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# Laterality of Eye Use by Bottlenose (*Tursiops truncatus*) and Rough-Toothed (*Steno bredanensis*) Dolphins While Viewing Predictable and Unpredictable Stimuli

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Laterality of eye use has been increasingly studied in cetaceans. Research supports that many cetacean species keep prey on the right side while feeding and preferentially view unfamiliar objects with the right eye. In contrast, the left eye has been used more by calves while in close proximity to their mothers. Despite some discrepancies across and within species, laterality of eye use generally indicates functional specialization of brain hemispheres in cetaceans. The present study aimed to examine laterality of eye use in bottlenose dolphins (*Tursiops truncatus*) and rough-toothed dolphins (*Steno bredanensis*) under managed care. Subjects were video-recorded through an underwater window while viewing two different stimuli, one predictable and static and the other unpredictable and moving. Bottlenose dolphins displayed an overall right-eye preference, especially while viewing the unpredictable, moving stimulus. Rough-toothed dolphins did not display eye preference while viewing stimuli. No significant correlations between degree of laterality and behavioral interest in the stimuli were found. Only for bottlenose dolphins were the degree of laterality and curiosity ratings correlated. This study extends research on cetacean lateralization to a species not extensively examined and to stimuli that varied in movement and degree of predictability. Further research is needed to make conclusions regarding lateralization in cetaceans.

*Keywords*: laterality, lateralization, bottlenose dolphins, rough-toothed dolphins, eye use

Lateralization of brain function, the functional specialization of each brain hemisphere, is a topic of interest that has been increasingly explored with studies involving visuospatial abilities and social interactions in humans and many species of non-human animals. Research on lateralization ranges from studies on personality in rainbow fish (*Melanotaenia nigrans*) to studies on human and primate language abilities (Brown & Bibost, 2014; Fitch & Braccini, 2013). A better understanding of lateralization across taxa allows for cross-species comparisons involving the evolutionary pressures that shaped these patterns. Cetaceans are often compared to humans and nonhuman primates in their cognitive abilities and social characteristics, thus making the study of cetacean lateralization of particular interest. Pertinent to the present study is research on visual laterality in cetaceans and the connection between laterality and personality.

## Visual Laterality in Cetaceans

### *Anatomy*

Given cetacean anatomical features, laterality of eye use in this taxon reveals hemispheric brain specialization. One anatomical feature is the lateral position of cetacean eyes, which allows researchers to determine the field of vision used by animals to perform tasks or view objects. Although binocular vision is sometimes used, the physical positions of the eyes allow monocular vision to be frequently used. Additionally,

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in comparison to humans, the smaller size of the cetacean corpus callosum relative to brain mass suggests that brain hemispheres in cetaceans function more independently of each other (Tarpley & Ridgway, 1994). Furthermore, the complete decussation of the optic nerve indicates that visual information taken in by one eye is directed to the opposite brain hemisphere for processing (Tarpley et al., 1994). Knowledge about these anatomical characteristics has allowed researchers to explore questions regarding cetacean eye use during social behaviors, feeding behaviors, and visual discrimination tasks. Eye-use preference and/or enhanced performance when using a particular eye are used to infer specialization in the opposite brain hemisphere (Blois-Heulin et al., 2012; Kilian et al., 2000).

***Social Behavior***

Research suggests that the right cerebral hemisphere of dolphins is responsible for processing social information (Karenina et al., 2010; Sakai et al., 2006; Winship et al., 2017). Sakai et al. (2006) found that bottlenose dolphins preferred to use the left flipper for flipper rubbing with social partners. The same dolphin population preferred to use the left eye during this social behavior, suggesting that left-flipper preference may be related to left-eye preference. The absence of flipper preference during object carrying discarded the hypothesis that left-flipper preference was related to laterality of motor abilities. Taken together, these results support a specific function of the right cerebral hemisphere to process information during flipper rubbing (a social behavior) but not object carrying (an independent behavior). If there was an overall preference for flipper use in dolphins, comparable to the handedness in humans, the authors would expect to see similar flipper preference for carrying objects and rubbing conspecifics (Sakai et al., 2006). Another study assessing pectoral fin use in a managed-care group of bottlenose dolphins found age differences for fin preference during social interactions. Calves used the right pectoral fins more frequently, whereas sub-adults and adults used the left pectoral fins more frequently (Winship et al., 2017). Lateralized behavior involving flipper preference was also found in orcas; the right pectoral flipper was used more frequently than the left during flipper slapping at the surface (Giljov et al., 2016).

