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Responses to Familiar and Unfamiliar Humans by Belugas (*Delphinapterus leucas*), Bottlenose Dolphins (*Tursiops truncatus*), & Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*): A Replication and Extension

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Previous research has documented that cetaceans can discriminate between humans, but the process used to categorize humans still remains unclear. The goal of the present study was to replicate and extend previous work on the discrimination between familiar and unfamiliar humans by three species of cetaceans. The current study manipulated the familiarity and activity level of humans presented to 12 belugas (*Delphinapterus leucas*) housed between two facilities, five bottlenose dolphins (*Tursiops truncatus*), and six Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) during free-swim conditions. Two measures of discrimination were coded from video recordings of each trial: lateralized visual processing and gaze duration. No clear lateralization effects emerged at the species level, primarily due to extensive individual variability. The results also indicated that activity level influenced gaze durations across species, and for some individuals, the interaction between human familiarity and activity level influenced gaze durations and eye preferences. Unexpectedly, bottlenose dolphins had longer gaze durations for familiar humans whereas belugas and Pacific white-sided dolphins had longer gaze durations for unfamiliar humans. All three groups displayed longer gaze durations for active humans as compared to neutral humans, and belugas and bottlenose dolphins had significantly longer gaze durations than Pacific white-sided dolphins. These results indicated that the cetaceans discriminated between unfamiliar and familiar humans and preferred active humans. The results of this study are discussed within the contexts of attention and individual differences across animals of different species.

Visual laterality is the ability to process incoming visual information in one hemisphere or the other. The lateralized processing of visual information may enhance a species' survival by enabling individuals to process incoming information more efficiently; said information can be distributed to areas that are better at processing types of information (Bisazza, Rogers, & Vallortigara, 1998; MacNeilage, Rogers, & Vallortigara, 2009; Rogers, Vallortigara, & Andrew, 2013; Rogers, Zucca, & Vallortigara, 2004; Vallortigara & Rogers, 2005). For example, the superiority of the right hemisphere in facial recognition has been replicated in humans and non-human species. When human faces were presented in the left-eye field of vision, participants responded more rapidly than when compared to the right-eye field of vision (Ellis, Shepherd, & Davies, 1979). This example of lateralized visual processing suggests that the ability to recognize conspecifics particularly during social interactions may be hemispheric-specific. A broad range of taxa have demonstrated such hemispheric lateralization, including domesticated birds, fish (reviewed by Bisazza et al., 1998; Johnsson, 1997), crustaceans (Karavanich & Atema, 1998), amphibians (reviewed by Bisazza et al., 1998), reptiles (reviewed by Bisazza et al., 1998), birds (Wilkinson, Specht, & Huber, 2010), and mammals (Kendrick, Atkins, Hinton, Heavens, & Keverne, 1996; Rosa Salva, Regolin, Mascalzoni, & Vallortigara, 2012; Tibbetts & Dale, 2007).

Research with birds consistently shows lateralized behavioral responses to various visual stimuli and differences in attention between some species (Bisazza et al., 1998; Scheid, Range, & Bugnyar, 2007). The interaction of two mechanisms, (1) a small to non-existent corpus callosum and (2) the complete decussation of the optic chiasm (Bisazza et al., 1998;ˌ Tarpley, Gelderd, Bauserman, & Ridgway, 1994), seems to facilitate lateralized processing in birds. Cetaceans also display these neurophysiological characteristics (Marino, Sudheimer, McLellan, & Johnson, 2004; Ridgway, 1986; Supin et al., 1978; Tarpley et al., 1994), suggesting that they too should demonstrate lateralized processing of visual stimuli. While cetaceans, such as belugas (*Delphinapterus leucas*) and dolphins, depend on echolocation or sonar as their primary sensory system, their visual acuity is similar when tested above or below water (Herman, Peacock, Yunker, & Madsen, 1975; Mass & Supin, 2002; Pepper & Simmons, 1973; Pilleri, 1982; Spong & White, 1971). In addition to basic sensory perceptual tests, dolphins (*Tursiops* spp.) appear to respond with different lateralized preferences depending on the type of visual stimuli tested, but the findings have produced contradictory yet intriguing patterns of results (MacNeilage, 2013).

When discriminating various familiar and unfamiliar objects (Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; Kuczaj & Walker, 2006), bottlenose dolphins in managed care approached and examined objects with their right eye (Kilian, von Fersen, Güntürkün, 2000; Ridgway, 1986; Yaman, Fersen, Denhardt, & Güntürkün, 2003). More recent research indicated that bottlenose dolphins in managed care displayed a group-level, left-eye preference when viewing familiar stimuli and a right-eye preference when viewing unfamiliar objects (Blois-Heulin, Crevel, Boye, & Lemassen, 2012). Additionally, bottlenose dolphins in managed care gazed longer at unfamiliar humans than familiar humans, but showed a left-eye preference when examining either familiar or unfamiliar humans (Thieltges, Lemasson, Kuczaj, Böye, & Bois-Heulin, 2011). The results of the single study using a similar protocol with a group of wild striped dolphins (*Stenella coeruleoalba*) corroborated the previous bottlenose dolphin study testing familiar and unfamiliar objects (Blois-Heulin et al., 2012); striped dolphins also displayed a right-eye preference when inspecting unfamiliar stimuli (Siniscalchi, Dimatteo, Pepe, Sasso, & Quaranta, 2012). Of the studies summarized above, the research testing responses to humans produced laterality results that conflicted with the research testing responses to objects. Thieltges and colleagues (2011) proposed that dolphins in managed care may view familiar and unfamiliar humans as a single social category rather than an object category that should be discriminated between familiar and unfamiliar. In summary, while dolphins appeared to utilize the left hemisphere during the visual inspection and processing of novel objects by displaying a right-eye preference, the categorization of humans remains unclear as both familiar and unfamiliar humans were processed with a left-eye preference.

In an effort to replicate and extend the earlier research with bottlenose dolphins, an initial investigation into the discrimination of familiar and unfamiliar humans was conducted with two additional cetaceans: belugas and Pacific white-sided dolphins, *Lagenorhyncus obliquidens* (Yeater, Hill, Baus, Farnell, & Kuczaj, 2014). Using a similar methodology to Thieltges et al. (2011), the beluga and Pacific white-sided dolphin results were ambiguous as lateralized processing was observed at the individual level but not at the group level (Yeater et al., 2014) in part due to large individual differences within species. In contrast, neutral (i.e., passive), unfamiliar humans elicited longer gaze durations than neutral, familiar humans (Yeater et al., 2014).

The current study was a replication of the Yeater et al. (2014) study, using almost all of the same individual belugas and Pacific white-sided dolphins tested previously. The study also served as a replication of the Thieltges et al. (2011) by testing another sample of bottlenose dolphins. Although the previous studies tested responses to neutral humans who stood passively while facing the animals with neutral facial expressions, the subjects of the study by Yeater and colleagues (2014) had experience with a training technique called the least reinforcing stimulus in which a trainer produces a neutral or passive response such that no

movement is made for at least 3 s in response to an incorrect behavior performed by the animal during a training session (Scarpuzzi, Lacinek, Turner, Thompson, & Force, 1999). This experience may have affected the gaze durations displayed at neutral, familiar humans as compared to neutral, unfamiliar humans. To address this possibility and extend the study by Yeater et al. (2014) an additional condition in which the humans were active was tested.

Based on the previous research by Thieltges et al. (2011) and Yeater et al. (2014) we expected that our subjects would (1) have longer gaze durations when viewing experimental conditions (any human stimuli) versus the control (apparatus only), (2) have longer gaze durations when viewing unfamiliar versus familiar humans, and (3) have a left-eye preference when viewing familiar or unfamiliar humans. Visual laterality has been observed in many species, with a pattern showing a right hemisphere dominance in many species in regards to discrimination of social companions, and individual familiarity-based recognition (Rosa Salva et al., 2012), including belugas and killer whales (*Orcinus orca*; Karenina, Giljov, Baranov, et al., 2010; Karenina, Giljov, Malaschichev, Baranov, & Bel'kovich, 2010; Karenina, Giljov, Ivkovich, Burdin, & Malaschichev, 2013). Thus, we generalized and expected the animals to display a preferential use of the left eye when viewing familiar humans and a preferential use of the right eye when viewing novel humans.

With the extension of the activity level variable, we expected the subjects to show longer gaze durations in the active human versus the passive human condition for all the cetaceans when viewing both familiar and unfamiliar humans. Activity level was expected to interact with familiarity with active unfamiliar humans eliciting longer gaze durations than any other condition. This result was anticipated because the subjects have a previous reinforcement history with the social behaviors of trainers and guests at the underwater viewing windows. Finally, based on Yeater et al. (2014) and the reported gaze durations of bottlenose dolphins in Thieltges et al. (2011), belugas were expected to have the longest average gaze duration of the three species.

