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Underwater Visual Acuity of Florida Manatees (*Trichechus manatus latirostris*)

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In Experiment 1 underwater visual acuity was assessed in two Florida manatees, *Trichechus manatus latirostris*, using grating stimuli in three conditions: Vertical gratings presented in freshwater, vertical gratings in saltwater, and horizontal gratings in saltwater. All stimuli were tested in a free-swimming format from a minimum distance of one meter. Substantial differences were found between the two subjects. One subject's minimum angles of resolution (MAR) were 56 min for vertical stimuli in freshwater, 38 min for vertical stimuli in saltwater, and 24 min for horizontal grating stimuli in saltwater. When only trials under brightest light conditions were analyzed, MARs improved for vertical stimuli to 24 min in freshwater and 21 min in saltwater. No improvement was found for horizontal stimuli with brighter light conditions. The MARs of the second subject measured over a degree for all test conditions. In Experiment 2 only the first subject was tested from a closer viewing distance. He showed no improvement when allowed to approach targets to within 30 cm. The limited resolution of both subjects and absence of increased acuity at closer distances in one suggests that manatees use vision for intermediate or longer distance inspection of large objects. The disparity in visual resolution between subjects has possible implications for variability in acuity within the species.

Endangered Florida manatees (*Trichechus manatus latirostris*) inhabit shallow waters of rivers, bays, estuaries, and coastal areas (Reynolds & Odell, 1991), where their primary food source, light-dependent vegetation, concentrates them near the surface. Much of their environment overlaps with humans, and as a result they suffer mortality and injury from boats, water control structures, and

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fisheries gear. Habitat degradation from coastal development and recreational use of shore areas also present a serious threat to manatee survival. Humans introduce stimuli (noise, chemicals, turbidity) that have the potential to disrupt what animals perceive and how well they can react to their surroundings. Unless we know what animals sense, it will be difficult to develop effective conservation recommendations to mitigate the various influences humans have on habitats. Reduction in manatee casualties requires a multi-faceted effort. The Florida Manatee Recovery Plan (U.S. Fish and Wildlife Service, 2001) explicitly recognizes this need in calling for study of sensory processes.

The published literature on manatee sensory processes is limited (Wartzok & Ketten, 1999). To our knowledge there are only a few experimental, behavioral studies of manatee senses supplemented by several evoked potential studies, physiological/anatomical reports, and naturalistic observations. Tactile senses have been minimally investigated. Bachteler and Dehnhardt (1999) report good tactile discrimination by the perioral bristles and related facial structures of the Antillean manatee (*Trichechus manatus manatus*). Marshall et al. (1998) have studied the role of the perioral bristles in feeding behavior. In addition, Reep, Marshall, and Stoll (1999) have discovered that the postcranial hairs are all of the sinus type, typically tactile in function. Little is known about the chemical senses (Wartzok & Ketten, 1999), although observational evidence suggests a possible role in a number of contexts: coprophagy (eating of excrement; Reynolds & Rommel, 1996), specific rubbing posts (Hartman, 1979; Rathbun & O'Shea, 1984; Wells, Boness, & Rathbun, 1999), mating behavior (Rathbun et al., 1995), and location of fresh water (Ortiz, Worthy, & MacKenzie, 1998). Hearing has been studied in diverse ways (see Supin, Popov, & Mass, 2001) including anatomically (see Ketten, Odell, & Domning, 1992), physiologically through evoked-potential techniques (Bullock, Domning, & Best, 1980; Bullock, O'Shea, & McClune, 1982; Klishin et al., 1990), and behaviorally using psychophysical methods (Gerstein et al., 1999). Despite the range of research approaches to audition there is still insufficient information to address important conservation issues such as the ability of manatees to acoustically detect boats (U.S. Fish and Wildlife Service, 2001).

Several aspects of manatee vision have been investigated. Griebel and Schmid (1997) tested brightness discrimination in West Indian manatees (*Trichechus manatus*) and found sensitivity, measured by relative reflection of targets in a two choice discrimination procedure to be similar to fur seals, although considerably less than humans. The authors note that it was surprising to find the similarity with fur seals, a fish-hunting predator that would presumably have greater need for brightness discrimination ability than the herbivorous manatee.

Three lines of evidence indicate that manatees have dichromatic color vision with sensitivity in the short (blue) and medium (green) wavelength region. Griebel and Schmid (1996) demonstrated that manatees were able to discriminate blue and green from a series of comparably bright grays in a two choice discrimination task. Cohen, Tucker, and Odell (1982) reported two different types of cones that differed morphologically. Ahnelt and Bauer (unpublished data), using antibody labeling of opsins, confirmed the presence of two types of photoreceptors, short wavelength, S-cones (blue) and longer wavelength sensitive cones in the retina of the Florida manatee. Current opsin labeling techniques do not permit differ-

entiation of medium wavelength, M-cones (green) and long wavelength, L-cones (red), but the behavioral findings of Griebel and Schmid (1996) suggest that the longer cones are of the M-class. The two types of cones found in manatee retinas differentiates them from the monochromatic cetaceans and pinnipeds, but is consistent with the dichromatism found in elephants and hyraxes, the manatee's closest terrestrial relatives (see Ahnelt & Kolb, 2000).

