



Do Belugas (*Delphinapterus leucas*), Bottlenose Dolphins (*Tursiops truncatus*), & Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*) Display Lateralized Eye Preference when Presented with Familiar or Novel Objects?

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Lateralization of behaviors and information processing are common across species. Hypothesized to be crucial for more efficient responding to environmental stimuli, lateralization has been investigated for a number of topics. Cetaceans are proposed to be hemispheric specialists, given a small corpus callosum, complete decussation of the optic nerve, and the ability to respond to a different visual stimulus presented to each eye simultaneously. Research with cetaceans has shown strong biases in a number of behaviors, including swimming, foraging, social interactions, and responses to myriad visual stimuli. Given similar evolutionary pressures, different species of cetaceans should display similar lateralized preferences. Previous research with bottlenose dolphins in managed care and wild striped dolphins indicated a right eye preference when viewing unfamiliar objects. The purpose of the current study was to evaluate the eye preference of belugas, bottlenose dolphins, and Pacific white-sided dolphins (lags) in managed care when viewing familiar and unfamiliar objects. The results from 11 belugas, 5 bottlenose dolphins, and 5 lags indicated that consistent group level eye preferences were not present. The belugas preferred to view both types of objects with both eyes, with the majority of the belugas showing a left-eye preference when a monocular gaze was used. Bottlenose dolphins tended to view both objects with their right eye while lags used their left eye when viewing objects. These results may have been affected by viewing objects below water versus above water. The belugas and the Pacific white-sided dolphins were able to view the objects below water, which may have elicited more naturalistic visual examinations of the objects (i.e., greater ecological validity). Viewing objects within one's habitat may facilitate the discrimination of an object rather than simply its detection, which is may be more likely when encountering stimuli above the surface of the water as the bottlenose dolphins had to do in the present and past research. Future research should compare if presentation of the stimulus above water versus below water affects the eye preference displayed.

Lateralized behaviors have been the subject of study across a number of species. Cetaceans are well-known for hemispheric independence, documented by behavioral, neuroanatomical, and neurophysiological evidence. Described very early in cetacean research, dolphins were able to examine two completely independent visual stimuli, one presented to each eye simultaneously, and respond to each stimulus appropriately and virtually simultaneously (Ridgway, 1986). Following these early observations, more systematic studies were conducted. A broad range of studies supported the presence of unihemispheric slow-wave sleep, which allows cetaceans and pinnipeds to maintain high levels of vigilance while moving about their environments and resting (Hill, Carder, & Ridgway, 2008; Lyamin, Manger, Ridgway, Mukhametov, & Siegel, 2008; Ridgway et al., 2006, 2009). Neuroanatomical evidence indicates that the corpus callosum is extremely small for all cetaceans examined (Tarpley & Ridgway, 1994) and the optic nerves are completely decussated at the optic chiasm, which indicates that all visual input is processed in the contra-lateral hemisphere (Tarpley, Gelderd, Bauserman, & Ridgway, 1994).

There is growing evidence for laterality in natural behaviors and social interactions with conspecifics across several taxa. All great apes except for orangutans, show a right-hand dominance (MacNeilage, 2007).

Asian elephants demonstrate individual preference for trunk curling directions (Haakonsson & Semple, 2009). Vallortigara and Rogers (2005) found evidence suggesting that brain lateralization may benefit individuals/species while foraging or protecting themselves from predators. For example, while engaging in foraging behaviors, domestic chicks demonstrate a right eye/left hemisphere preference. Further evidence of lateralized processing in the left eye/right hemisphere for social interactions is supported by many species across taxa. Visual laterality has been demonstrated in several vertebrate species, including fish, birds, amphibians, reptiles, and land mammals (i.e., Rosa Salva, Regolin, Mascalcioni, & Vallortigara, 2012). For all of these species there was consistent evidence for a left eye/right hemisphere preference during socio-sexual interactions with conspecifics. Rosa Salva and colleagues (2012) concluded that many species displayed a left eye/right hemisphere preference when discriminating between social companions. There is also evidence for the significance of visual laterality in aggressive interactions among conspecifics. In one example, female striped plateau lizards (*Sceloporus virgatus*) frequently show more aggressive displays toward courting males if the male appears on the left side of the female or if the male is in the female's binocular visual field, not on the right side (Hews, Castellano, & Hara, 2004). Aggressive interactions are also more intense if experienced in the left eye/right hemisphere. Gelada baboons (*Theropithecus gelada*) prefer to process social visual cues from conspecifics with their right hemisphere even during non-aggressive approaches (Casperd & Dunbar, 1996). Social recognition in some mammalian species (such as sheep and monkeys) may also be influenced by the emotional valence, such as in discrimination tasks with neutral, negative (sad) or positive (happy) facial expressions (i.e., Tate, Fischer, Leigh, & Kendrick, 2006). For example, in humans it has been suggested that perception of negative valence relies preferentially on the left eye/right hemisphere, and the perception of positive valence utilizes both hemispheres (Adolphs, Jansari, & Tranel, 2001; Jansari, Tranel, & Adolphs, 2000).

