

Left and right visual preferences during paired swimming in bottlenose dolphins (*Tursiops truncatus*)

Ashley Reese

Christine Johnson
Faculty Advisor

Jeremy Karnowski
Graduate Advisor

Edwin Hutchins
Faculty Advisor

2014 Cognitive Science Honors Thesis
University of California, San Diego
Email: anreese@ucsd.edu

ABSTRACT

Bottlenose dolphins (*Tursiops truncatus*) maintain visual access to each other with their left and right laterally positioned eyes as they swim together in pairs. Their vision is primarily monocular, and signals from each eye cross completely to the contralateral brain hemisphere. The dolphins' visual anatomy and observed behavior suggest that bottlenose dolphins may be lateralized for vision. One outcome of lateralized vision may be a preference for swimming with a particular eye towards another dolphin. In this study, six bottlenose dolphins were observed through video recordings over 26 days at the Brookfield Zoo in Chicago. The instantaneous scan sampling method was used to record the bottlenose dolphins' positions as they swam together in the tank. Eye position, body orientation, horizontal and vertical positions were recorded. Out of the five observed dolphin pairs, three of the pairs showed eye position preferences consistent with their rank. Three pairs also showed a position preference along the tank wall, where one dolphin swam next to the underwater windows in the tank wall, while the other maintained closer proximity to the other dolphins in the tank. One pair, composed of two adolescents of the same rank, showed neither an eye position preference nor a tank position preference. Lateralized vision and rank in bottlenose dolphins may be two factors driving their left and right side position preferences.

INTRODUCTION

Vision is a mechanism for communication between bottlenose dolphins. Bottlenose dolphins use vision to observe each other as they swim together in groups. Their eyes are located laterally on their heads, and they see primarily using monocular vision. Bottlenose dolphins can see both in front and behind their bodies by moving their eyes independently of each other (Supin et al. 2001; McIntyre, 1974). It has been estimated that dolphins have 130 degree horizontal range of vision and 100 degree vertical range of vision (Dral, 1977; Supin et al., 2001). The region below and in front of bottlenose dolphins' heads is a narrow, 20-30 degree field where dolphins see binocularly (McIntyre, 1974; Dral, 1977). Bottlenose dolphins have blind spots above their heads, as well as behind their dorsal fin and tail (McIntyre, 1974; Supin et al., 2001).

The neuroanatomy of the bottlenose dolphin brain shows that optic nerve fibers cross completely to the opposite brain hemisphere (Jacobs et al., 1975; Ridgway, 1990). The corpus callosum, a set of fibers connecting the two brain hemispheres, is smaller than expected in dolphins given their large mammalian brain size (Manger, 2010; Ridgway, 1990). The neuroanatomy of the dolphins' visual system suggests that there may be relatively little transfer of visual information between brain hemispheres.

Based on the bottlenose dolphins' laterally positioned eyes and neuroanatomy, dolphins may be lateralized for vision. Visual lateralization has been observed across vertebrate and invertebrate species in a variety of functions, such as prey detection, prey escape, recognition of conspecifics, social cognition, and spatial cognition (Rogers, 2002; Tommasi, 2009; Vallortigara & Rogers, 2005). Researchers have begun to study and observe lateralized eye function in dolphins.

In a pattern matching task, five bottlenose dolphins paired 2D patterns with either their left or right eye (Yaman et al., 2003). The bottlenose dolphins required fewer trials to learn the pattern matching task and were more accurate when they used their right eye. In a similar pattern discrimination task, one bottlenose dolphin was tested using either his left or right eye (von Fersen et al., 2000). This dolphin was more accurate with his right eye than his left eye. In yet another pattern task using 2D black and white stimuli, a bottlenose dolphin was trained to choose the pattern with the fewest number of white stimuli (Kilian et al., 2005). The dolphin's right eye accuracy was nearly equivalent to its accuracy when it used both its eye, and its left eye performance was significantly worse.

In a visuospatial task, two female bottlenose dolphins swam through three hoops in a tank. The dolphins initially learned the task with both eyes. Then, one eye was covered and the dolphins were measured on their accuracy of swimming through the hoops with one eye open. The two bottlenose dolphins performed as well with their right eye as when both eyes were uncovered, but they had worse accuracy when using just their left eye (Ridgway et al., 1988).

