

Visual Acuity of Juvenile Loggerhead Sea Turtles (*Caretta caretta*): A Behavioral Approach

Soraya Moein Bartol
Woods Hole Oceanographic Institution, U.S.A.

Roger L. Mellgren
University of Texas at Arlington, U.S.A.

and
John A. Musick
College of William and Mary, U.S.A.

Studies focusing on the visual cues sea turtles use to orient between the nesting site and the sea indicate that sea turtles use diffuse images for orientation and are highly myopic on land. The visual environment encountered by sea turtles, however, is very different in water than on land. In this study, operant conditioning techniques were used to explore the visual acuity of juvenile loggerhead sea turtles (*Caretta caretta*) in the marine environment. Turtles were trained, in a tank setting, to distinguish between a 45 mm striped panel and 50% gray panel by using squid as a food reward. Though the pace of training was limited by our guidelines for holding these animals in captivity and the amount of food we could give each animal in a week, all turtles were trained in under a month. Once training was achieved, the stripes were reduced in size (stripe width ranging from 45.0 – 0.035 mm) until the turtle chose the striped panel over the 50% gray panel based on chance; this level of choice was designated as threshold. Mean acuity threshold level for all turtles tested was found to be 0.078 (visual angle of 12.89 minutes of arc). These results are similar to those of other marine species and indicate that loggerhead sea turtles use distinct visual cues in the aquatic environment.

Sea turtles have been the subjects of many behavioral studies that have explored the perceptions of these animals as they search for a suitable nesting site or orient towards water, either post-nesting or post-hatching. Anthropogenic light sources can deter female sea turtles from choosing a nesting site and can disorient hatchlings on their path to the sea, causing a decrease in the number of nesting sites and a high hatchling mortality rate (Witherington & Martin, 1996). Conservation efforts have focused on the role of visual cues in these behaviors. Moreover, as Ehrenfeld & Carr (1967) pointed out in their investigation of sea-finding orientation by turtles, the nesting female and recently emerged hatchling are the two life history stages of the sea turtle where behavior can be easily studied in the natural environment. Many of these terrestrial studies have tested brightness cues, shapes, silhouettes, wavelength, and the horizon as environmental cues for sea turtles to find water. Various methods have been used, from observing the reaction

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of turtles to visual stimuli (e.g., Ehrenfeld & Carr, 1967; Salmon, Wyneken et al., 1992) to using operant conditioning methods to test color and intensity preferences (e.g., Fehring, 1972; Witherington & Bjorndal, 1991). Though researchers have found orientation on land to be dependent on visual cues, these cues are often diffuse images or brightness contrasts (see Ehrenfeld & Carr, 1967; Ehrenfeld, 1968; Mrosovsky & Shettleworth, 1968; Salmon et al., 1992; Salmon & Wyneken, 1990; 1994; Witherington & Bjorndal, 1991).

Based on morphological and electrophysiological studies, the visual capabilities of sea turtles are very different in water than on land, unlike semiaquatic turtles that have developed adaptations for both media (Duke-Elder, 1958; Walls, 1942). The sea turtle lens is nearly spherical and morphological studies have shown it to be static and unpliant. Sea turtles, moreover, do not appear to have the musculature needed for accommodation (Ehrenfeld & Koch, 1967; Granda, 1979; Walls, 1942). Focusing of the lens for any animal is often achieved either by changing the shape of a pliable lens (as in freshwater turtles) (Granda, 1979; Walls, 1942) or by moving the lens along a rostral-caudal axis (as in most teleosts) (Fernald, 1990; Munk, 1973; Walls, 1942). For sea turtles, however, the sphincter muscle, which is needed to deform the lens shape, is weakly developed, and the ciliary processes, which is needed in the movement of the lens, do not come in contact with the lens itself (Ehrenfeld & Koch, 1967; Granda, 1979). Lens shape and an apparent lack of accommodative mechanisms cause sea turtles to be highly myopic on land, and thus only close objects are in focus for the sea turtle. However, when submerged in water, the extreme convexity of the lens elevates the overall refractive index of the eye (Sivak, 1985, 1990). When the refractive index of the green turtle eye was tested in water, these animals were found to be emmetropic, and images over a range of distances were focused onto the photoreceptive elements of the retina (Ehrenfeld & Koch, 1967). Using visual evoked potentials (VEPs) to measure neural responses to striped stimuli, Bartol, Musick, and Ochs (2002) also found a difference in the response of the animal when the eye was tested in water and in air. When sea turtles were tested with their eye out of water, these researchers were unable to collect any discernable VEP response, even when using the largest striped panel as the stimulus, suggesting that the sea turtle eye operates much differently in the two media.