Assessment of manatee visual acuity, the ability to discriminate fine detail, lacks the confluence seen in color studies. In an early review, Walls (1967) suggested that the manatee eye was built for sensitivity, not acuity, based on an apparent absence of cones and a paucity of ganglion cells. In other words, the manatee has an eye adapted to dim light conditions. Although some subsequent reports provided support (e.g., Piggins, Muntz, & Best, 1983; West et al., 1991), noting that the small manatee eye had relatively few retinal ganglion cells and no apparent accommodation mechanism, other investigations indicated a better performing eye. A more recent study of ganglion cell density by Mass et al., (1997) indicated that the Florida manatee had limited visual resolution, 20 min of visual arc. Hartman (1979) suggested that manatees could see well over considerable distances in clear water, based on observations in natural settings. Gerstein (1994) noted that they could detect shape, size, and pattern differences, although no data were provided. Woodyard (1984) and Woodyard and Piggins (1994) reported that manatees demonstrated substantial learning skills in a variety of visual discrimination tasks.

Because vision is a product of multiple, integrated stages of processing (e.g., optics at the level of the cornea and lens, physiology at the level of the retina, and complex higher order perceptual/cognitive analysis), the ultimate tests of visual capability are behavioral. In order to alleviate some of the confusion concerning manatee visual acuity, behavioral experiments were initiated in 1999 at Mote Marine Laboratory and Aquarium utilizing grating stimuli in two-choice discrimination tests. Minimum angle of resolution (MAR), a measure of acuity, was determined for two subjects. The visual angle subtended by a stimulus is a measure of the size of the retinal image, the smaller the visual angle the smaller the retinal image. The MAR indicates the size of that image at threshold. Because similar techniques have been used with a variety of animals, MARs allow for comparisons with different species (Nachtigall, 1985).

Two experiments are described. In the first experiment, visual grating stimuli, black and white equal width bands, presented at a minimum distance of one meter in both horizontal and vertical planes were tested to determine manatee MARs in a two choice discrimination task. Tests are also reported separately for fresh and saltwater environments.

The second experiment addressed the focusing power of the manatee eye. Depending on the source, manatee vision might be hypermetropic (farsighted), suggested by naturalistic observation of the Florida manatee (Hartman, 1979) or emmetropic (normal focus on the retina), suggested by morphology of a related species, *Trichechus inunguis* (Piggins, Muntz, & Best, 1983). Hartman (1979) also indicated that at least some researchers considered manatees to be myopic (near-sighted). As an initial step in assessing focusing power, the decision point on discrimination trials was shortened from one meter to 30 cm.

Experiment 1

Method

Subjects. The subjects were two male Florida manatees, *Trichechus manatus latirostris*, named Hugh and Buffett and aged 15 and 12 years respectively, at the beginning of training. Both manatees were born and raised in captivity. They were maintained in the same habitat during training and testing. Throughout the study Hugh was approximately 545 kg, a normal weight for the species. Buffett weighed approximately 908 kg at the beginning of training, but his weight was reduced to 816 kg under veterinary supervision for health reasons.

Apparatus. Training was done in the 265,000 L manatee habitat at Mote Marine Laboratory and Aquarium. The exhibit had three connected areas: the visitor display area, 9.14 m in diameter and 3.05 m deep; the shelf area, 4.57 x 5.18 x 1.52 m; and the medical pool, 4.57 x 3.66 x 1.52 m. Testing was conducted in the shelf area or medical pool. The facilities changed in certain critical aspects during the course of training because of aquarium decisions made on the basis of health and display considerations. A roof was placed over the visitor display area, which generated shadows on the shelf, necessitating movement of testing to the medical pool area. From the beginning of testing in 1999, through 2000, the manatees were kept in freshwater and the sides and bottom of the testing area were white in color. All testing in 2001-2002 was done in saltwater and the color of the test area was changed to light brown. Tests in freshwater/white environment and saltwater/brown environment are separated for analysis in the results.

Visual grating targets were 32 cm squares with a black border. They were made of 3M ControlTac Vinyl digitally printed using solvent-based inks, laminated with Lustre UV overlamine, and mounted on 1/8 inch PVC. The targets were attached to black, Sintra Material plastic holders and inserted into a 195 x 128 cm display board also made of the same material. The target holders were periodically changed among stimuli to control for possible confounding cues. The standard stimulus had 1mm gratings. The gratings on the other targets were 8.00, 4.00, 2.29, 1.60, 1.23, 1.00, 0.84, 0.73, 0.57, and 0.47 cm wide. The targets were high contrast, with a Michelson contrast ratio of 0.83. This ratio is measured as $L_{\max} - L_{\min} / L_{\max} + L_{\min}$, where L_{\max} is the luminance of the white bar and L_{\min} the luminance of the black bar. Black and white gratings were equal in number and width on each target in order to control for brightness cues. Targets were presented with centers 66 cm apart through windows in the display board. The top of the target was 4 cm beneath the water surface. A PVC divider bisected the distance between the targets and extended one meter perpendicular to the display board. The display board had a curtained window in the center through which the trainer could feed the subject for correct responses (Figure 1).

Suitability of water clarity for testing was determined by visual inspection. For many sessions it was quantified in nephelometric turbidity units (NTU) with a Hach 2100P Portable Turbidimeter. Light intensity was measured in all blocks kept for analysis. For the freshwater tests light was measured as radiant flux in microEinsteins at the beginning and end of each block and for saltwater tests it was measured as illuminance in lux for every trial. MicroEinsteins were measured using a Licor LI-192-S Underwater Quantum Sensor, which fed into a Licor LI-1000 data logger. Lux were measured using an Ikelite Dm 4200 Underwater Digital Exposure Meter.

Procedure. Most training was conducted between 08:00 and 10:00 h, before the exhibit was opened to the public. The manatees' daily ration of food, 84 heads of romaine lettuce and 12 bunches of kale, was placed in the display area after each session was concluded. The food was usually consumed by 17:00, providing a nighttime fast of approximately 15 h before the beginning of training the next day. Foods not available outside of training including apple wedges, beet slices, peeled baby carrots, and Zupreem monkey biscuits, were used as reinforcers in order to increase motivation (Colbert & Bauer, 1999; Colbert et al., 2000). A specific trainer's whistle for each manatee was used as a secondary reinforcer to provide rapid feedback to the subject when its behavior was correct.

