



Lateralization in accuracy, reaction time and behavioral processes in a visual discrimination task in an Indo-Pacific bottlenose dolphin (*Tursiops aduncus*)[☆]

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ARTICLE INFO

Keywords:

Laterality
Reaction time
Visual discrimination
Bottlenose dolphin

ABSTRACT

Perceptual and behavioral asymmetry has been observed in a wide range of vertebrate and invertebrate species with its origin estimated to go back over 500 million years. Previously, hemispheric lateralization in marine mammals has been recorded during foraging, parental care, preferred swimming direction as well as when solving cognitive challenges. Visual laterality has been demonstrated in preferred eye use and performance accuracy. A female Indo-Pacific bottlenose dolphin was trained to associate eight pairs of non-identical visual stimuli. Her performance was tested and compared under binocular and monocular conditions. No significant difference was found in accuracy, while a clear left eye advantage was demonstrated in reaction time. In addition, behavioral asymmetry was observed in movement pattern preference during the stimulus discrimination.

1. Introduction

Behavioral laterality, preferred use of one side over the other is an indication of the differences between the left and the right brain. Lateralization has been observed during preferential use of one hand/paw over the other (Lonsdorf and Hopkins, 2005; Westergaard and Suomi, 1996; Wells and Millsopp, 2009), favored swimming direction (Blois-Heulin et al., 2012; Marino and Stowe, 1997a, b; Ridgway, 1972), frequented use of one eye (Delfour and Marten, 2006; Farmer et al., 2010; Thielges et al., 2011) and even during tail wagging (Quaranta et al., 2007; Siniscalchi et al., 2013). Previously hemispherical lateralization was considered to be found exclusively in humans, however recent studies suggested its presence since 500 million years ago, when vertebrates emerged (MacNeilage et al., 2009). Experiments with non-human primates (McGrew and Marchant, 1997), birds (Franklin and Lima, 2001; Hunt et al., 2002), reptiles (Bisazza et al., 1998; Robins et al., 2005), amphibians (Bisazza et al., 1998; Robins et al., 1998) and fish (Bisazza et al., 2007; Takeuchi and Hori, 2008) confirmed general manifestation of lateralization in vertebrates. Moreover, studies conducted with nematodes and insects showed examples for lateralization of the nervous system in invertebrates

(Frasnelli, 2013; Frasnelli et al., 2012). Comparative studies on behavioral lateralization provided valuable data for understanding how animals perceive the world around them and how are these sensory inputs are being processed (Rogers, 2010). The anatomy of the cetacean brain makes them ideal candidates for hemispherical lateralization studies, given that they possess an asymmetrical brain structure, with bigger right hemispheres (Ridgway and Brownson, 1984) and have a relatively less-developed corpus callosum (Tarpley and Ridgway, 1994). Behavioral laterality in cetaceans has been observed in various contexts. Right-side bias was observed during feeding, such as intentional breaching on the right or lunging towards the right (Karenina et al., 2016). Right-side preference was noted in parental care having the calf swimming more on the right than on the left side of the mother (Hill et al., 2017; Karenina et al., 2010) and right-side bias was also noted in suckling patterns (Zoidis and Lomac-MacNair, 2017). However, during initiation of physical contact left pectoral fin was favored (Johnson and Moewe, 1999; Sakai et al., 2006; Winship et al., 2017) and dolphins under human care showed a counter-clockwise swimming preference (Sobel et al., 1994).

Experiments on sensory perception lateralization have mainly focused on vision. Due to the complete decussation of the optic nerve,

[☆] The project was approved by the Animal Welfare, Ethics and Care Committee of Ocean Park Conservation. Ocean Park gained accreditation from the Association of Zoos and Aquariums (AZA), it is also a member of the World Association of Zoos and Aquariums (WAZA). The animal welfare standards at the Park were also approved by the American Humane Association under its Humane Conservation™.