Method

Subjects

As a direct replication and extension study of Yeater et al. (2014) and a modified replication of Thieltges et al. (2011), the subjects of the study included a beluga population (*n* = 9) housed in a facility in the southern United States (Facility A) and a beluga population (*n* = 3) housed in a facility in the northeastern United States (Facility B), and two species of dolphins, a bottlenose dolphin population (*n* = 5) and a Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) population (*n* = 6), both housed at Facility A. To facilitate the distinction between the two dolphin species, the bottlenose dolphins will be identified as *bottlenose dolphins* and the Pacific white-sided dolphins will be identified as *lags*. Two of the adult belugas at Facility A were believed to have some visual impairments. As in Yeater et al. (2014), these two animals were excluded from analyses involving laterality but were included in analyses involving gaze duration as their distributions were similar to the other belugas in the current study. Additionally, one of the calves at Facility A that was studied in Yeater et al. (2014) was not present for the trials in the current study, and two of the beluga calves at Facility A in the current study were not present in the population for Yeater et al. (2014). These calves were 3-5 months old and still nursing from their mothers during the current study. All subjects were in good health as determined by regular veterinary exams. Table 1 summarizes the demographic characteristics of all individuals tested in this study.

Table 1

Sex and Age Characteristics of Belugas, Bottlenose Dolphins, and Pacific White-Sided Dolphins

Individual code	Sex	Age class
Facility A belugas		
STE[a]	Female	Calf
SAM[a]	Male	Calf
ATL	Female	Juvenile
OLI	Male	Juvenile
LUN	Female	Adult
CRI	Female	Adult
IMA	Male	Adult
MAR	Female	Adult
NAT	Female	Adult
Facility B belugas		
JUN	Male	Sub-adult
KEL	Female	Adult
NAL	Male	Adult
Facility A dolphins		
AIN	Male	Sub-adult
CIS	Male	Sub-adult
FAT	Male	Adult
BRA	Male	Adult
GIL	Male	Adult
Facility A lags		
BOL	Male	Juvenile
HAL	Female	Adult
DAR	Male	Adult
CAT	Female	Adult
AVA	Female	Adult
BET	Female	Adult

Note. [a] identifies belugas that were not present in Yeater et al. (2014).

Materials

The current study utilized the experimental equipment of Yeater et al. (2014). A curtain apparatus, consisting of a PVC-based frame (W: 1.8 m x H: 2.1 m) upon which opaque curtains were hung was placed approximately 1-2 m from the side of each pool. A stationary table (W: 1.5 m x H: 1.0 m) was positioned directly in front of the curtain apparatus. Digital video camera(s) (Sony HandyCam HD or JVC), located near the apparatus, recorded the responses of each animal viewing the objects presented during each trial. The belugas and the lags were tested using underwater viewing windows located in their primary pools. The bottlenose dolphins did not have underwater viewing access so all trials were conducted from the side of their pool with surface viewing only. To facilitate the line of sight for the bottlenose dolphins, the apparatus and table were positioned approximately 1.5 m from the side of the pool. The pools in which testing occurred had different wall heights, which necessitated that the table be raised approximately 0.5 m for one of the pools to display the objects. All animals were given 10-15 min to habituate to the experimental set-up before each experimental session.

Measures

The dependent variables for the current study included gaze duration and eye preference coded from video recordings of each trial. Gaze duration was defined as the time (s) elapsed from the first eye orientation at the object until the animal looked away or departed. If an animal looked at the same object multiple times within the presentation window, the total amount of time the animal

gazed was summed from all looks in that trial. Eye preference was based on converting the frequency of gazes based on which eye (right, left, or both) was used to view a stimulus to a percentage. The percentage of eye preference was calculated by dividing the frequency of each eye gaze by the total gaze frequency and multiplying by 100.

Procedure

The same experimental protocol was used for all populations. The animals were grouped according to the current social grouping determined by the trainers and free to swim and investigate a presented human independently. The experimental protocol called for 30 trials of familiar humans, 30 trials of unfamiliar humans, and 10 trials of the control for each animal in a population. Familiar humans were trainers who had worked with the animals for a least a year, and unfamiliar humans had never worked with the animals directly or were novel to the animals. Control trials were performed randomly during a session such that each session conducted had a control trial. The purpose of the control trial was to determine if the apparatus alone had any effect on gaze durations. Familiar and unfamiliar human trials were divided into two activity levels (the second independent variable): passive and active. Passive trials consisted of a human standing in a single location facing the pool with a neutral facial expression. Active trials consisted of one of four behaviors: (1) *Peek-A-Boo*—human popped head out from behind the curtain and brought it back behind the curtain seconds later before repeating the action, (2) *Jumping Jacks*—human moved arms and legs in an outward and inward motion simultaneously while jumping up and down, (3) *Crazy Hands*—human moved hands above head in any crazy motion, and (4) *Dancing*—human chose any style of dance to move the body around during the presentation. The human familiarity and activity trials were further divided into different types of attire (the third independent variable), which included wearing either the person's typical clothing (standard work uniform for familiar humans and street clothes for unfamiliar humans) or a standardized, long-sleeve blue chambray shirt that was worn over the human's typical clothes.

Eight unique conditions, 2 (familiarity) x 2 (activity) x 2 (attire) plus random control trials were tested across sessions. Not all eight conditions were tested in every session as multiple presentations or trials were conducted for the conditions selected to be presented in a given session. Within a session, two to three conditions were presented in a randomized order using a block of four trials per condition. For example, an active familiar t-shirt condition was selected and four trials of that condition (i.e., the four different activities described above) were performed before the second set of trials was conducted, e.g., a passive unfamiliar regular clothing condition tested with four presentations (illustrated in Figure 1). All trials for active conditions (e.g., crazy hands, jumping jacks, dancing, or peek-a-boo) were performed in a random order selected by each participant acting as the stimulus for the set of trials. Sessions conducted at Facility A lasted 10-20 min, as determined by the attention of the animals, and typically produced 8-12 trials, or two to three blocks of trials of a particular condition. The same human was used across the pre-determined trials that were presented as blocks of four trials (Figure 1). While this protocol was not ideal (potentially subject to habituation effects), it allowed session time to be maximized while minimizing trainer time. In transitioning between each block of trials, a 3-5 min break was given to ensure the animals were in free swim and not focused on the previous trials (Figure 1). A trial consisted of a free-swimming animal having 1 min to view the stimulus. Each combination of conditions was presented two times over the course of the study to provide all animals present the opportunity to view each condition on at least eight independent trials. A trial was initiated once the human opened the curtain and stepped out in front of the curtain apparatus, closing the curtain behind himself or herself. The trial ended once the human had moved behind the curtain and was no longer in view. All sessions with belugas and lags were performed between 07:00-09:30. Sessions with dolphins were performed between 07:00-09:30 or 13:00-15:00.

At Facility B, a session consisted of four trials and each trial lasted exactly one min. Each trial was separated by a minimum of 5 min. If multiple sessions with varying conditions were conducted in the same day, a minimum of 15 min delay was incorporated in between sessions and different conditions were randomly presented across the day. Due to differences in facilities (trainer availability and the continuous presence of guests), all trials conducted at Facility B presented a different human than the previous trial. Sessions were conducted between 09:00-14:00.
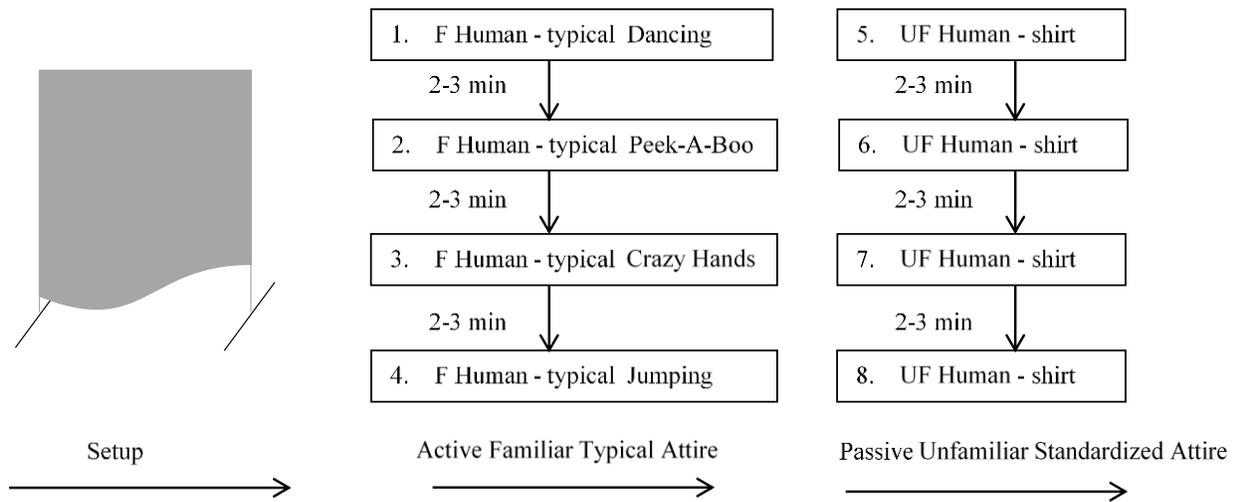
1. F Human - typical Dancing	5. UF Human - shirt
2-3 min	2-3 min
2. F Human - typical Peek-A-Boo	6. UF Human - shirt
2-3 min	2-3 min
3. F Human - typical Crazy Hands	7. UF Human - shirt
2-3 min	2-3 min
4. F Human - typical Jumping	8. UF Human - shirt

Setup   Active Familiar Typical Attire   Passive Unfamiliar Standardized Attire

Figure 1. **Session protocol used at Facility A.** Protocol at Facility B differed slightly. All subjects had a 10-15 min habituation period to the apparatus prior to the start of a session. In this illustration, an Active Familiar condition with humans in their typical attire was selected for the first block of 4 trials, randomly selected order of activity. A 4-5 min break occurred before the next set of trials. The second block of trials included a second randomly selected condition, such as a Passive Unfamiliar condition with humans in a standardized shirt. Each trial consisted of each animal having at least one minute to view the stimulus with 2-3 min between trial presentations. At Facility A, humans remained the same for a block of four trials. At Facility B, humans changed across each trial.

