions that were originally caused by sleep deprivation (e.g., Alhola and Polo-Kantola 2007; Xie et al. 2019; Kim et al. 2022; Siegel 2001, 2021).

In agreement with the results of human studies, the majority of animal studies reported cognitive impairment with sleep deprivation through using a number of working memory tests including those which measure the ability to retain visual–spatial information (Piérard et al. 2007; Alhaider et al. 2010). However, some reports demonstrated that sleep deprivation is not necessarily accompanied by a decrease in cognitive processes, including memory, and rather may even suggest improvement (Vaseghi et al. 2021; Hunter 2019). It seems that the outcome of TSD in animal as in human studies may be attributed to many factors including differences in the type of memories tested, complexity of the tasks, stage of sleep, and the experimental protocols. This has been discussed in the literature (see above). When initiating this study, we intended to continue evaluating the effects of TSD on cognitive performance of the northern fur seal, a non-laboratory animal with unusual sleep phenomenology (unihemispheric sleep, reduction of REM sleep in water; Lyamin et al. 2017, 2018) and biological cycle (long range migrations), and performance of a laboratory animal with the sleep pattern, resembling the sleep in humans while using the same cognitive test. Following our prior studies on the effects of TSD on discriminant processes (Lyamin et al. 2015) we

believe that DMTS task is a good tool to examine working memory and to compare the results of these studies with those in other mammals.

We have so far found that under the conditions of TSD, apart from human studies, a DMTS test has been used to study cognitive functions only in rhesus monkeys (Porrino et al. 2005; Deadwyler et al. 2007). In agreement with the majority of the human studies, the primate studies reported impairment effects of TSD on performance in a DMTS test in the rhesus monkey. For instance, 30–36 h of TSD significantly reduced overall DMTS performance (in baseline conditions $75\% \pm 0.3\%$, during TSD—$62.7\% \pm 2.5\%$; $p < 0.001$ for all delays and number of objects; Porrino et al. 2005). The effect of TSD on performance was not different with respect to delay with an increased number of images. On average, it accounted for a 10% decrease in the percentage of correct choices and a 18% increase in the MRL in trials with the same delays and number of objects (from 2 to 6 images). The same is true for the most often reported effects of TSD on performance in different visual–spatial memory test in the rat and mice models, while they employed a longer delay phase than in a usual DMTS task (e.g., Piérard et al. 2007; Alhaider et al. 2010).

Effect of sleep deprivation on performance of fur seals in a DMTS task

Our data suggest that a 108-h TSD did not impair the fur seals' performance in DMTS test as measured by the overall percentage of errors. On the contrary, during TSD both female fur seals performed better than in baseline conditions, especially for long delays. All 3 animals, including the male, continued to improve over the recovery period. In addition, during TSD the average MRLs in two of the 3 fur seals studied were not different from those in non-deprived conditions. In the third fur seal, in half of the cases, the MRLs were significantly less during TSD than in the baseline conditions for the same delays and the positions of the match objects. This is opposite of what has been reported for rhesus monkeys subjected to 30–36 h of TSD, in which the percentage of correct response significantly decreased during TSD regardless of the number of objects and delay time. The MRLs in the task in rhesus monkeys also increased during TSD for the respected number of images. The increase was significant for 3 and more images (Porrino et al. 2005; Deadwyler et al. 2007).

In this study we also used parameters of behavioral lateralization (asymmetry) to characterize the performance of fur seals in a DMTS task, including the direction and the strength. Lateralization can be sensitive to a variety of factors (discussed above). Over the period of TSD the behavioral lateralization with respect to the percentage of errors was retained only in one of the two females; however, the "disliked" matched object became different. The preference for one object faded in the other female, which substantially improved the overall performance in comparison with the baseline conditions. In the third animal, a preference for one object became significant during TSD, while it was not evident in the baseline conditions. Thus, we concluded that the directions of changes of this lateralization pattern in 3 fur seals were not consistent, although there was a general trend toward a decrease in the strength of the lateralization during the entire period of experiments (background, deprivation and control). There is no reason to suggest any impact of experimental conditions (TSD or following recovery period) on this type of lateralization

as measured by the percentage of errors, regardless of the type of such asymmetry (sensory or motor). The degree of lateralization was minimal during the recovery period in each fur seal during peak performance. This is consistent with the data that extensive training may reduce the expression of motor asymmetry (Sankey et al 2011; Rogers 2021).

The degree of behavioral asymmetry as measured by MRLs was higher than by percentage of errors. As for the MRL, in the conditions of a 108 h of TSD, both females retained the same direction of behavior lateralization for selecting the matched object as in the baseline conditions. The degree of asymmetry of the MRL during TSD in the females was comparable with that during baseline, but it decreased during the recovery period suggesting that the strength of the asymmetry was linked to the level of training on the task. No preference of this sort was recorded in the male. Therefore, there is no reason to suggest any specific impact of experimental conditions (TSD or recovery period) on this type of lateralization as well.

Sleep deprivation in humans and rodents may or may not be accompanied by acute or chronic stress. The outcome is primarily determined by the nature of the sleep deprivation procedure, while moderated by other variables, such as sex and age (e.g., Nollet et al 2020). Stress itself can affect cognitive functions (e.g., Shields et al. 2016; Kulshreshtha et al. 2023), as well as the degree and direction of behavioral lateralization (Ocklenburg et al. 2016). We did not measure cortisol in fur seals in this study and we cannot say anything about stress levels in fur seals under the conditions of TSD. However, regardless of the stress level a 108-h TSD did not affect the performance of fur seals in a visual DMTS test based on the parameters we used (percentage of errors, response latency and behavioral lateralization). This is different from the results of studies in primates and in humans which reported a detrimental effect of sleep deprivation on working memory (Porrino et al. 2005; Deadwyler et al. 2007; Lieberman et al. 2002; Habeck et al. 2004; Alhola and Polo-Kantola 2007).

Among non-laboratory animals, cognitive performance under conditions of reduced sleep has been evaluated in several species. The first group of studies reported that sleep loss impaired cognitive performance, e.g., auditory discrimination in European starlings (*Sturnus vulgaris*, Brawn et al. 2010), reversal learning in Australian magpies (*Cracticus tibicen*, Johnsson et al. 2022), or avoidance learning in zebrafish (*Danio rerio*, Pinheiro-da-Silva et al. 2018). However, in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*), which is one of the migratory avian species, accuracy and response times on a repeated-acquisition task during the migratory period was as high in the migratory period as in the non-migratory time. This level of performance was maintained despite the fact that birds slept about 70% less at this time compared to pre-migratory conditions (Rattenborg et al. 2004). The ability to maintain auditory and visual vigilance was also tested in the bottlenose dolphin (*Tursiops truncatus)* under experimental conditions of continuous vigilance, that is of reduced sleep time. As reported, the dolphins were able to maintain a high level of performance for at least 120 h (Ridgway et al. 2009). Despite the obvious analogies between the results of the sparrow, dolphin and our studies, both the reduction in sleep time and the complexity of the evaluated cognitive functions were quite different. At the same time, the results of all these

studies clearly support the idea that sleep deprivation or restriction does not necessarily have to be accompanied by cognitive impairment in all animals.