Behavioral evidence in cetaceans has been observed both within spontaneous responses to natural stimuli and with manipulated and controlled stimuli. Beluga calves and killer whale calves tend to swim on their mothers' right side to maintain social contact with their left visual field in their natural habitats (Hill et al., 2016; Karenina et al., 2010a; Karenina, Giljov, Glazov, & Malashichev, 2013). A similar trend has also been observed with beluga calves in managed care (Hill et al., 2016). Bottlenose dolphins (*Tursiops truncatus* and *T. aduncus*) in both their natural habitats and managed care display a left pectoral fin contact preference when initiating social interactions (Dudzinski, Gregg, Ribic, & Kuczaj, 2009; Dudzinski, Gregg, Paulos, & Kuczaj, 2010; Sakai, Hishii, Takeda, & Kohshima, 2006). For example, Sakai et al. (2006) found that Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) engaged in social flipper rubbing more often when viewing a partner with the left eye.

In experimental settings, the right visual field was associated with superior performance in audio-visual discrimination tasks for eight bottlenose dolphins in managed care (Delfour & Marten, 2006; Kilian, von Fersen, & Güntürkün, 2005; von Fersen, Schall, & Güntürkün, 2000; Yaman, von Fersen, Dehnhardt, & Güntürkün, 2003). More recent research has indicated that some bottlenose dolphins in managed care preferred to examine familiar and unfamiliar human stimuli with their left eye (Thieltges, Lemasson, Kuczaj, Boye, & Blois-Heulin, 2011). In contrast, other bottlenose dolphins displayed a trend for a right-eye preference when viewing humans, although the trend was not statistically significant (Hill et al., 2016). Belugas in managed care preferred to view humans in general with both eyes, only showing a left-eye tendency toward familiar humans while Pacific white-sided dolphins viewed familiar and unfamiliar humans with their left eye (Hill et al., 2016; Yeater, Hill, Baus, Farnell, & Kuczaj, 2014). When objects were tested, different responses emerged based on the familiarity of the object. Wild belugas preferred to examine an unfamiliar object (i.e., an underwater video camera) with their left eye (i.e., right hemisphere bias; Karenina, Giljov, Malashichev, Baranov, & Bel'kovich, 2010b), but wild striped dolphins (*Stenalla coeruleoalba*) preferred to examine

unfamiliar objects with their right eye, demonstrating a left-hemisphere bias (Siniscalchi, Dimatteo, Pepe, & Sasso, 2012). For bottlenose dolphins in managed care, a left-eye preference was observed when viewing unfamiliar objects (Blois-Heulin, Crevel, Boye, & Lemasson, 2012).

These mixed results have led to several working hypotheses. As discussed earlier, for many other animal species, the right hemisphere is implicated in the specialized processing of social information, including emotions, social interactions with familiar conspecifics, and holistic perspectives (reviewed by Rosa Salva et al., 2012). Thus, when viewing conspecifics, cetaceans may prefer to utilize their left eye/right hemisphere when processing visual information about those individuals to facilitate social interactions (e.g., Karenina et al., 2010a; Ridgway, 1986; Rosa Salva et al., 2012; Thieltges et al., 2011). An alternate hypothesis suggests that the categorization of novel (unfamiliar) stimuli may be processed by the right eye/left hemisphere as details of the stimuli are assembled into a more cohesive picture (Blois-Heulin et al., 2012; Delfour & Marten, 2006; Kilian et al., 2005; Siniscalchi et al., 2012; von Fersen et al., 2000; Yaman et al., 2003).

The purpose of the current study was to evaluate the eye preference of three cetaceans when viewing objects outside of their aquatic habitat that had either been never experienced or seen by the animals (i.e., novel, unfamiliar objects) or that have been part of their typical enrichment program (i.e., familiar objects), extending the initial study in which gaze duration was assessed for belugas, bottlenose dolphins, and Pacific white-sided dolphins (Guarino, Yeater, Lacy, Dees, & Hill, 2017). The results of the initial object study conducted in a free swim, variable social setting indicated that while Pacific white-sided dolphins had significantly shorter gaze durations than either belugas or bottlenose dolphins, all three species looked longer at unfamiliar stimuli than at the control apparatus. Significant differences in gaze duration between familiar and unfamiliar objects did not emerge, which may have been due to competing contingencies between the object presentations and ongoing social states/interactions or a lack of power combined with individual differences. Evaluation of visual laterality is independent of gaze time and findings from previous studies indicated that familiarity of an object influenced the eye used to investigate it. Thus, we expected all three species to display a right-eye preference when viewing unfamiliar objects and a left-eye preference when viewing familiar objects.

Method

Subjects

Eleven belugas (*Delphinapterus leucas*, five males and six females), ranging between 15 months and late 30 years were housed at two separate facilities. Additionally, five male bottlenose dolphins (*Tursiops truncatus*), ranging between 8 and 25+ years, and five Pacific white-sided dolphins (*Lagenorhynchus obliquidens*, lags, two males and three females), ranging between 6 and 30+ years, were housed at the same facility as one of the beluga populations. Two adult female belugas were excluded from the analyses due to visual impairments. See Guarino et al. (2017) for specific details about the subjects.