At both facilities, all research assistants present remained hidden to avoid influencing the results. Once the trials were conducted, each videotaped trial was coded by a trained coder for gaze durations and eye presentations of each animal that viewed the presented human. Approximately 10% of the trials (with all conditions represented at least once) were also viewed by a senior author to assess the reliability of the coder. Disagreements were resolved through discussion.

Statistical Analyses

Almost all animals received the pre-determined number of trials, but each animal responded to a different number of trials (Table 2). Preliminary analyses were conducted to determine if facility influenced gaze durations of the belugas and if attire influenced the gaze durations for all three species. The results of an independent *t*-test indicated that there was no difference between the two facilities in gaze duration, enabling the data to be analyzed together. Dependent *t*-tests were conducted to determine if attire influenced the gaze durations for each species, using each animal's averaged gaze duration in each condition. The results indicated that there was no difference in gaze duration when human stimuli were wearing a standardized shirt or their typical clothing. Attire was therefore examined as a separate factor in all subsequent analyses, and the data were collapsed into the two remaining variables: familiarity and activity level. All approaches displayed by each animal during a trial were included in group and individual analyses. For group analyses, the average gaze durations and percentages for eye preference (laterality) were calculated across all trials of a given condition related to familiarity (familiar, unfamiliar, or control), activity level (passive or active), and the interaction between familiarity and activity for each individual animal. Gaze duration was tested initially using familiarity x activity level repeated measures factorial ANOVAs while laterality was tested initially using familiarity x activity x laterality repeated measures factorial ANOVAs. Fisher's least significance differences (LSD) post hocs were performed when appropriate. Given the amount of individual variability observed in the previous study (Yeater et al., 2014) and the variability observed in the current study, we selected this liberal post hoc test to maximize the opportunity of detecting any significant differences. Mauchley's test of sphericity was conducted to investigate the variance assumption for all repeated measures tests. If the assumption was violated, a Huyhn-Feldt correction was applied. Additionally, the averaged gaze durations were used to assess if differences in gaze duration existed across the three species, using a between subjects one-way ANOVA. Given the degree of individual variability, additional descriptive analyses were conducted for each individual animal using all of the trials animals were presented and attended (Table 2).

Table 2

Presentation Responses by Belugas, Bottlenose Dolphins, and Pacific White-Sided Dolphins

Animal	Trials presented	Trials attended	Control %	Familiar %	Unfamiliar %
Facility A belugas					
STE	75	13	20	7	23
SAM	75	8	20	19	5
ATL	40	14	0	45	41
OLI	66	17	11	25	32
LUN	75	10	0	15	14
CRI	75	45	20	70	58
IMA	76	17	11	46	12
MAR	89	37	50	54	33
NAT	65	19	11	30	35
Facility B belugas					
JUN	76	43	81	27	73
KEL	76	22	6	63	7
NAL	76	6	0	17	3
Facility A dolphins					
AIN	51	38	71	70	82
CIS	51	34	43	67	76
FAT	51	13	29	19	35
BRA	45	27	75	60	53
GIL	45	26	50	45	76
Facility A lags					
BOL	91	8	0	1	14
HAL	91	7	0	8	8
DAR	91	4	0	0	8
CAT	91	18	0	32	14
AVA	91	30	0	26	41
BET	91	9	0	5	14

Note. "Trials presented" correspond to the number of object presentations each animal had an opportunity to view. The presented trials include all of the attempted presentations, which included successful trials and mistrials. A successful trial was defined as at least one animal viewed the presented human. A mistrial was defined as no animals viewed the presented human. "Trials attended" correspond to the total number of object presentations each animal viewed. "Control %" is the calculated percent of the number of control trials viewed divided by the total control trials presented to that animal. "Familiar %" and "Unfamiliar %" were calculated the same way with the relevant numbers.

Results

General Trends in Attention to Stimuli

As summarized in Table 2, not every animal received the expected 70 trials. Related to different social groupings that occurred during the course of the study, some animals had more opportunities to experience different conditions than other animals ("Trials presented" column, Table 2). Individual animals also attended the different stimuli with varying degrees of interest ("Trials attended" column, Table 2). Eight of the 12 belugas, all five bottlenose dolphins, and two of the six lags attended and responded to approximately 30% or more of the presented trials. When overall gaze durations were averaged across all three conditions and

examined for species differences in attention, it appeared that bottlenose dolphins gazed the longest at stimuli (M = 9.6 s, SD = 2.3 s) followed by belugas (M = 8.1 s, SD = 5.4 s) and then lags with the shortest overall gaze duration (M = 1.3 s, SD = 0.6 s). The results of the one-way ANOVA indicated that there was a significant effect of species on gaze duration, $F(2, 20) = 6.85$, $p = 0.005$, $\eta^2 = 0.41$. LSD post hocs indicated that bottlenose dolphins displayed significantly longer gazes than lags ($p = 0.004$), and belugas displayed significantly longer gazes than lags ($p = 0.004$; Figure 2).
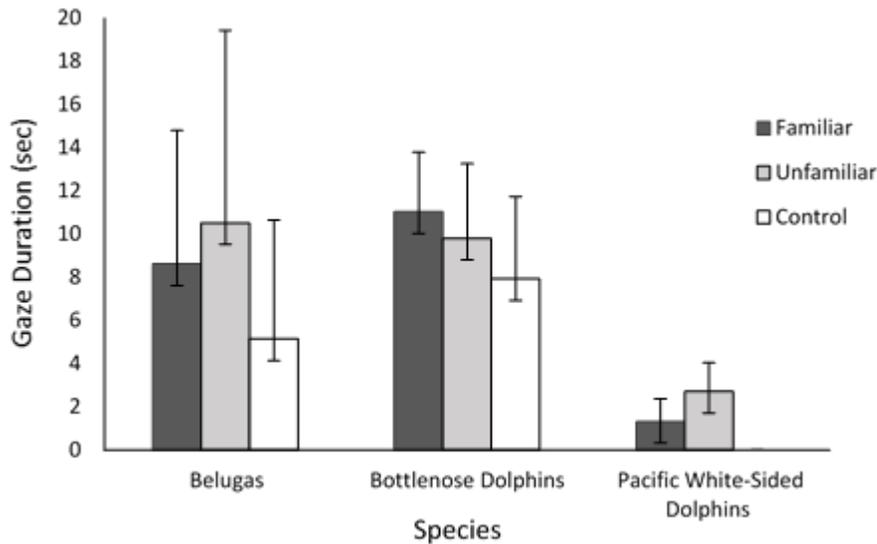

Figure 2. **Average gaze duration (s) across familiarity (trial type) per species.** Error bars represent standard

Group-level Discrimination

Gaze duration. Based on previous work, all three species were expected to gaze longer at unfamiliar humans than at familiar humans as a measure of discriminative ability. We also expected humans of any kind to elicit longer gaze times than the apparatus by itself, the control. Gaze durations were expected to be longer for active conditions compared to neutral conditions, and activity level was expected to interact with familiarity with active unfamiliar humans eliciting longer gaze durations than any other condition.

Three 3 (familiarity) x 2 (activity) repeated measures ANOVAs were conducted to test the main effects of human familiarity and activity and the interaction between the two variables on gaze duration for each species. The results for the belugas indicated that the main effect for familiarity approached significance, $F(2, 22) = 2.97$, $p = 0.07$, $\eta^2 = 0.21$, partially supporting the hypothesis that gaze durations would be longer for humans than the curtain apparatus. LSD post hocs indicated that both types of humans approached significance from the control ($p = .06$) but not from each other, although unfamiliar humans produced slightly longer gaze durations (Figure 3a; Control: $M = 5.2$ s, $SD = 5.5$ s; Familiar: $M = 8.6$ s, $SD = 6.2$ s; Unfamiliar: $M = 10.5$ s, $SD = 8.9$ s). No other evidence for the remaining hypotheses emerged from this omnibus test (Figure 3a).

The results for the bottlenose dolphins were different than expected. No main effect for familiarity was observed with the factorial omnibus test (Figure 3b), but a significant main effect did occur for activity level,

$F(1, 4) = 13.85$, $p = 0.02$. The active condition ($M = 17.3$ s, $SD = 8.8$ s) produced significantly longer gaze durations than the neutral condition ($M = 5.3$ s, $SD = 1.0$ s). However, the interesting results came from the significant interaction between activity level and familiarity, $F(2, 8) = 9.25$, $p = 0.008$. Unexpectedly, the bottlenose dolphins gazed the longest at the active familiar condition than any other condition (LSD post hocs, $p < 0.05$) and longer gaze durations for active familiar humans ($M = 15.6$ s, $SD = 5.1$ s) were consistent across most conditions (i.e., neutral familiar humans: $M = 6.5$ s, $SD = 1.7$ s; neutral unfamiliar humans: $M = 3.6$ s, $SD = 0.9$ s; curtain apparatus: $M = 7.9$ s, $SD = 3.8$ s; see Figure 3b). In partial support of the effect of unfamiliar humans, longer gaze times were associated with active unfamiliar humans ($M = 16.0$ s, $SD = 7.7$ s) compared to neutral unfamiliar humans ($p < 0.05$).