The benefits of using the same methodologies to test cognition between the animal groups may be affected by the ecological relevance of the test, and by the difficulty of the task for the tested species. Vision is among the most important sensory systems in pinnipeds, which, unlike cetaceans, do not have echolocation. The visual system of the northern fur seals is highly efficient both in water and on land based on visual acuity, capabilities to precisely aim visually driven behavior, as well as by the well-developed visual brain centers (Mass and Supin 2018). In addition, while sleeping unihemispherically in the water, fur seals appear to use vision to monitor the environment for predators by directing the open eye toward the water from where they expect danger (Lyamin et al. 2017; Kendall-Bar et al. 2018). Therefore, there is no reason to consider that visual DMTS task (as a measure of working memory) ecologically irrelevant for the northern fur seals. In future studies, it would be interesting to evaluate the effect of TSD on the performance of fur seals in a DMTS task with other modalities, such as auditory and olfactory. Regarding the difficulty of the task, it was delay-dependent. The fur seals completed the task well at minimal delays but acted mostly randomly at the longest delays, suggesting the DMTS task at these delays was quite difficult. It is clear that the number of images is another parameter which makes the task more difficult and controls performance in the same manner as the delay. In rhesus monkeys a 36-h TSD was found to produce significant impairment of animal performance regardless of the number of images (from 2 to 6, Porrino et al. 2005). In our study, three times longer TSD in fur sea seals did not impair performance in a 2-choice DMTS task. Without questioning the importance of factors of ecological relevance and difficulty of the task, duration of TSD and parameters of the DMTS task, we see an obvious difference between the results of our studies in fur seals and currently available data in primate and human subjects which used a similar methodology.

In this study cognitive performance of fur seals in a DMTS task varied clearly between the fur seals. Female 1 was the leader at all 3 stages of the experiment. She demonstrated the most improvement over the study period for all delays, including during TSD. The largest number of errors in all experimental conditions was made by the male. He improved performance only for a minimum delay. Differences between the animals first appeared at the training stage, as individual preference of the matching objects and the side of their presentation. The male took longer to learn the task, consistently opting for either one of the two figures or a particular side of presentation for several days. The pairs of figures were selected individually, and it is possible that the percentage of correct responses at all stages of the experiment was linked to the degree of differences between the figures. In females, the figures differed more in area than in the male. Of the two females, the one whose figures differed more performed better. Second, both females made fewer errors than the male did. The females' training period was shorter. Therefore, differences between the seals could be related to sex as well as it is for the direction of rotation in the water (Pryaslova et al. 2009b). The time of year when the experiments were conducted could be a third reason. For females, it was summer, a warmer season and the middle of the land period, when fur seals spend most of their time on land while molting and breeding. In the male, the experiments were conducted in the fall, during a colder time and the migratory period. It appeared he

had less sleep pressure during the period of TSD. His rebound of resting behavior was minimal and limited to the 1st day, while on the 2nd day, he swam almost continuously. In our prior studies we recorded such periods of prolonged activity in captive fur seals and walruses (Pryaslova et al. 2009a, b). They may be similar to restlessness in birds during the migration season (Rattenborg et al. 2004). Thus, differences in fur seal performance in a DMTS task could be determined not only by the individual characteristics of the animals (preference and sex), but also by the degree of differences between the matching objects (difficulty of the task at the stage of discrimination), as well as by the season during which the experiments were conducted. Given the small total number of animals studied, we cannot say to what extent each of these factors affected the fur seal performance in a visual DMTS task. It is possible that additional experiments (or increasing the sample size) will detect some evidence for impaired performance in the same test in another group of fur seals. This would mean that performance of fur seals in a visual DMTS task does not primarily depend on TSD, but suggest the role of some other factors, which may or may not be related to the TSD procedure.

In conclusion, the main result of this study reveals that a 108-h TSD did not adversely affect the performance of fur seals in a visual DMTS task, as determined by the overall percentage of errors and MRLs. Furthermore, TSD did not change the direction and the strength of two behavioral lateralizations. Over the course of the study, northern fur seals continuously improved their ability to perform this task. These findings suggest that TSD did not interfere with cognitive processes in northern fur seals, such as working memory, learning and visual discrimination. We also suggest that different animal species, especially those that are forced to change behavioral strategies (such as fur seals switching annually from the terrestrial to aquatic style of life and birds between non-migratory and migratory states), are much more resistant to the effects of sleep deprivation than animals living in more stable conditions (such as primates and rodents).

Acknowledgements

Data availability

Data used in this study are available on request.

References

Adamson C, Foster TM, McEwan JS (2000) Delayed matching to sample: the effects of sample-set size on human performance. Behav Processes 49:149–161. 10.1016/s0376-6357(00)00087-5 [PubMed: 10922528]

Alhaider IA, Aleisa AM, Tran TT, Alzoubi KH, Alkadhi KA (2010) Chronic caffeine treatment prevents sleep deprivation-induced impairment of cognitive function and synaptic plasticity. Sleep 33:437–444. 10.1093/sleep/33.4.437 [PubMed: 20394312]

Alhola P, Polo-Kantola P (2007) Sleep deprivation: Impact on cognitive performance. Neuropsychiatr Dis Treat 3:553–567 [PubMed: 19300585]

Austin NP, Rogers LJ (2007) Asymmetry of flight and escape turning responses in horses. Laterality 12:464–474. 10.1080/13576500701495307 [PubMed: 17712716]

Banks S, Dinges DF (2007) Behavioral and physiological consequences of sleep restriction. J Clin Sleep Med 3(5):519–528 [PubMed: 17803017]

Berretz G, Wolf OT, Güntürkün O, Ocklenburg S (2020) Atypical lateralization in neurodevelopmental and psychiatric disorders: What is the role of stress? Cortex 125:215–232. 10.1016/ j.cortex.2019.12.019 [PubMed: 32035318]

Boulinguez-Ambroise G, Pouydebat E, Disarbois É, Meguerditchian A (2020) Human-like maternal left-cradling bias in monkeys is altered by social pressure. Sci Rep 10:11036. 10.1038/ s41598-020-68020-3 [PubMed: 32620801]

Braccini SN, Lambeth SP, Schapiro SJ, Fitch WT (2012) Eye preferences in captive chimpanzees. Anim Cogn 15:971–978. 10.1007/s10071-012-0523-9 [PubMed: 22733385]

Brawn TP, Nusbaum HC, Margoliash D (2010) Sleep-dependent consolidation of auditory discrimination learning in adult starlings. J Neurosci 30:609–613. 10.1523/ JNEUROSCI.4237-09.2010 [PubMed: 20071524]

Cousins JN, Fernández G (2019) The impact of sleep deprivation on declarative memory. Prog BrainRes 246:27–53. 10.1016/bs.pbr.2019.01.007

Daniel TA, Katz JS, Robinson JL (2016) Delayed match-to-sample in working memory: a BrainMap meta-analysis. Biol Psychol 120:10–20. 10.1016/j.biopsycho.2016.07.015 [PubMed: 27481545]

Deadwyler SA, Porrino L, Siegel JM, Hampson RE (2007) Systemic and nasal delivery of orexin-A (Hypocretin-1) reduces the effects of sleep deprivation on cognitive performance in nonhuman primates. J Neurosci 27:14239–14247. 10.1523/JNEUROSCI.3878-07.2007 [PubMed: 18160631]