Although not tactile in nature, visual laterality has been observed during mother-calf interactions in belugas (*Delphinapterus leucas*). In both wild and managed-care beluga populations, calves spent significantly more time on the right side of the mother, thus observing her with the left eye (Hill et al., 2017; Karenina et al., 2010). Similar laterality of eye use was found in orcas. In one study, when orca mother-calf pairs were in close proximity to the observation watercraft, orca calves swam on the mother's left side more frequently; however, these positions were reversed when the distance from the observation watercraft increased (Karenina et al., 2013). Another study assessing laterality of eye use in wild orcas found that adult females used the left eye more than the right eye while viewing human swimmers (Chanvallon et al., 2017). Results from these studies of laterality in social behaviors provide evidence of left-eye preference across cetacean species, implicating the function of the right cerebral hemisphere in processing social information.

***Feeding Behavior***

In contrast to the left eye/right hemisphere specialization for socialization, right eye/left hemisphere specialization has been hypothesized for feeding behavior. In wild settings, laterality of feeding behavior has been noted in diverse species of cetaceans. Lunging or rolling to the right side to capture prey has been observed in North Atlantic humpback whales (*Megaptera novaeangliae*; Canning et al., 2011), gray whales (*Eschrichtius robustus*; Woodward & Winn, 2006), bottlenose dolphins (Kaplan et al., 2019), and orcas (Karenina et al., 2016).

### *Visual Discrimination*

Many studies regarding cetacean brain lateralization have focused on the visuospatial abilities of these animals with regard to pattern discrimination, numeric abilities, and investigatory behavior. Two separate studies reported the ability of bottlenose dolphins to discriminate between different patterns of visual stimuli (von Fersen et al., 2000; Yaman et al., 2003). The results of these studies indicated that dolphins performed better while viewing the patterns with the right eye, which suggests the left hemisphere processed information about visual patterns more accurately. Yaman et al. (2003) also recorded animals' daily activities and found that the right eye was used significantly more while viewing unfamiliar objects and during daily activity, such as training sessions. This observation led the authors to hypothesize that the counter-clockwise swim pattern exhibited by most dolphins is the result of using the right eye to examine objects or monitor activity around the perimeter of the enclosure (Sobel et al., 1994).

Furthermore, specific forms of visuospatial processing, including numeric abilities, obstacle navigation, and audiovisual stimuli discrimination, have been attributed to left hemisphere dominance. Kilian et al. (2005) found that bottlenose dolphins performed better in numeric tasks while viewing the test stimuli with the right eye. Similarly, this bottlenose dolphin group completed more successful trials in a navigation task when using the right eye (Kilian et al., 2000). A different bottlenose dolphin group tested in an audiovisual matching task performed better when using the right eye, suggesting left hemisphere dominance for visual and auditory stimuli (Delfour & Marten, 2006). In contrast, a study assessing accuracy of visual processing in a single bottlenose dolphin indicated that this animal responded faster when using the left eye (Matrai et al., 2019).

### *Familiarity of Humans*

The degree of familiarity of stimuli presented to subjects has also been examined for its effect of laterality of eye use. One study found a left eye/right hemisphere dominance when dolphins viewed both familiar and unfamiliar human stimuli (Thieltges et al., 2010). Additionally, regardless of eye use, dolphins gazed significantly longer at unfamiliar humans. The ability of dolphins to discriminate between the two categories of human stimuli suggested that humans may be socially significant visual stimuli in this managed-care dolphin group (Thieltges et al., 2010). Laterality of eye use while viewing familiar and unfamiliar humans was also examined in belugas, bottlenose dolphins, and Pacific white-sided dolphins (Hill et al., 2016; Yeater et al., 2014). Despite the lack of species-level laterality, eye-use preference emerged at the individual level, with some subjects using the left eye more than the right eye (Hill et al., 2016; Yeater et al., 2014). Furthermore, Hill et al. (2016) examined if laterality varied if the human stimuli were stationary or moving but found no laterality of eye use based on movement.