The extent to which sea turtles can resolve objects in the marine environment is an important consideration when developing conservation plans for these endangered species. For example, an issue at the forefront of current conservation efforts is the entanglement and incidental capture of sea turtles in fishing gear, which has been implicated in population declines of several species of sea turtles (Lutcavage et al., 1997). In several fisheries, there are ongoing efforts to develop fishing techniques that reduce or eliminate the incidental entanglement/capture of sea turtles without reducing the capture rate of target species. In order to develop fishing gear that does not attract sea turtles, researchers must first understand how sea turtles perceive this gear. The degree of visual environmental perception exhibited by sea turtles can also play an important role in the protection of these animals from an array of other anthropogenic threats, such as ship strikes, entrainment by dredges, and incidental capture by trawlers

(Lutcavage et al., 1997). Eliminating or incorporating visual cues that attract or repel sea turtles to vessels, respectively, may go a long way in reducing mortalities.

One approach to explore the aquatic visual acuity of sea turtles is the application of operant conditioning-based psychophysical procedures, a practice frequently used to test the sensory capacities of non-verbal animals. Psychophysical methods have been used successfully with hatchling sea turtles in the tank environment to study hue discrimination (Fehring, 1972), underwater chemosensory behavior (Manton, Karr, & Ehrenfeld, 1972a, 1972b), and learning capacity (Mellgren & Mann, 1996; Mellgren, Mann, & Zurita, 1994). Recent studies have shown that hatchlings were easily conditioned to bite a tube for a reward, a basic operant conditioning procedure (Mellgren & Mann, 2000). These studies provide a starting point for using juvenile sea turtles as subjects in behavioral experiments.

For this study, we investigated the visual acuity of juvenile loggerhead sea turtles (*Caretta caretta*) in the aquatic medium using psychophysical methods. To accomplish this objective, operant conditioning methods were developed to train juvenile sea turtles to identify a suprathreshold visual stimulus. Once training was achieved, the size of the visual angle of the stimulus was manipulated to determine behavioral acuity.

Method

Subjects

Six juvenile loggerhead sea turtles (*C. caretta*), averaging approximately 63 cm straight notch-to-notch carapace length, were used in this study. These loggerheads were incidentally captured in poundnets in the Potomac River, a tributary of the Chesapeake Bay. Due to their threatened status under the Endangered Species Act, these animals were obtained for an ongoing conservation program at the Virginia Institute of Marine Science. They were placed in individual recirculating riverwater tanks with water temperature maintained between 23 and 27°C. After at least 24 h of acclimation, the animals were examined to determine their health status by the attending veterinarian, and if favorable, considered ready for testing. At the conclusion of this study, all animals were released back into the Chesapeake Bay as healthy individuals.

Apparatus

Testing was performed in a rectangular tank 250 cm long, 128 cm wide, and 59 cm deep filled with filtered riverwater. A plywood barrier running the width of the tank was positioned at one end of the tank. Two sections (9 cm by 9 cm) were cut out on the barrier and covered with Plexiglas. The sections were equally spaced and were the sites for the two stimuli. Behind the barrier, a food chute was connected to a PVC pipe. The PVC pipe extended through the barrier below each stimulus. Lights of equal intensity were mounted behind each stimulus panel and a single on/off switch controlled these lights simultaneously. Finally, an end of PVC pipe protruded equidistant between each stimulus panel and acted as an observer key (Figure 1). The entire tank was covered prior to testing to prevent the turtle from reacting to the observer and to reduce ambient light levels and a small strip was cut out of the covering to allow for observation of the turtle's responses. Testing was conducted in a greenhouse and light levels in these facilities were not under experimental control.

Stimuli were panels with black and white stripes of equal size and a uniform 50% gray panel. All stimuli were printed on transparencies and mounted onto Plexiglas. Stimulus panels were positioned in the cutout sections of the plywood barrier with clips so that they could be easily switched from one side to the other. Contrast ratios, differences in light intensities between black and white stripes, exceeded 90% for all patterns. Eight gratings, parallel stripes of equal width, were used

and the widths of the stripes were 45.0, 22.5, 11.3, 5.6, 2.8, 1.4, 0.7, and .035 mm (Figure 2). The brightness level of the 50% gray panel equaled that of each of the eight gratings.