Drummond SP, Anderson DE, Straus LD, Vogel EK, Perez VB (2012) The effects of two types of sleep deprivation on visual working memory capacity and filtering efficiency. PLoS ONE 7:e35653. 10.1371/journal.pone.0035653 [PubMed: 22530064]

Farmer K, Krueger K, Byrne RW (2010) Visual laterality in the domestic horse (Equus caballus) interacting with humans. Anim Cogn 13:229–238. 10.1007/s10071-009-0260-x [PubMed: 19618222]

Gravett N, Bhagwandin A, Sutcliffe R, Landen K, Chase MJ, Lyamin OI, Siegel JM, Manger PR (2017) Inactivity/sleep in two wild free-roaming African elephant matriarchs - does large body size make elephants the shortest mammalian sleepers? PLoS ONE 12:e0171903. 10.1371/ journal.pone.0171903 [PubMed: 28249035]

Habeck C, Rakitin BC, Moeller J, Scarmeas N, Zarahn E, Brown T, Stern Y (2004) An event-related fMRI study of the neurobehavioral impact of sleep deprivation on performance of a delayed-match-to-sample task. Brain Res Cogn Brain Res 18:306–321. 10.1016/j.cogbrainres.2003.10.019 [PubMed: 14741317]

Hagewoud R, Havekes R, Novati A, Keijser JN, Van der Zee EA, Meerlo P (2010) Sleep deprivation impairs spatial working memory and reduces hippocampal AMPA receptor phosphorylation. J Sleep Res 9:280–288. 10.1111/j.1365-2869.2009.00799.x

Hahn LA, Rose J (2020) Working memory as an indicator for comparative cognition - detecting qualitative and quantitative differences. Front Psychol 11:1954. 10.3389/fpsyg.2020.01954 [PubMed: 32849144]

Havekes R, Meerlo P, Abel T (2015) Animal studies on the role of sleep in memory: from behavioral performance to molecular mechanisms. Curr Top Behav Neurosci 25:183–206. 10.1007/7854_2015_369 [PubMed: 25680961]

Hoffman ML, Beran MJ, Washburn DA (2009) Memory for "what", "where", and "when" information in rhesus monkeys (Macaca mulatta). J Exp Psychol Anim Behav Process 35:143–152. 10.1037/ a0013295 [PubMed: 19364223]

Hunter AS (2019) Short-term REM deprivation does not affect acquisition or reversal of a spatial learning task. Behav Processes 169:103985. 10.1016/j.beproc.2019.103985 [PubMed: 31678636]

Johnsson RD, Connelly F, Gaviraghi Mussoi J, Vyssotski AL, Cain KE, Roth TC 2nd, Lesku JA (2022) Sleep loss impairs cognitive performance and alters song output in Australian magpies. Sci Rep 12:6645. 10.1038/s41598-022-10162-7 [PubMed: 35459249]

Kendall-Bar JM, Williams TM, Mukherji R, Lozano DA, Pitman JK, Holser RR, Keates T, Beltran RS, Robinson PW, Crocker DE, Adachi T, Lyamin OI, Vyssotski AL, Costa DP (2023) Brain activity of diving seals reveals short sleep cycles at depth. Science 380:260–265. 10.1126/science.adf0566 [PubMed: 37079694]

Kendall-Bar JM, Vyssotski AL, Mukhametov LM, Siegel JM, Lyamin OI (2018) Eye state asymmetry during aquatic unihemispheric slow wave sleep in northern fur seals (Callorhinus ursinus). PLoS ONE 14(5):e0217025. 10.1371/journal.pone.0217025

Kim T, Kim S, Kang J, Kwon M, Lee SH (2022) The common effects of sleep deprivation on human long-term memory and cognitive control processes. Front Neurosci 16:883848. 10.3389/fnins.2022.883848 [PubMed: 35720688]

Kulshreshtha A, Alonso A, McClure LA, Hajjar I, Manly JJ, Judd S (2023) Association of stress with cognitive function among older black and white US adults. JAMA Netw Open 6(3):e231860. 10.1001/jamanetworkopen.2023.1860 [PubMed: 36881411]

Leong RLF, Chee MWL (2023) Understanding the need for sleep to improve cognition. Annu Rev Psychol 74:27–57. 10.1146/annurev-psych-032620-034127 [PubMed: 35961036]

Lesku JA, Rattenborg NC, Valcu M, Vyssotski AL, Kuhn S, Kuemmeth F, Heidrich W, Kempenaers B (2012) Adaptive sleep loss in polygynous pectoral sandpipers. Science 337:1654–1658. 10.1126/science.1220939 [PubMed: 22878501]

Lieberman HR, Tharion WJ, Shukitt-Hale B, Speckman KL, Tulley R (2002) Effects of caffeine, sleep loss, and stress on cognitive performance and mood during U.S Navy SEAL training. Sea-Air-Land Psychopharmacology (berl) 164:250–261. 10.1007/s00213-002-1217-9 [PubMed: 12424548]

Lind J, Enquist M, Ghirlanda S (2015) Animal memory: a review of delayed matching-to-sample data. Behav Processes 117:52–58. 10.1016/j.beproc.2014.11.019 [PubMed: 25498598]

Lyamin OI, Mukhametov LM (1998) Organization of sleep in the northern fur seal. In: Sokolov VE, Aristov AA, Lisitzina TU (eds) The Northern Fur Seal. Systematic, Morphology, Ecology, Behavior. Nauka, Moscow, pp 280–302

Lyamin OI, Mukhametov LM, Siegel JM (2017) Sleep in the northern fur seal. Curr Opin Neurobiol 44:144–151. 10.1016/j.conb.2017.04.009 [PubMed: 28505502]

Lyamin O, Pryaslova J, Kosenko P, Siegel J (2007) Behavioral aspects of sleep in bottlenose dolphin mothers and their calves. Physiol Behav 92:725–733. 10.1016/j.physbeh.2007.05.064 [PubMed: 17599365]

Lyamin OI, Kosenko PO, Lapierre JL, Mukhametov LM, Siegel JM (2008) Fur seals display a strong drive for bilateral slow-wave sleep while on land. J Neurosci 28:12614–12621. 10.1523/JNEUROSCI.2306-08.2008 [PubMed: 19036955]

Lyamin OI, Korneva SM, Obukhova ED, Mukhametov LM, Siegel JM (2015) Evaluation of the ability of northern fur seals to perceive and visually discriminate images under the conditions of sleep loss. Dokl Biol Sci 463:211–214. 10.1134/S0012496615040080 [PubMed: 26335972]

Lyamin OI, Kosenko PO, Korneva SM, Vyssotski AL, Mukhametov LM, Siegel JM (2018) Fur seals suppress REM sleep for very long periods without subsequent rebound. Curr Biol 28:2000–2005.e2. 10.1016/j.cub.2018.05.022 [PubMed: 29887309]

Mass AM, Supin AY (2018) Vision. In: Würsig B, Thewissen JGM, Kovacs KM (eds) Encyclopedia of Marine Mammals (Third Edition). Academic Press, London

Mundorf A, Matsui H, Ocklenburg S, Freund N (2020) Asymmetry of turning behavior in rats is modulated by early life stress. Behav Brain Res 393:112807. 10.1016/j.bbr.2020.112807 [PubMed: 32673705]