Another group of experiments studied lateralized vision in bottlenose dolphins by presenting stimuli to the dolphins and recording which eye the dolphins used to look at those stimuli. Blois-Heulin et al. presented objects to five bottlenose dolphins (2012). The objects ranged from very familiar, familiar, to unfamiliar to the dolphins. The dolphins more frequently looked at the very familiar objects with their left eye, and the unfamiliar objects with their right eye. In a similar study with wild beluga whales, unfamiliar objects were placed in the beluga whales' environment (Karenina et al., 2010b). The beluga whales turned to look at the unfamiliar objects more frequently with their left eye and for a longer period of time than with their right eye. This contrasts with the results of the above-described Blois-Heulin et al. (2012) study which

found that bottlenose dolphins looked at unfamiliar objects mainly with their right eye.

Two additional studies presented humans as stimuli to bottlenose dolphins. Thieltges et al. (2011) presented unfamiliar and familiar humans to five bottlenose dolphins in captivity. The bottlenose dolphins used their left eye more frequently to look at these humans, whether familiar or unfamiliar. In a similar study, wild bottlenose dolphins in the Indo-Pacific Ocean were recorded when they turned to look at underwater videographers with their left or right eye (Sakai et al., 2006). When the dolphins approached the videographers, they more frequently looked at the videographers with their left eye. While these studies suggest that dolphins may have a visual preference for their left or right eye on particular tasks, the implications for particular eye functions are unclear with the limited number of studies.

In related work, several studies have found lateralized behavior during pectoral fin rubbing events. Sakai et al. (2006) recorded bottlenose dolphins (*Tursiops aduncus*) rubbing each other with either their left or right pectoral fin in the Indo-Pacific Ocean. The wild bottlenose dolphins used their left pectoral fin 79% of the time to rub another dolphin's body, suggesting that the dolphins have a left side preference when rubbing another dolphin. In a similar pectoral fin rubbing study, Johnson and Moewe (1999) found significant left pectoral fin preferences in a group of captive Commerson's dolphins (*Cephalorhynchus commersonii*). The male dolphins initiated the pectoral fin contact with females more frequently with their left pectoral fin, which tended to be the fin with serrations. Male Commerson's dolphins exhibit a population-wide tendency to have serrations on their left pectoral fin. Unlike Commerson's dolphins, bottlenose dolphins do not have serrations on their pectoral fins and both males and females engage in pectoral fin rubbing behavior. Lateralization in this fin rubbing behavior may be driven by lateralized eye function.

Another behavior observed in the wild and in captivity that may be driven by eye preference is group swimming. During group swimming, when two or more dolphins swim together in close proximity, they position themselves staggered above and below each other such that they can also see other individuals in the group (Norris and Dohl, 1980). It is less common for bottlenose dolphins to swim in parallel with each other than staggered vertically and horizontally in the water.

A study with wild orca (*Orcinus orca*) mothers and calves found side preferences when the pairs swam together (Karenina et al., 2013b). Calves were more frequently observed on their mother's right side with their left eye towards their mother. The side position changed when the research vessel was in close proximity to the orca pairs. When the research vessel was close to the pairs, the mother was more frequently seen on the calf's right side with her left eye towards the calf, regardless of which side the research vessel approached the pair. This study suggests that there may be an eye position preference that changes under particular social contexts. In another study, Karenina et al. (2010a; 2013a) analyzed wild beluga mother and calf pairs. The study found that the majority of the calves positioned themselves to their right of their mother, consistent with the wild orca mother and infant side position preferences. Furthermore, when the young calves in that study swam with older juveniles, the younger calves were observed more frequently to the right of the older calves (Karenina et al. 2010a).

The role of vision and eye position preferences in bottlenose dolphin mother-calf pairs have also been observed during sleep. Bottlenose dolphins sleep with one hemisphere of their brain at a time (Mukhametov, 1985). Only the eye associated with the "awake" hemisphere remains open while they swim in this state. The study on three newborn bottlenose mother-calf pairs found that the calves tended to have the eye facing its mother open more frequently than

the eye away from its mother (Lyamin et al., 2007). This study suggests that the three calves preferred to have the eye facing the mother open during sleep.

When bottlenose dolphins swim upright in a pair, one dolphin has its left eye towards the other dolphin, and the other dolphin has its right eye towards that dolphin. If vision is lateralized for a particular function, there may be a preferred left or right eye position. Given their laterally positioned eyes, only one dolphin can occupy a preferred eye position. The focus of this study was to observe how bottlenose dolphins positioned themselves when they were swimming in pairs. The study addressed the following questions: Do bottlenose dolphins have eye position preferences? And are eye position preferences related to the rank of the dolphins?