### *Familiarity of Objects*

A study examining preference of eye use while viewing familiar and unfamiliar objects in three cetacean species reported that each species displayed a different pattern of eye use (Yeater et al., 2017). Regardless of familiarity, bottlenose dolphins used the right eye more than the left eye while viewing objects, belugas used both eyes or used the left eye monocularly, and Pacific white-sided dolphins used the left eye more than the right eye (Yeater et al., 2017).

A right-eye preference was found for wild striped dolphins (*Stenella coeruleoalba)* while viewing unfamiliar stimuli (Siniscalchi et al., 2012) and for bottlenose dolphins in managed care while viewing very familiar, familiar, and unfamiliar objects (Blois-Heulin et al., 2012). Additionally, the bottlenose dolphins used the right eye to observe unfamiliar objects and familiar objects with which the subjects had not previously interacted and the left eye to observe very familiar objects with which the subjects had previously interacted. Blois-Heulin et al. (2012) suggested that the right hemisphere may process more general features of familiar objects, especially those with which the dolphin has interacted, while the left hemisphere may process the details of an unfamiliar object. In a study of dolphins' behavior, while using an underwater maze task, the two subjects that used the maze the most displayed a right eye preference for viewing the maze (Clark & Kuczaj, 2016).

Based on the studies discussed thus far, the right hemisphere appears to process socially significant visual information and more familiar visual stimuli. In contrast, the left hemisphere may be more adept at analyzing local details of visuospatial and unfamiliar stimuli while also being used more often during feeding behavior. Despite some discrepancies in previous research, most findings have been relatively consistent in finding the lateralized function of the left hemisphere for controlling movement and appendage usage across humans and marine mammals (MacNeilage, 2013).

### Personality and Lateralization

Some research has suggested that lateralization and personality may be linked. Brown and Bibost (2014) found that a higher level of boldness in fish was related to stronger laterality of eye use in front of a mirror. Similarly, Found and St. Clair (2017) reported that laterality of front limb use in elk was correlated with boldness and increased migration. Also, subordinate dairy cows were more likely to use the left eye while viewing other cows and unfamiliar humans as compared to dominant individuals' eye-use (Phillips et al., 2015). Ungulates, including elk and cows, are distant evolutionary relatives of cetaceans (Shimamura et al., 1997), thus increasing the likelihood that this trend may be preserved across species and also observed in dolphins.

### Present Study

The present study extended previous research to examine laterality of eye use in bottlenose (*Tursiops truncatus*) and rough-toothed dolphins (*Steno bredanensis*) while subjects viewed an unpredictable, moving jack-in-the-box stimulus and a predictable, static cylinder stimulus. Previous research found subjects had longer gaze durations for the unpredictable, moving stimulus compared to the predictable, static stimulus, but there were individual differences in curiosity-related behaviors, and laterality was not assessed (Lilley et al., 2018). Laterality has not been extensively examined in rough-toothed dolphins; however, based on prior research in cetaceans, it was hypothesized that both bottlenose and rough-toothed dolphins would predominantly use the right eye while viewing both stimuli, but would use the right eye significantly more while viewing the unpredictable stimulus.

## Method

#### Subjects

The subjects of this study were 15 bottlenose dolphins (*Tursiops truncatus*; 5 males, 9 females; 7 adults, 5 juveniles, 3 calves) and 5 rough-toothed dolphins (*Steno bredanensis*; 3 males, 2 females; 4 adults, 1 juvenile) housed at Gulf World Marine Park in Panama City Beach, Florida. Estimated age was used for individuals who were rescued after stranding, and age classes were defined as calf (0-2 years), juvenile (3-10 years), and adult (11+ years) per Eskelinen et al. (2015). Subjects had daily interactions with training staff, visitors, and environmental enrichment. These interactions took multiple forms, from in-water swims with guests to husbandry sessions, and varied greatly on a day-to-day basis. Social groupings also varied on a daily basis.

### Procedure

Data were collected by video recording subjects' behavior while viewing an unpredictable, moving jack-in-the-box stimulus, which was manually opened via a mechanism at the back of the jack-in-the-box at random intervals between 1 and 15 s, and a predictable, static cylinder stimulus. Subjects were given the opportunity to observe each object at separate times through an underwater viewing window for five 5-min trials. This procedure was part of data collection for a previously published study (see Lilley et al., 2018, Experiment 1, for details). Videos were coded according to the procedure of Lilley et al. (2018) with the addition that eye use (left eye, right eye, and both eyes) was coded to produce a duration in seconds for each eye use category for each experimental session. Eye use was defined as the visibility of subjects' eyes from the perspective of the stimuli, and therefore the camera. Additionally, caretakers' ratings of subjects' curiosity on a 7-point Likert scale item and the total time spent viewing stimuli were measures used for this study, both taken from Lilley et al. (2018).