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<https://doi.org/10.1016/j.beproc.2019.02.003>

Received 21 November 2018; Received in revised form 26 January 2019; Accepted 11 February 2019

Available online 16 February 2019

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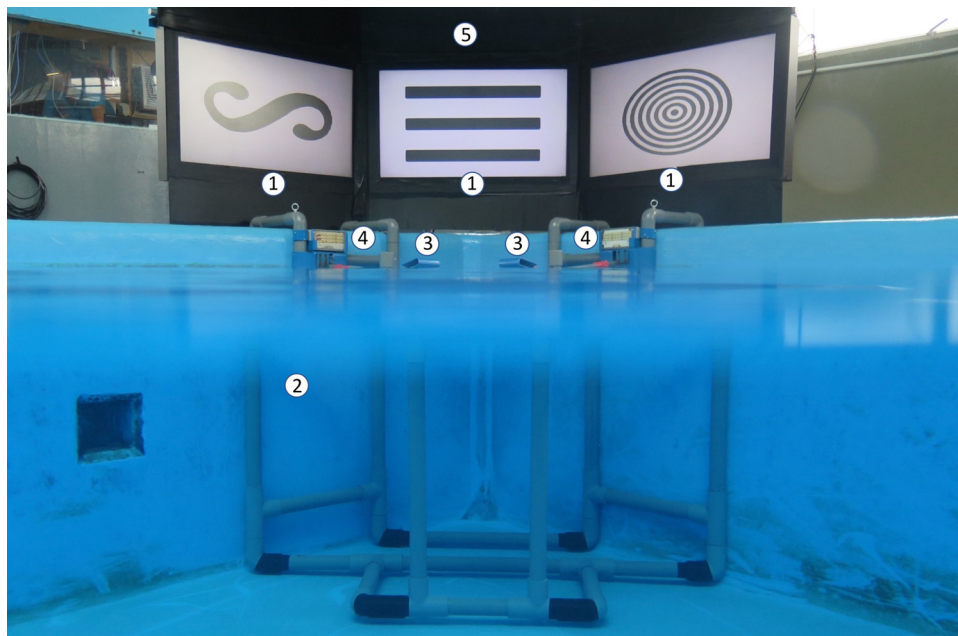


Fig. 1. Complete research setup including three TV screens (1), the stationing device (2) with two response paddles (3) respective to the location of the screens on the left and right, two visual feed-back boxes mounted above the response paddles (4) and a black corrugated plastic board top cover (5).

information registered through the right eye is processed in the left brain hemisphere, while visual information registered by the left eye travels to the right hemisphere (Jacobs et al., 1975). Moreover, dolphins' eyes are positioned laterally, resulting in a wide visual field of 120–130° with the two eyes overlapping only 20–30° (Mass and Supin, 2009). Visual laterality was demonstrated during the presentation of objects with different degrees of familiarity (Blois-Heulin et al., 2012; Siniscalchi et al., 2012; Yeater et al., 2017), observation of familiar and non-familiar humans (Thieltges et al., 2011; Hill et al., 2016; Yeater et al., 2014) as well as during cognitive challenges: Dolphins demonstrated right eye preference when provided with visuospatial cognitive tasks (Clark and Kuczaj, 2016; Kilian et al., 2000). Higher frequency of counter-clockwise swimming rotation was displayed at the presence of a cognitive enrichment, called the underwater maze device, that was interpreted as right eye lateralization (Clark and Kuczaj, 2016). In a three-choice spatial discrimination task dolphins were trained to swim through three hoops in any sequence they preferred but without omitting or re-using one of them. When tested under monocular conditions, their performance was significantly higher when they used their right eye than the left (Kilian et al., 2000). Right visual field advantage was also observed during a two-choice relational discrimination task between numerical stimuli under monocular view (Kilian et al., 2005). Monocular pattern acquisition and interhemispheric transfer tests supported a left hemisphere dominance in visual processing (von Fersen et al., 2000; Yaman et al., 2003).

This paper aimed to investigate and compare a bottlenose dolphin's performance in a two-alternative choice visual discrimination task under both binocular and monocular conditions, focusing on lateralization in accuracy, reaction time and behavioral processes.

2. Materials and methods

2.1. Subject and housing

The subject of this study was a 14-year old, female Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), named Dumisa. Dumisa was born in Bayworld South Africa in 2004. She was relocated to Ocean Park Hong Kong (OPHK) in 2009 and has been involved in acoustic and cognitive studies since 2012. Dumisa was housed with 14 other

dolphins in the Marine Mammal Breeding and Research Centre (MMBRC) of OPHK. The experiment was conducted in one of the six interconnected pools of MMBRC (L 17 m, W 20 m and D 4 m) between March 2017 and September 2017. Research sessions were conducted twice daily during the week, that coincided with the dolphin's feeding time. The regular medical check-ups of Dumisa's eyes by the veterinarian team at OPHK, found no unusual conditions or differences between the two eyes.