The results of the lags also partially supported the effect of familiarity with a significant main effect, $F(2, 10) = 12.13$, $p = 0.002$ (Figure 3c; Control: $M = 0.0$ s, $SD = 0.0$ s; Familiar: $M = 3.3$ s, $SD = 1.2$ s; Unfamiliar: $M = 1.4$ s, $SD = 1.2$ s). LSD post hoc analyses indicated that the lags gazed at unfamiliar objects significantly longer than the control ($p < 0.05$). The main effect for activity did not achieve statistical significance at an $\alpha = 0.05$, $F(1, 5) = 4.38$, $p = 0.09$, as the interaction between activity level and familiarity also did not, $F(2, 10) = 3.74$, $p = 0.06$. However, the results were intriguing and therefore explored a little more (Figure 3c). LSD post hocs suggested that the active familiar condition ($M = 1.4$ s; $SD = 0.8$ s) was significantly longer than the control ($M = 0.0$ s, $SD = 0.0$ s; $p = 0.009$) as was the neutral unfamiliar condition ($M = 1.5$ s, $SD = 0.6$ s; $p = .001$). Additionally, the active unfamiliar condition ($M = 3.9$ s, $SD = 2.7$ s) produced longer gaze durations than the neutral unfamiliar condition ($p < 0.05$) while the neutral familiar condition ($M = 1.3$ s, $SD = 1.4$ s) produced longer gaze durations than the neutral unfamiliar condition ($p < 0.05$). Although these analyses did not achieve statistical significance, the trends partially supported the expected interaction effect although the lags appeared to prefer the familiar humans over the unfamiliar humans, countering the expected outcome of longer gaze durations for unfamiliar humans.
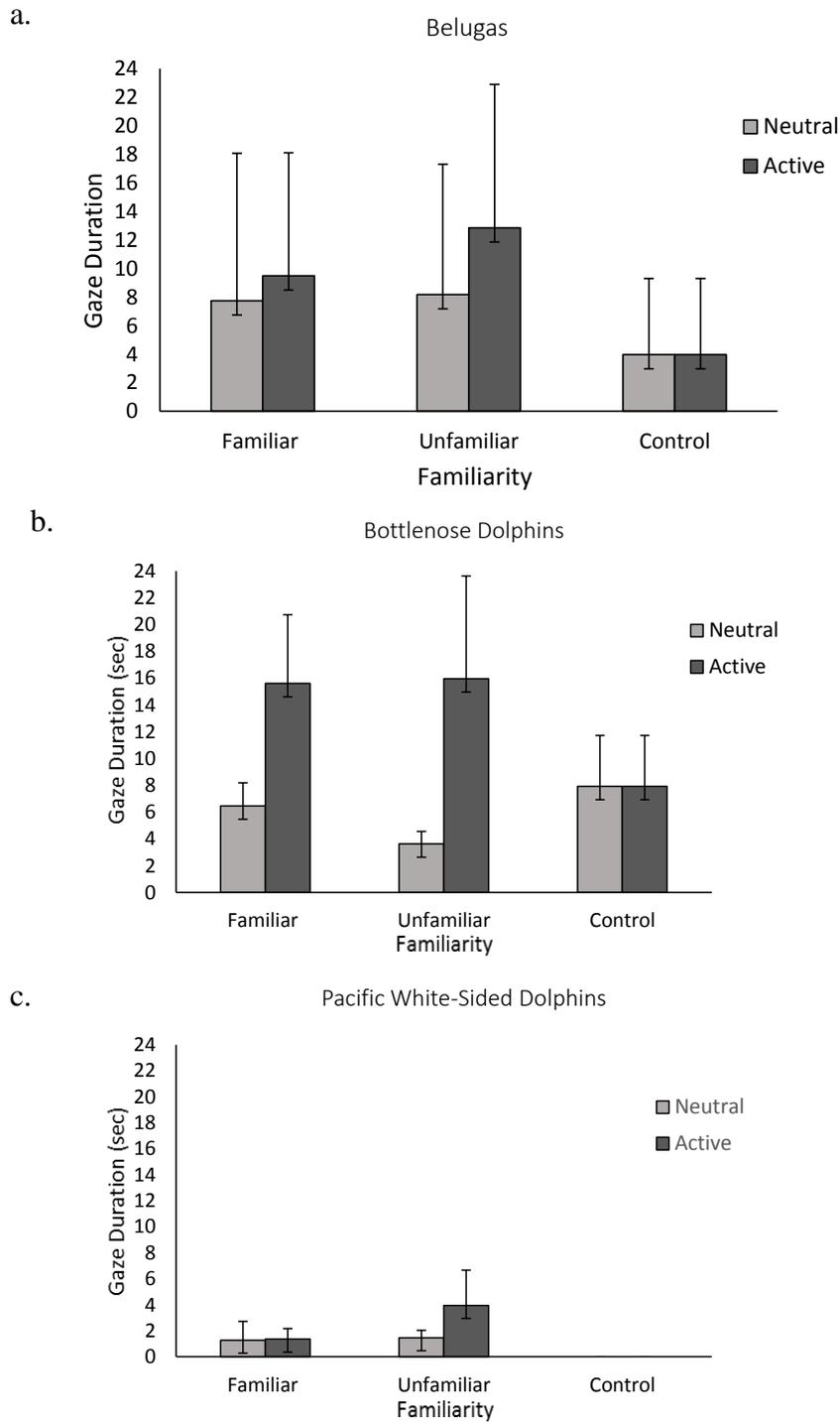
a. Belugas

b. Bottlenose Dolphins

c. Pacific White-Sided Dolphins

Figure 3. **Average gaze duration (s) across conditions (interaction between familiarity and activity level) per species: (a) belugas, (b) bottlenose dolphins, (c) Pacific white-sided dolphins (lags).** A significant interaction was found for bottlenose dolphins only. The interaction for the lags approached significance. Belugas were consistent in gaze durations across all five conditions. Error bars represent standard error of the mean. See text for specific information.

Laterality. Three 3 (laterality) x 3 (familiarity) x 2 (activity) repeated measures ANOVAs were conducted with averaged percentages of gazes to determine if each species displayed any lateralized processing while viewing unfamiliar and familiar humans. The omnibus test was performed so that each main effect and the critical interactions could be tested. There was no indication of laterality as related to familiarity or any other combination for the belugas, the bottlenose dolphins, or the lags. Additional one-way repeated measures ANOVAs were performed within each familiarity condition as the factorial was likely under powered. The results of these ANOVAs for unfamiliar humans indicated that only the lags had a significant effect, $F(2, 10) = 6.39$, $p = 0.02$, $\eta^2 = 0.56$, but this effect was driven by the absence of using binocular vision when viewing unfamiliar humans. LSD post hocs indicated that the lags were more likely to use their right eye ($M = 27.0\%$, $SD = 24.0\%$) or their left eye ($M = 39.6\%$, $SD = 32.9\%$) when compared to both eyes ($M = 0.0\%$, $SD = 0.0\%$; $p < 0.05$).

The results of these ANOVAs for familiar humans were similar to the results about unfamiliar humans. The lags again displayed a significant effect for laterality when viewing familiar humans, $F(2, 10) = 16.23$, $p = 0.001$, $\eta^2 = 0.76$, but again this effect was driven by the absence of binocular vision. LSD post hocs indicated that the lags were more likely to use their right eye ($M = 39.2\%$, $SD = 18.8\%$) or their left eye ($M = 60.8\%$, $SD = 18.8\%$) when compared to both eyes ($M = 0.0\%$, $SD = 0.0\%$; $p < 0.05$). The results of the interaction between laterality and familiarity did not achieve significance for the belugas, $F(2, 18) = 3.32$, $p = 0.06$, $\eta^2 = 0.27$. LSD post hocs suggested that the belugas preferred a binocular view ($M = 47.3\%$, $SD = 36.6\%$) over a lateralized, monocular view (Right: $M = 11.7\%$, $SD = 17.3\%$; Left: $M = 29.5\%$, $SD = 0.5\%$; $p < 0.05$).

Finally, the results of the ANOVAs for the curtain apparatus indicated that no lateralized preferences emerged at the group level for belugas or lags, as expected. However, the bottlenose dolphins displayed a significant effect for laterality on control trials, $F(2, 10) = 4.77$, $p = 0.04$, $\eta^2 = 0.76$. LSD post hocs indicated that the bottlenose dolphins preferred to use their left eye ($M = 24.9\%$, $SD = 15.3\%$) above both eyes ($M = 15.2\%$, $SD = 13.2\%$) when examining the apparatus ($p < 0.05$).