Materials

The current study replicated the experimental equipment and video recording set-up used by Yeater et al. (2014) and Guarino et al. (2017). The belugas and the lags were tested using underwater viewing windows located in their primary pools. Underwater viewing access was not available for the bottlenose dolphins, and 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 time to habituate to the experimental set-up before each session. However, all animals had experienced this experimental set-up repeatedly for two studies conducted previously and did not demonstrate increased interest or aversion to the experimental apparatus at any point of the current study.

Familiar and unfamiliar objects were presented to the animals. Familiar objects, selected by trainers, included previously manipulated environmental enrichment devices (EEDs, e.g., buoy balls, buoy bumpers, plastic flower pots) regularly given to the animals as “toys.” Unfamiliar objects included different three-dimensional and colored objects, similar in size to familiar objects, (e.g., stuffed animals, 3-dimensional PVC objects, fake plants, posters, large human toys) that had not been presented or manipulated previously by the animals. Familiar objects were presented multiple times throughout the project due to the limited availability and unfamiliar objects were presented only one time for each species. As documented in the supplementary material in Guarino et al. (2017), some objects produced longer gaze durations and/or frequency of views, and numbers of individuals viewing the object (Supplementary Tables 2-4). No clear pattern emerged for unfamiliar or familiar objects or for specific objects, suggesting that salience of individual stimuli varied unpredictably.

Procedure

The same experimental protocol was used for all populations and described in detail in Guarino et al. (2017). Experimental sessions were conducted using a free swim context and daily social groupings. During testing, animals could continue their social activities or swim by the apparatus where objects were presented. The experimental protocol called for 30 trials of familiar objects (i.e., objects with which the animals had regular interactive experience), 30 trials of unfamiliar objects (i.e., objects with which the animals had no prior experience), and 10 trials of the control (i.e., curtain apparatus) for each animal. For the facility with belugas, bottlenose dolphins, and lags, a session held 5-8 randomly determined trials (i.e., familiar, unfamiliar, and control trials were intermixed randomly through the session determined by a block randomization schedule), with each trial lasting approximately two minutes. For the facility with belugas only, four randomly determined trials were conducted per session with one minute given to view the stimulus. A trial consisted of either a familiar or an unfamiliar object presented in front of the curtain apparatus on top of the table or hanging from the apparatus. Although almost all animals received the pre-determined number of trials, individual animals ultimately responded to a different number of trials (see Guarino et al., 2017 for specific details). Trained research assistants coded the videotaped trials. To assess the reliability of the coders, approximately 10% of the trials were viewed and confirmed by the principal investigator with any discrepancies resolved. Each trial was coded for swimming direction at approach and eye preference used by each animal when viewing the object. Eye preference was based on converting the frequency of gazes based on the eye (right, left, or both) used to view a stimulus to a percentage. The percentage of eye preference was calculated by dividing the frequency of each eye look by the total number of gazes in a trial and multiplying by 100.

Statistical Analyses

All approaches displayed by each animal during a trial were included in group and individual analyses. For group analyses, the average percentages were calculated across all trials of a given condition related to object familiarity (familiar, unfamiliar, or control) for each individual animal. Age and sex analyses were not conducted due to the small number of available animals per condition. However, data for the belugas from both facilities were analyzed together as similar object familiarity trends were found for both populations. These measures were tested for a significant effect of object familiarity using repeated measures ANOVAs for each species and Least Significant Differences (LSD) post hocs when appropriate. These post hocs were selected to maximize the possibility of detecting any significant pairwise differences given the degree of individual variability.

Results

Group Laterality

Belugas. No significant interaction between object familiarity and laterality was observed for belugas when averaged percentages of gaze frequency were examined with a mixed model ANOVA. However, when the different conditions were examined separately some lateralized preferences emerged (Table 1). The results of repeated measures ANOVAs reported significant effects for eye preference for both familiar objects and unfamiliar objects analyses. When investigating familiar objects, belugas used the left eye more frequently than the right eye ($p = 0.050$), but both eyes more frequently than the right eye ($p = 0.015$) and the left eye ($p < 0.05$), supporting the assumed hypothesis. When investigating unfamiliar objects, belugas also used both eyes more frequently than the right eye ($p = 0.030$; left eye: $p = 0.090$, Table 1). An additional analysis was

conducted to determine if these preferences were influenced by swim pattern. The results of a binomial test indicated the belugas approached the stimuli from both directions equally, suggesting that swim pattern did not influence their results.