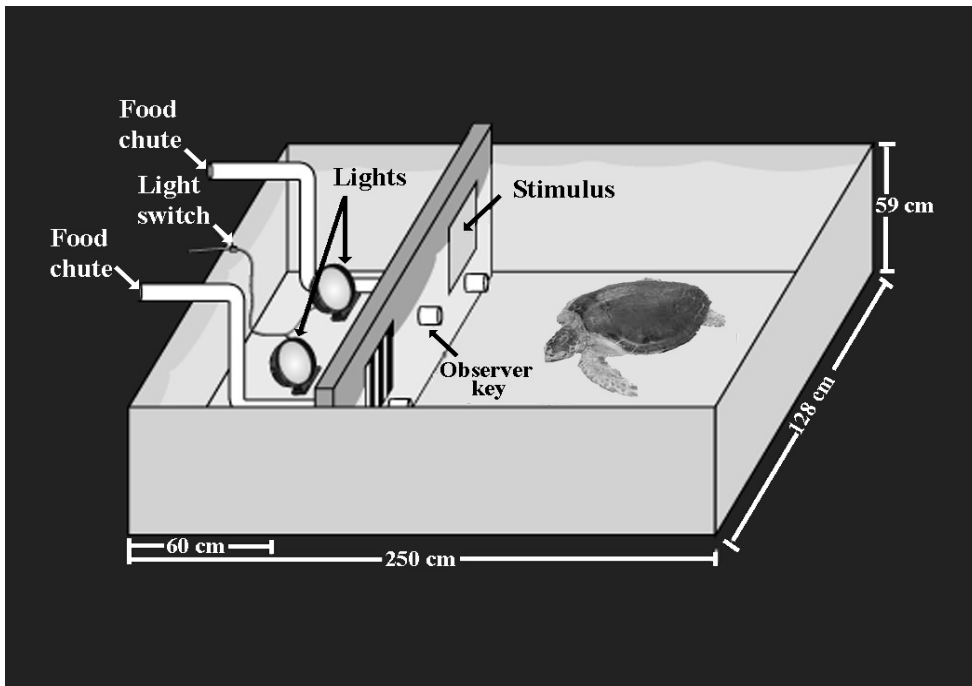


Figure 1. Schematic diagram of tank design used to test the behavioral visual acuity thresholds of the juvenile loggerhead sea turtle (*C. caretta*). One striped and one 50% gray Plexiglas stimulus panel were attached to the barrier in the tank. Below each panel extended the food chute and squid was always present in both chutes. Lights of equal intensity were mounted behind the stimulus panels and controlled by a single switch. The lights were switched on when the turtle bit the observer key, PVC pipe mounted between the stimuli panels. The entire tank was covered and a strip was cut out of the covering to allow for observation of the turtle's responses.

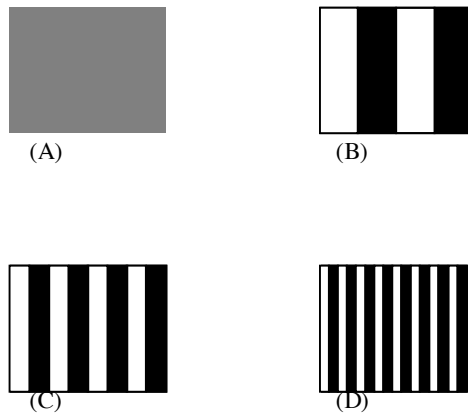


Figure 2. Four examples of stimuli panels used in the training and testing of visual acuities of juvenile loggerhead sea turtles (*C. caretta*). During training, the 45mm and 50% gray panels were always used. Once threshold trials began, the 50% gray panel was paired with varying striped panels of descending size. Contrast ratios between black and white stripes exceeded 90% for all patterns and brightness levels were equal for all panels. (A) 50% gray panel (B) 45mm stripe panel (C) 22.5mm stripe panel (D) 11.3mm stripe panel.

Training, and all ensuing trials, proceeded using an operant conditioning technique commonly called the two-response, forced-choice method. Using this method, the subject animal is presented with two stimuli and is reinforced to choose the “correct” stimulus by the presentation of an associated reward. The position of the correct stimulus, either on the left panel or the right panel, is randomly determined for each trial to ensure that the learned behavior is in connection with the stimulus and not its location (Blough & Blough 1977; Blough & Yager 1972). For our experiment, the turtles were trained to choose the striped panel over the 50% gray panel, and this correct response was rewarded with the presentation of a piece of squid.