2.2. Apparatus

The apparatus consisted of a custom-made stationing device equipped with two response paddles and two visual feedback boxes, three TV screens (LG 42LE5500 42" full HD) and a black, corrugated plastic board top cover. The stationing device was made of schedule 80 PVC pipes and fittings and was mounted at the corner of the pool. The three screens were positioned behind the stationing device, with one in the center and two aligned with the response paddles on the left and the right. The two visual feedback boxes were placed above the response paddles below the center of the left and right TV screens. They were equipped with light emitting diodes (LED) and also contained a radio transmitter, that relayed a paddle press to the computer system. When the response paddles were pressed, the front panel of the box containing the LEDs lit up and the outcome of the trial ("yes" for correct and "call her back" for incorrect trials) was triggered through a loudspeaker. The display of the stimuli was controlled by a computer (Mac Pro, 2013) from the "recording studio" at the poolside. Max software (Max 7, Cycling '74) was used for the control of the whole experiment including the presentation of the stimuli as well as for recording the outcome, reaction time and length of the inter-trial intervals. The top cover was placed diagonally across the top of the TVs to reduce any reflection on the screens (Fig. 1). To test Dumisa's performance under monocular condition, she was partially blind-folded using a set of connected eyecups, consisting of two rubber suction cups (8 cm in diameter) connected through a 46 cm long rubber hose. The custom-made eyecups had been used in previous experiments, thus Dumisa was familiar with them. To achieve a monocular test condition, one of the suction cups was placed over her eye while the other one was attached contra-laterally behind her melon (Fig. 2). Video data was collected with a GoPro

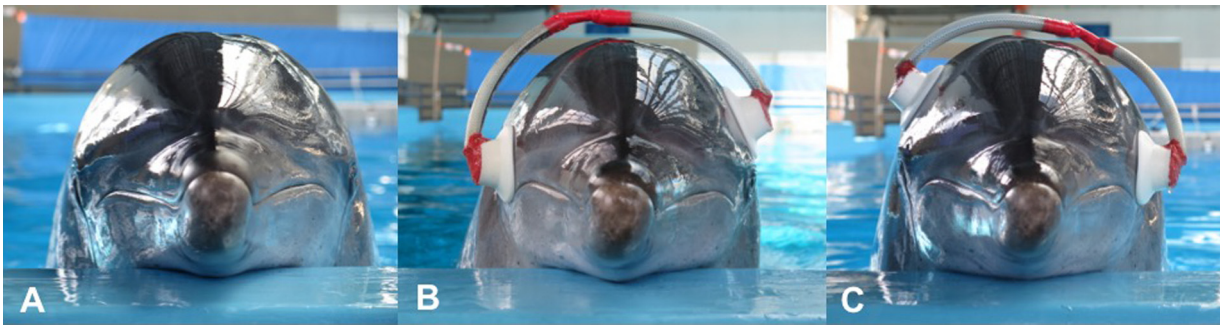


Fig. 2. Front view of the subject under the three experimental conditions: A) binocular, B) right monocular and C) left monocular.

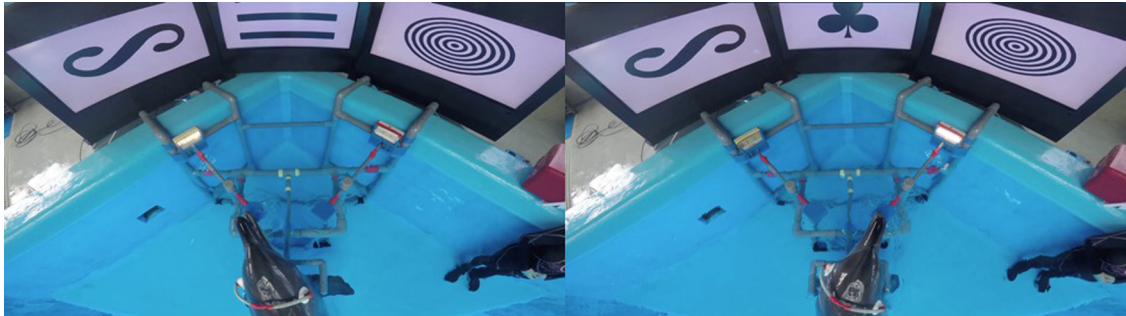


Fig. 3. Screenshots of two research trials on Set 1 stimuli under right monocular condition with Dumisa selecting the correct choice on the left and the right.