Shaping by reinforcement of successive approximations (Pepper & Defran, 1975) was used to train all new behaviors. Time outs were used to reduce undesirable behaviors such as leaving the test area. The manatee not engaged in acuity testing was trained on alternative tasks such as husbandry procedures (Colbert et al., 2000), ophthalmic procedures, and tactile studies in a separate area of the habitat.

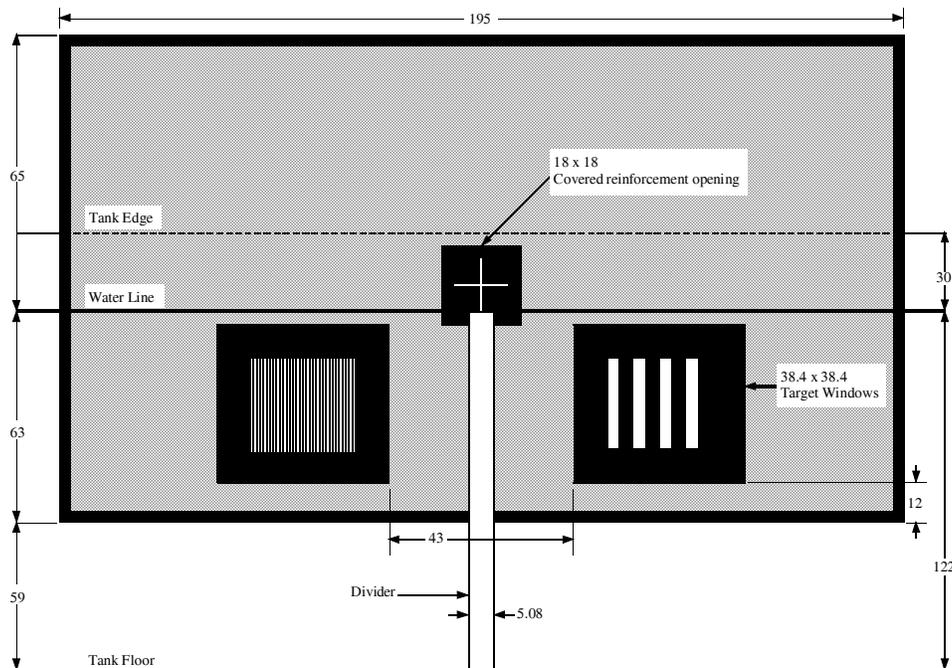


Figure 1. Schematic diagram of the apparatus for testing manatee visual acuity (not to scale). All measurements are in centimeters.

Subjects were presented with pairs of grating stimuli in a two choice discrimination in which one of the targets was a standard and the other stimulus was selected from a set that varied in spatial frequency. The standard stimulus, which had 1 mm stripes, presumably appeared as uniformly “gray” solid to the subjects at the distance targets were tested. A modified method of constant stimuli was used for testing (cf. Kling & Riggs, 1971). In this method, multiple grating stimuli were paired randomly with the standard grating stimulus within a block of 10 or 12 counterbalanced trials, Gellermann (1933) or Fellows Scales (1967), respectively. The same target was presented twice within each block. Because of the large number of stimuli tested, all were not presented in the same block. Sessions ranged in length from one to five blocks for Buffett and one to four for Hugh.

Testing for this study was modeled after a procedure used by Schusterman (1972) to assess vision in pinnipeds. The task for the manatees was to station three meters from the paired targets, the standard grating stimulus and the variable stimulus, and swim towards them. A divider extending from the display board forced the subject to make a choice at a distance of no less than one meter. The standard was always the incorrect stimulus. Subjects were determined to have made their choice as soon as their muzzle passed the leading edge of the divider, although they were trained to continue forward to touch the variable stimulus. The subjects never changed their decision once they passed the leading edge of the divider. The acuity threshold was set by tradition at the 75% correct level. The free-swimming format was adopted because of inconsistencies in the literature concerning the focusing power of the manatee eye, ranging from hypermetropic to myopic. This format allowed the subject the freedom to rely on far or near distance vision. The MAR was determined using the formula, *tangent of the visual angle = size of the grating/subject distance from target*. The distance at which the manatee made its choice was conservatively assumed to be at the leading edge of the divider. Decision distance was measured as 1 m plus the subject’s muzzle length (tip of the muzzle to the eyes), 20 cm for Buffett and 17 cm for Hugh. The minimum intertrial interval was 30 seconds. Blocks were included for analysis if the subject (1) was not interrupted by the other manatee more than three times, (2) left no more than three times, or (3) did not show a side bias as indicated by more than 80% selection of the same target side. These measures were used to control for motivational effects.

Three trainers conducted experimental sessions: one trainer, with her back to the display board, stationed the animal at three meters; a second assistant, hidden behind the display board, placed targets for each trial and provided reinforcement; the third assistant, standing out of the manatee’s view, behind and to the side of the experimental tank, identified correct/incorrect responses.

Testing was done using both vertical and horizontal stimuli. Testing of vertical stimuli was done in both fresh and saltwater. Horizontal stimuli were tested in salt water only.

Results and Discussion

Measured water clarity ($N = 120$, $M = 0.18$ NTU, $SD = 0.044$) was not significantly correlated with visual discrimination performance. This does not mean that vision was unaffected by water clarity. More likely it indicates that experimenter’s visual judgments concerning turbidity were sufficient to avoid running sessions when clarity would be a problem. Sessions were conducted under bright light conditions (Table 1). These light levels are within the range of those taken in natural manatee environments in Southwest Florida between 0.5 and 3 m deep at midday (unpublished data).