### Analysis

For each eye use category, gaze duration was converted to percentage of the time, dividing the duration of each eye use by the total time a subject spent viewing a stimulus. For each species, an ANOVA was conducted to compare percentage of eye use (left, right, and both eyes; between-subjects factor) across conditions (static/predictable, moving/unpredictable; repeated-measures factor). To obtain the degree of laterality that each subject displayed, the laterality index ([R-L]/[R+L]) was calculated (Thieltges et al., 2010). The absolute value of this calculation was used to determine degree of laterality (i.e., the extent to which a subject displayed lateralized behavior). The degree of laterality was then correlated with overall gaze duration and human caretakers' ratings of the subjects as "curious."

## Results

For bottlenose dolphins, there was a significant interaction between stimuli displayed and eye use, $F(2, 39) = 10.93$, $p < 0.01$, $\eta_p^2 = 0.36$ (Figure 1). There was also a significant main effect of eye use, $F(2, 39) = 8.96$, $p < 0.01$, $\eta_p^2 = 0.32$. Post-hoc follow-up analyses revealed that bottlenose dolphins were more likely to use their right eye ($M = 45.82$, $SD = 17.33$) compared to the left eye ($M = 27.83$, $SD = 14.44$; $p < 0.01$) and both eyes ($M = 27.41$, $SD = 13.83$; $p < 0.01$) regardless of the stimuli presented. For the predictable, static object, there was a significant difference in eye use, $F(2, 39) = 10.61$, $p < 0.01$, $\eta_p^2 = 0.35$, with the right eye ($M = 48.01$, $SD = 19.54$) being used significantly more than both eyes ($M = 19.60$, $SD = 11.98$; $p < 0.01$), a trend for the right eye being used more than the left eye ($M = 33.81$, $SD = 16.55$; $p = 0.08$), and the left eye being used more than both eyes ($p = 0.08$). For the unpredictable, moving object, there was a significant effect of eye use, $F(2, 42) = 9.90$, $p < 0.01$, $\eta_p^2 = 0.32$, with the right eye ($M = 44.04$, $SD = 14.66$) being used significantly more than the left eye ($M = 21.50$, $SD = 11.96$; $p < 0.01$) and both eyes ($M = 35.11$, $SD = 15.11$) being used significantly more than the left eye ($p = 0.03$).

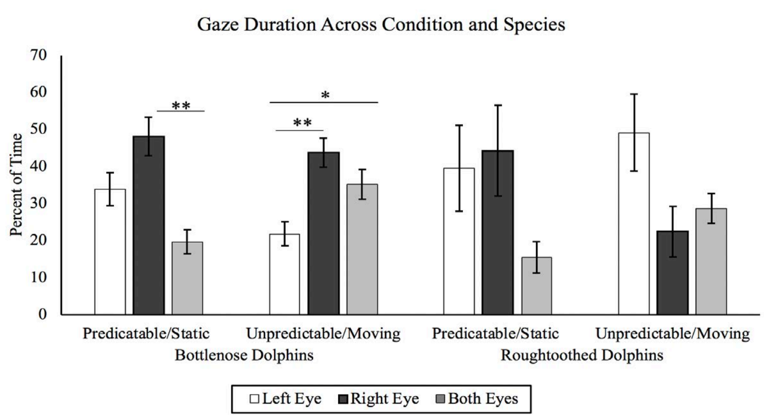


*Figure 1*. **Gaze duration across condition and species.** * $p < .05$ and ** $p < .001$. Error bars represent standard error for each eye.

An assessment of individual differences in bottlenose dolphins indicated that the majority of individuals had a right-eye preference while viewing the unmoving, predictable stimulus as well as the moving, unpredictable stimulus. However, many bottlenose dolphins switched to using both eyes more while viewing the moving, unpredictable object (Table 1; Subjects 1-15).