Nollet M, Wisden W, Franks NP (2020) Sleep deprivation and stress: a reciprocal relationship. Interface Focus 10:20190092. 10.1098/rsfs.2019.0092 [PubMed: 32382403]

Ocklenburg S, Korte SM, Peterburs J, Wolf OT, Güntürkün O (2016) Stress and laterality - The comparative perspective. Physiol Behav 164(Pt A):321–329. 10.1016/j.physbeh.2016.06.020 [PubMed: 27321757]

Pack AA, Herman LM, Roitblat HL (1991) Generalization of visual matching and delayed matching by a California sea lion (Zalophus californianus). Anim Learn Behav 19:37–48. 10.3758/BF03197858

Peng Z, Dai C, Cai X, Zeng L, Li J, Xie S, Wang H, Yang T, Shao Y, Wang Y (2020) Total sleep deprivation impairs lateralization of spatial working memory in young men. Front Neurosci 14:562035. 10.3389/fnins.2020.562035 [PubMed: 33122988]

Piérard C, Liscia P, Philippin JN, Mons N, Lafon T, Chauveau F, Van Beers P, Drouet I, Serra A, Jouanin JC, Béracochéa D (2007) Modafinil restores memory performance and neural activity impaired by sleep deprivation in mice. Pharmacol Biochem Behav 88:55–63. 10.1016/j.pbb.2007.07.006 [PubMed: 17698177]

Pinheiro-da-Silva J, Tran S, Luchiari AC (2018) Sleep deprivation impairs cognitive performance in zebrafish: a matter of fact? Behav Processes 157:656–663. 10.1016/j.beproc.2018.04.004 [PubMed: 29656092]

Porrino LJ, Daunais JB, Rogers GA, Hampson RE, Deadwyler SA (2005) Facilitation of task performance and removal of the effects of sleep deprivation by an ampakine (CX717) in nonhuman primates. PLoS Biol 3:e299. 10.1371/journal.pbio.0030299 [PubMed: 16104830]

Pryaslova JP, Lyamin OI, Siegel JM, Mukhametov LM (2009a) Behavioral sleep in the walrus. Behav Brain Res 201:80–87. 10.1016/j.bbr.2009.01.033 [PubMed: 19428620]

Pryaslova YP, Lyamin OI, Mukhametov LM (2009b) Lateralized behavior in northern fur seals. Dokl Biol Sci 425:171–174. 10.1134/S0012496609020252

Rattenborg NC, Mandt BH, Obermeyer WH, Winsauer PJ, Huber R, Wikelski M, Benca RM (2004) Migratory sleeplessness in the white-crowned sparrow (Zonotrichia leucophrys gambelii). PLoS Biol 2:E212. 10.1371/journal.pbio.0020212 [PubMed: 15252455]

Rattenborg NC, Voirin B, Cruz SM, Tisdale R, Dell'Omo G, Lipp HP, Wikelski M, Vyssotski AL (2016) Evidence that birds sleep in mid-flight. Nat Commun 7:12468. 10.1038/ncomms12468 [PubMed: 27485308]

Rechtschaffen A, Gilliland MA, Bergmann BM, Winter JB (1983) Physiological correlates of prolonged sleep deprivation in rats. Science 221:182–184. 10.1126/science.6857280 [PubMed: 6857280]

Ridgway S, Keogh M, Carder D, Finneran J, Kamolnick T, Todd M, Goldblatt A (2009) Dolphins maintain cognitive performance during 72 to 120 hours of continuous auditory vigilance. J Exp Biol 212(Pt10):1519–1527. 10.1242/jeb.027896 [PubMed: 19411545]

Rodriguez JS, Zürcher NR, Bartlett TQ, Nathanielsz PW, Nijland MJ (2011) CANTAB delayed matching to sample task performance in juvenile baboons. J Neurosci Methods 196:258–263. 10.1016/j.jneumeth.2011.01.012 [PubMed: 21276821]

Rogers LJ (2021) Brain lateralization and cognitive capacity. Animals (basel) 11:1996. 10.3390/ani11071996 [PubMed: 34359124]

Salgirli DY, Isparta S, Saral B, Keskin YN, Adıay DM, Töre-Yargın G, Musa SA, Atilgan D, Öztürk H, Kul BC, afak CE, Ocklenburg S, Güntürkün O (2023) Acute and chronic stress alter behavioral laterality in dogs. Sci Rep 13:4092. 10.1038/s41598-023-31213-7 [PubMed: 36906713]

Sankey C, Henry S, Clouard C, Richard-Yris MA, Hausberger M (2011) Asymmetry of behavioral responses to a human approach in young naive vs. trained horses. Physiol Behav 104:464–468. 10.1016/j.physbeh.2011.05.009 [PubMed: 21605580]

Siegel JM (2001) The REM sleep-memory consolidation hypothesis. Science 294:1058–1063. 10.1126/science.1063049 [PubMed: 11691984]

Siegel JM (2021) Memory consolidation is similar in waking and sleep. Curr Sleep Med Rep 7:15–18. 10.1007/s40675-020-00199-3 [PubMed: 34485023]

Shields GS, Sazma MA, Yonelinas AP (2016) The effects of acute stress on core executive functions: a meta-analysis and comparison with cortisol. Neurosci Biobehav Rev 68:651–668. 10.1016/j.neubiorev.2016.06.038 [PubMed: 27371161]

Sobel N, Supin AY, Myslobodsky MS (1994) Rotational swimming tendencies in the dolphin (Tursiops truncatus). Behav Brain Res 65:41–45. 10.1016/0166-4328(94)90071-X [PubMed: 7880453]

Stafne GM, Manger PR (2004) Predominance of clockwise swimming during rest in Southern Hemisphere dolphins. Physiol Behav 82:919–926. 10.1016/j.physbeh.2004.08.001 [PubMed: 15451659]

Teutsch J, Kätzel D (2019) Operant assessment of DMTP spatial working memory in mice. Front Behav Neurosci 13:193. 10.3389/fnbeh.2019.00193 [PubMed: 31507388]

Vaseghi S, Arjmandi-Rad S, Kholghi G, Nasehi M (2021) Inconsistent effects of sleep deprivation on memory function. EXCLI J 20:1011–1027. 10.17179/excli2021-3764 [PubMed: 34267613]

Walker MP, Stickgold R (2004) Sleep-dependent learning and memory consolidation. Neuron 44:121–133. 10.1016/j.neuron.2004.08.031 [PubMed: 15450165]

Wee N, Asplund CL, Chee MW (2013) Sleep deprivation accelerates delay-related loss of visual short-term memories without affecting precision. Sleep 36:849–856. 10.5665/sleep.2710 [PubMed: 23729928]

Wells DL, Irwin RM, Hepper PG (2006) Lateralized swimming behaviour in the California sea lion. Behav Proc 73:121–123. 10.1016/j.beproc.2006.04.004

Wickens CD, Hutchins SD, Laux L, Sebok A (2015) The impact of sleep disruption on complex cognitive tasks: a meta-analysis. Hum Factors 57:930–946. 10.1177/0018720815571935 [PubMed: 25850114]