Hero 4, mounted on the top cover, centered above the dolphin (Fig. 3) as well as through an IP camera mounted across the pool behind the test station.

2.3. Procedure

Dumisa had previously been trained (as part of a separate experiment) to associate four sets of non-identical stimuli pairs. Each set included two stimuli pairs and each pair consisted of an ‘A’ and a ‘B’ stimulus (Table 1). The stimuli were black clipart images displayed on a white background. During the two-alternative choice discrimination task, Dumisa was stationed in front of the three TV screens using the stationing device. A sample stimulus (one of the eight ‘A’ stimuli) was shown on the central screen for 2 s, then the two alternative choices (the two corresponding of the eight ‘B’ stimuli) appeared simultaneously on the left and the right screens. Dumisa was trained to indicate her choice between the two ‘B’ stimuli by pressing the response paddle

Table 1
The four sets of research stimuli that were used in the visual discrimination tasks.

Set	Stimuli pair	Stimuli A	Stimuli B
Set 1	A01 – B01		S
	A02 – B02	♣	🌀
Set 2	A03 – B03	▲	☺
	A04 – B04	+	☔
Set 3	A05 – B05	✂	🍷
	A06 – B06	⚽	🐛
Set 4	A07 – B07	🌳	≡
	A08 – B08	📏	●

corresponding to the location of the selected image. One of the two ‘B’ stimuli was associated with the sample image and represented the correct choice (S^+), while the other one was the unrewarded stimulus (S^-). For example, if the sample was A01, the correct response was B01 and not B02. Dumisa’s performance was tested on each set separately. Each set included two pairs of stimuli in four possible combinations. For example, the combinations for Set 1 were: 1) A01 sample with B01 on the left and B02 on the right; 2) A01 sample, with B02 on the left and B01 on the right; 3) A02 sample with B01 on the left and B02 on the right; 4) A02 sample with B02 on the left and B01 on the right. A total of 576 trials were conducted. Each set was tested on 144 balanced trials (72 trials/sample), in three experimental conditions (48 trials/condition/set): I. binocular, II. the first monocular, III. the other monocular condition (Figs. 2 and 3). One research session consisted of 24 trials, thus each set was tested for six sessions (144 trials) with two consecutive sessions for each condition (48 trials). In total 192 trials were conducted under binocular and 384 under monocular (192 for left and 192 for right) conditions. The testing of each set started with binocular view, that was followed by testing with right then left monocular conditions or left then right monocular conditions. During the sessions, the trials were presented in a pseudo-random manner, with a balanced use of the four combinations. An A stimulus did not appear on more than two consecutive trials, nor did the S^+ appear on the same side for more than two consecutive trials. The position of the trainer (left or right to the setup) was also balanced for the experiment. The outcome (correct or incorrect) and the reaction time of each trial was recorded.

Dumisa’s head turning movements during the discrimination task were analyzed through a post-session video analysis. Only four patterns were observed:

- Pattern A - Single head turn towards the left, followed by a clear left paddle press
- Pattern B - Left then a right turn, followed by a clear right paddle press
- Pattern C - Single head turn towards the right, followed by a clear right paddle press
- Pattern D - Multiple (two or more) head turns, followed by a clear left paddle press