The training phase of this project proceeded in several steps. In the first stage of the training session the turtles were conditioned to bite the observer key by simply placing squid within this pipe. Upon biting the key both stimulus lights were turned on simultaneously, and both panels were illuminated. The purpose of the observer key was twofold; first the action of biting the pipe placed the turtle equidistant between each panel at the start of a trial, and second, the illumination of the panels acted as an indicator to the turtle that a trial had begun. Once the lights were switched on, the turtles entered the second phase of the training sessions and were presented with three possible choices: (1) if the turtle bit the pipe under the 45 mm striped panel, it immediately received a piece of squid through that very pipe via the food chute, and then the lights were extinguished; (2) if the turtle bit the pipe under the 50% gray panel, both lights were immediately turned off and the turtle received no squid reward; and (3) if the turtle failed to respond at all within 30 s, both lights were turned off and no reward was given. Irrespective of the response, once the lights were extinguished, they could not be re-illuminated by the turtle biting the observer key until 30 s had lapsed. This period of time was needed to change position of the stimuli and to refill the reward chutes (if necessary). Squid was present in both reward chutes so that olfaction could not bias the response. For each trial, the position of the stimulus on the barrier was determined by a coin toss. The duration of training sessions was based on our protocols for holding these animals in captivity. The juvenile loggerhead’s weekly diet was restricted to 1–3 % of their total body weight. Based on these limitations, training for each turtle occurred only every other day for one to two hours, or until all of the allotted squid was consumed. The turtle was deemed fully trained when it chose the 45 mm stripe panel at least 80% of the time.

Once training was achieved, threshold trials began for each animal. Each day of threshold testing consisted of a warm-up period of 10 trials using the 45 mm stripe panel vs. the 50 % gray panel and then eight blocks of 10 trials (each stripe size represented a block). As the block of trials progressed in the session, the stripe width decreased. This block method is commonly used in animal psychophysical studies (Blough & Blough, 1977). An observer recorded both correct (choosing the striped panel) and incorrect (choosing the 50% gray panel or no response) responses. Multiple threshold sessions were performed on each turtle on multiple days.

Calculation of Visual Acuity and Statistical Analysis

Visual acuity is the reciprocal of the visual angle and is a measure of the ability to resolve details of an object. Visual angle, measured in minutes of arc, is the angle subtended at the eye by the size of the viewed object and is calculated as follows:

$$\text{Visual angle} = \tan^{-1} \left(\frac{\text{width } \frac{1}{2} \text{ cycle}}{\text{distance between stimulus and turtle's eye}} \right)$$

The width of one half cycle is the distance from the middle of one black stripe to the middle of one white stripe. The distance between the stimulus and the turtle was standardized at 15 cm (the distance from each stimulus when the turtle was biting the observer key).

Percent correct responses for each block of tests were plotted as a function of the reciprocal of visual angle for individual turtles and all turtles combined. Linear regression analysis was performed on these data (Sokal & Rohlf, 1981). Acuity threshold was identified when the turtle chose the panels based on chance. Therefore the intercept of the regression line at the 50% correct level was used to approximate acuity threshold.

Results

Training

First, the suitability of these animals for behavioral experimentation was examined. During the training portion of this project, several response behaviors were tested; the action of biting a pipe was by far the most consistent response of unconditioned turtles. The turtles also associated the lights with the possibility of food early in the training process. All turtles were highly motivated by the food reward of squid, and fasting prior to testing was not necessary.

Five of the six turtles were successfully trained during the span of these experiments (three months). For those five turtles, training occurred in under a month (averaging approximately 22 days; Figure 3), with one turtle being trained in only 11 days. After training was achieved, no turtle dropped below the 80% correct criterion when tested with the 45 mm stripe panel during the warm-up trials (Figure 3).