Xie W, Berry A, Lustig C, Deldin P, Zhang W (2019) Poor sleep quality and compromised visual working memory capacity. J Int Neuropsychol Soc 25(6):583–594. 10.1017/S1355617719000183 [PubMed: 31030699]

Yeater DB, Hill HM, Baus N, Farnell H, Kuczaj SA 2nd (2014) Visual laterality in belugas (Delphinapterus leucas) and Pacific whitesided dolphins (Lagenorhynchus obliquidens) when viewing familiar and unfamiliar humans. Anim Cogn 17:1245–1259. 10.1007/s10071-014-0756-x [PubMed: 24831888]
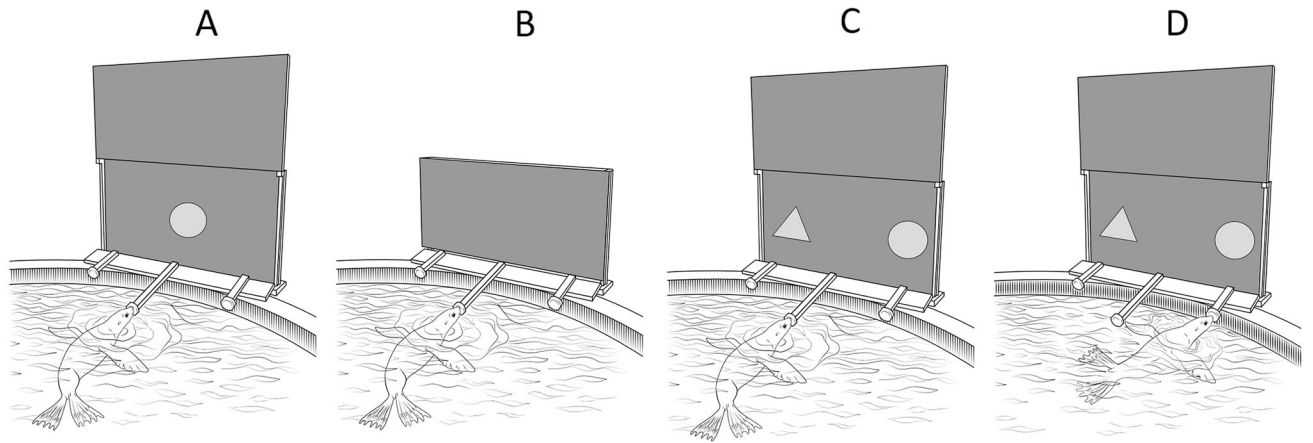
Fig. 1.
Experimental setup. **A** At the start of the trial the sample object was presented to the animal for 3 s. **B** Delay phase lasted 5, 10, 15, 20 or 25 s. **C**, **D** Match phase was followed by the matching object selection (touching the target beneath the object)
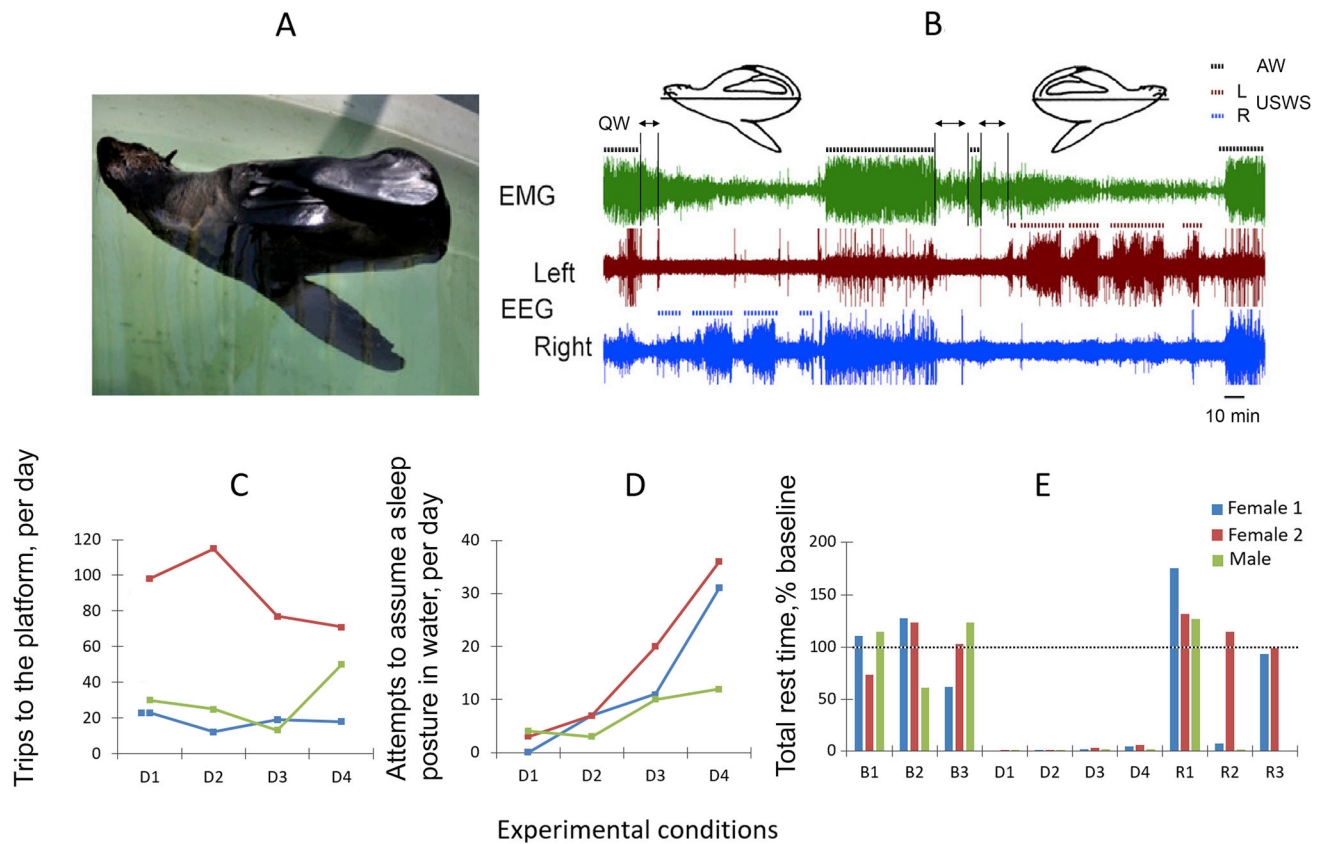
Fig. 2.