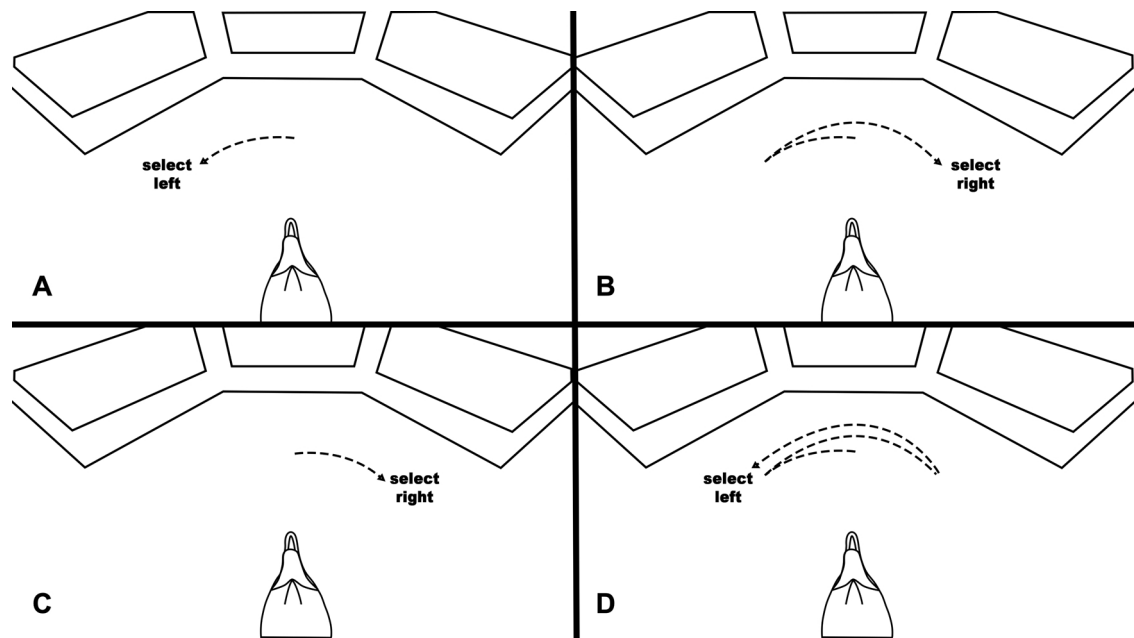


Fig. 4. The four head movement patterns (A, B, C and D) during the discrimination task, including a single example for Pattern D.

The four movement patterns are illustrated in Fig. 4, with one possible example for pattern D.

3. Results

3.1. Correct performance

Dumisa showed significantly correct performance levels (Binomial test, $P < 0.05$) under all three conditions (binocular, right monocular, left monocular) (Fig. 5). With each condition tested with a total of 192 trials (48 trials/set), she made only 2 mistakes on binocular (99% correct performance), 9 right monocular (95% correct performance) and 17 on left monocular (91% correct performance) conditions. The comparison of Dumisa’s performance on the four sets under monocular condition showed no significant difference (one-way ANOVA, F -

stat = 0.986, $P > 0.05$). Her performance during the binocular condition was significantly better than under left monocular condition (Wilcoxon Signed-Rank test, $P < 0.05$). However, no significant difference was found between performances in binocular and right monocular conditions (Wilcoxon Signed-Rank test, $P > 0.05$). There was also no significant difference between her performances under the two monocular conditions (Wilcoxon Signed-Rank test, $P > 0.05$). During the experiment the rewarded stimuli (S^+) were equally displayed on the left (288 trials, from which 96 in binocular and 192 in monocular conditions) and the right (288 trials, from which 96 in binocular and 192 in monocular conditions) screen. Dumisa showed no significant difference in her performance in correlation to the location of S^+ under binocular condition (Wilcoxon Signed-Rank test, $P > 0.05$). However, she made less mistakes under monocular condition when S^+ was on the same side as her uncovered eye. Under right