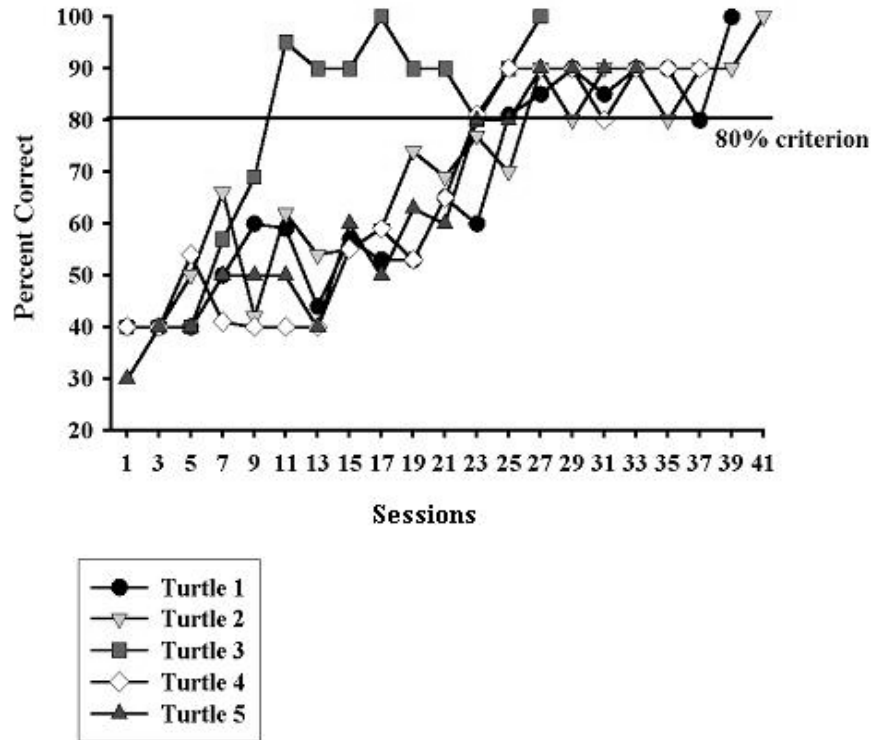


Figure 3. Learning curves and warm-up trial responses of five loggerhead sea turtles (*C. caretta*) trained to discriminate between an illuminated gray panel and 45mm striped panel. Training occurred every other day for one to two hours per day. A turtle was successfully trained when it chose the striped panel at least 80% of the time. After training was achieved, each day of threshold testing consisted of a warm-up period of 10 trials using the 45 mm striped panel vs. the 50% gray panel to ensure that training had been retained.

Threshold Trials

For all five turtles, the linear regressions of the plotted data were significant ($p < 0.05$) and explained 43.0 to 69.1% of the variance (Figure 4, Table 1). The range of extrapolated visual acuity thresholds, at the 50% correct criterion, was from 0.069 – 0.088 (visual angle = 14.50 – 11.36 minutes of arc). Furthermore, when the data from all five turtles were pooled, the linear regression was significant and the extrapolated acuity threshold at the 50% correct criterion was 0.078 (visual angle = 12.89 minutes of arc; Figure 5, Table 1).

Table 1
Linear Regression Analysis of Visual Performance.

Turtle	P-value	r ²	50% intercept (minutes of arc)	Visual Acuity
Turtle 1	<0.001	0.430	14.50	0.069
Turtle 2	<0.001	0.610	13.89	0.072
Turtle 3	<0.001	0.474	13.33	0.075
Turtle 4	<0.001	0.688	13.51	0.074
Turtle 5	<0.001	0.691	11.36	0.088
All Turtles Combined	<0.001	0.747	12.89	0.078