**Table 1**

*Individual Differences in Eye Use [M(SD) as Measured in Seconds] Across Conditions*

| Subject | Predictable/Static | | | Unpredictable/Moving | | |
|---|---|---|---|---|---|---|
| | Left Eye | Right Eye | Both Eyes | Left Eye | Right Eye | Both Eyes |
| 1 | **56.10(14.84)** | 25.54(22.14) | 18.36(16.92) | 27.97(27.05) | **45.57(29.24)** | 26.46(27.87) |
| 2 | 7.53(13.04) | **74.19(44.70)** | 18.28(31.66) | 9.22(10.80) | **51.74(34.8)** | 39.04(30.21) |
| 3 | **50.26(43.41)** | 29.32(27.06) | 20.43(18.13) | 14.79(10.87) | **42.93(38.05)** | 42.28(28.64) |
| 4 | 16.67(21.28) | 43.89(43.90) | **45.00(40.18)** | 4.70(6.47) | 45.4(34.14) | **49.90(31.04)** |
| 5 | 27.78(25.46) | **60.19(37.71)** | 12.04(12.53) | 11.56(16.68) | **54.86(34.65)** | 33.58(22.18) |
| 6 | **59.32(28.95)** | 17.26(19.80) | 23.42(16.79) | 9.03(5.36) | 25.68(15.44) | **65.28(16.22)** |
| 7 | 19.05(0.00) | **76.19(0.00)** | 4.76(0.00) | 18.42(0.00) | **71.05(0.00)** | 10.53(0.00) |
| 8 | 27.69(0.00) | 29.23(0.00) | **43.08(0.00)** | 24.14(0.00) | 27.59(0.00) | **53.45(0.00)** |
| 9 | 31.15(10.07) | **52.68(15.85)** | 16.17(10.71) | 27.43(9.77) | **40.93(10.92)** | 31.64(9.41) |
| 10 | **54.56(39.23)** | 31.18(28.45) | 14.26(17.30) | **48.76(20.26)** | 23.55(9.57) | 27.69(16.52) |
| 11 | 15.56(14.21) | **63.56(33.49)** | 20.88(19.57) | 17.04(16.99) | 37.59(33.22) | **45.37(22.51)** |
| 12 | 30.01(23.26) | **71.56(23.65)** | 3.43(6.86) | **39.22(10.85)** | 22.94(16.42) | 37.84(12.52) |
| 13 | 42.76(12.15) | **43.04(15.64)** | 22.54(23.57) | 30.04(34.21) | **60.42(34.71)** | 14.27(15.55) |
| 14 | 34.98(16.19) | **54.33(18.36)** | 11.69(12.78) | 23.55(8.35) | **60.40(21.17)** | 16.05(16.15) |
| 15 | - | - | - | 16.67(11.79) | **50.00(35.36)** | 33.33(47.14) |
| 16 | 10.53(14.89) | **81.58(26.05)** | 7.89(11.16) | **75.88(8.09)** | 3.03(5.25) | 21.09(12.12) |
| 17 | 32.11(45.95) | **47.15(39.07)** | 20.74(21.71) | 13.31(15.64) | **45.40(33.3)** | 41.30(23.43) |
| 18 | 26.93(23.88) | **41.10(24.58)** | 27.66(17.48) | **48.77(35.84)** | 18.39(20.06) | 32.84(30.64) |
| 19 | **48.61(46.83)** | 47.22(41.74) | 4.17(7.22) | **45.7(39.73)** | 25.97(21.02) | 28.33(33.94) |
| 20 | **79.17(26.02)** | 4.17(7.22) | 16.67(28.87) | **61.95(44.91)** | 19.39(27.73) | 19.54(33.11) |
| Avg | 35.85(29.08) | **46.53(31.18)** | 18.58(19.87) | 28.29(27.02) | **38.18(28.44)** | 33.90(24.56) |

*Note.* Bold values indicate the eye(s) used for the majority of time for each subject in each condition. Subject 15 did not participate in any trials for the predictable, static object.