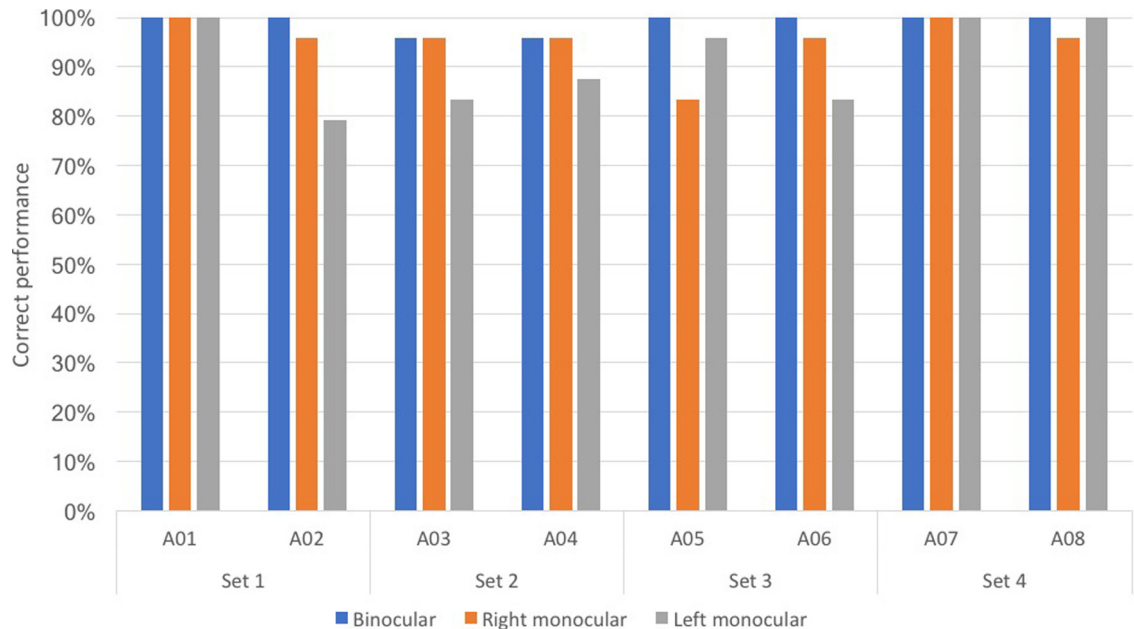


Fig. 5. Dumisa’s correct performance on the eight stimuli pairs under binocular (blue) and monocular (orange and grey) conditions.

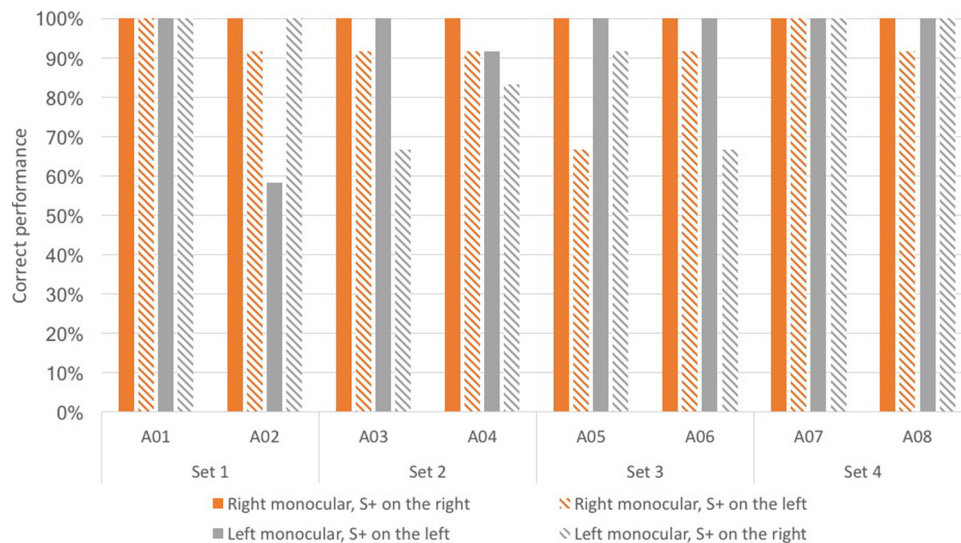


Fig. 6. Dumisa's correct performance on the eight stimuli pairs under monocular conditions (right in orange, left in grey) showing the difference between having the rewarded stimuli displayed on the same (full) and the opposite (stipes) side to the covered eye.

monocular condition, she responded correctly on all 96 trials (100%) with S^+ was displayed on the right and correct on 87/96 (91%) when it was displayed on the left side. Under left monocular condition, she responded correctly on 90/96 (94%) of the trials when S^+ was displayed on the left and 85/96 (89%) when displayed on the right (Fig. 6).