Table 1
Mean Light Levels for Viewing Distance at 1 m and 30 cm.

Subject	Test Condition	Trials	Distance	Mean	SD	Min	Max
Buffett	FW Vertical	2,328	1 m	1,088	413	140	1,887
	SW Vertical	852	1 m	52,790	32,521	3,159	116,117
	SW Horizontal	1,548	1 m	51,787	33,676	5,500	153,217
	SW Vertical	480	30 cm	63,226	24,591	9,576	116,117
Hugh	FW Vertical	652	1 m	1,069	487	307	2,252
	SW Vertical	372	1 m	69,416	38,410	11,000	176,000
	SW Horizontal	742	1 m	57,902	34,511	7,778	133,383

Note. FW = Freshwater (light measured in microEinsteins); SW = Saltwater (light measured in lux).

Buffett’s first 60 blocks and Hugh’s first 50 blocks were dropped from analysis because of apparent learning effects as indicated by improving accuracy. Total trials for each subject and condition are reported in Table 1. For Buffett, no individual target was tested less than 68 times. For Hugh one target was tested only 46 times; of the remainder, none was tested less than 62 times.

Both subjects scanned the targets on approach by orienting both left and right. They performed with better than 90% accuracy on targets with the widest gratings, suggesting that the discrimination task was well learned (Figure 2 for Buffett and Figure 3 for Hugh). However, there was a substantial difference in visual acuity performance between the two subjects, so their results are discussed separately. Figures 2 and 3 show composite data across all light levels; data for brightest light conditions are described in the text.

Buffett’s interpolated MARs were 56 min of vertical stimuli in freshwater, 38 min for vertical stimuli in saltwater, and 24 min for horizontal stimuli in saltwater (Figure 2). However, the relationship between visual angle and accuracy was not smoothly linear and performance approached threshold at smaller visual angles. When the near-threshold angles were analyzed only for brightest light trials Buffett achieved smaller MARs for vertical stimuli, which were more consistent with the horizontal threshold. For example, in freshwater at bright light levels,

greater than 1,500 microEinsteins, the MAR was 24 min ($N = 28$). In saltwater at greater than 44,000 lx, the MAR was 21 min ($N = 48$). No improvement in performance was seen under brighter light conditions for tests of horizontal stimuli. Although the overall thresholds across all tested light levels suggest that Buffett's performance was better in saltwater than in freshwater, performance under brightest light conditions casts that assumption into doubt. The negligible effect of the difference in refractive index between freshwater and saltwater makes it reasonable to assume that there would not be a difference.

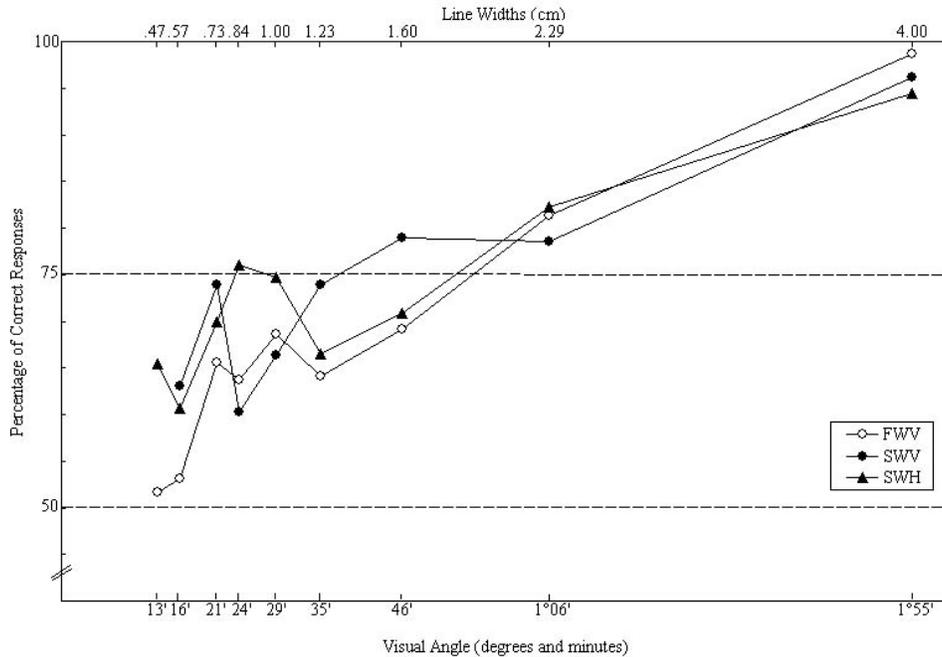


Figure 2. Percentage of correct responses as a function of visual angle and grating width for Buffett at a distance of 1.2 m. Distance was determined as the length of the divider plus Buffett's muzzle length of 20 cm. The 8 cm grating width stimulus is not shown since the percentage correct was similar to the 4 cm stimulus. FWV (freshwater vertical), SWV (saltwater vertical), SWH (saltwater horizontal).

The threshold for Hugh indicated comparatively dreadful vision, with acuity over 1° of visual arc for all three conditions (Figure 3). Hugh's interpolated MAR for freshwater, vertical stimuli was 1 degrees 06 min; for saltwater vertical stimuli, 1 degrees 12 min; and for saltwater horizontal stimuli, 1 degrees 06 min. There was no variability across light intensity measures. Elimination of blocks in which performance on the easiest targets was less than perfect (a motivational check) did not change that conclusion in any consistent or substantive way; MARs remained over a degree.