For rough-toothed dolphins, there was not a significant interaction between stimuli displayed and eye use, $F(2, 12) = 2.17$, $p = 0.16$, $\eta_p^2 = 0.27$ (Figure 1). Additionally, there was not a significant main effect of eye use, $F(2, 12) = 3.39$, $p = 0.07$, $\eta_p^2 = 0.36$, though a trend was present (left eye: $M = 44.30$, $SD = 24.67$; right eye: $M = 33.34$, $SD = 21.43$; both eyes: $M = 22.02$, $SD = 9.22$). For the predictable, static object, there was not a difference in eye use, $F(2, 12) = 2.35$, $p = 0.14$, $\eta_p^2 = 0.28$ (left eye: $M = 39.47$, $SD = 26.02$; right eye: $M = 44.24$, $SD = 27.51$; both eyes: $M = 15.43$, $SD = 9.53$), although there was a trend for a difference in eye use for the unpredictable, moving object, $F(2, 12) = 3.41$, $p = 0.07$, $\eta_p^2 = 0.36$ (left eye: $M = 49.12$, $SD = 23.32$; right eye: $M = 22.44$, $SD = 15.34$; both eyes: $M = 28.62$, $SD = 8.91$).

An assessment of individual differences in rough-toothed dolphins indicated that the majority of individuals had a right-eye preference while viewing the predictable, static object and a left-eye preference while viewing the moving, unpredictable stimulus (Table 1; Subjects 16-20).

For bottlenose dolphins, laterality of eye use was not significantly correlated with overall gaze duration, $r(13) = -0.12$, $p = 0.45$, but there was a significant correlation between laterality and caretakers' ratings of the subjects' curiosity, $r(13) = -0.63$, $p = 0.01$. For rough-toothed dolphins, laterality of eye use was not significantly correlated with overall gaze duration, $r(3) = -0.06$, $p = 0.93$, nor was there a significant correlation for laterality and caretakers' ratings of the subjects' curiosity, $r(3) = -0.28$, $p = 0.65$.

## Discussion

The present study sought to further explore cetacean laterality of eye use in bottlenose and rough-toothed dolphins. Previous studies have used human and object stimuli that varied in their degree of familiarity and found that bottlenose dolphins typically use the right eye more while viewing objects, especially unfamiliar objects (e.g., Blois-Heulin et al., 2012; Yeater et al., 2017). Bottlenose dolphins typically used the left eye more while viewing human stimuli, although these patterns have not been corroborated by all previous studies (e.g., Hill et al., 2016). In the present study, bottlenose and rough-toothed dolphins were shown a static, predictable object and a moving, unpredictable object through an underwater viewing window. These stimuli were viewed by the dolphins several times through the underwater viewing windows during the study, but, prior to the study, the stimuli were novel for the subjects, and at no point during the study did the subjects have tactile contact with the stimuli.

For bottlenose dolphins, there was a significant effect of eye use for the static, predictable object, with the right eye being used significantly more than both eyes and the right eye being used descriptively, but not significantly, more than the left eye. While viewing the moving, unpredictable stimulus, bottlenose dolphins used the right eye significantly more than the left eye and both eyes significantly more than the left eye. Descriptively, the right eye was also used more than both eyes while viewing the moving, unpredictable stimulus. At the individual level, the majority of bottlenose dolphins displayed a right-eye preference while viewing the static, predictable stimulus, and this pattern was even more pronounced when they viewed the moving, unpredictable stimulus. Many individual bottlenose dolphins also increased their use of binocular vision to look at the moving, unpredictable stimulus. This finding was consistent with past literature that showed cetaceans typically used the right eye more while viewing unfamiliar stimuli (Blois-Heulin et al., 2012), moving objects such as prey (Karenina et al., 2016), and during visual discrimination tasks (von Fersen et al., 2000; Yaman et al., 2003). Due to cetacean brain anatomy (Tarpley et al., 1994; Tarpley & Ridgway, 1994), use of the right eye for these tasks indicates that bottlenose dolphins' left cerebral hemisphere is likely more specialized to process this visual information. This study extends previous research that compared laterality for familiar and unfamiliar objects (Blois-Heulin et al., 2012) by using two unfamiliar objects that varied in movement and degree of predictability.

Rough-toothed dolphins have not been extensively examined in the cetacean cognition literature. Previous research on cetacean species other than bottlenose dolphins generally confirms the right-eye visual advantage, especially during feeding (e.g., Karenina et al., 2016). However, several studies have found a lack of species-level laterality for other species, such as belugas, Pacific white-sided dolphins, and Yangtze finless porpoises (*Neophocaena asiaeorientalis asiaeorientalis*; Platto et al., 2017; Yeater et al., 2014). The rough-toothed dolphins in the present study did not display significant laterality at the group level, although, descriptively, the left eye was used more than the right eye in the moving, unpredictable condition. When examining eye use at the individual level, there was a large variation in individual preference, consistent with previous studies (Yeater et al., 2017). The small sample size of rough-toothed dolphins combined with individual variability likely contributed to a lack of significant differences in eye use.