Individual-level Discrimination

Gaze duration. When examining the descriptive statistics (Table 3) and figures (Figures 4-6) for gaze durations exhibited by each individual animal, it is clear that individuals across each species showed greater attention while other individuals appeared to be much less interested in the humans as indicated by shorter gaze durations and less variability. Two belugas consistently displayed a wide range of variability in interest in all the conditions tested and relatively long gaze durations (Figure 4). As indicated in Table 3 and Figure 4, five belugas, displayed longer gaze durations while viewing familiar humans than unfamiliar humans, three belugas displayed longer gaze durations when viewing unfamiliar humans than familiar humans, and four belugas displayed similar gaze durations when viewing familiar or unfamiliar humans. As indicated in Table 3, seven belugas displayed longer gaze durations when examining active humans than neutral humans, and three belugas displayed similar gaze durations when viewing active or neutral humans.

Four bottlenose dolphins displayed consistent interest in unfamiliar humans with longer gaze durations when examining active humans, familiar or unfamiliar (Table 3; Figure 5). The remaining bottlenose dolphin, BRA, displayed longer gaze durations when examining familiar humans being active or neutral (Table 3; Figure 5).

Finally, four lags displayed more interest for unfamiliar humans than familiar humans, one lag, HAL, displayed similar interest when examining familiar or unfamiliar humans, and one lag, CAT, displayed more interest for familiar humans. No lags displayed trend differences according to the activity condition. Rather, lags engaged in much shorter gaze durations and fewer looks at the humans in general (Table 3; Figure 6).

Table 3

Average Gaze Duration per Individual Animal per Condition

Animal	Control		Active Familiar		Active Unfamiliar		Neutral Familiar		Neutral Unfamiliar	
	M	*SE*	*M*	*SE*	*M*	*SE*	*M*	*SE*	*M*	*SE*
Facility A belugas										
STE	3.0	--	5.5	2.5	21.6	4.6	--	--	30.0	6.0
SAM	2.0	--	--	--	3.0	1.0	3.0	0.7	--	--
ATL	--	--	20.0	9.5	20.0	6.7	6.5	4.5	7.0	2.0
OLI	7.0	--	2.0	--	8.5	2.8	2.3	0.3	3.2	0.8
LUN	--	--	8.7	2.9	16.7	7.6	22.0	--	3.0	0.6
CRI	4.0	--	18.9	6.7	24.9	5.9	3.7	0.8	17.2	6.0
IMA	2.0	--	10.8	4.5	6.7	1.8	1.6	0.2	3.0	0.7
MAR	13.8	5.4	13.0	9.0	24.9	7.8	4.2	0.9	17.9	5.5
NAT	5.0	--	3.0	1.0	3.3	1.0	9.8	7.8	2.2	0.3
Facility B belugas										
JUN	17.0	3.8	3.3	1.5	25.0	5.4	32.7	9.4	14.6	5.6
KEL	8.0	--	8.6	2.2	--	--	3.3	1.0	1.3	0.3
NAL	--	--	7.0	2.5	3.0	--	2.0	--	2.0	--
Facility A dolphins										
AIN	7.8	2.2	21.0	6.1	19.9	6.9	6.0	2.1	2.8	0.9
CIS	13.7	4.3	15.6	4.9	19.3	7.1	6.8	1.6	4.0	1.7
FAT	4.5	0.5	23.5	8.5	46.5	18.6	6.3	0.9	6.5	0.5
BRA	9.2	1.5	14.4	3.4	9.7	3.1	10.8	4.9	3.6	1.1
GIL	4.5	1.1	9.8	3.6	6.8	4.2	5.7	2.3	5.4	1.6
Facility A lags										
BOL	0.0	0.0	3.0	--	4.0	1.6	--	--	2.0	0.6
HAL	0.0	0.0	3.0	--	2.0	0.4	3.0	0.6	1.5	0.5
DAR	0.0	0.0	--	--	5.5	3.5	--	--	1.0	--
CAT	0.0	0.0	3.0	0.6	6.3	2.4	3.8	0.5	3.0	1.0
AVA	0.0	0.0	2.7	0.7	3.5	0.6	3.0	0.8	2.1	0.3
BET	0.0	0.0	2.0	1.0	1.0	--	--	--	1.4	0.2

Note. Dashes (--) in both *M* and *SE* columns indicate that those animals never attended that trial condition. Dashes (--) in the *SE* column indicate that those animals attended that trial condition once.
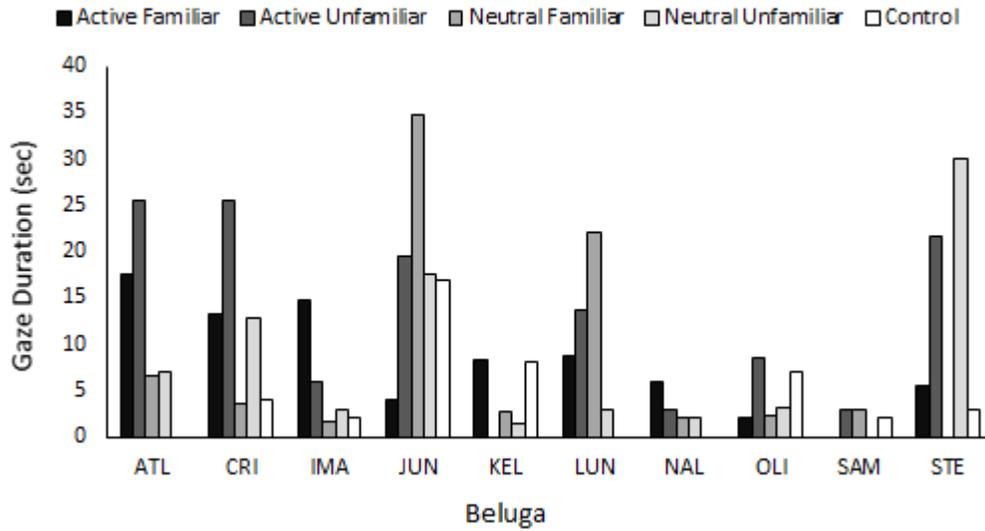
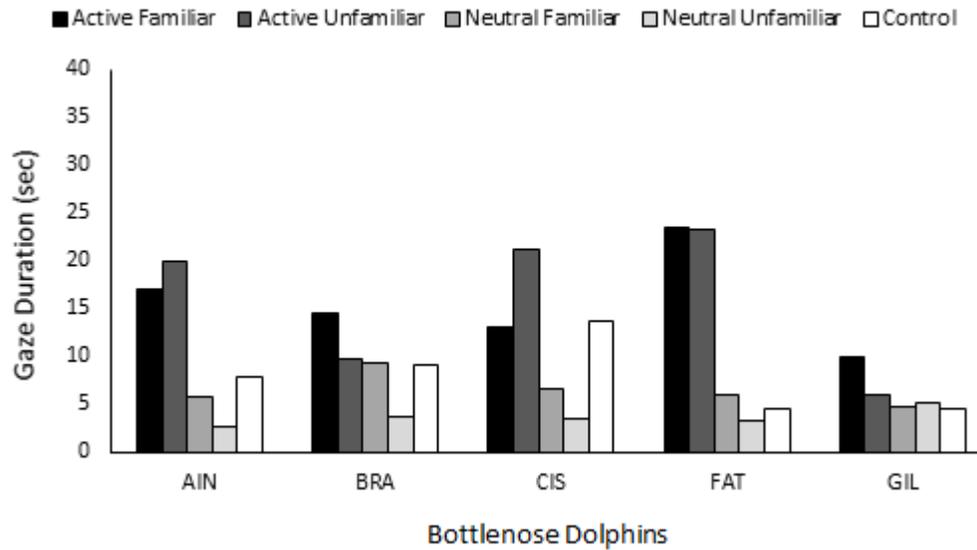*Figure 4.* **Individual gaze durations per conditions for belugas.**

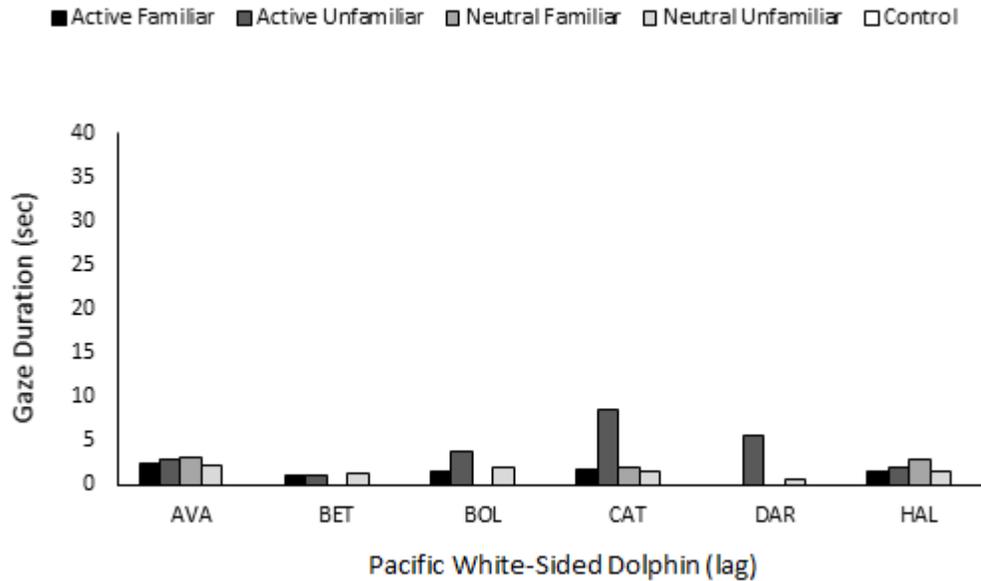*Figure 5.* **Individual gaze durations per conditions for bottlenose dolphins.**

Figure 6. **Individual gaze durations per conditions for Pacific white-sided dolphins.** The lags did not attend to any control trials.