METHODS

Subjects

The subjects of the study were six bottlenose dolphins (*Tursiops truncatus*). There were five female dolphins and one male dolphin (See Table 1). The subjects varied in age, and they were 7, 10, 11, 24, 30, and 31 years old at the time of the study. The 31-year-old dolphin was a high ranking adult female who had two daughters in the tank, ages 7 and 10. The rank of the dolphins was associated with the age of the dolphins (Table 1). The dolphins were classified into four rank categories by the trainers at the Brookfield Zoo. The youngest dolphin was in rank category 4, the two adolescents were ranked together in rank category 3, the 24-year-old adult female who was relatively new to the group was in rank category 2, and the two highest ranking adults were in rank category 1.

Table 1

Rank Categories of the dolphins at the Brookfield Zoo.

Rank Category	Gender-Rank	Dolphin Identity	Age
1	F-1, M-1	Tapeko (T), Chinook (C)	31, 30
2	F-2	Allie (E)	24
3	F-3, F-4	Noelani (N), Spree (S)	10, 11
4	F-5	Allison (A)	7

Note. In the Gender-Rank column, *F* refers to female, *M* refers to male, and the numbers correspond to the dolphins' ordered rank for each gender.

Brookfield Zoo, Chicago

The bottlenose dolphins were housed at the Seven Seas exhibit at the Brookfield Zoo in Chicago. The exhibit consisted of four, round, interconnected tanks of varying sizes. The main tank was the largest tank, followed by two smaller holding tanks and a medical pool. All of the walls in the four tanks had extensive windows for the trainers and zoo visitors to view the dolphins. The dolphins were also able to see through the windows to view the trainers and human visitors.

The UCSD Distributed Cognition Lab and the Brookfield Zoo had previously installed ten underwater cameras and three above water cameras. The dolphins were recorded using the video cameras from 8am-5pm daily.

Procedure

The video recordings were analyzed over 26 days in the mornings from March to April in 2013. Observations were taken from 8:30am to the first feed of the day, which occurred around 9:45am. The dolphins were observed in the three largest tanks, which included the main tank and the two holding tanks.

Observations were recorded using the instantaneous scan sampling method. Every time a group of two or more dolphins passed a particular window frame, data was recorded on their position. Data was only recorded after the dolphins had completed one lap of the tank together. The dolphins were considered to be swimming together if there was one body length or less between two animals. In addition, a dolphin had to be within one body length in front of or behind another dolphin. In groups of more than two dolphins, the length criteria followed the “chain rule”, meaning that each dolphin had to meet the length criteria for the dolphin closest to it in the group. The dolphins were recorded until one or more dolphins broke off from the swimming group. The dolphins’ swim direction, eye use, body orientation, and spatial position were recorded. The detailed explanations for each position are below.

Scored Positions

Swim direction: *Counterclockwise* or *clockwise* swimming direction in the round tanks.

Eye: The eye recorded was the eye that was oriented to the other dolphin(s) with whom they were swimming. The eye positions recorded were: *left*, *right*, *no*, *binocular*. The dolphins primarily positioned their *left* or *right* eye towards another dolphin. However, there were instances when the dolphin would rotate 90 degrees, turning its back to the other dolphin and thus having *no* eyes oriented to its partner, or instead, turning its ventrum to the other dolphin and thus having both eyes oriented to the other dolphin (*binocular* vision). It was not possible with the video recordings to see when the dolphins were actively looking at another dolphin. The eye positions only indicate which eye had direct access to the other animal.

Body orientation: The body orientations scored were *upright*, *inverted*, *belly to*, and *back to*. *Upright* referred the dolphins’ most common position, which was when their dorsal fins were

upright and towards the surface of the water. The *inverted* position was when the dolphins' dorsal fins were facing the bottom of the tank and their belly was facing the surface of the water. The *belly to* position was when the dolphin was turned 90 degrees to have its belly facing another dolphin. The *back to* position referred to when the dolphin was turned 90 degrees with its dorsal fin oriented to another dolphin.

Spatial position: Spatial position was classified into vertical, longitudinal, horizontal and inside/outside tank position, as follows:

Vertical position: The dolphins' vertical position was recorded as *above*, *below*, *parallel*, *floor*, *top-overlapping*, or *bottom-overlapping*. The *above* or *below* position was scored when the dolphin was above or below another dolphin with no body overlap of the body, dorsal, or pectoral fins. If there was overlap of two dolphins' body or fins, then the dolphin's position was recorded as either *top-overlapping* or *bottom-overlapping*. Occasionally, the dolphins swam parallel with no dolphin in a position above or below the other dolphin. This position was scored as *parallel*. When the dolphins swam in parallel along the bottom floor of the tank, this was scored as *floor*, since it was presumed that such a position constrained the range of relative positions available to the dolphins.