Subjects of both species tended to use binocular vision more while viewing the moving, unpredictable stimulus. It is possible that the use of both eyes increased due to subjects seeking more visual information or depth perception, given that they could not use their echolocation skills through the underwater viewing windows to explore the objects. There were also individual differences in laterality for members of both species, a finding consistent across many previous studies (e.g., Yeater et al., 2017). These differences could reflect individual variations in brain lateralization much like individual lateralization of speech areas in the human brain, often corresponding to dominant hand usage (Hund-Georgiadis et al., 2002).

Previous research in other species, including fish and elk, found a connection between boldness and the degree to which subjects were lateralized in their behavior (Brown & Bibost, 2014; Found & St. Clair, 2017). For marine mammals, personality traits are often assessed using behavioral measures and/or caretaker ratings of individual differences (Frick et al., 2017). No significant correlations between laterality and interest in stimuli were found in the present study; however, for bottlenose dolphins only, there was a negative correlation for ratings of subjects as curious and degree of laterality. Compared to previous research on personality and laterality of behavior (Brown & Bibost, 2014; Found & St. Clair, 2017), the correlation between personality and laterality of eye use in bottlenose dolphins and rough-toothed dolphins was in the opposite direction. The present study suggests that as subjects are more lateralized, they are rated as less curious. This pattern, which is inconsistent with previous research, may be due to how laterality was measured (i.e., hoof use, Found & St. Clair, 2017; eye use toward social stimuli, Brown & Bibost, 2014). Furthermore, subjects were not tested on boldness in the same way that other species have been (i.e., migration, Found & St. Clair, 2017; emergence test, Brown & Bibost, 2014), and curiosity can be considered distinct from boldness (Lilley et al., 2018). For example, although Clark and Kuczaj (2016) found that the two bottlenose dolphins who used a maze the most preferentially used the right eye to search the maze for a hidden object, all of the dolphins had the opportunity to interact with the maze, presumably decreasing their curiosity regarding the object. Previous research found the ratings of the subjects in the present study to be positively correlated with their behavioral interest, thus validating the caretaker ratings as reflecting information about subjects' behavior (i.e., time spent viewing the stimuli; Lilley et al., 2018). Future research could examine whether "handedness," the degree to which pectoral fin contact is lateralized, is correlated with any aspect of personality in a larger sample size.

**Limitations**

One limitation of the present study was the inability to tease apart the effects of motion and predictability of stimuli on the subjects' eye use. Having a third condition, a moving, but predictable, stimulus would have suggested if differences in eye use were due to the objects' movement, predictability, or both.

Another limitation in this study was the small number of subjects, especially rough-toothed dolphins. Additionally, the rough-toothed dolphins in the present study were all stranded, rehabilitated, and deemed non-releasable, meaning that they are potentially, but not definitively, behaviorally and/or physiologically nonrepresentative of their species in some ways. Limited conclusions can be made from this small sample, and it is necessary that further research on this species be conducted to learn more about their lateralization and other aspects of their cognition.

Finally, data for the present study were collected opportunistically while subjects were not interacting with caretakers. Subjects were housed in varying social groups for the duration of the study and could choose whether or not to attend to the stimuli presented. When only monocular vision was used to attend to the stimuli, it is possible that subjects were visually attending to other stimuli in the environment with the opposite eye.

## Conclusions

Despite some limitations, these results help to extend the laterality hypotheses in bottlenose dolphins to include objects that have variable movement, as well as being unfamiliar. The lack of consistency in rough-toothed dolphins may indicate that lateralization in this species is different from other cetacean species, or the lack of significant results could be due to a small and possibly nonrepresentative sample size. Regardless, more research is needed to better understand the functional organization of the cetacean brain and explore if lateralization relates in any consistent way to personality. Examining laterality of cetacean behavior allows for extrapolation of cognition and brain specialization while providing minimal interference into the daily life or social interactions of the subjects. In addition, understanding aspects of cetacean cognition, including lateralization of function, facilitates the exploration of cross-species comparisons and insight into the evolution of this phenomenon.

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