Laterality. The belugas displayed many different eye preferences when viewing the control, familiar humans, or unfamiliar humans. Five of the belugas that examined the humans preferred to investigate familiar and unfamiliar humans with both eyes. Two other belugas preferred to investigate both types of humans with their left eye while NAT preferred to investigate both types of humans with her right eye (Figure 7). In comparison, three of the five bottlenose dolphins used their right eye primarily to investigate both familiar and unfamiliar humans while one dolphin used his left eye to view both familiar and unfamiliar humans (Figure 8). The fifth dolphin used both eyes to view familiar humans and the right eye to view an unfamiliar human. The lags tended to use their left eye overall to view familiar and unfamiliar humans (Figure 9). However, one lag, BOL, preferred to use each eye equally for familiar humans, but then switched to a right-eye preference when viewing unfamiliar humans. Another lag preferred to use the right eye to view familiar humans and switched to the left eye to view unfamiliar humans. None of the lags used both eyes to view humans.
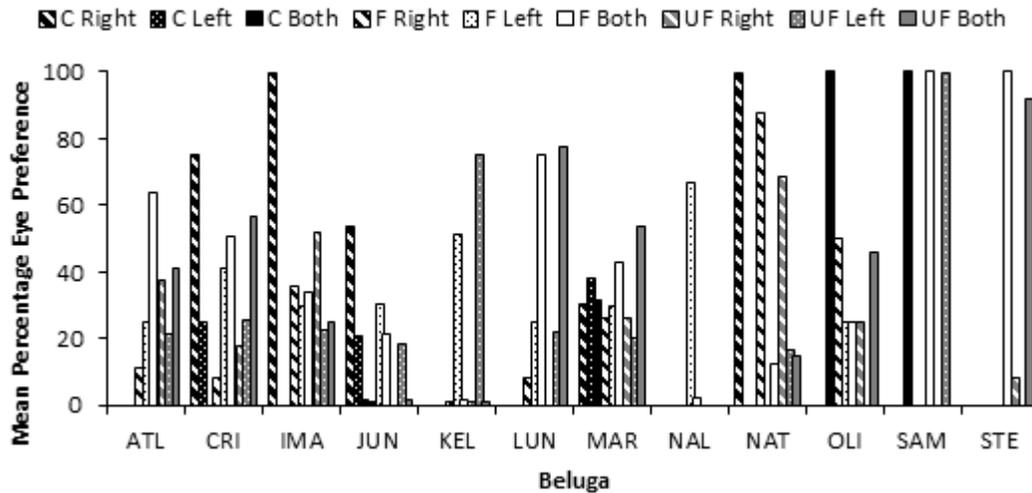
Figure 7. **Eye preferences per individual across familiarity trials for belugas.** MAR and NAT, were removed from statistical analyses due to possible visual impairment but are displayed in the figure for comparison purposes.
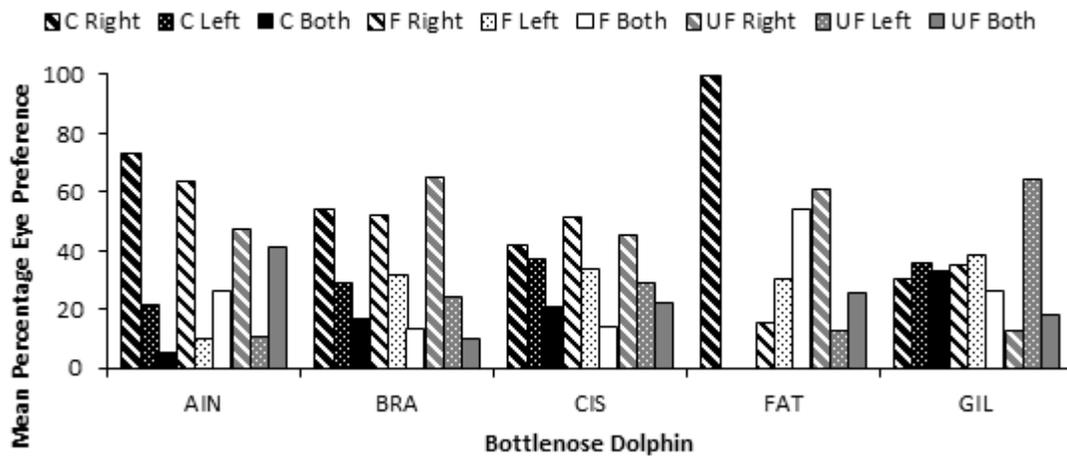

Figure 8. **Eye preferences per individual across familiarity trials for bottlenose dolphins.**
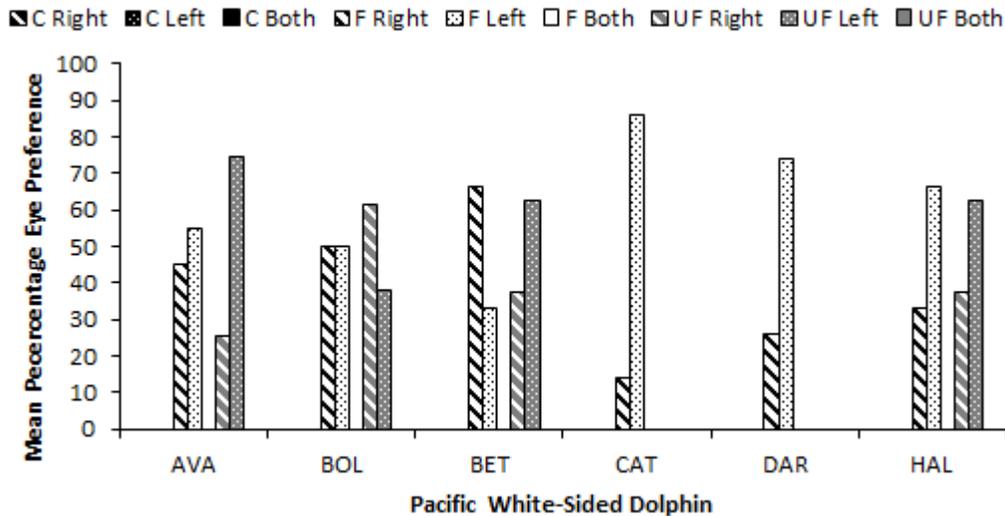
Figure 9. **Eye preferences per individual across familiarity trials for Pacific white-sided dolphins.**

Discussion

As a replication and extension of previous research (Thieltges et al., 2011; Yeater et al., 2014), the present study offered a unique perspective on the abilities of cetaceans to distinguish between familiar and unfamiliar humans, and to determine if level of activity by the human affected the gaze durations or lateralized responses of three species of cetaceans in managed care.

Discrimination between Categories of Humans

Gaze duration. Humans were expected to produce longer gaze durations than the curtain apparatus in all three species. Although gaze durations for the lags were not as long as the belugas or the bottlenose dolphins in general, the lags clearly gazed at humans longer than the curtain apparatus itself. Belugas also gazed longer at humans than the curtain apparatus, but the differences were significant at $p = 0.07$. In contrast, bottlenose dolphins tended to gaze at the curtain apparatus with durations similar to humans, except when the human was active and familiar. Lags did not gaze at the control trials with the curtain apparatus alone. These results suggested that the lags and belugas were more attentive to human stimuli as compared to an inanimate object whereas the bottlenose dolphins found any type of stimulus almost equally engaging. It is possible that the different experimental set-up (below water viewing vs above water viewing) could account for this difference in the gaze duration trends. This explanation seems unlikely as the bottlenose dolphins gaze durations were similar to the beluga gaze durations. Perhaps a better explanation for the unexpected bottlenose dolphin results is related to the study itself. The stimuli and procedure used in the study may have been highly reinforcing and unexpected and therefore elicited longer, but similar, gaze durations across the conditions.

Some insight about this explanation may be provided by the more specific results addressing the expectation that all three species would discriminate between familiar and unfamiliar humans by looking longer at unfamiliar humans (Thieltges et al., 2011; Yeater et al., 2014). Although gaze durations were longer

for unfamiliar humans for all three species, the variability between individuals was extensive and affected the overall statistical results; no significant differences in gaze durations were found between familiar and unfamiliar humans, especially for lags and belugas (Figures 2, 4-6). The lack of statistical significance between classes of humans is most likely related to the large degree of individual variability in gaze duration. However, the lack of significant results could also have been due to the limited sensitivity of gaze duration as a measure of discrimination in a free-swim paradigm. Greater sensitivity in gaze duration as a measure of discrimination may require a different paradigm in which animals are under trainer control and given a two-choice discrimination, or more animals may simply need to be tested with a greater number of presentations. The results for the belugas and lags in the current study were similar to the original study conducted with the same populations, even with slightly longer gaze durations (Yeater et al., 2014). The results of the bottlenose dolphins were more ambiguous as this species displayed similar gaze durations for familiar and unfamiliar humans as well as the curtain apparatus when comparing those three conditions. However, the interaction between type of human and activity level of the human, suggested that the bottlenose dolphins tended to gaze longer at active familiar humans than almost any other combination of human. Although we expected active unfamiliar humans to be the most interesting to the animals and produce longer gaze durations, it is possible that the bottlenose dolphins found their trainers much more engaging because the trainers' active behavior was unexpected from their previous history with the familiar humans. This interpretation is partially supported by the longer gaze durations by the bottlenose dolphins when viewing active unfamiliar humans compared to neutral familiar humans. These results partially replicated the findings by Thieltges et al. (2011) using a different group of bottlenose dolphins tested solely with neutral familiar and unfamiliar humans in a similar free-swim paradigm.