3.2. Reaction time

Dumisa's average reaction time was the fastest under left monocular condition, 1.15 ± 0.16 s. Her average reaction time was 1.22 ± 0.21 s under binocular condition, while it was 1.34 ± 0.23 s under right monocular condition. Significant differences were found between binocular and right monocular conditions (one-tailed Paired T-test, $T\text{-stat} = -6.321$, $P < 0.0001$), binocular and left monocular condition (one-tailed Paired T-test, $T\text{-stat} = 4.177$, $P < 0.0001$) as well as between the two monocular conditions (one-tailed Paired T-test, $T\text{-stat} = 11.529$, $P < 0.0001$). There was no significant difference in reaction time across the sets for binocular or left monocular conditions (one-way ANOVA, $F\text{-stat} = 1.219$, $P > 0.05$). However, under right condition, significant differences were found between the eight stimuli pairs (one-way ANOVA, $F\text{-stat} = 3.669$, $P = 0.001$, Turkey HSD, 95% level, $P < 0.05$) (Fig. 7). The position of the S^+ showed a significant effect on Dumisa's response time, she was faster when it was displayed on the left screen than on the right under binocular, right monocular, as well as left monocular condition (one-tailed Paired T-test, $T\text{-stat} = -10.870$, $P < 0.0001$). No correlation was found between the reaction time and the percentage of correct performance.

3.3. Movement pattern

Out of the four observed Patterns three indicated a left turn start (Pattern A, B and D), thus Dumisa's first motion was nearly exclusively (570/576, 99%) a left turn. Two different movement patterns were documented for both left and right responses. Dumisa selected the left paddle on 284 occasions, of which her action matched Pattern A 98% of the time and Pattern D only 2% of the time (Binomial test, $P < 0.0001$). The right side was chosen on 292 occasions with movement Pattern B on 98 % of the time, while Pattern C was exhibited only on 2% of the trials (Binomial test, $P < 0.0001$).

4. Discussion

Significant correct performance on the eight stimuli pairs under binocular condition proved Dumisa's ability to successfully discriminate and map the visual patterns to the displayed sample stimulus. When the same task was presented under monocular conditions she made more mistakes but her performance stayed well above chance level. Previously documented left hemisphere advantage in visual processing (von Fersen et al., 2000; Yaman et al., 2003) was not found in this study. No significant difference in performance accuracy was documented between the two monocular conditions. The absence of significant asymmetry could be due to a ceiling effect: Familiarity-dependent asymmetry was demonstrated in previous studies (Blois-Heulin et al., 2012; Kilian et al., 2005; Fagot and Vaclair, 1994; Laeng et al., 1999), when significant lateralization emerged with the presentation of novel stimuli or more demanding discrimination tasks. As a result of ongoing training to acquire new associations and to maintain familiar ones, Dumisa was highly familiar with the discrimination of the eight test stimuli pairs. Thus, the restriction to use a single visual field did not affect her performance significantly. On the other hand, Dumisa demonstrated a significantly higher effort under right eye monocular condition by spending longer time observing and selecting her choice. Earlier studies (Richards et al., 1984; Swensson, 1972) demonstrated a tradeoff between accuracy and speed during decision making. In this experiment, a correlation between the ratio of correct trials and the reaction time under monocular conditions was absent.

Under monocular conditions higher percentages of correct performances were documented when the S^+ was displayed at the side of the uncovered eye than opposite to it, suggesting stimulus proximity dependence. The dolphins' visual field is estimated to be as wide as 120° – 130° with a 20° – 30° overlap of the two eyes (Mass and Supin, 2009). The center of the left and the right TV screens were separated by an angle of about 70° from Dumisa's position, thus it is probable that she was not able to view both alternative choices simultaneously under the monocular condition. As a result, the stimulus that was displayed on the side of the uncovered eye could have been viewed earlier than the one on the opposite side. Thus, a delay in appearance of the rewarded stimulus could have contributed to the observed performance bias.

Hemispheric asymmetry in visual pattern processing has previously been documented, showing differential hemispheric activation during global and local processing (Fink et al., 1997; Hillger and Koenig, 1991). Shape recognition could be accomplished by the matching of global features, guided by the right hemisphere (Laeng et al., 1999;