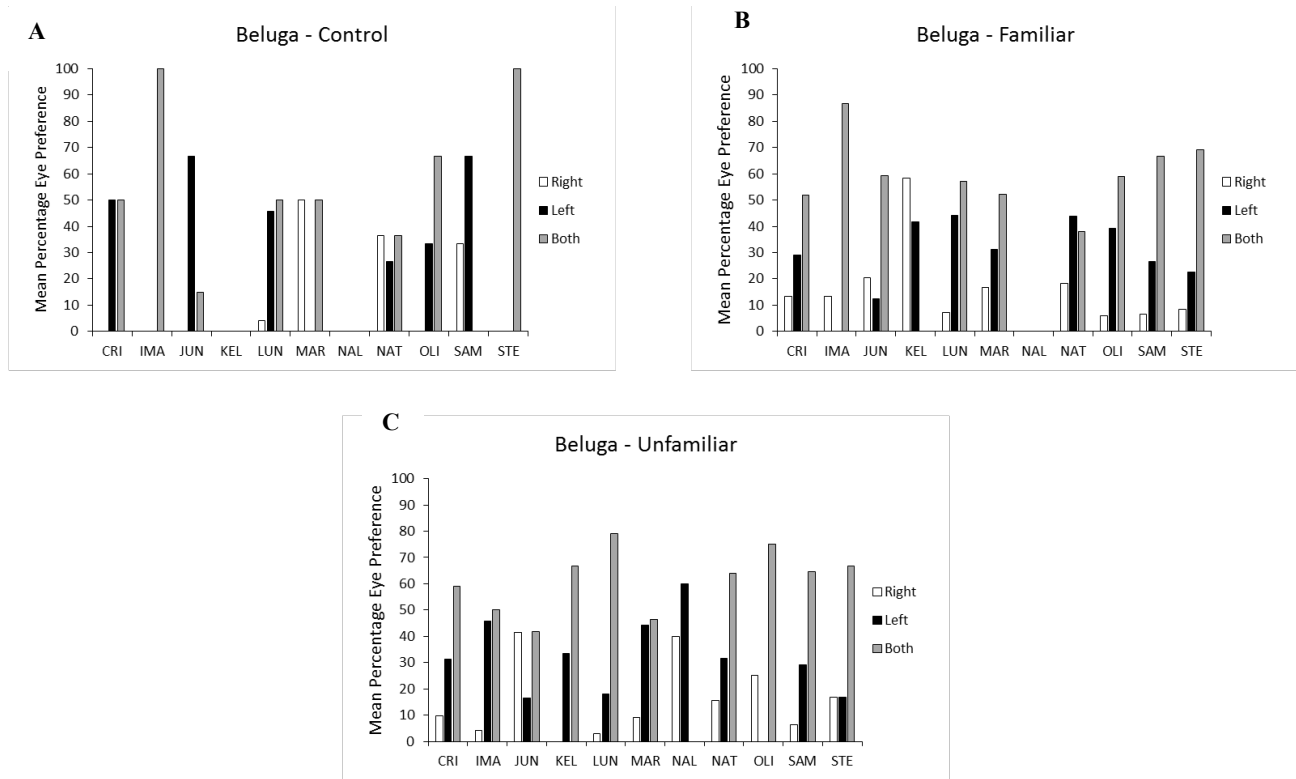


Figure 1. Eye preferences per individual for control (a), familiar (b), and unfamiliar (c) trials for belugas. MAR and NAT, were removed from statistical analyses due to possible visual impairment but are displayed in the figure for comparison purposes.

Bottlenose dolphins. No significant interaction between object familiarity and laterality was observed for bottlenose dolphins when averaged percentages of gaze frequency were examined with a mixed model ANOVA. However, when the different conditions were examined separately some lateralized preferences emerged (Table 1). The results of repeated measures ANOVAs reported a significant effect for eye preference for familiar objects, but not for unfamiliar objects. When investigating familiar objects, bottlenose dolphins used the right eye more often than the left eye ($p = 0.040$) or both eyes ($p = 0.040$). These results did not support the assumed hypothesis that the left eye would be used more frequently than the right eye. A similar pattern of results was indicated by the eye preference analyses for unfamiliar objects, but no significant differences were found (Table 1). The results of a binomial test indicated the dolphins approached the stimuli from both directions equally.

Lags. No significant interaction between object familiarity and laterality was observed for lags when averaged percentages of gaze frequency were examined with a mixed model ANOVA. However, when the different conditions were examined separately a strong lateralized preference emerged (Table 1). The results of repeated measures ANOVAs reported significant effects for eye preference for both familiar objects and unfamiliar objects analyses. When investigating familiar objects, lags used the left eye more frequently than the right eye ($p = 0.008$) and both eyes ($p = 0.001$), supporting the assumed hypothesis. When investigating

unfamiliar objects, lags once again used the left eye more frequently than the right eye ($p = 0.003$) or both eyes ($p < 0.001$) (Table 1). A strong swim direction preference was observed for the lags such that the lags approached presented stimuli significantly more often with their left eye than the right eye, as determined by a binomial test, $z(N = 20) = 7.06$, $p < 0.001$.