Sleep posture in fur seals in water and their behavior during TSD. **A** Characteristic sleep posture in fur seals in water. **B** Polygram of sleep in water in a fur seal. It shows electroencephalogram (EEG) of the left and right hemispheres and electromyogram (EMG) during sleep in the posture on the right or left side. Dotted lines mark episodes of active waking (AW) and unihemispheric sleep (USWS) in the left (L) and right (R) hemispheres. The black arrows mark episodes when the fur seal was in the sleep posture but was awake (QW—quiet waking). The photo and a polygram (modified) are from Lyamin et al. 2018. **C, D** Number of trips of 3 fur seals (two females and one male) from the water to a platform and attempts to assume a sleep posture in the water during the period of TSD. D1–4 are the days of TSD. The numbers for the last 12-h period of TSD are not shown. **E** Total rest time in 3 fur seals during baseline (B), a 108-h total sleep deprivation (D) and in a following recovery period (R). The numbers are days. The recovery period lasted 3 days in the females and 2 days in the male
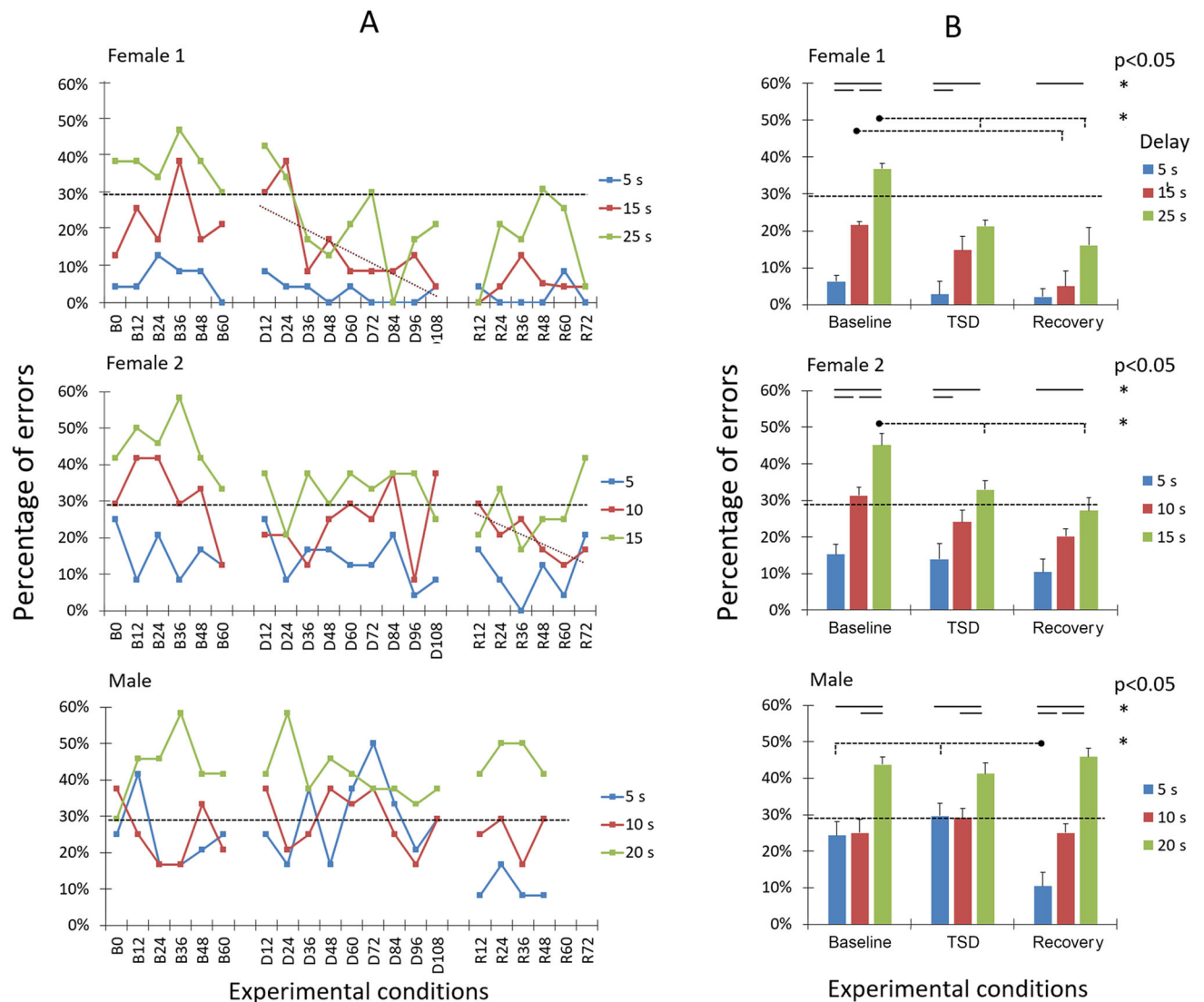
Fig. 3.
Performance of northern fur seals in a DMTS task in different experimental conditions as measured by the overall percentage of errors. **A** Percentage of errors in different experiments in 3 fur seals (female1, female 2 and male) at different delays during baseline (B), a 108-h total sleep deprivation (D) and in a following recovery period (R). Abscissa shows hours from the start of the experimental conditions. The black dotted lines are drawn for the error value corresponding to the percentage of random selection of one of the two items for 24 trials (29.2%). Regression lines are drawn for a significant correlation between the percentage of errors and the experiment number in the series ($p < 0.05$). **B** Overall average percentage of errors ($\pm$ SEM) in 3 fur seals during baseline (B), a 108-h total sleep deprivation (D) and in a following recovery period (R). * Indicates statistically significantly difference (Tukey's post hoc test, $p < 0.05$). Solid lines show significant difference for the delays, and dashed lines for the conditions
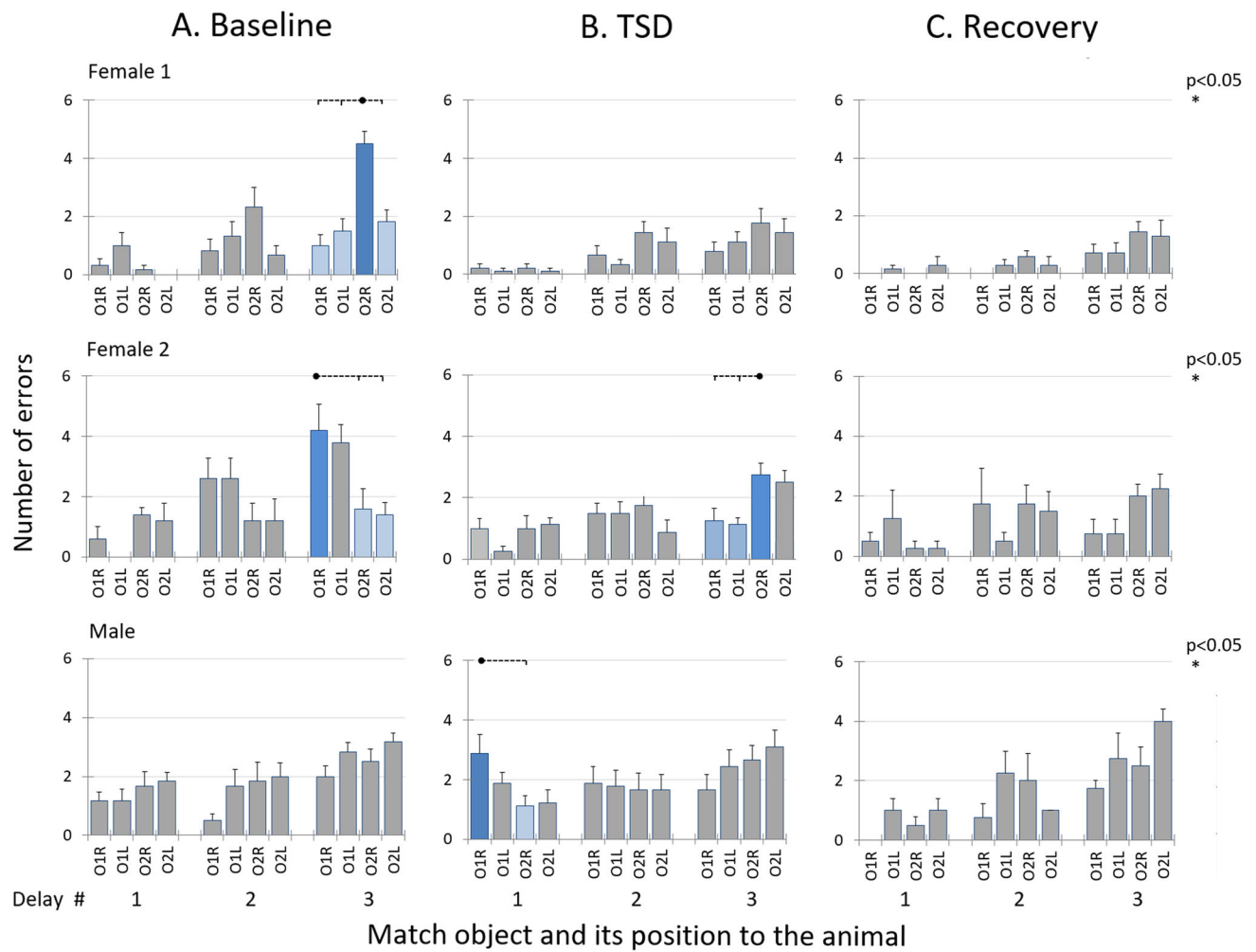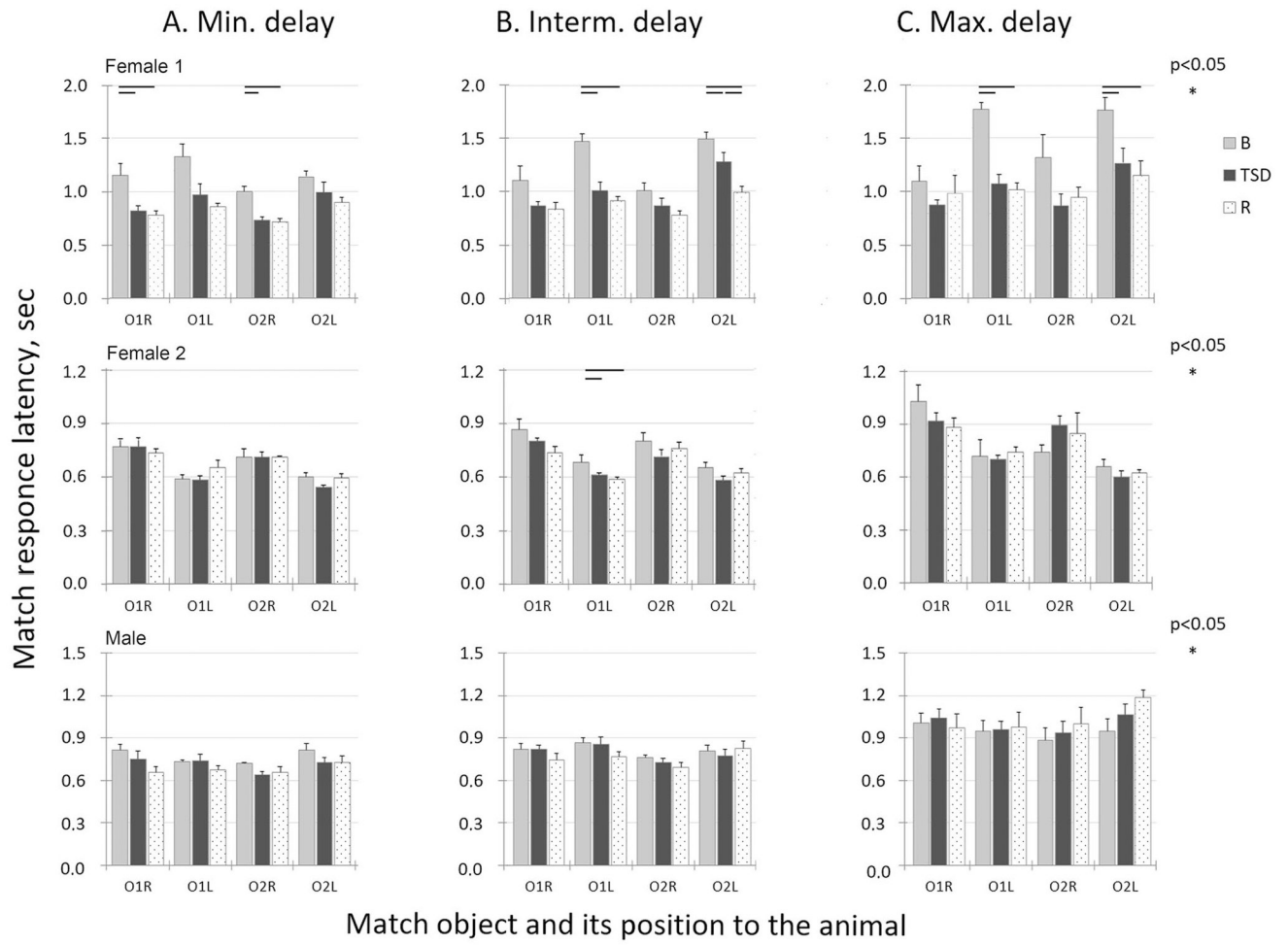
Fig. 4.