Longitudinal position: The longitudinal position of the dolphins was also recorded. The longitudinal positions were *ahead*, *behind*, *head-to-head*, or *head-to-body*. The positions *ahead* and *behind* referred to when the dolphins were in front or behind another dolphin with no overlap of their bodies. *Head-to-head* was scored when one dolphin's rostrum was overlapping with another dolphin's head region, defined as the area from the dolphin's rostrum to the foremost part of its pectoral fin. *Head-to-body* was scored when one dolphin's rostrum was between another dolphin's pectoral fin and tail.

Horizontal position: The horizontal distance between two dolphins was scored as *length*, *reach*, or *overlap*. *Length* referred to one body length between two dolphins. *Reach* was scored when two dolphins were within one body width of each other, such that they could potentially touch one another with extended pectoral fins. *Overlap* was scored when the body of a dolphin overlapped with the body of another dolphin. These three scored horizontal positions were later not analyzed as the distance between pairs was relatively consistent within pairs.

Tank position: After the data had been collected, an additional recording was created based on the dolphin's position relative to the tank wall. If the dolphin was next to the tank wall, and thus next to the underwater windows, their position was recorded as the *outside* position. If the dolphin was in the position closest to the center of the tank, such that they had greater body and visual access to other dolphins in the tank, this was recorded as the *inside* position. The position was determined from the dolphins' swim direction and eye position.

When the recordings of the dolphins were analyzed, several classifications of spatial positions were condensed. In the vertical position classifications, the *top-overlapping* and *bottom-overlapping* were condensed into the *above* and *below* categories. In the longitudinal position classifications, the *head-to-head* and *head-to-body* recordings were condensed into either *ahead* or *behind* categories, based on which dolphin was in front or behind another dolphin. The horizontal distance between two dolphins swimming together, scored as *length*, *reach*, or *overlap*, were not analyzed.

The majority of the time, the dolphins swam in pairs in the *upright* position. In this configuration, they had either their *left* or *right* (and not *both* or *no*) eye towards another dolphin. For the purposes of answering the original research question of a left or right eye position preference, only the instances when the dolphins were in pairs and swimming upright were

analyzed. While there were 15 possible pairings of the dolphins, only five pairs were observed frequently enough to be analyzed. Three dolphins were observed with multiple partners, while the other three dolphins were observed with only one partner.

Statistical Analysis

The first statistical analyses were conducted on left and right eye position, inside and outside position, and swim direction. The analyses were run for each observed dolphin pair using a two-sided binomial test. The two-sided binomial test was run based on the observed frequencies of one dolphin in a particular pair. The observed frequencies of a dolphin's position in the tank would be the exact opposite of the other dolphin's observed position frequencies. Thus, the observed frequencies of either dolphin in the pair would result in the same p-value. The dolphin chosen for analysis in each pair was based on alphabetical order of the dolphins' first letter initial.

A secondary analysis was conducted to determine if the left and right eye, and inside and outside positions, changed when the pairs' swim direction changed. A two-sided Fisher's Exact test was used to compare counterclockwise and clockwise swim direction with left and right eye positions. The same test was used to compare swim direction with inside and outside position for dependence. Again, the observed frequencies of one dolphin in a pair were analyzed as the resulting p-value would be the same for either dolphin in the pair.

A final analysis was conducted to determine how other factors, such as rank, horizontal and vertical position influenced the dolphins' side positions when swimming in pairs. The factors were modeled using a General Linear Model Regression (GLM). The responsive variable in the GLM was either eye position or tank position. The secondary variables in the model were

dolphin identity, horizontal position, vertical position, and rank. The residual differences from the null model were compared to the residual differences from the test model using an ANOVA test.