Table 1

Descriptive and Inferential Statistics for Averaged Percentages of Eye Preferences (Right, Left, Vs. Both) for Belugas, Bottlenose Dolphins, and Pacific White-Sided Dolphins for the Two Object Familiarity Conditions

Animal	Familiar						F	df	η_p^2
	Right		Left		Both				
	M	SD	M	SD	M	SD			
Belugas	10.7 ^a	10.4	24.5 ^b	15.9	43.3 ^c	26.6	12.01	2, 16	0.60
Dolphins	61.1 ^d	74.4	16.1 ^e	10.6	22.8 ^e	8.3	15.22	2, 8	0.79
Lags	11.0 ^f	12.4	86.5 ^g	13.2	2.5 ^f	3.5	62.47	2, 8	0.94
Animal	Unfamiliar						F	df	η_p^2
	Right		Left		Both				
	M	SD	M	SD	M	SD			
Belugas	17.3 ^a	15.3	22.8 ^a	18.5	60.0 ^b	25.8	7.80	2, 16	0.49
Dolphins	54.1	23.9	21.9	14.8	23.5	19.8	4.35	2, 8	--
Lags	11.3 ^c	11.5	86.2 ^d	15.8	2.5 ^c	5.6	51.37	2, 8	0.93

Note. Within familiarity condition, means with different superscripts (i.e., a, b, c, d, e, f, g) are significantly different from each other and means with the same superscripts are not different from each other, per LSD post hoc tests, $p < 0.05$.

Individual Laterality

The belugas displayed many different eye preferences when viewing the experimental apparatus, familiar objects, or unfamiliar objects. Belugas that examined all three types of stimuli clearly preferred to investigate any type of object with both eyes. When both eyes were not considered, there were some lateralized preferences that were independent of object familiarity. For example, six belugas preferred to investigate familiar and unfamiliar objects with the left eye as opposed to the right eye (Figure 1). In comparison, three of the five bottlenose dolphins used the right eye primarily to investigate both familiar and unfamiliar objects while the other two bottlenose dolphins investigated familiar objects primarily with the right eye and unfamiliar objects with either the left eye or both eyes. Two of these animals then switched from a monocular view to a binocular view (Figure 2). The lags, however, did not differ from one another in their preference between familiar and unfamiliar objects as all lags displayed a very strong preference for the left eye over the right or both eyes when investigating objects (Figure 3). Two of the lags did use both eyes occasionally, although this use was relatively rare compared to bottlenose dolphins and belugas.

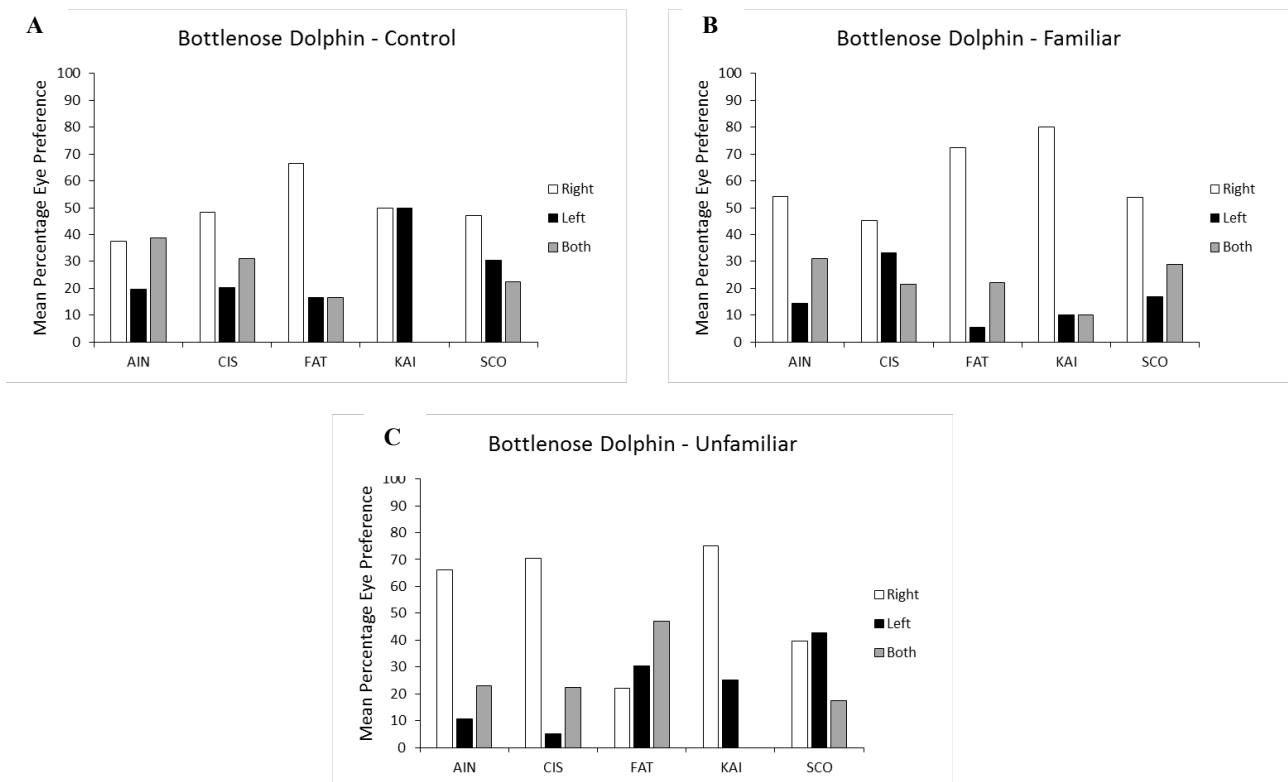


Figure 2. Eye preferences per individual for control (a), familiar (b), and unfamiliar (c) trials for bottlenose dolphins.

