

Role of chemical and visual cues in food recognition by leatherback posthatchlings (*Dermochelys coriacea* L)

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Received January 28, 2003 · Accepted April 27, 2003

Summary

We raised leatherback posthatchlings in the laboratory for up to 7 weeks to study the role of visual and chemical cues in food recognition and food-seeking behavior. Turtles were reared on a formulated (artificial gelatinous) diet and had no contact with test materials until experiments began. Subjects were presented with visual cues (a plastic jellyfish; white plastic shapes [circle, square, diamond] similar in surface area to the plastic model), chemical cues (homogenates of lion's mane jellyfish, *Cyanea capillata*; moon jellyfish, *Aurelia aurita*; and a ctenophore, *Ocyropsis* sp., introduced through a water filter outflow), and visual and chemical cues presented simultaneously. Visual stimuli evoked an increase in swimming activity, biting, diving, and orientation toward the object. Chemical cues elicited an increase in biting, and orientation into water currents (rheotaxis). When chemical and visual stimuli were combined, turtles ignored currents and oriented toward the visual stimuli. We conclude that both cues are used to search for, and locate, food but that visual cues may be of primary importance. We hypothesize that under natural conditions turtles locate food visually, then, as a consequence of feeding, associate chemical with visual cues. Chemical cues then may function alone as a feeding attractant.

Key words: leatherbacks, feeding, food recognition, food-seeking behavior, chemoreception

Introduction

Female marine turtles dig a nest on oceanic beaches, deposit a clutch of eggs, then return to the ocean. There is no post-nesting parental care (Hirth, 1980). Hatchlings emerge from those nests at night, crawl down the beach to the surf zone, enter the sea, and migrate offshore. After a few days their yolk supply is exhausted and the turtles (known as "posthatchlings") begin feeding.

Since posthatchlings lead solitary lives, some capacity to recognize and orient toward appropriate food must be "built-in", that is, functionally developed by the time feeding is initiated. However, no information is available because posthatchlings are rarely seen, let alone studied, in the open ocean.

Leatherback sea turtles (*Dermochelys coriacea* L.) are dietary specialists; they feed upon gelatinous zooplankton (Bleakney, 1965; Den Hartog, 1980; Eisenberg and Frazier, 1983; Davenport, 1998; Bjørndal, 1997).

Adults feed both during the day and at night, often diving hundreds of metres to the deep scattering layer (Eckert et al., 1987). Field observations of posthatchlings 2–10 weeks old indicate that they perform shallow dives only (Salmon et al., in press). Gelatinous prey are attacked the first time they are encountered. In some instances, dives by young turtles were directed straight toward prey, suggesting that orientation is visual (Salmon et al., in press).

Many marine animals, especially those active at night, use chemical cues to detect and locate food items (Prosser, 1973; Weissburg and Zimmer-Faust, 1993; Derby and Steullet, 2001). Experiments conducted with freshwater (*Pseudemys* spp.; *Chelydra serpentina*) as well as marine (*Caretta caretta* L) turtles indicate that feeding experience early in development can result in olfactory-mediated orientation and food preferences that persist for days or weeks (Owens et al., 1986). Posthatchling leatherbacks, unlike other marine turtles

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of the same age, show some nocturnal activity (Wyneken and Salmon, 1992). Thus, young leatherbacks might find prey using visual cues during the day, and chemical cues at night.

To explore the role of external cues in prey recognition and food-seeking behavior, we reared leatherbacks in the laboratory, then presented them with visual and chemical stimuli. Our objectives were to determine (i) if these stimuli evoke food-searching behavior, (ii) whether the two stimuli release similar (or different) responses, and (iii) how prey recognition develops.

Materials and methods

Collection and maintenance

Hatchlings (19 turtles from 6 nests) were captured as they emerged from nests in Palm Beach County, Florida, USA (26° 41' N, 80° 6' W), between early July and late September 2000. Within 2–4 h, the turtles were transported in Styrofoam™ coolers to our laboratory at Florida Atlantic University.