In the free-swimming testing format the distance of the divider from the targets represented the minimum estimate of resolution. If the subjects were in fact making their decisions at a greater distance, visual acuity would have been better than our estimates. If it is assumed that subjects made their target decision at the one-meter distance, Buffett's threshold visual acuity under bright light conditions, 21 min to 24 min, was similar, although somewhat short of the limit suggested by

Mass et al. (1997) imposed by ganglion cell separation. This acuity range is intermediate between pinnipeds and bottlenose dolphins (5 min – 9 min; Herman, et al., 1975, Schusterman & Balliett, 1970; 1971;) and the Amazon River dolphin (40 min – 45 min; Mass & Supin, 1989). Hugh's vision was considerably worse at over a degree. To put these MARS in some perspective, Wartzok and Ketten (1999) note that the diameter of a full moon subtends a visual angle of 30 min, within the resolution capacity of only one of our two subjects. Hugh's results indicate the need for an ophthalmologic examination and the disparity between subjects make general comments about manatee vision tentative.

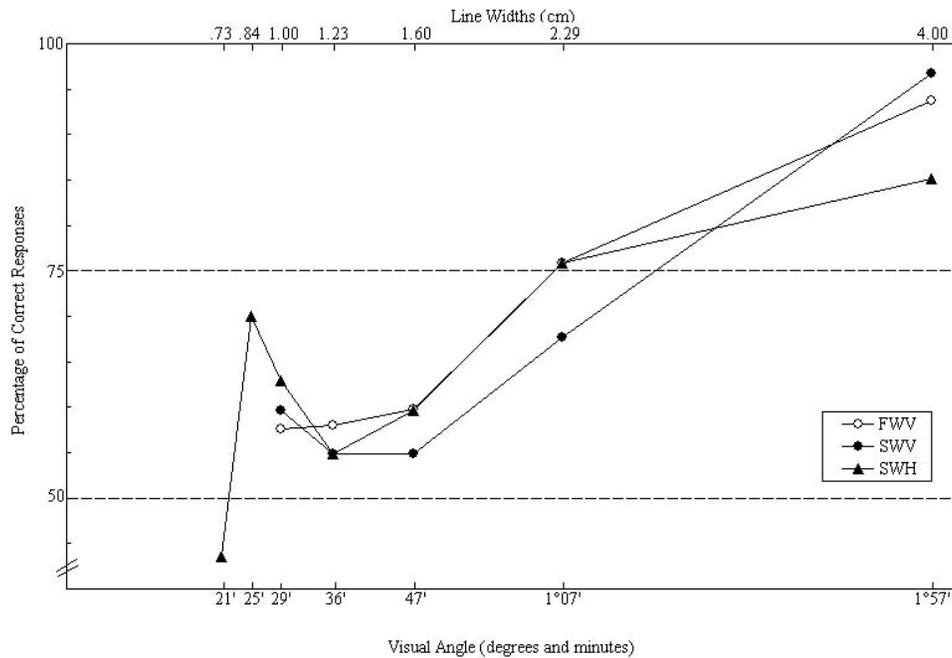


Figure 3. Percentage of correct responses as a function of visual angle and grating width for Hugh at a distance 1.17 m. Distance was determined as the length of the divider plus Hugh's muzzle length of 17 cm. The 8 cm grating width stimulus is not shown since the percentage correct was similar to the 4 cm stimulus. FWV (freshwater vertical), SWV (saltwater vertical), SWH (saltwater horizontal).

Experiment 2

Method

One manatee from the Experiment 1, Buffett, participated in this study.

Experimental characteristics were similar to those of Experiment 1. All blocks of trials were run in the medical pool and were counterbalanced using Fellows scales. Only vertical grating stimuli were used in testing. All testing was done in saltwater. The critical difference was that the divider extended only 30 cm from the targets, instead of 1 m, allowing the manatee to approach the targets more closely. The grating widths on the targets were 0.72, 0.57, 0.47, 0.4, 0.33, 0.25, and 0.20 cm. The standard had 1 mm gratings.

Results and Discussion

Light levels were slightly higher than were found in the first experiment, $M = 63,226$ lx, $SD = 24,591$ (Table 1). The stimulus with a grating width of 0.20 cm was dropped because of a possible confounding artifact in the target. All stimuli were tested 76 times except grating width 0.72 cm, which was tested 22 times. Buffett's MAR, including trials at all light levels, again did not show a smooth trend (Figure 4). Although his 76.3% accuracy at 32.5 min suggests a lower MAR across light levels at the near distance compared to performance from 1 m (overall MAR = 38 min in saltwater), the general trend of the function indicates similar performance to that of the greater viewing distance tests. Differences in light levels did not yield consistent changes in response accuracy. Although it is possible that Buffett did not switch strategies to take advantage of the closer viewing distance, it is plausible to conclude that his vision does not improve at distances under a meter.