RESULTS

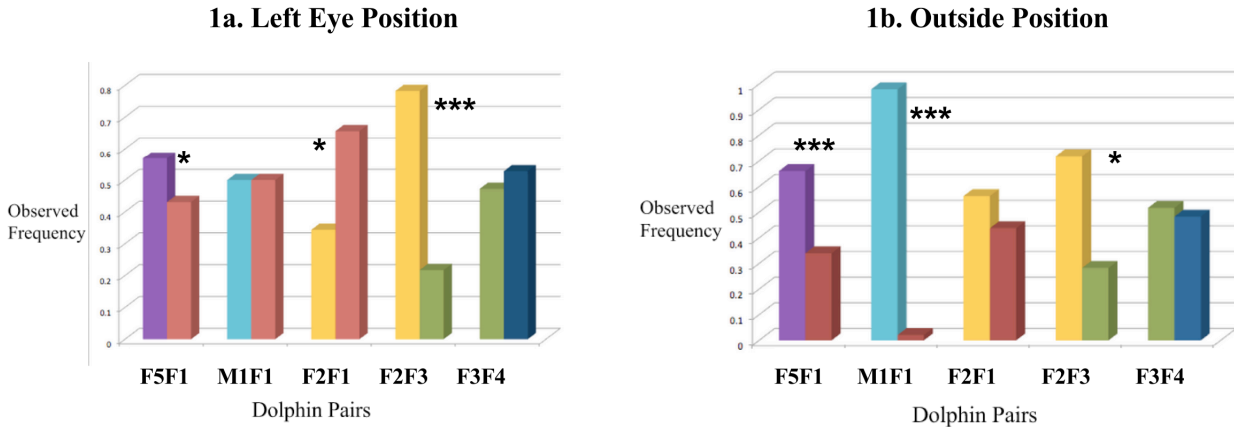
Binomial Test

1. The primary hypothesis was that left and right eye position preferences would vary based on the dolphins' rank. Three of the five dolphin pairs (F1F5, F1F2, F2F3) showed an eye position preference (Binomial test, $2P(Y \geq 181 | n = 318, p < .02)$; $2P(Y \leq 22 | n = 64, p < .02)$; $2P(Y \geq 36 | n = 46, p = .0001)$). The three pairs that showed eye position preferences were composed of dolphins from different rank categories. The two pairs that did not show an eye position preference (F1F5, F3F4) were dolphins from the same rank category.

2. Three of the five observed dolphin pairs (F1F5, F3F4, F2F3) preferred to swim in particular direction. Two pairs (F1F5, F2F3) preferred to swim in the counterclockwise direction (Binomial test, $2P(Y \geq 239 | n = 318, p < .0001)$; $2P(Y \geq 31 | n = 46, p < .03)$). Another pair (F3F4) preferred to swim in the clockwise direction (Binomial test, $2P(Y \geq 341 | n = 470, p < .0001)$).

Figure 1

Observed Position Preferences



Note. Five dolphin pairs are represented in the graph above. Each bar corresponds to a dolphin’s left eye position when swimming in that pair. Each dolphin is represented by a different color.

Note. The same five dolphin pairs are represented in the graph above. Each bar corresponds to a dolphin’s outside position when swimming in that pair. The colors represent the same dolphins as in Figure 1a.

3. One of the pairs (M1F1) that did not have an eye position preference did have an outside and inside position preference (Binomial test, $2P(Y \geq 47 | n = 48, p < .0001)$). The pair that showed this preference was the highest ranking adult female and male in rank category 1. Two other pairs (F2F3, F1F5) showed an outside and inside position preference (Binomial test, $2P(Y \geq 33 | n = 46, p < .01; 2P(Y \geq 210 | n = 318, p < .0001)$).

Two-sided Fisher’s Exact Test

4. A post-hoc analysis of the data revealed that certain dolphin pairs had position preferences that were dependent on swim direction. When certain pairs swam in a different direction, they either maintained their eye position, or they maintained their inside and outside position. A test for dependence of swim direction and eye position revealed that for two dolphin

pairs (F1F4, M1F1), their eye position was dependent on swim direction, meaning that when the dolphins changed swim direction, they changed their eye position but maintained their tank position (Two-sided Fisher's exact test, $p < .0001$; $p < .0001$). The other two other pairs (F1F2, F2F3) showed the opposite pattern. Their tank position was dependent on their swim direction, meaning their tank position varied by swim direction, but they maintained an eye position regardless of swim direction (Two-sided Fisher's Exact Test, $p < .01$; $p < .002$). The fifth dolphin pair (F3F4) showed variability in both eye positions and tank positions in both swim directions. Neither eye position nor tank position was dependent on swim direction.

ANOVA

5. An analysis of how the secondary factors of rank, horizontal, and vertical spatial positions were associated with side position, were analyzed. Rank, horizontal, and vertical spatial positions were significant predictors for both eye position, and inside and outside position (Table 2).