Each turtle was measured (straight-line carapace length to the nearest 0.1 mm using vernier calipers) and weighed (to the nearest 0.01 g) using an electronic scale (Sartorius model BP 410). Thereafter, measurements were made weekly to monitor growth. Posthatchlings were maintained in groups of four within five circular blue plastic pools (0.9 m diameter \times 0.18 m deep) filled with ~ 100 l of seawater, maintained at 23–27 °C. Water in each pool was continuously circulated through a UV sterilizer (by a 25 W UV Startronics™ unit) and filter (“Skilter” Supreme 400™ with protein skimmer, ground carbon and fiberglass mat; flow rate = 25.3 l/min; dimensions = 37 \times 12 \times 20 cm deep). An overhead light 0.5 m above each pool (100 W UVA/UVB incandescent lamp) was provided to promote basking. Ten 100 W Vita-lite™ fluorescent tubes, suspended approximately 3.0 m overhead, provided full spectrum lighting on a 14 L:10 D cycle. Water quality (pH, salinity and ammonia level) was monitored daily. Partial water changes were made every three days using fresh, sterilized seawater.

A 1.0 cm² hooked Velcro™ patch was fixed with a drop of surgical grade cyanoacrylic cement to the posterior end of each turtle’s carapace (Fig. 1). This patch served for the attachment of a monofilament tether, 10 cm long. These tethers restricted each turtle to a quarter of the pool, and prevented contact with the other turtles or with the pool’s side or bottom. Tethering was required because leatherbacks swim continuously, do not recognize barriers, and will injure themselves unless their movements are restricted to “open” water (Witham, 1977).



Fig. 1. Tethered posthatchling in its holding tank. Arrow shows location of velcro® patch.

Five to 7 days after collection, hatchlings were fed once daily to satiation using a custom formulated gelatinous diet (Jones et al., 2000). Rectangular strips (1 \times 4.5 \times 0.5 cm thick, tan in color) were offered to the turtles at water surface level. Only feeding, growing, and apparently vigorous turtles were used in experiments.

Test pools

Turtles were between 18 and 35 d post emergence when testing began, and within 49 d post emergence when tests were completed. Trials were conducted during the day. A turtle was removed from its holding pool and tethered alone in a separate (test) pool (Fig. 2), identical in size, color and shape to the holding pools. Transferred turtles were allowed 1.5 h to recover from handling and to acclimate to their new surroundings. A longer tether (30 cm, fixed at the tank center) allowed the turtle to contact the pool bottom (“dive”), but prevented contact with the pool’s side. The test pool was subdivided by external marks (not visible to the turtle) into four equal quarters. In tests using chemical stimuli (see below), the pool contained a filter centered in one quarter. Its outflow was used to introduce chemical stimuli into the pool water. The filter was removed during tests with visual stimuli (Fig. 2).

Turtles 1–11 were captured early in the season, allowing time to expose each turtle to up to five tests. Turtles 12–19 were captured later and exposed to only two tests so they could be returned to the wild at a seasonally appropriate time. All subjects were released in deep water, several km from shore (within the Gulf Stream).

Test stimuli

Visual stimuli were shapes (circle, diamond, square) cut from opaque white plastic sheeting (2 mm thick), or a soft plastic (red, pink and brown) model jellyfish of comparable size (22 cm²) when viewed from above