Although the current study did not support the discrimination between familiar and unfamiliar humans unequivocally through the use of gaze durations, there is evidence that individuals within the subjects and species tested did discriminate between the two classes of humans (Figures 2, 4-6) much like the previous studies (Thieltges et al., 2011; Yeater et al., 2014). Interestingly, attire did not appear to be used by the animals to facilitate a discrimination between the two classes of humans. Whether a familiar human or an unfamiliar human wore a standardized shirt or typical clothing, the animals did not differ in their gaze durations between the two conditions. These results suggest that the animals may use other characteristics to classify humans they encounter. Additional research could explore which characteristics are critical in discriminating between these two classes of humans, as this information might help trainers understand some of the factors that may play a role in training animals (Kuczaj & Xitco, 2002). While it appears that cetaceans in managed care can discriminate between classes of humans differing in terms of familiarity or between language-based categories, such as verbs and nouns (Herman, 1986; Herman, Pack, & Wood, 1994), more studies should incorporate different discrimination or categorization paradigms to better understand cetacean cognitive abilities (e.g., Mercado, Killebrew, Pack, Macha, & Herman, 2000).

Laterality. One measure suggested by previous research was visual laterality, as cetaceans appear to display lateralized processing when viewing familiar and unfamiliar stimuli (Blois-Heulin et al., 2012; Karenina, Giljov, Baranov, et al., 2010; Karenina, Giljov, Malaschichev, et al., 2010; Karenina et al., 2013; Kilian, von Fersen, & Güntürkün, 2005; Siniscalchi et al., 2012; Thieltges et al., 2011; Yeater et al., 2014) and other animals (reviewed by Rosa Salva et al., 2012; Vallortigara & Rogers, 2005). Thieltges et al. (2011) concluded that bottlenose dolphins should display a left-eye preference when viewing familiar or unfamiliar humans, potentially categorizing both types of humans as part of the same *social* category. In contrast, research by Karenina, Giljov, Baranov, et al. (2010), Karenina, Giljov, Malaschichev, et al. (2010), and Rosa Salva et al. (2012) suggested that belugas and the Pacific white-sided dolphins would display a left-eye preference when viewing familiar humans and a right eye preference when viewing unfamiliar humans, to reflect the

hemispheric specialization of visually processing social information with the left eye and subsequently the right hemisphere and processing novel information with the right eye and subsequently the left hemisphere.

No evidence for lateralized visual processing at the group level was observed for any species. Much like the study by Yeater et al. (2014), the animals in the current study again displayed large degrees of individual variability in attention (Table 2) as well as the eye used to inspect the stimuli (Figures 7-9). To accommodate the lack of power related to the small sample sizes and inter-individual variability, additional analyses were conducted within each condition of familiarity. The results of these tests were intriguing as they partially supported the hypothesized outcomes. When examining unfamiliar humans, none of the three species showed any statistical tendency for lateralized processing, despite the presence of possible eye preferences (e.g., belugas tended to use both eyes, bottlenose dolphins tended to use their right eye, and lags tended to use their left eye). The results for familiar humans were also unclear. Again, the belugas tended to prefer to use both eyes to investigate familiar humans while the bottlenose dolphins were equally likely to use their right, left, or both eyes to gaze at familiar humans. Lags tended to use their left eye to view familiar humans but it was not statistically more than their right-eye use. The current laterality results replicated those of Yeater et al. (2014) even with a different operational definition used for eye preference. While the individual variability may have affected the results, perhaps the lack of a lateralized preference when discriminating between unfamiliar and familiar humans is not unexpected for animals in managed care, as humans may be viewed as a complex stimulus that is familiar instead of as two classes of the category of human.

Discrimination of Activity Level in Humans

As an extension of previous studies investigating the lateralized processing and discrimination of familiar and unfamiliar humans, we expected longer gaze durations for humans being active as opposed to being passive, independent of familiarity. Ultimately, when activity level was tested independently, all three species showed a clear preference for active humans over neutral humans with longer gaze durations. Although the purpose of the current study was to explore the ability of three species of cetaceans to discriminate between two classes of humans differing in their familiarity, the inclusion of activity level of the human did result in longer gaze times than using passive presentations alone. These results suggest that humans elicit attention from the animals, especially novel humans, but active humans elicit even greater attention. This pattern appeared to be true for belugas and bottlenose dolphins for both familiar and unfamiliar humans, with unfamiliar humans having larger differences between active and passive humans (Figure 3). Unfortunately, none of the differences reached statistical significance with the current sample. A similar effect occurred for the lags but not as strongly and only for unfamiliar humans. Future studies should incorporate these additional activity elements to promote attention to the stimuli, if free-swim paradigms are used.

Interest in Stimuli

Observed to manipulate a variety of natural and man-made objects and investigating humans in their natural habitats, bottlenose dolphins and belugas, particularly those habituated to the presence of humans, are frequently described as curious and interested in stimuli within their environments (e.g., Scheer, 2010). In contrast, lags have not been observed engaging in similar types of curious and investigative behaviors as often. Following these anecdotal observations and the results of the previous study, species differences in interest as measured by gaze duration were expected. As expected, lags showed the least interest in humans with the shortest gaze durations while the bottlenose dolphins and the belugas showed significantly longer gaze times although they did not differ from one another. Although the bottlenose dolphins may have had to exert greater

effort to view the presented stimuli (i.e., surface viewing only) compared to the belugas or lags who were able to view the stimuli from a more naturalistic perspective (i.e., underwater viewing), it was clear this difference in testing procedure did not alter the gaze durations of the bottlenose dolphins from the belugas.

The difference in gaze durations between the lags and the bottlenose dolphins and the belugas instead may have been related to their species-specific morphology. Belugas are much larger and tend to swim slower than bottlenose dolphins and lags during free-swim contexts. When combined with flexible (unfused) neck vertebrae (e.g., belugas and bottlenose dolphins), these physical characteristics might have produced longer gaze durations as compared to the lags. Although we did not measure speed specifically, all three species appeared to swim at relatively similar speeds when viewing the stimuli, which may rule out speed and size as a potential confound. The differences in gaze durations may have also been a product of life-history parameters (Connor, Wells, Mann, & Read, 2000; Heise, 1997; Luque & Ferguson, 2010; Morton, 2000) or personality differences (see discussion in Yeater et al., 2014). At a species-level, bottlenose dolphins and belugas may be able to spend more time investigating stimuli than lags because the physical size, social compositions, and natural habitats of belugas and bottlenose dolphins facilitate reduced predation risk. Additionally, these differences may have been enhanced due to individual differences in attention by specific animals. Some animals consistently attended the trials while other animals rarely attended the trials (Table 2), and within trials individual animals differed in their eye preferences and gaze durations when viewing humans within the same familiarity category (Figures 4-9). Reliable differences in personality at the individual level have already been demonstrated for bottlenose dolphins (Highfill & Kuczaj, 2007; Kuczaj, Highfill, & Byerly, 2012) and likely exist for both belugas and lags. Perhaps future investigations into personality could use a similar paradigm to elicit individualized responses to novel and familiar stimuli.

Conclusion

This replication and extension study successfully reproduced trends observed in a study conducted two years prior with the same populations of belugas and lags under slightly different methodological conditions (the addition of two manipulated variables, activity level and attire, and a modified operational definition for laterality). In a free-swim context with a limited number of available animals, competing social demands (e.g., dominance conditions, breeding season, mother-calf interactions), and wide ranges of animals in terms of age, sex, curiosity, and overall interest in stimuli external to their immediate environments, the results of the current study are suggestive. At the group level, few reliable statistical trends were found. There was some evidence that unfamiliar humans were discriminated from familiar humans for bottlenose dolphins, belugas, and lags although not always in the direction expected. Like Yeater et al. (2014), lateralized preferences appeared to be more likely at the individual level than at the group level. Ultimately, the addition of an active human condition may have helped to sustain the interest of an animal although it did not necessarily elicit the interest of the animals any more than the simple presence of a human. This condition did however produce different patterns of responses across the three species, suggesting that this combination of variables promoted choice and differing enriching experiences for individual animals. Studies such as these will improve our understanding of the cognitive processes (e.g., attention and object categorization) in cetaceans while also providing opportunities to enhance the wellbeing of animals in managed care.

References

Bisazza, A., Rogers, L. J., & Vallortigara, G. (1998). The origins of cerebral asymmetry: A review of evidence of behavioral and brain lateralization in fishes, amphibians, and reptiles. *Neuroscience and Behavioral Reviews*, *22*, 411–426.

Blois-Heulin, C., Crevel, M., Boye, M., & Lemasson, A. (2012). Visual laterality in dolphins: Importance of the familiarity of stimuli. *BMC Neuroscience*, *13*, 1–8.

Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies* (pp. 91–125). Chicago, IL: The University of Chicago Press.

Ellis, H., Shepherd, J., & Davies, G. (1979). Identification of familiar and unfamiliar faces from internal and external features: Some implications for theories of face recognition. *Perception*, *8*, 431–439.

Heise, K. (1997). Life history and population parameters of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). *Report of the International Whaling Commission*, *47*, 817–825.

Herman, L. M. (1986). Cognition and language competencies of bottlenosed dolphins. In R. J. Schusterman, J. A. Thomas, & F. G. Wood (Eds.), *Dolphin cognition and behavior: A comparative approach* (pp. 221–252). Hillsdale, NJ: Erlbaum.

Herman, L., Pack, A., & Wood, A. (1994). Bottlenose dolphins can generalize rules and develop abstract concepts. *Marine Mammal Science*, *10*, 70–80.

Herman, L. M., Peacock, M. F., Yunker, M. P., & Madsen, C. (1975). Bottlenosed dolphin: Double-slit pupil yields equivalent aerial and underwater diurnal acuity. *Science*, *139*, 650–652.

Highfill, L. E., & Kuczaj, S. A. II. (2007). Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities. *Aquatic Mammals, 33*, 380–389.

Johnsson, J. (1997). Individual recognition affects aggression and dominance relations in rainbow trout, *Oncorhynchus mykiss*. *Ethology*, *103*, 267–282.

Karavanich, C., & Atema, J. (1998). Individual recognition and memory in lobate dominance. *Animal Behaviour*, *56*, 1553–1560.

Karenina, K., Giljov, A., Baranov, V., Osipova, L., Krasnova, V., & Malashichev, Y. (2010). Visual laterality of calf–mother interactions in wild whales. *PLoS ONE*, *5*, 1–6.

Karenina, K., Giljov, A., Ivkovich, T., Burdin, A., & Malashichev, Y. (2013). Lateralization of spatial relationships between wild mother and infant orcas, *Orcinus orca*. *Animal Behaviour*, *86*, 1225–1231.

Karenina, K., Giljov, A., Malashichev, Y., Baranov, V., & Bel'kovich, V. (2010) Visual lateralization in the wild: perceiving of novel object in beluga whale (*Delphinapterus leucas*). *Asymmetry Journal*, *4*, 3–12.

Kendrick, K., Atkins, K., Hinton, M., Heavens, P., Keverne, B. (1996). Are faces special for sheep? Evidence from facial and object discrimination learning tests showing effects of inversion and social familiarity. *Behavioural Processes*, *38*, 19–35.

Kilian, A., von Fersen, L., & Güntürkün, O. (2000). Lateralization of visuospatial processing in bottlenose dolphin (*Tursiops truncatus*). *Behavioural Brain Research*, *116*, 211–215.

Kilian, A., von Fersen, L., & Güntürkün, O. (2005). Left hemispheric advantage for numerical abilities in the bottlenose dolphin. *Behavioural Processes*, *68*, 179–184.

Kuczaj, S. A., II, Makecha, R. N., Trone, M., Paulos, R. D., & Ramos, J. A. (2006). The role of peers in cultural transmission and cultural innovation: Evidence from dolphin calves. *International Journal of Comparative Psychology*, *19*, 223–240.

Kuczaj, S. A. II, Highfill, L. E., & Byerly, H. C. (2012). The importance of considering context in the assessment of personality characteristics: Evidence from ratings of dolphin personality. *International Journal of Comparative Psychology*, *25*, 309–329.

Kuczaj, S. A., II, & Walker, R. (2006). Problem solving in dolphins. In T. Zentall & E. Wasserman (Eds.), *Comparative cognition: Experimental explorations of animal intelligence* (pp. 580–601). New York, NY: Oxford University Press.

Kuczaj, S. A. II, & Xitco, M. J., Jr. (2002). It takes more than fish: The psychology of marine mammal training. *International Journal of Comparative Psychology*, *15*, 186–200.

Luque, S. P., & Ferguson, S. H. (2010). Age structure, growth, mortality, and density of belugas (*Delphinapterus leucas*) in the Canadian Arctic: Responses to environment?. *Polar Biology*, *33*, 163–178.

MacNeilage, P. F. (2013). Vertebrate whole-body-action asymmetries and the evolution of right handedness: A comparison between humans and marine mammals. *Developmental Psychobiology*, *55*, 577–587.

MacNeilage, P., Rogers, L., & Vallortigara, G. (2009). Origins of the left and right brain. *Scientific American*, *301*, 60–67.

Marino, L., Sudheimer, K., McLellan, W. A., & Johnson, J. I. (2004). Neuroanatomical structure of the spinner dolphin (*Stenella longirostris orientalis*) brain from magnetic resonance images. *The Anatomical Record. Part A, Discoveries in Molecular, Cellular, and Evolutionary Biology*, *279*, 601–610.

Mass, A., & Supin, A. Y. (2002). Visual field organization and retinal resolution of the beluga, *Delphinapterus leucas* (Pallas). *Aquatic Mammals*, *28*, 241–250.

Mercado, E., Killebrew, D., Pack A., Macha, B., & Herman, L. (2000). Generalizations of 'same-different' classification abilities in bottlenose dolphins. *Behavioral Processes*, *50*, 79–94.

Morton, A. (2000). Occurrence, photo-identification and prey of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in the Broughton Archipelago. *Marine Mammal Science*, *16*, 80–93.

Pepper, R., & Simmons, J. (1973). In-air visual acuity of the bottlenose dolphin. *Experimental Neurology*, *41*, 271–276.

Pilleri, G. (1982). Observations on the behaviour sense of vision and sonar field of some cetaceans in captivity. *Investigations of Cetacea*, *13*, 167–176.

Ridgway, S. (1986). Physiological observations of the dolphins brain. In R. Schusterman, J. Thomas, & F. Wood (Eds.), *Dolphin cognition and behavior: A comparative approach* (pp. 31–59). Hillsdale, NJ: Lawrence Erlbaum Associates.

Rogers, L. J., Vallortigara, G., & Andrew, R. J. (2013). *Divided brains: The biology and behaviour of brain asymmetries*. Cambridge, MA: University Press.

Rogers, L. J., Zucca, P., & Vallortigara, G. (2004). Advantages of having a lateralized brain. *Proceedings of the Biological Sciences*, *271*, 420–422.

Rosa Salva, O., Regolin, L., Mascalzoni, E., & Vallortigara, G. (2012). Cerebral and behavioural asymmetries in animal social recognition. *Comparative Cognition & Behaviour Reviews*, *7*, 110–138.

Scarpuzzi, M., Lacinak, T., Turner, T., Tompkins, C., & Force, D. (1999). Decreasing the frequency of behavior through extinction: An application for the training of marine mammals. In K. Ramirez (Ed.), *Animal training, successful animal management through positive reinforcement* (pp. 103–107). Chicago, IL: Shedd Aquarium.

Scheer, M. (2010). Review of self-initiated behaviors of free-ranging cetaceans directed towards human swimmers and waders during open water encounters. *Interaction Studies*, *11*, 442–466.

Scheid, C., Range, F., & Bugnyar, T. (2007). When, what, and whom to watch? Quantifying attention in ravens (*Corvus corax*) and jackdaws (*Corvus monedula*). *Journal of Comparative Psychology*, *121*, 380–386.

Siniscalchi, M., Dimatteo, S., Pepe, A., Sasso, R., & Quaranta, A. (2012). Visual lateralization in wild striped dolphins (*Stenella coeruleoalba*) in response to stimuli with different degrees of familiarity. *PLoS ONE*, *7*, 1–6.

Spong, P., & White, D. (1971). Visual acuity and discrimination learning in the dolphin (*Lagenorhynchus obliquidens*). *Experimental Neurology*, *31*, 431–436.

Supin, A. Y., Mukhametov, L. M., Ladygina, T. F., Popov, V. V., Mass, A. M., & Poliakova, I. G. (1978). *Electrophysiological studies of the dolphin's brain*. Moscow: Izdatel'ato Nauka.

Tarpley, R. J., Gelderd, J.B., Bauserman, S., & Ridgway, S. H. (1994). Dolphin peripheral visual pathway in chronic unilateral ocular atrophy: Complete decussation apparent. *Journal of Morphology*, *222*(1), 91–102.

Thieltges, H., Lemasson, A., Kuczaj, S., Böye, M., & Bois-Heulin, C. (2011). Visual laterality in dolphins when looking at (un)familiar humans. *Animal Cognition*, *14*, 303–308.

Tibbetts, E. A., & Dale, J. (2007). Individual recognition: It is good to be different. *Trends in Ecology & Evolution*, *22*, 529–537.

Vallortigara, G., & Rogers, L. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*, *28*, 575–589.

Wilkinson, A., Specht, H., & Huber, L. (2010). Pigeons can discriminate group mates from strangers using the concept of familiarity. *Animal Behaviour*, *80*, 109–115.

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.

Yeater, D. B., Hill, H. M., Baus, N., Farnell, H., & Kuczaj, S. A. (2014). Visual laterality in belugas (*Delphinapterus leucas*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) when viewing familiar and unfamiliar humans. *Animal Cognition*, *17*, 1245–1259. doi:10.1007/s10071-014-0756-x