Lateralization of the number of errors in fur seals in a DMTS task for different matched objects and their positions to the animals in different experimental conditions. TSD is a 108-h sleep deprivation. Abscissa is the match object and its position to the animal for 3 delays. O1 and O2, the match object 1 and 2; R and L—right or left side relative to the animal. Delays 1, 2 and 3: female 1–5, 15 and 25 s, female 2–5, 10 and 15 s, male—5, 10 and 20 s, respectively. Ordinates are average numbers of errors (± SEM) per experiment (the maximum number was 6). * and blue bar color indicate statistically significantly difference (Tukey's post hoc test, $p < 0.05$). Grey bar color means no difference between the bars ($p > 0.05$)
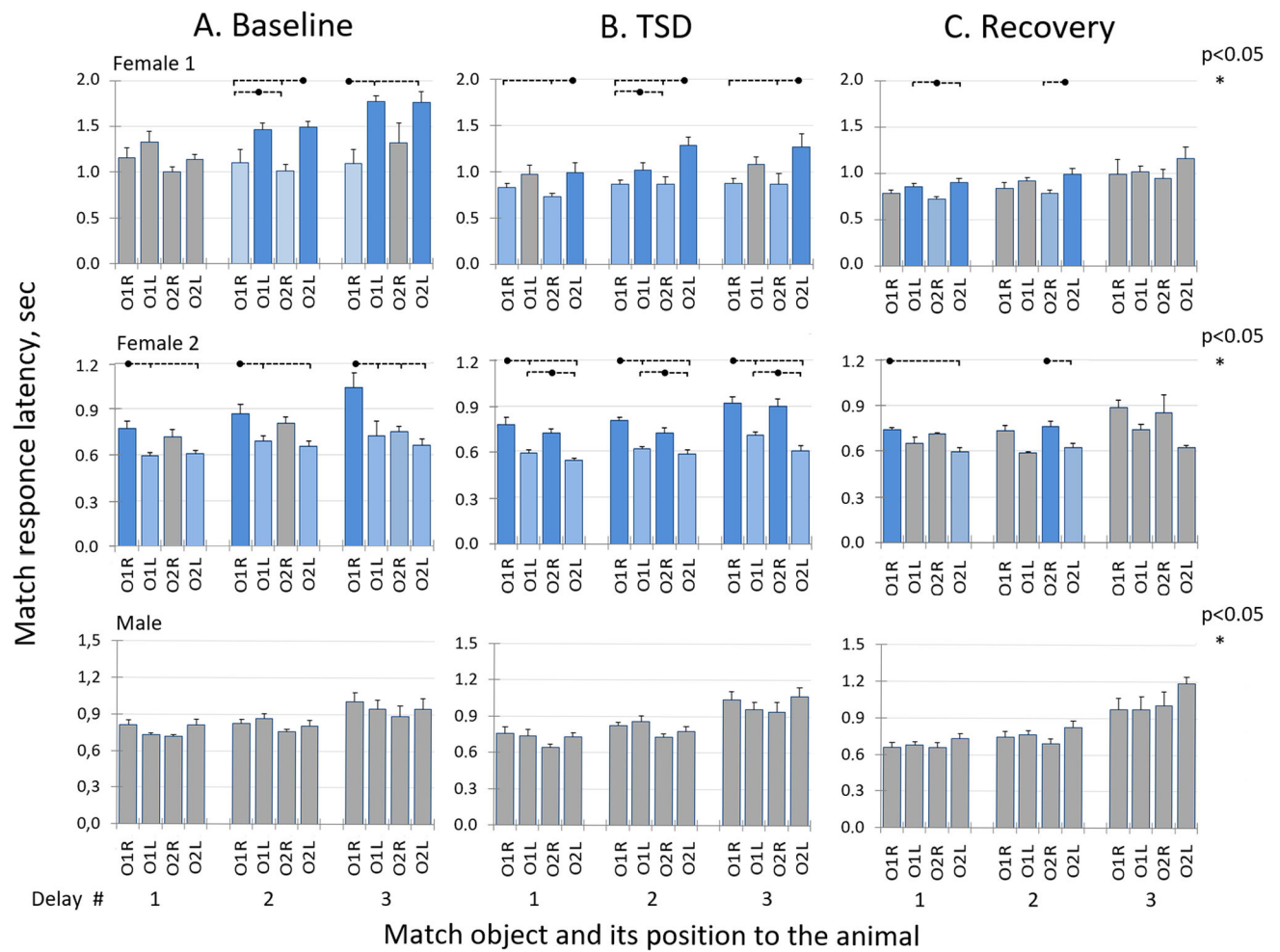
Fig. 5.