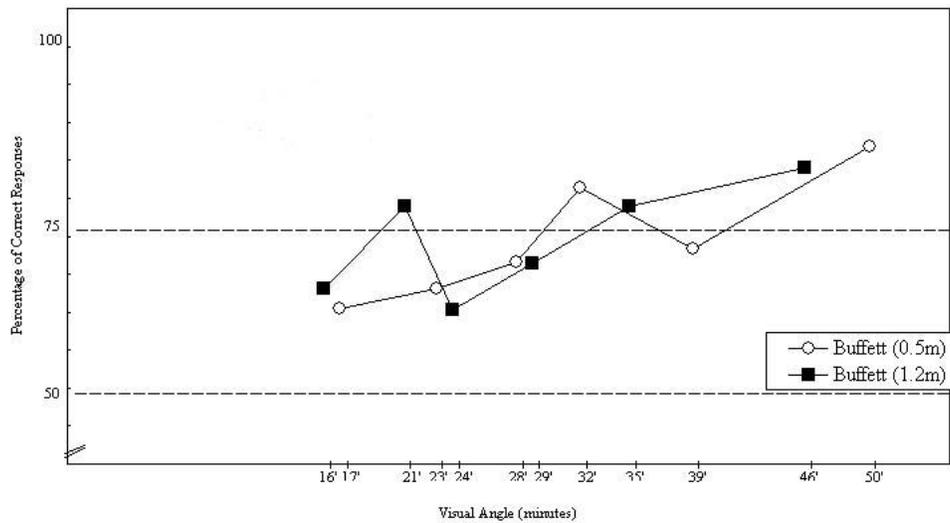


Figure 4. Percentage of correct responses to vertical grating stimuli in saltwater as a function of visual angle calculated at distances of 1.2 and 0.5 m. Distance was determined as the length of the divider plus Buffett's muzzle length of 20 cm.

As already noted, some evidence suggests that myopia is not likely among manatees. For example, Hartman (1979) noted that poor near vision in manatees was indicated by a tendency to bump heads into objects at close distances. Curiously, we observed this same behavior in Buffett, but not Hugh. Buffett's behavior, characterized by slow speed collisions with display windows and other objects, suggests an animal that is focusing from a distance but losing resolution on close approach. In contrast, in fifty hours of observation (Morgan and Bauer, unpublished data), Hugh was never observed to bump his head into the glass display windows, while for Buffett this was a frequent behavior. Hugh's behavior suggests that of an essentially blind animal that has learned to rely on nonvisual means for orientation, such as tactile and kinesthetic memory.

General Discussion

From the standpoint of manatee conservation, three issues need to be addressed: (1) the tested visual characteristics of the subjects; (2) the implications for manatees in captivity including the constraints on testing imposed by the endangered species status of the subjects; and (3) the application of results to behavior in natural settings. The first issue relates to the basic biology of manatees. Although small sample sizes in psychophysical studies of other marine mammals have generated fairly consistent results when similar methods were used (see Nachtigall, 1985), the current studies with manatees generated disparate results that need to be addressed. Concerning captive settings, the relatively poor vision of the subjects needs to be considered in light of the fact that all healthy manatees in captivity in the United States are eligible for release. Ultimately, the relevance of laboratory studies to conservation lies in their application to behavior in natural settings.

Substantial differences between subjects in visual acuity, especially the poor resolution of one of the subjects, Hugh, might not be worthy of note under most circumstances. Although all species presumably have some individuals with uncharacteristically deficient sensory processing in some modality, there is reasonable justification for considering the possibility that the results might reflect real variability in the population. Motivational differences cannot be ruled out completely, but the high performance of Hugh on wide gratings suggests that his motivation was adequate. Further support is indicated by the analysis demonstrating that removing sessions where performance on wide gratings was less than perfect, did not substantively affect performance on narrow grating stimuli. A more promising direction for analysis is the difference in vision itself.

One hypothesis, currently under investigation, is that differences in corneal vascularization might account for the differences in acuity. Samuelson and colleagues (Samuelson, et al., 1994; Samuelson, Lewis, & Pinkwasser, 1997; Young Harper & Samuelson, unpublished data) have noted the proliferation of capillaries and occasional arterioles and venules in postmortem examination of manatee eyes. Although neovascularization of the corneas of terrestrial mammals is usually a sequela of trauma, no injury has been correlated with the vascularization of the manatee eye; it appears to be a naturally occurring condition. Samuelson (personal communication, May 15, 2003) suggests the hypothesis that since there is variation in the degree of vascularization in salvaged manatee eyes, and the presence of blood vessels in the eyes of terrestrial animals can impair vision, it is possible that manatee vision might be differentially impaired by vascular occlusion. The lower resolving power of the manatee eye by both subjects compared to predictions based on ganglion cell density (Mass et al., 1997) and the substantial differences in acuity between subjects are consistent with the vascularization hypothesis. Manatees may have the unusual characteristic of having an optical apparatus that is at variance with their retinal resolution potential.

Color vision greatly enhances pattern recognition, and may consequently compensate for some deficiencies in resolution, at least in comparison to monochromatic cetaceans. Nevertheless, the utility of the manatee eye for imaging remains suspect. Although the retinal attributes have been found to be considerably superior to those originally proposed by Walls (1967), the optics of the eye might compromise them.

Because the subjects were born and raised in captivity the possible effects of an artificial environment are of concern. Bright light conditions in shallow aquarium exhibits with reflective walls and chlorination of habitats are two factors that might be considered for their potential impact on captive manatee vision. However, the disparate resolution of the two subjects, raised in the same environments for most of their lives, does not provide strong support for this hypothesis. Nevertheless it suggests the need for testing a broader spectrum of manatees from both captive and natural settings. The release of a captive manatee with substantial limits in a sensory modality has different implications for policy if those same limitations are found among healthy animals in the wild population, than if they are absent.

The clear need for larger sample sizes carries with it a need to find more efficient testing techniques. Although behavioral testing probably provides the most accurate assessments of sensory abilities, the slow manatee response rate makes it difficult to provide relevant information in a timely manner. In addition, U.S. Fish & Wildlife Service policy encourages release of captive manatees. Multi-year testing, which is required in behavioral studies, is not congruent with this policy. A potentially more efficient technique for future sensory work is the use of evoked potential techniques. These have been used for studying hearing in manatees (Bullock, Domning, & Best, 1980; Bullock, O'Shea, & McClune, 1982; Klishin et al., 1990; Popov & Supin, 1990). They are most effective for obtaining a clear picture of subject sensory characteristics when they can be anchored to behavioral tests. The flexibility of evoked potential methods was recently demonstrated in studies of visual acuity in juvenile loggerhead turtles, another endangered, aquatic species. Visual evoked potentials (VEPs) were collected from subdermal electrodes placed over the optic nerve and optic tectum while grating stimuli were presented onto a screen (Bartol, Musick, & Ochs, 2002). Similar techniques might be attempted with manatees.