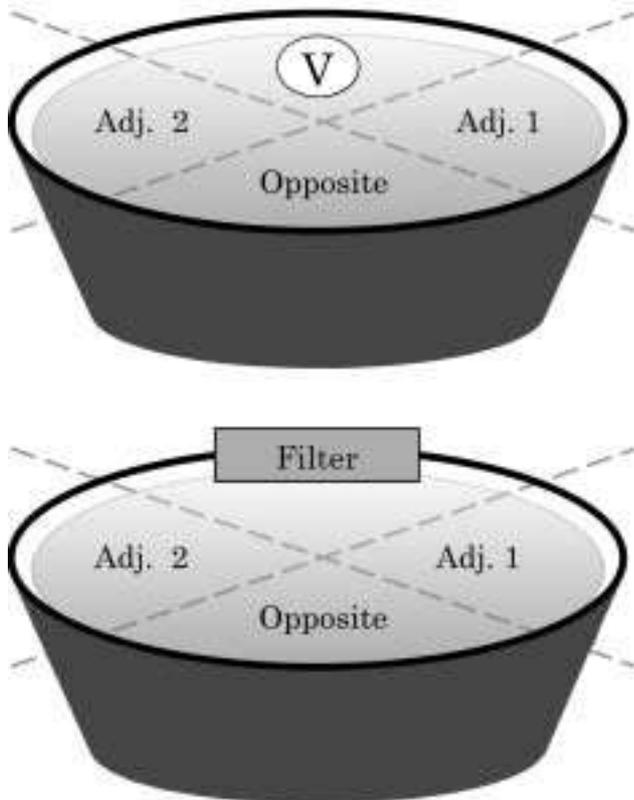


Fig. 2. Test pools with quarters indicated for visual (top), chemical, or chemical plus visual (bottom) stimuli. When the filter was present, the visual stimulus was randomly assigned to one of the other three pool quarters.

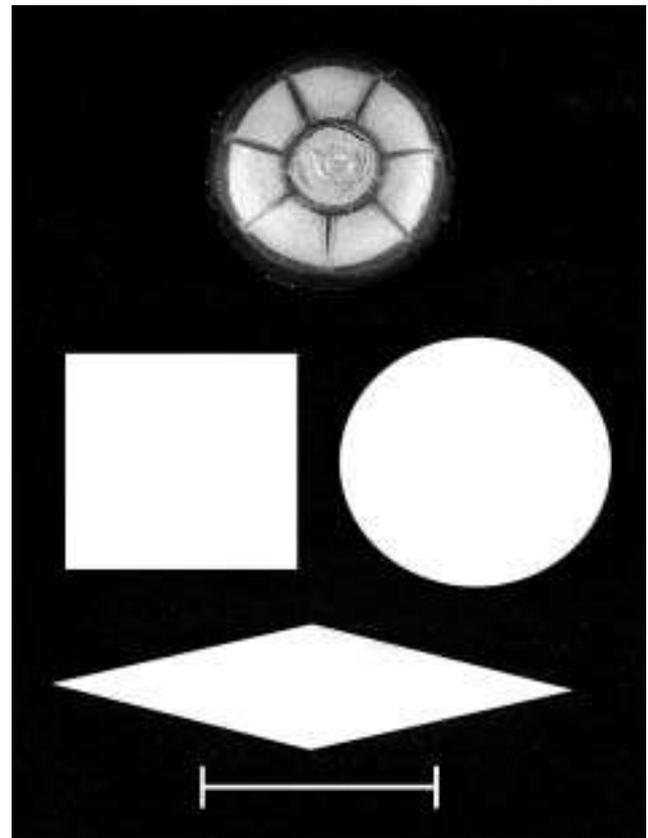


Fig. 3. Visual stimuli. Top: jellyfish model; middle: square and circle; bottom: diamond. Scale line is 7.0 cm (diameter of the jellyfish model).

(Fig. 3). Each stimulus was fixed to the lower pool wall with a transparent suction cup, not visible to the turtle. Stimuli were always placed in the middle of a tank quarter.

Chemical stimuli were homogenates of live prey. Two were cnidarians (*Cyanea capillata* [lion's mane], *Aurelia aurita* [moon jelly]), while the third was a ctenophore (*Ocyropsis* sp.). Prey were blended for 2 min, then aliquoted into 20 ml sealed vials and stored at -70°C until use. Two homogenates were the color of the intact organism (*C. capillata* was reddish-brown while *A. aurita* was pink). However, at the dilutions used these colors were not visible to us. The homogenate made from *Ocyropsis* was clear.

Test protocols

Each experiment consisted of a 15 min control period (no stimulus), immediately followed by a 15 min test period (stimulus presented). No turtle received the same stimulus or stimulus combination twice, and stimulus order varied for each animal. Turtles were tested

no more than once every 24 h. After a test, they were immediately returned to their holding tank.

Visual tests began with a control period, followed immediately by the introduction of a stimulus (at the onset of the test period) into one of the four pool quarters (assigned randomly).