Lateralization of the match response latency in fur seals in a DMTS task for different matched objects and their positions to the animals in different experimental conditions. Ordinates are average latencies (± SEM). All other details are same as in Fig. 4
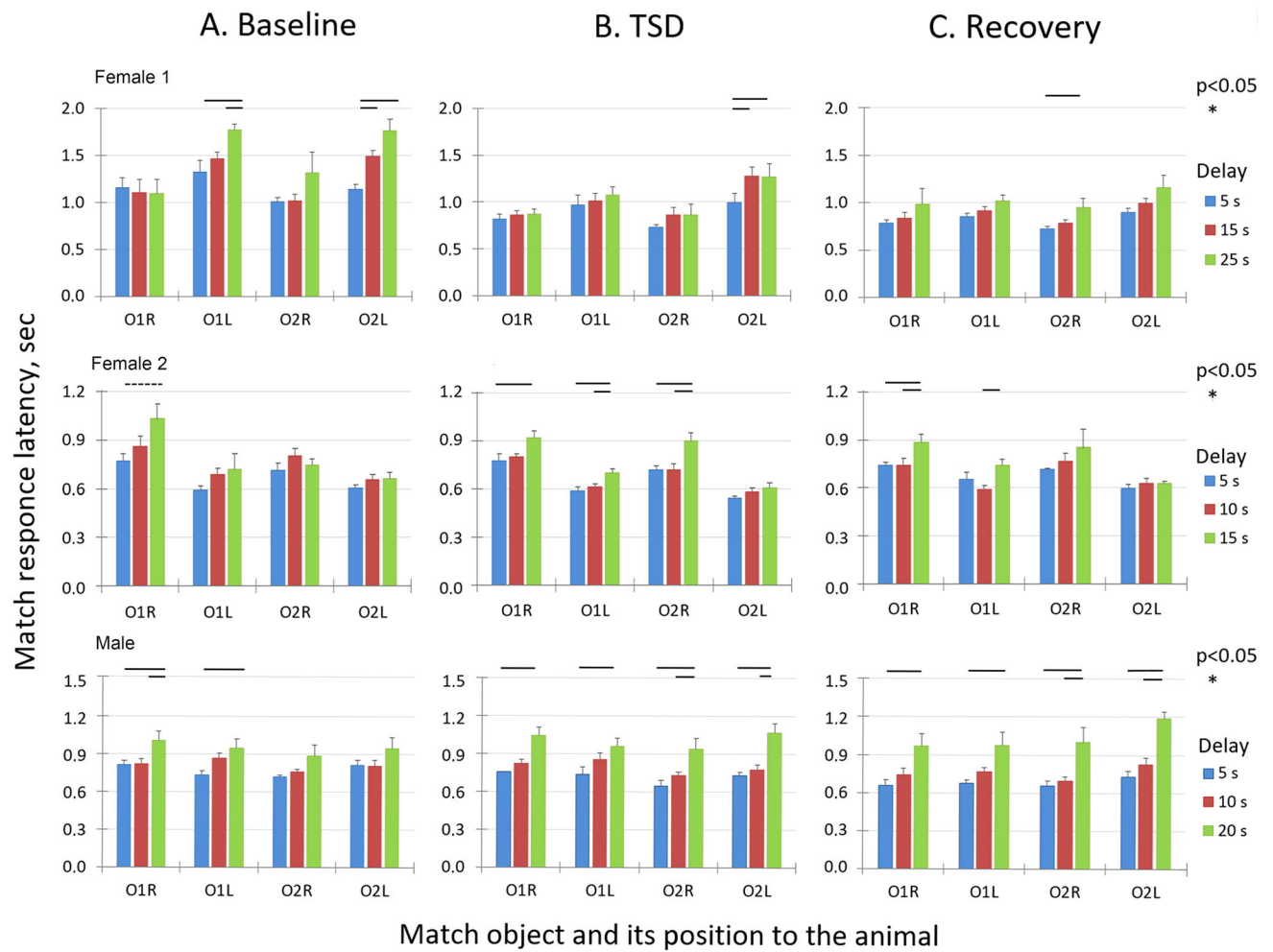
Fig. 6.
Match response latency in fur seals in a DMTS task at different delays for different matched objects and their positions to the animals in different experimental conditions. Ordinates are average MRLs (± SEM). All other details are same as in Fig. 4

Fig. 7.
Match response latency in fur seals in a DMTS task in different experimental conditions for different matched objects and their positions to the animals and different delays. Ordinates are average MRLs (± SEM). All other details are same as in Fig. 4