Manatee vision is probably not of great utility in evaluating the fine features of objects, especially at close distances. Hartman (1979) noted that vision was the preferred means of exploration by manatees in natural settings. Gerstein (1994) observed the readiness of manatees to explore captive environments, at least in part through vision, with terminal exploration by touch. The current psychophysical assessment of vision in conjunction with these previous reports of visual behavior suggests an animal that uses vision as an intermediate or longer distance orientation cue for large stimuli, but relies on direct contact for closer inspection. These characteristics might contribute to injuries and mortality suffered in water control structures and entanglement in fishing gear as close investigation of fine detail cannot be done visually, but instead demands touch. However, this is obviously an incomplete explanation. Manatees have evolved in frequently turbid environments where vision would be of little use. They clearly have evolved orientation mechanisms that rely on sensory modalities in addition to vision. For a full understanding of the threats to manatees and development of conservation strategies, a broad-scale effort, studying multiple senses and their integration, will be necessary in both laboratory and natural settings.

References

- Ahnelt, P. K., & Kolb, H. (2000). The mammalian photoreceptor mosaic-adaptive design. *Progress in Retinal and Eye Research*, **19**, 711-777.
- Bachteler, D., & Dehnhardt, G. (1999). Active touch performance in the Antillean manatee: evidence for a functional differentiation of the facial tactile hairs. *Zoology*, **102**, 61-69.
- Bartol, S. M., Musick, J. A., & Ochs, A. L. (2002). Visual acuity thresholds of juvenile loggerhead sea turtles (*Caretta caretta*): an electrophysiological approach. *Journal of Comparative Physiology A*, **187**, 953-960.
- Bullock, T. H., Domning D. P., & Best, R. C. (1980). Evoked brain potentials demonstrate hearing in a manatee (*Trichechus inunguis*). *Journal of Mammalogy*, **61**, 130-133.
- Bullock, T. H., O'Shea, T. J., & McClune, M. C. (1982). Auditory evoked potentials in the West Indian manatee (*Sirenia: Trichechus manatus*). *Journal of Comparative Physiology*, **148**, 547-554.
- Cohen, J. L., Tucker, G. S., & Odell, D. K. (1982). The photoreceptors of the West Indian manatee. *Journal of Morphology*, **173**, 197-202.
- Colbert, D. E., & Bauer, G. B. (1999). Basic husbandry training of two West Indian manatees, *Trichechus manatus latirostris*. *Soundings*, **24**, 18-21.
- Colbert, D. E., Fellner, W., Bauer, G. B., Manire, C. A., & Rhinehart, H. L. (2001). Husbandry and research training of two Florida manatees (*Trichechus manatus latirostris*). *Aquatic Mammals*, **27**, 16-23.
- Fellows, B. J. (1967). Change stimulus sequences for discrimination tasks. *Psychological Bulletin*, **67**, 87-92.
- Gellerman, L. W. (1933). Chance orders of alternating stimuli in visual discrimination experiments. *Journal of Genetic Psychology*, **42**, 207-208.
- Gerstein, E. R. (1994). The manatee mind: Discrimination training for sensory perception testing of West Indian manatees (*Trichechus* [sic] *manatus*). *Marine Mammals: Public Display and Research*, **1**, 10-21.
- Gerstein, E., Gerstein, L., Forsythe, S., & Blue, J. (1999). The underwater audiogram of the West Indian manatee (*Trichechus manatus*). *Journal of the Acoustical Society of America*, **105**, 3575-3583.
- Griebel, U., & Schmid, A. (1996). Color vision in the manatee (*Trichechus manatus*). *Vision Research*, **36**, 2747-2757.
- Griebel, U., & Schmid, A. (1997). Brightness discrimination ability in the West Indian manatee (*Trichechus manatus*). *Journal of Experimental Biology*, **200**, 1587-1592.
- Hartman, D. S. (1979). Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. *American Society of Mammalogists, Special Publication No. 5*, Lawrence, KS.
- Herman, L. M., Peacock, M. F., Yunker, M. P., & Madsen, C. J. (1975). Bottlenose dolphin double slit pupil yields equivalent aerial and underwater diurnal acuity. *Science*, **189**, 650-652.
- Ketten, D. R., Odell, D., & Domning, D. (1992). Structure, function and adaptation of the manatee ear. In J.A. Thomas, R. A. Kastelein, & A. Y. Supin (Eds.), *Marine mammal sensory systems* (pp. 77-95). New York: Plenum Press.
- Kling, J. W., & Riggs, L. A. (1971). *Experimental psychology*. New York: Holt, Rinehart and Winston.
- Klishin, V. O., Diaz, R. P., Popov, V. V., & Supin, A. Y. (1990). Some characteristics of hearing of the Brazilian manatee, *Trichechus inunguis*. *Aquatic Mammals*, **16**, 140-144.
- Marshall, C. D., Huth, G. D., Edmonds, V. M., Halin, D. L., & Reep, R. L. (1998). Prehensile use of perioral bristles during feeding and associated behaviors of the Florida manatee (*Trichechus manatus latirostris*). *Marine Mammal Science*, **14**, 274-289.
- Mass, A. M., & Supin, A. (1990). Best vision zones in the retinae of some cetaceans. In J.A. Thomas & R.A. Kastelein (Eds.), *Sensory abilities of cetaceans* (pp. 505-517). New York: Plenum Press.
- Mass, A. M., Odell, D. K., Ketten, D. R., & Supin, A. Y. (1997). Ganglion layer topography and retinal resolution of the Caribbean manatee *Trichechus manatus latirostris*. *Doklady Biological Sciences*, **355**, 392-394.
- Nachtigall, P. E. (1985). Vision, audition, and chemoreception in dolphins and other marine mammals. In R.L. Schusterman, J. A. Thomas, & F.G. Wood (Eds.), *Dolphin cognition and behavior: A comparative approach* (pp. 79-113). Hillsdale, NJ: Erlbaum.
- Ortiz, R. M., Worthy, G. A. J., & MacKenzie, D. S. (1998). Osmoregulation in wild and captive West Indian manatees (*Trichechus manatus*). *Physiological Zoology*, **71**, 449-457.