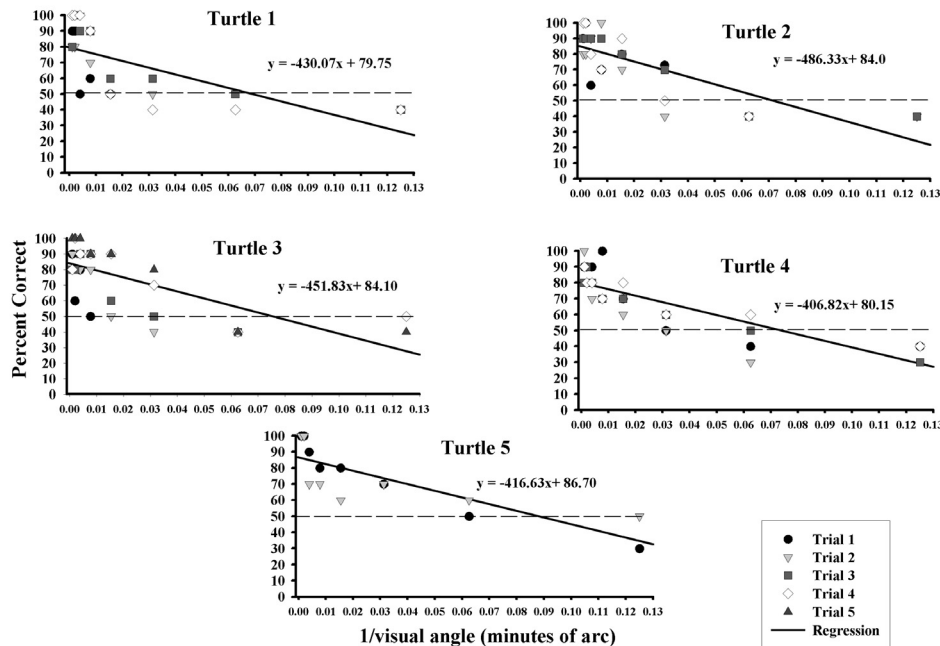


Figure 4. Percent correct responses plotted as a function of stimulus stripe size for five juvenile loggerhead sea turtle (*C. caretta*). Each graph is a combination of multiple acuity trials performed on separate days for the turtles. Percent correct responses consistently decrease with stripe size. The intercept of the regression line at the 50 % correct level is an approximation of threshold. The symbols represent separate days of trials.

All Turtles All Trials

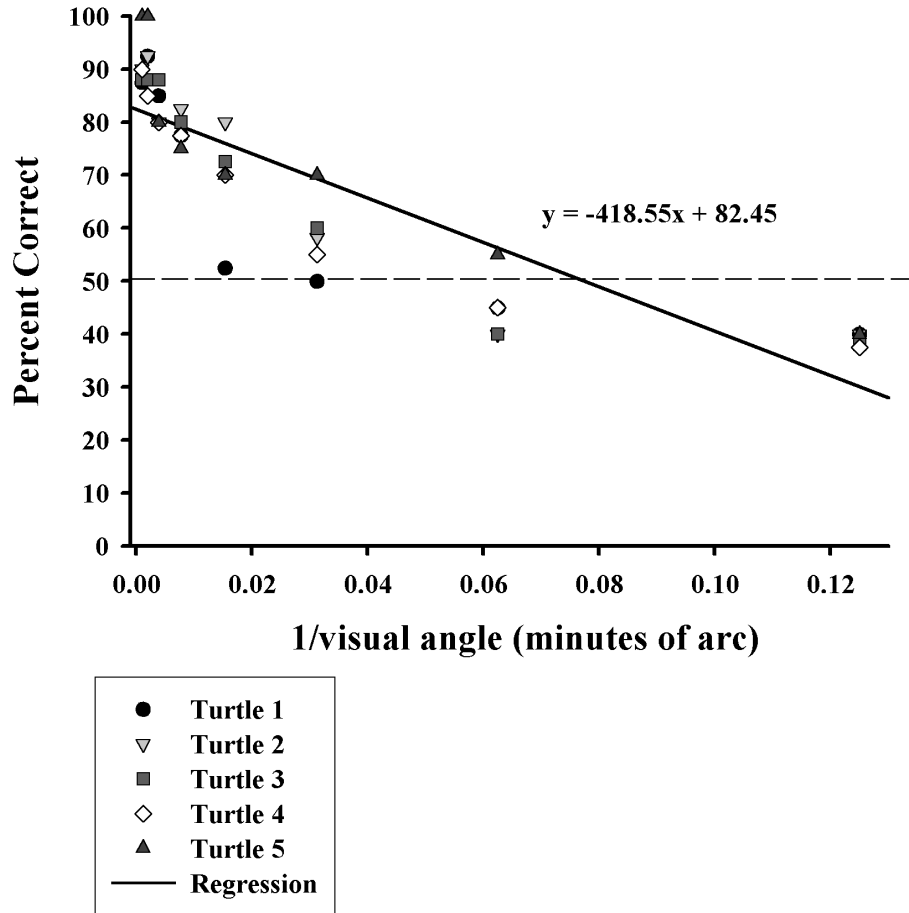


Figure 5. Percent correct responses plotted as a function of stimulus stripe size for all juvenile loggerhead sea turtles (*C. caretta*) tested. Percentage of correct responses by the turtles consistently decreased with visual angle. The intercept of the regression line at the 50% correct level approximated acuity threshold to be 0.078 (12.89 minutes of arc). The symbols represent each turtle tested.