Discussion

Many vertebrates display lateralized visual preferences when examining different types of familiar and unfamiliar stimuli (MacNeilage, 2013; Rosa Salva et al., 2012). For example, bottlenose dolphins displayed a right eye advantage in studies requiring visual processing (Delfour & Marten, 2006; Kilian et al., 2005; Yaman et al., 2003; von Fersen et al., 2000) while two additional studies suggested that captive bottlenose dolphins (Blois-Heulin et al., 2012) and wild striped dolphins (Siniscalchi et al., 2012) preferentially used the right eyes to investigate unfamiliar objects (Table 2). As noted by MacNeilage (2013), this right-eye preference for unfamiliar stimuli was counter to most other vertebrate species tested in which the right eye was used to view familiar stimuli while the left eye was used preferentially to view unfamiliar stimuli (Vallortigara & Rogers, 2005).

Group-based laterality. Like the previous study using a similar paradigm with humans as the visual stimuli and similar beluga and lag populations (Yeater et al., 2014), no clear preference for any species emerged at the group level using averaged percentages (Table 2). A large degree of variability existed among the individuals of each species (Figures 1-3), and although five to eight cetaceans is considered a “large” sample, the power to detect significant effects was limited. To better understand the possibility of lateralized processing, we examined each condition separately. Some preferences emerged with belugas (Figure 1). Like the results of a similar study testing this species’ ability to discriminate between familiar and unfamiliar humans (Yeater et al., 2014), the belugas again showed a bias for binocular vision followed by a left-eye preference for familiar objects, but not for unfamiliar objects (Table 2). In contrast, bottlenose dolphins displayed a right-eye preference for familiar objects and curtain apparatus, but did not show any preference for unfamiliar objects, which countered previous results in a similar study (Blois-Heulin et al., 2012). Bottlenose dolphins also used

binocular vision, but not as often as belugas. Finally, lags displayed a very strong left-eye preference for familiar and unfamiliar objects and for the control apparatus. This left-eye preference was likely related to the lags' swim pattern. The lags almost never used both eyes to view any object. Although previous studies using the free swim paradigm reported that binocular vision was rarely used by bottlenose dolphins (Blois-Heulin et al., 2012; Delfour & Marten, 2006; Thieltges et al., 2011), both the bottlenose dolphins and the belugas tended to use binocular vision frequently with belugas preferring it. In comparison, the lags were more likely to use monocular vision, a behavior that may be influenced by their fused and inflexible neck vertebrae. The lags also showed much less interest in viewing these objects by swimming at faster speeds and looking for shorter periods of times compared to the other two species, much like the previous study examining their responses to humans (Yeater et al., 2014).