Table 2

ANOVA Results

	Null Model	Test Model	ANOVA
Test 1	Eyes ~ names	Eyes ~ names + horiz + vertical + horiz*vertical	$p < .04$
Test 2	In.out ~ names	In.out ~ names + horiz + vertical + horiz*vertical	$p < .001$
Test 3	Eyes ~ horiz*vertical	Eyes ~ rank + horiz*vertical	$p < .02$
Test 4	In.out ~ horiz*vertical	In.out ~ rank + horiz*vertical	$p < .001$

6. A qualitative analysis of rank on eye position revealed that for two dolphin pairs (F1F2, F2F3) that were of different ranks, the highest ranking dolphin had its left eye towards the

low ranking dolphin. This eye position preference was consistent across rank for the two female pairs. The two dolphin pairs (F3F4, M1F1) that had individuals of the same rank showed no eye position preference. However, one of those two dolphin pairs showed an inside and outside position preference. The higher ranked position that was consistent with a left eye preference for two pairs did not hold true for the adult female and her juvenile daughter (F1F5). The juvenile daughter was observed more frequently in the left eye position.

DISCUSSION

Certain dolphin pairs, composed of individuals from different rank categories, showed eye position preferences. The three dolphins that were observed with multiple partners changed their eye position depending on if their swim partner was a lower or higher ranking individual. In two of the three pairs that had mixed ranked dolphins, the higher ranked female of a given pair swam with her left eye towards the other dolphin. In contrast, the lower ranked female had her right eye towards her swim partner. In the third pair, the eye positions of the highest ranked female and her juvenile daughter were inconsistent with the previous two pairs' eye position and rank associations. The higher ranking mother had her right eye towards her lower ranking daughter. Although their eye position preferences were not consistent with the other two pairs, their eye position preference was consistent with wild orca and beluga whale mother-infant studies, where young infants were observed with their left eye towards their mother (Karenina et al., 2010a; 2013b). While the daughter in this study was not an infant, she was the youngest daughter of the adult female and may have continued to position herself with her left eye towards her mother.

The two dolphin pairs that were in the same rank category did not show eye position preferences. Upon closer examination of the high ranking adult male and female pair, they showed a preference for an outside and inside position along the tank wall, with the male on the outside. The other dolphin pair, composed of the two adolescent dolphins both in rank category 2, showed no significant results for eye position or tank position.

When the highest ranking male and female swam together, the adult male was observed nearly always in the outside position and below the adult female. The position below the female may be a herding position observed in the wild. However, if the male dolphin was using “herding” as a way to “sequester” the female from others, as male bottlenose dolphins are often observed doing in the wild (Connor et al, 2000; Wells, Irvine & Scott, 1980), we might have expected the male dolphin to have positioned himself in the inside position to herd the female away from the other animals. But, with no other males in the tank, he may instead have been “sequestering” her from the humans at the windows. With only one male dolphin in the tank at the time of the study, the role of gender remains unclear.

The adult male and female were not the only pairs that had an inside and outside position preference. In fact, three dolphin pairs showed an inside and outside preference. For the mother and her juvenile daughter, it was found that their eye position was dependent on swim direction, while their inside and outside positions were maintained regardless of swim direction. However, for the second highest ranking female and lower ranking female adolescent pair, it was found that their inside and outside spatial positions were dependent with swim direction. Their eye position was maintained regardless of swim direction. This would suggest that these pairs had a stronger eye position preference than tank position preference.

At the Brookfield Zoo, the outside position afforded visual access to the humans through the underwater windows, while the inside position in the tank allowed visual access to other dolphins swimming in the tank. The inside position also allowed body access to the other dolphins in the tank. That is, the inside position put the dolphins in a position where they could break away from their partner and swim towards another dolphin in the tank. In the wild, having a particular eye oriented away from the group may be used to monitor the behavior of other dolphins nearby. Having a particular eye oriented away from the group may also have the function of monitoring for predators. The dolphins may have had individual preferences for being in the inside position or the outside position

Yet another alternative hypothesis to their position preferences is swim direction. Previous studies have suggested that bottlenose dolphins in captivity often have a swim direction preference (Marino & Stowe, 1997a; 1997b) , although the direction appears to vary with facility. In this study at the Brookfield Zoo, the dolphins' swim direction varied in the tank. Two of the five pairs swam in either direction with no significant direction preference, while the other three pairs did have swim direction preferences. The direction varied by pair; two dolphin pairs swam more frequently in the counterclockwise direction, while the third pair swam more frequently in the clockwise direction.

If the dolphins were positioning themselves such that their left eye was to the window to look at the humans, the results would have indicated a swim direction preference for the clockwise direction. Both dolphins in a pair would have the same eye towards the window as they swam together in the circular tanks. Previous studies have suggested a left eye preference for looking at humans (Sakai et al., 2006; Thieltges et al., 2011). However, the results of the study at the Brookfield Zoo do not indicate a clockwise swim direction preference across pairs.