General Aspects of Behavior

It was further noted that the general behavior of the animal drastically changed upon nearing threshold. In suprathreshold trials, the response of the animal was swift and distinctive. After biting the observer key and initiating the trial by turning on the lights, the turtles would make a rapid choice of the panels, frequently within 10 s of biting the observer key. However, with all five loggerhead sea turtles, the turtle often would not choose either pipe as threshold was approached. Instead, the turtle would swim back and forth in front of the two panels, until the lights were switched off due to time limitations. If the turtle did not make a selection within 30 s, the response was recorded as incorrect.

Discussion

Juvenile loggerhead sea turtles proved to be suitable subject animals for in-tank behavior studies. Adapting an appropriate response to these loggerheads was relatively simple; these turtles readily bit any protuberance in a tank. Consequently, training mainly involved directing the turtles to associate the pipe with the above stimulus. Several methods were attempted, but the observer key was the most successful in focusing the turtle's attention on to the trial. Even before the observer key was introduced into these experimental procedures, these turtles associated the presence of light with the possibility of finding squid. By adding the extra step of biting the observer key to turn on the lights, the turtles became more alert to finding the squid. More importantly, this step positioned the turtle equidistant from both stimuli, preventing a location bias at the beginning of a trial.

One limitation in the duration of training was the restriction in diet for sea turtles maintained in captivity. The juvenile loggerhead's diet was limited to 1-3% of their body weight per week; this diet restriction reduces the possibility of obesity often associated with captive sea turtles. Squid is not a complete diet for sea turtles, and outside of the training sessions their diet was augmented with blue crabs and dietary supplements (George, 1997), two items that would not work as a reward. Consequently, sessions had to be terminated when the allotted squid was consumed, even though the subject animal was motivated to continue with the training. Despite these limitations, training of the sea turtles was accomplished in under one month.

Using these operant conditioning methods, we computed the acuity threshold for juvenile loggerheads to be approximately 0.078 (visual angle = 12.89 minutes of arc). Comparisons of these results to previous sea turtle work are problematic. Most prior behavioral research examined actions of these animals directly on the beach, providing an estimate of natural behavior on land rather than in water. However, recent non-behavior based studies on loggerhead sea turtles addressed the issue of visual acuity in the marine environment (Bartol et al., 2002; Bartol & Musick 2001; Oliver et al., 2000). Oliver et al. (2000) examined the ganglion cell densities of multiple species of hatchling sea turtles, and *C. caretta* were found to have a wide dorso-ventral streak, indicating a higher acuity along the horizon field of view. Bartol and Musick (2001) also identified a horizontal concentration of cells in the retina of juvenile loggerheads; cone photoreceptor cells and corresponding ganglion cells were found to be higher in concentration along the horizontal area centralis. According to Bartol and Musick (2001), this horizontal area centralis should provide sharp visual acuity for juvenile loggerheads along the benthos when foraging in shallow waters. Electrophysiological techniques have also been employed to investigate the visual acuity of juvenile loggerhead sea turtles (Bartol et al. 2002). Bartol et al. (2002) recorded VEPs to test for visual acuity thresholds with the eye of the turtle submerged in water. In this study, researchers used a modified goggle filled with seawater over the stimulated eye and presented black and white striped patterns of decreasing size to the sea turtle. Acuity thresholds were found to be approximately 0.187 (visual angle = 5.34 minutes of arc). Visual evoked potential acuity thresholds are measurements of the physiological limits of the visual system, and

thus it was not surprising that these thresholds were lower than those collected behaviorally.

The behavioral acuity results presented here also may be compared to visual acuity results for other aquatic species determined using psychophysical methods (Table 2). Though Table 2 encompasses a wide range of species, habitats, and experimental procedures, studies performed on other marine species provide a frame of reference when evaluating the acuity of loggerhead sea turtles. All of these animals, except for the nautilus whose eye acts as a simple pin-hole camera, have a behavioral visual acuity threshold between 3.7-17 minutes of arc and all are hypothesized to use visual cues extensively in the aquatic environment. Juvenile loggerhead sea turtles' acuity falls within this range at 12.9 minutes of arc. Morphologically derived visual acuity estimates are also reported in Table 2. Though these visual acuity approximations frequently over-estimate the behavioral response to a visual stimulus by a subject animal, they are useful for making comparisons between loggerheads and other benthic, shallow water marine species that have not been tested using behavioral acuity methods. Species, such as the lemon shark and the banded toadfish, have a morphological visual acuity ranging from 3.75-10 minutes of arc, and are reported to use visual cues to feed on active epibenthic and benthopelagic prey (Collin and Pettigrew, 1989; Heuter & Gruber, 1982). Juvenile loggerhead sea turtles used in this study occupy a similar habitat and spend part of the year in temperate latitudes (such as the Chesapeake Bay waters of Virginia and Maryland) to forage along the shallow waters of the channel edges (Musick & Limpus 1997). Based on these comparisons, it is reasonable to assume that juvenile loggerheads are also using distinct visual cues to function in the marine environment. The level of acuity reported in the present study would permit loggerheads to discern prey, such as horseshoe and blue crabs, as well as large predators.