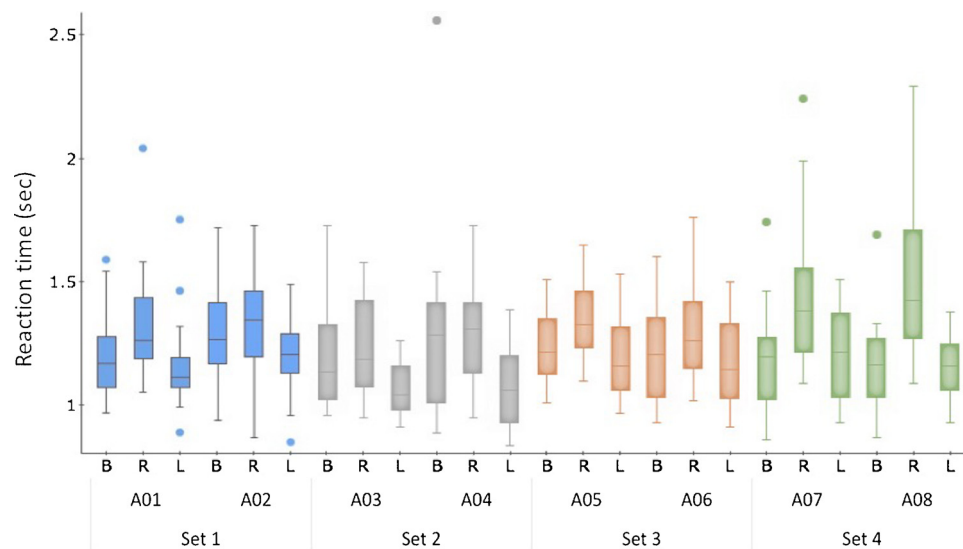


Fig. 7. Boxplots of Dumisa's reaction time on the eight stimuli pairs under binocular and monocular conditions with B indicating binocular, while R stands for right and L stand for left monocular conditions, Set 1 represented in blue, Set 2 in gray, Set 3 in orange and Set 4 in green color.

Hellige, 1993). This hemispheric asymmetry could facilitate different cognitive strategies. Under the binocular condition Dumisa could analyze the stimuli by both local and global features, while in the monocular conditions she might have been restricted to the use of only one of the two (either local or global features). Her significant levels of correct performance indicate that she may have been able to perform the task relying on either or both strategies. However, it is important to note that all stimuli used in this study were familiar to Dumisa. In order to investigate shape recognition strategies, trials involving novel stimuli would have to be considered. When analyzing Dumisa's reaction times in correlation with the locations of the rewarded stimulus, she was significantly faster when the S^+ was displayed on the left side than on the right, in all three experimental conditions. This significant reaction time difference can be explained by her recorded movement pattern preference. During her training Dumisa was required to station using the apparatus (Fig. 1) at constant distance from the screens, however she could freely choose her preferred viewing direction and eyesight. As a result, she developed a habit of first turning towards the left response paddle and would only switch direction if she was going to select the image on the right. This behavior was independent from the location of the trainer (next to the left or right side of the setup), which was balanced over the experiment. If this behavior was to be exhibited only under binocular condition, it could be interpreted as a result of the preferred use of her right eye. However, she displayed the same movement patterns even under the left eye monocular view condition. Preference in behavioral sequences by dolphins has been documented during a visuospatial challenge, when certain locations of the research setup were visited prior to others (Kilian et al., 2000). Moreover, rotational and turning tendencies in humans and rats during spatial navigation tasks (Bradshaw and Bradshaw, 1988; Yuan et al., 2014) have also been documented, in possible relation to dopamine asymmetries in the basal ganglia (Bradshaw and Bradshaw, 1988) or the age and the sex of the participants (Yuan et al., 2014). Dumisa's preferential movement patterns could be related to a hemispheric asymmetry or it may just be an individual preference.

Our study was based to the involvement of a single subject, which could have been a limiting factor. However, our findings highlight the importance of psychophysiological studies focusing on the deeper understanding of the linkage between behavioral and hemispheric lateralization.

5. Conclusion

In summary, laterality was demonstrated on two of the three factors of this study. Visual pattern discrimination on associations that had been acquired under binocular condition was successfully demonstrated under both monocular conditions without any prior training specific to the task. Dumisa's correct performance showed no significant difference between the two monocular conditions. However, behavioral laterality was found in Dumisa's movement pattern, favoring a left turn start independently from the viewing conditions (binocular or monocular). Her reaction time under the three conditions differed significantly, with left eye monocular condition being the fastest and right eye monocular condition the slowest.

Declarations of interest

None.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Acknowledgements

We thank the Marine Mammal Department of Ocean Park Hong Kong for their support during our experiment, the interns and volunteers for their valuable help with data collection.

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