Pepper, R. L., & Defran, R. H. (1975). Dolphin Trainers Handbook, part 1: Basic Training. Naval Undersea Center, San Diego, California, 1-50.

Piggins, D. J., Muntz, W. R. A., & Best, R. C. (1983). Physical and morphological aspects of the eye of the manatee, *Trichechus inunguis*. Natterer 1883: (Sirenia: Mammalia). *Marine Behaviour and Physiology*, **9**, 111-130.

Popov, V. V., & Supin, A. Y. (1990). Electrophysiological studies on hearing in some cetaceans and a manatee. In J. A. Thomas & R. A. Kastelein (Eds.), *Sensory abilities of cetaceans: Laboratory and field evidence* (pp. 417-426). New York: Plenum Press.

Rathbun, G.B., & O'Shea, T. J. (1984). The manatee's simple life. In D. Macdonald (Ed.), *The encyclopedia of mammals* (pp. 300-301). New York: Facts on File.

Rathbun, G. B., Reid, J. P., Bonde, R. K., & Powell, J. A. (1995). Reproduction in free-ranging Florida manatees. In T. J. O'Shea, B. B. Ackerman, & H. F. Percival (Eds.), *Population biology of the Florida manatee*, U.S. Department of the Interior, National Biological Service, Information and Technology Report 1 (pp. 135-156). Washington, D.C.

Reep, R. L., Marshall, C. D., & Stoll, M. L. (1999). *The sirenian lateral line: Postcranial tactile hairs in manatees*. Paper presented at the 13th Biennial Conference on the Biology of Marine Mammals, Nov. 28 – Dec. 3, Wailea, U.S.A.

Reynolds, J. E., III, & Odell, D. K. (1991). *Manatees and dugongs*. New York: Facts on File.

Reynolds, J. E., III, & Rommel, S. A. (1996). Structure and function of the gastrointestinal tract of the Florida manatee, *Trichechus manatus*. *Anatomical Record*, **245**, 539-558.

Samuelson, D. A., Lewis, P. A., & Pinkwasser, M. (1997) Corneal vascularization in the West Indian manatee (*Trichechus manatus*). *Investigative Ophthalmology Visual Science (ARVO Supplement)*, **38**, 5514.

Samuelson, D., Reep, R., Lewis, P., & Chisholm, M. (1994). The ocular anatomy of the West Indian manatee. *First International Manatee and Dugong Conference*, **1**, 33-34.

Schusterman, R. J. (1972). Visual acuity in pinnipeds. In H. E. Winn, & B. L. Olla (Eds.), *Behavior of marine animals, vol. 2, Vertebrates* (pp. 469-492), New York: Plenum Press.

Schusterman, R. J., & Balliet, R. F. (1970). Conditioned vocalization as a technique for determining visual acuity thresholds in the sea lion. *Science*, **169**, 498-501.

Schusterman, R. J., & Balliet, R. F. (1971). Aerial and underwater visual acuity in the California sea lion (*Zalophus californianus*) as a function of luminance. In H. E. Adler (Ed.), *Annals of the New York Academy of Sciences*, **188**, 37-46.

Supin, A. Y., Popov, V. V., & Mass, A. M. (2001). *The sensory physiology of aquatic Mammals*. Boston, MA: Kluwer Academic Publishers.

U.S. Fish and Wildlife Service (2001). Technical/Agency Draft, Florida Manatee Recovery Plan (*Trichechus manatus latirostris*), Third Revision. U.S. Fish and Wildlife Service, Atlanta, Georgia. 138 pp.

Walls, G. L. (1963). *The vertebrate eye and its adaptive radiation*. New York: Hafner.

Wartzok, D., & Ketten, D. R. (1999). Marine mammal sensory systems. In J. E. Reynolds III, & S. A. Rommel (Eds.), *Biology of marine mammals*. Washington, DC: Smithsonian Institution Press.

Wells, R. S., Boness, D. J., & Rathbun, G. B. (1999). Behavior. In J. E. Reynolds, III & S. A. Rommel (Eds.), *Biology of marine mammals* (pp. 324-422). Washington, DC: Smithsonian Press.

West, J. A., Sivak, J. G., Murphy, C. J., & Kovacs (1991). A comparative study of the anatomy of the iris and ciliary body in aquatic mammals. *Canadian Journal of Zoology*, **69**, 2594-2607.

Woodyard, H. D. (1984). *Visual information processing in captive manatees*. Paper presented at the Conference of the International Society of Comparative Psychology, Acapulco, Mexico.

Woodyard, H. D., & Piggins, D. (1994). *Sirenia vision: A status report*. Paper presented at the Conference of the International Society for Comparative Psychology, Sao Paulo, Brazil.

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