In addition to threshold levels, the reaction time for choosing a panel was noted, but not measured, for both suprathreshold and threshold trials. Once the animals were trained to choose the striped panel over the 50% gray panel, and threshold trials began, the turtles always chose the largest striped panel (45 mm) at least 80% of the time and the reaction time was generally very quick (~ 10 s). Thus, the turtles were not disrupted in their training over the course of time and did not hesitate when choosing a panel. Conversely, the reaction time varied over the course of the threshold trials within a session. As stripe width decreased and threshold was approached, the latency of response by the turtle increased. Near threshold the turtle would bite the observer key and then pace back and forth between the two stimulus panels, often not making a selection before time expired. Manton et al. (1972b) also found that when chemosensory stimuli could not be detected, the behavior of sea turtles changed significantly. They reported that subthreshold chemical levels elicited erratic swimming behavior, characterized by pacing between the response keys. If this association of reaction time and stimulus level were confirmed in future behavioral studies with sea turtles, it would be possible to use this response as a technique for evaluating not only thresholds but also the similarity of suprathreshold stimuli by testing for more than one visual variable at a time (Blough & Yager, 1972). For example, brightness levels or contrast ratios could be varied for several suprathreshold gratings and latencies of

responses by turtles noted for each. From the resulting latency curves, correlations between acuity and brightness or contrast could be made.

Table 2.
Visual Acuities (minutes of arc), of Various Aquatic Species Measured Using Psychophysical Techniques (except for those noted).

	Species	Visual Acuity (min. of arc)	Reference
Mammals	<i>Phoca vitulina</i>	8.3	Schusterman & Balliet 1970
	<i>Eumetopias jubata</i>	7.1	Schusterman & Balliet 1970
Teleost Fishes	<i>Katsuwonus pelamis</i>	5.6	Nakamura, 1968a
	<i>Euthynnus affinis</i>	7.4	Nakamura, 1968a
	<i>Thunnus albacares</i>	3.7	Nakamura, 1968b
	<i>Scophthalmus maximus</i>	11	Neave, 1984
	<i>Salmo gairdneri</i>	14	Rahmann, Jeserich, & Zeutzius, 1979
	<i>Lepomis macrochirus</i>	14.2	Hairston, Kao, & Easter, 1982; Breck & Gitter, 1983
		17.0	
	<i>Dasson variabilis</i>	7.5 (morphological)	Collin & Pettigrew, 1989
	<i>Halophryne diemensis</i>	7.5-10 (morphological)	Collin & Pettigrew, 1989
	<i>Amblyglyphidodon curacao</i>	3.75-5 (morphological)	Collin & Pettigrew, 1989
Elasmobranchs	<i>Negaprion brevirostris</i>	4.1 (morphological)	Heuter & Gruber, 1982; Heuter, 1991
Cephalopods	<i>Nautilus pompilius</i>	330-670	Muntz & Raj, 1984
	<i>Octopus pallidus</i>	9.7	Muntz & Gwyer, 1988
Reptiles	<i>Caretta caretta</i>	12.9	
		5.34 (visual evoked potentials)	Bartol et al. 2002

Based on this behavior experiment, we confirm that it is possible to examine the behavioral response of juvenile loggerhead sea turtles to visual stimulation in the aquatic medium. These behavioral data indicate that loggerheads are capable of using visual cues for prey identification, predator avoidance, locomotion, territory selection and defense, and other basic behaviors in their aquatic surroundings. These data may also be applied to sea turtle conservation efforts. Understanding the extent to which sea turtles perceive their surroundings is fundamental for predicting how these threatened animals might react to anthropogenic changes in their environment and critical to developing preservation plans based on their sensory abilities.

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