Furthermore, for the two pairs who had an inside and outside position preference, only one pair had a swim direction preference. The pair that showed this swim direction preference was the juvenile daughter and high ranking adult female, and they swam more frequently in the counterclockwise swim direction. The other pair that showed the tank position preference swam in both directions with almost equal frequency. The observed swim direction frequencies in this study do not support the hypothesis that the dolphins were swimming such that their both left eyes were toward windows to observe the humans. However, it is important to recognize the differences between the previous studies, when the dolphins were observed actively looking at humans, and this study. In contrast to the previous studies, in this study the dolphins swam in groups and looked at the humans through glass windows. When the dolphins swam in pairs, they tended to swim by the windows without turning their heads or actively changing their head orientation to look at the humans. In contrast, when they swam by themselves in the tank, they would occasionally swim towards the windows and turn to their heads to look at the humans. This active looking behavior was rarely observed when the dolphins were swimming in pairs. This may indicate that the dolphins' use their vision differently in depending on the social context. Lateralized visual preferences may be observed differently depending on the behavioral and social contexts.

The dolphins observed in this study were recorded in the morning during group swimming. The dolphins were less aroused in the morning than at other times of the day during feeds and shows. Arousal and active social engagement, like pectoral fin rubbing, may show lateralized eye position preferences among pairs. Future studies on a larger population of dolphins, and their known rank and age, could provide insight into their left and right eye position preferences under varied social contexts. Casagrande et al. (2013) studied lateralized

behavior of Guiana dolphins under different behaviors: breaching, flippering, and tail slapping. The results indicated that, of these behaviors, only breaching was lateralized, occurring on the right side 63% of the time. In bottlenose dolphins, they too may have eye position preferences for flipper rubbing and active social behaviors. Lateralized vision and rank in bottlenose dolphins may be two factors driving their left and right side position preferences under varied social contexts.

ACKNOWLEDGEMENTS

Thank you to the Distributed Cognition Lab and the Brookfield Zoological Society for providing me with access to the video recordings of the dolphins. Thank you to Christine Johnson, Jeremy Karnowski, and Edwin Hutchins for advising me through my honors thesis. Lastly, thanks to Marta Kutas, Thanh Maxwell, and the entire UCSD Cognitive Science honors thesis class of 2014.

REFERENCES

- Blois-Heulin, C., Crevel, M., Boeye, M., Lemasson, A. (2012). Visual laterality in dolphins: Importance of the familiarity of stimuli. *BMC Neuroscience*, 13(9): 8pp.
- Casagrande, T., Lunardi, V. O., Lunardi, D. G. (2013). Lateralized behavior in Guiana dolphins, *Sotalia guianensis*, at Pipa Beach, RN, Brazil. *Brazilian Journal of Biology*, 73(1):223-224.
- Connor, R.C., R. Wells, J. Mann, and A. Read. (2000). The bottlenose dolphin: social relationships in a fission-fusion society. In J. Mann; R.Connor, P.Tyack, and H.

- Whitehead (Eds.) *Cetacean Societies: Field studies of whales and dolphins* (pp. 91-126). Chicago: University of Chicago Press.
- Dral, A.D.G. (1977). On the retinal anatomy of cetacea (mainly *Tursiops truncatus*). In: Harrison, R.J. (Ed.), *Functional Anatomy of Marine Mammals III*. (81–134). London: Academic Press.
- Jacobs, M.S., Morgane, P.J., McFarland, W.L. (1975) Degeneration of visual pathways in the bottlenose dolphin. *Brain Research*, 88:346–352.
- Johnson, C.M., Moewe, K. (1999). Pectoral fin preference during contact in Commerson's dolphins (*Cephalorhynchus commersonii*). *Aquatic Mammals*, 25:73–77.
- Karenina, K., Giljov, A., Baranov, V., Osipova, L., & Krasnova, V. (2010a). Visual laterality of calf–mother interactions in wild whales. *PLoS ONE* 5, e13787.
doi:10.1371/journal.pone.0013787
- Karenina, K., Giljov, A., Dmitry, G., Malashichev, Y. (2013a). Social laterality in wild beluga whale infants: comparisons between locations, escort conditions, and ages. *Behavioral Ecology and Sociobiology*, 67(7):1195-1204.
- Karenina, K., Giljov, A., Ivkovich, T., Burdin, A., Malashichev, Y. (2013b). Lateralization of spatial relationships between wild mother and infant orcas, *Orcinus orca*. *Animal Behavior*, 86(6):1225-1231.
- Karenina, A., Giljov, A.N., Malashichev, Y.B., Baranov, V.S., Bel'kovich, V.M. (2010b) Visual lateralization in the wild: perceiving of novel object in beluga whale (*Delphinapterus leucas*). *Asymmetry Journal*, 4:3–12.
- Kilian, A., von Fersen, L., Güntürkün, O. (2000). Lateralization of visuospatial processing in the bottlenose dolphin (*Tursiops truncatus*). *Behavioral Brain Research*, 116:211-215.