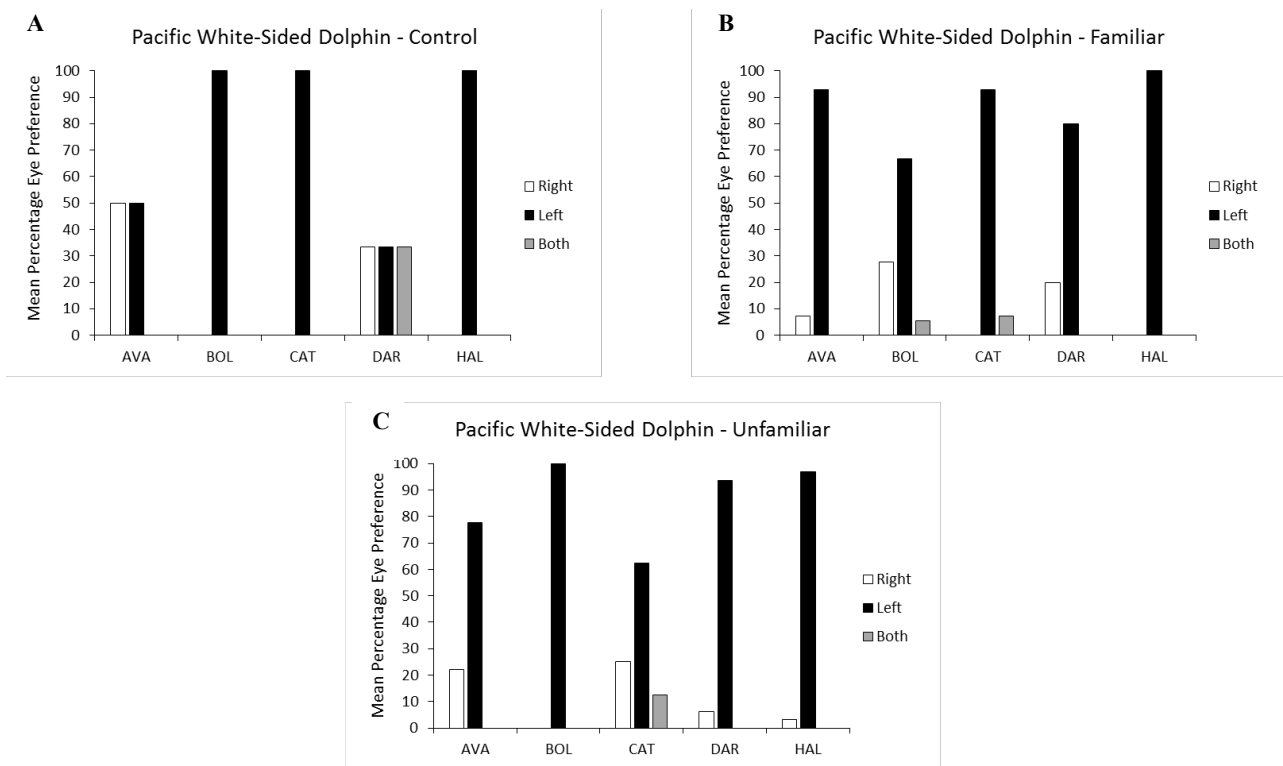


Figure 3. Eye preferences per individual for control (a), familiar (b), and unfamiliar (c) trials for Pacific white-sided dolphins.

The inconsistent laterality results across the three species suggests that individual differences were likely driving the visual processing of external stimuli during this free-swim paradigm. Research on animal personality has documented that some individuals are more likely to approach novel stimuli and investigate unfamiliar objects (see Gosling, 2001 for a review). Research has indicated that bottlenose dolphins have reliable individual personalities (Highfill & Kuczaj, 2007; Kuczaj, Highfill, & Byerly, 2012), and not all dolphins respond similarly to novel environmental enrichment objects (Eskelinen, Winship, & Borger-Tuner, 2015; Lopes, Borger-Turner, Eskelinen, & Kuczaj, 2016). Unfortunately, individual personality profiles have not been evaluated for the subjects for this study. However, consistent individual differences existed when one examines the frequency and gaze duration responses across comparable studies conducted with the same population (Guarino et al., 2017, Table 1 & Supplemental Table 1; Hill et al., 2016, Tables 2 & 3). The degree of individual variability in interest likely influenced the overall results for all three species.

However, methodological differences may have also affected the results. In an effort to better understand the mixed results and to examine the proposed hypotheses regarding the possible hemispheric functions during lateralized processing of visual information, the design differences and results for studies investigating lateralized object discrimination in cetacean species, including the data from the current study, were summarized (Table 2). As seen in Table 2, Blois-Heulin et al. (2012) and Siniscalchi et al. (2012) were the most similar methodologically to our current study. However, even with very similar research methods, the results for eye preference differed. In fact, the results for the bottlenose dolphins in the present study countered the findings reported by Blois-Huelin and her colleagues (2012), despite both studies having objects presented above water and allowing the animals to freely approach the stimuli. Possible explanations for these discrepancies may involve individual bottlenose dolphins used in both studies, group-influenced behavior as both studies tested the animals in group settings, or differences in definition used to evaluate eye preference. Furthermore, belugas and lags were able to view the objects below water, which simulates a context more likely to occur in their natural habitats (i.e., ecological validity). This underwater viewing (although still outside of their actual aquatic habitat) may enable the animals to visually discriminate between the different classes of stimuli (i.e., familiar or unfamiliar) easier, especially if this discrimination utilizes lateralized processing. For example, when animals experience objects while “on the go” and above water (i.e., the bottlenose dolphin experimental set-up), detection that an object is present most likely elicits the first response. However, to visually categorize objects that are removed from immediate visual access, animals have to spend more time at the surface, look up and outside to inspect these objects, and may expose them to potential threats. Additionally, as found with other studies with humans (i.e., Adolphs, et al., 2001; Jansarui, et al., 2000), the perceived emotional valence of a stimulus may affect the engagement and lateralized viewing preference. Thus, emotional valence of particular objects may influence the results of these studies as some familiar, preferred objects may have elicited stronger positive responses while unfamiliar, possibly threatening objects may have elicited stronger negative responses for specific individuals, which would have been very difficult to detect in the current paradigm.

Further research needs to be conducted on cetaceans’ ability to categorize familiar and unfamiliar objects by looking at stimuli, and indicating the concept followed by the measure of the number of correct choices based on eye preference. To be consistent with the majority of the literature, the research design should focus on tasks related to monocular viewing of stimuli. We believe that a performance-based task should be developed to assess laterality, such as combining a match-to-sample cognitive discrimination task that forces an animal to view stimuli monocularly and perform the task with only one eye at time (“blindfolded” with one eye cup). This design would provide an opportunity to test the animals with more than one set of novel stimuli (with emotional valence controlled), and to compare the data of each eye for each set of stimuli. Improved research design with the animals under stimulus control should allow for better assessment of performance based on visual processes. Based on the hypothesized theories, we would expect the right hemisphere to have an advantage over the left hemisphere in processing and discriminating visual information. If cetaceans are using global processing (as suggested by Delfour & Marten, 2006; Kilian et al., 2005; von Fersen et al., 2000; Yaman et al., 2003), the results should demonstrate better discrimination for novel (unfamiliar) stimuli when using the right eye. The social hypothesis (Karenina et al., 2010a, 2013; Rosa Salva et al., 2012) was demonstrated to be important (Yeater et al., 2014) for human stimuli. The present results using object discrimination offered support for the global versus detail (local) processing hypothesis as being more relevant for these species. We propose that future studies utilizing these proposed changes to the current methodologies may find corroborating support in more ecologically valid contexts such as lateralized visual responses during social interactions.