- Kilian, A., von Fersen, L., Güntürkün, O. (2005). Left hemispheric advantage for numerical abilities in the bottlenose dolphin. *Behavioral Processes*, 68(2):179–184.
- Lyamin, O., Pryaslova, J., Kosenko, P., Siegel, J. (2007) Behavioral aspects of sleep in bottlenose dolphin mothers and their calves. *Physiology & Behavior*, 92:725–733.
- McIntyre, J. (1974). *Mind in the waters*. New York: Scribner.
- Manger, P.R., Hemingway, J., Haagensen, M., Gilissen, E. (2010) Cross-sectional area of the elephant corpus callosum: comparison to other eutherian mammals. *Neuroscience*, 167:815–824.
- Marino, L. & Stowe, J. (1997a). Lateralized behavior in two captive bottlenose dolphins (*Tursiops truncatus*). *Zoo Biology*, 16:173-177.
- Marino, L. & Stowe, J. (1997b). Lateralized behavior in a captive beluga whale (*Delphinapterus leucas*). *Aquatic Mammals*, 23(2):101-103.
- Morrel-Samuels, P., & Herman, L. M. (1993). Cognitive factors affecting comprehension of gesture language signs: A brief comparison of dolphins and humans. In H. R. Roitblat, L. M. Herman, & P. Nachtigall (Eds.), *Language and communication* (311-327). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Mukhametov, L. M. (1985). Unihemispheric slow wave sleep in the brain of dolphins and seals. In: S.Inoue and A. A.Borbély (Eds) *Endogenous Sleep Substances and Sleep Regulation* (67-75). Tokyo: Japanese Scientific Societies Press, YNU Science Press BV, Utrecht.
- Norris, K.S., and Dohl, T.P. (1980). The structure and functions of cetacean schools. In: LM Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (211-261). NY: Wiley.
- Ridgway, S.H., and Wood, F.G. (1988). Cetacean Brain Evolution. *Behavioral and Brain*

Sciences, 11(1):99-100.

- Ridgway, S.H. (1990) The central nervous system of the bottlenose dolphin. In: S. Leatherwood & R.R. Reeves (Eds.), *The Bottlenose dolphin* (69-97). San Diego: Academic.
- Rogers, L.J. (2002) Lateralization in vertebrates: Its early evolution, general pattern, and development. *Advances in the Study of Behavior, 31:107-161.*
- Sakai, M., Hishii, T., Takeda, S. & Kohshima, S. 2006. Laterality of flipper rubbing behaviour in wild bottlenose dolphins (*Tursiops aduncus*): Caused by asymmetry of eye use? *Behavioural Brain Research, 170(2), 204-210.*
- Thieltges, H., Lemasson, A., Kuczaj, S., Boeye, M., Blois-Heulin, C. (2011). Visual laterality in dolphins when looking at (un)familiar humans. *Animal Cognition, 14(2):303-308.*
- Tommasi, L. (2009). Mechanisms and functions of brain and behavioural asymmetries. *Philos Trans R Soc Lond B Biol Sci. 364:855–859.*
- Vallortigara G, Rogers LJ (2005) Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences, 28:575–589.*
- von Fersen, L., Schall, W., Gunturkun, O. (2000). Visual lateralization of pattern discrimination in the bottlenose dolphin (*Tursiops truncatus*). *Behavioral Brain Research, 107:177-181.*
- Wells, R.S., Irvine, A.B. & Scott, M.D. (1980) The social ecology of inshore Odontocetes. In L.M. Herman. (Ed.) *Cetacean Behavior* (pp. 263-318). NY: John Wiley & Sons.
- Yaman, S., von Fersen, L., Dehnhardt, G., & Güntürkün, O. (2003). Visual lateralization in the bottlenose dolphin (*Tursiops truncatus*): Evidence for a population asymmetry? *Behavioural Brain Research, 142, 109–114.*