Table 2

Comparison of Studies Investigating Cetacean Responses to Visual Stimuli

Study	Cetacean	Setting	Type of Stimulus	Stimulus Location	Presentation Mode	Eye Preference Examined	Dependent Variable	Eye Preference		
								Familiar Stimulus	Unfamiliar Stimulus	Not indicated
von Fersen et al. (2000)	1 <i>Tt</i>	Managed care	Pattern discrimination	AW	Stimulus control	M	Percentage correct based on eye			R
Yaman et al. (2003)	3 <i>Tt</i>	Managed care	Pattern discrimination	AW	Stimulus control	M	Percentage correct based on eye			R
Kilian et al. (2005)	1 <i>Tt</i>	Managed care	Visual shapes for numerosity study	UW	Stimulus control	M	Percentage correct based on eye			R
Delfour & Marten (2006)	3 <i>Tt</i>	Managed care	Images on touch screen	UW	Stimulus control	M	1. Duration of gaze time 2. Number of correct responses per eye			1. No spontaneous preference (mixed between 3 <i>Tt</i>) 2. R
Karenina et al. (2010b)	Numerous <i>Dl</i>	Free-ranging	Video camera	UW	Free swim	M	1. Frequency of looks per eye 2. Duration of looks per eye		L	
Thieltges et al. (2011)	5 <i>Tt</i>	Managed care	Neutral Humans	AW	Free swim	M	Laterality Index ^a	L	L	
Blois-Heulin et al. (2012)	5 <i>Tt</i>	Managed care	Objects	AW	Free swim	M	Laterality Index	L	R	
Siniscalchi et al. (2012)	86 identified <i>Sc</i>	Free-ranging	Objects	AW	Free swim	M	Frequency of looks per eye	L	R	
Delfour & Herzing (2013)	66 identified <i>Sf</i>	Free-ranging	Mirror	UW	Free swim	B & M	Duration of gaze time per eye		R	
Yeater et al. (2014)	9 <i>Dl</i> 6 <i>Lo</i>	Managed care	Neutral Humans	UW	Free swim	B & M	Duration of gaze by an eye converted to a proportion ^b	<i>Dl</i> – B, then L <i>Lo</i> – L > R, ns	<i>Dl</i> – B, then L <i>Lo</i> – L > R, ns	

(continued)

Study	Cetacean	Setting	Type of Stimulus	Stimulus Location	Presentation Mode	Eye Preference Examined	Dependent Variable	Eye Preference		
								Familiar Stimulus	Unfamiliar Stimulus	Not indicated
Hill et al. (2016)	5 <i>Tt</i> 9 <i>Dl</i> 5 <i>Lo</i>	Managed care	Neutral & Active Humans	AW/UW	Free swim	B & M	Frequency of looks converted to percentage ^c	<i>Dl</i> – B <i>Tt</i> – B = R = L <i>Lo</i> – L > R, ns	<i>Dl</i> – B <i>Tt</i> – R, ns <i>Lo</i> – L, ns	
Yeater et al. (current study)	5 <i>Tt</i> 9 <i>Dl</i> 5 <i>Lo</i>	Managed care	Objects	AW/UW	Free swim	B & M		<i>Dl</i> – B, then L <i>Tt</i> – R <i>Lo</i> – L	<i>Dl</i> – B, R = L <i>Tt</i> – no preference <i>Lo</i> – L	

Note. Cetacean: *Tt*, *Tursiops truncatus* (bottlenose dolphin); *Sc*, *Stenella coeruleoalba*, striped dolphin; *Dl*, *Delphinapterus leucas*, beluga; *Lo*, *Lagenorhynchus obliquidens*, Pacific white-sided dolphin. Stimulus Location: UW = Underwater; AW = Above water. Eye Preference Examined: M = Monocular; B = Binocular. Eye Preference: R = Right; L = Left; B = Both; ns = non-significant. a “A visual laterality index (ILV) was calculated for each subject using the formula: $(R - L)/(R + L)$. R and L represent the numbers of times the right eye and the left eye were used. ILV reveals the direction of preference and varies from -1 to +1; negative values indicate preferential use of left eye and positive values indicate preferential use of right eye. The absolute value of ILV, Abs (ILV), was used to determine preference strength.” (Thieltges et al., 2011, p. 305). b “Eye preference was determined by which eye was presented the longest while viewing a given stimulus.” (Yeater et al., 2014, p. X). c “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.” (Hill et al., 2016, p. 5).

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