Chemical tests began with a control (the injection of 20 cc of sterile seawater into the pool filter), followed 15 min later by the test (injection of 20 cc of prey homogenate into the filter). Pilot tests with dye indicated that the odorant was distributed throughout the pool in <1 min. After each chemical test, the filter unit and pool were emptied and rinsed. Both were then filled with fresh sterile seawater.

Combined chemical plus visual tests began with the injection of 20 cc of sterile seawater into the pool filter. The test period began 15 min later with the injection of homogenate into the filter, and the placement of a visual stimulus into one of the three remaining pool quarters (selected randomly). Following each chemical plus visual test, the pool and filter were again rinsed and the water replaced as previously described.

Behavioral measurements

Each turtle's behavior during the control and test periods was recorded on videotape (60 fps), using a camera fixed above the tank. Records were later used to quantify any changes in behavior. The following behavior patterns were measured.

Stroke rate was measured as the number of synchronous fore flipper strokes/min. Initially, we measured relative changes in the stroke rate during minutes 5, 10, and 15 of the control period, and during minutes 5, 10, and 15 of the test period, as compared to the rate measured during min 1 of the control period. This analysis was used to establish that typically (1) stroke rates changed little during the 15 min control period, (2) could increase abruptly (depending upon the stimulus) during the initial part of the test period, then (3) declined toward the end of the test period. On the basis of these findings, we analyzed changes in stroke rate by comparing the actual stroke rate during the last 5 min of the control period with the rate during the first 5 min of the test period.

Orientation was quantified by noting the turtle's location (pool quarter) every 20 s during the last 5 min of the control period and during the first 5 min of the test period. Control and test distributions in the stimulus quarter (source of the stimulus) were then compared.

Bite frequency, *diving frequency*, and *diving duration* were quantified throughout the control and test periods. Diving was identified by the turtle's unique (almost vertical) swimming posture.

Data analysis

Since each animal served as its own control, data for turtles exposed to the same treatment were analyzed using paired Wilcoxon signed rank tests (Siegel and Castellan, 1988). We hypothesized that, if stimulatory, the stimuli we presented would cause an increase in stroke rate, orientation, biting, and diving frequency or duration during the test period. Significance was therefore based upon one-tailed tests (null hypothesis of no difference in behavior rejected when probabilities ≤ 0.05).

Table 1. Treatment order for each leatherback posthatching used in this study. Square, circle, diamond and "jellyfish model" are visual stimuli. Genera designate the chemical stimuli.

Turtle number	Stimulus 1	Stimulus 2	Stimulus 3	Stimulus 4	Stimulus 5
1	Square	Circle	<i>Cyanea</i>	<i>Cyanea</i> + square	
2	Diamond	Jellyfish model	<i>Cyanea</i> + jellyfish model	<i>Cyanea</i>	
3	Circle	Jellyfish model	Square	<i>Cyanea</i>	
4	Jellyfish model	Diamond	<i>Cyanea</i> + diamond	<i>Cyanea</i>	
5	<i>Cyanea</i>	Jellyfish model	<i>Cyanea</i> + jellyfish model		
6	<i>Cyanea</i> + diamond	<i>Cyanea</i> + jellyfish model	Square	Circle	<i>Aurelia</i>
7	<i>Ocyropsis</i>	<i>Cyanea</i> + square	<i>Cyanea</i> + circle	Circle	
8	<i>Ocyropsis</i> + square	<i>Aurelia</i> + circle	<i>Cyanea</i>	Square	Jellyfish model
9	<i>Cyanea</i>	Diamond	<i>Cyanea</i> + diamond		
10	<i>Aurelia</i> + diamond	<i>Aurelia</i> + jellyfish model	<i>Ocyropsis</i>	Square	
11	<i>Ocyropsis</i>	<i>Ocyropsis</i> + diamond	<i>Ocyropsis</i> + jellyfish model	Diamond	
12	<i>Cyanea</i>	<i>Aurelia</i>			
13	<i>Aurelia</i>	<i>Cyanea</i>			
14	<i>Aurelia</i>	<i>Cyanea</i>			
15	<i>Cyanea</i>	<i>Aurelia</i>			
16	<i>Aurelia</i>	<i>Cyanea</i>			
17	<i>Cyanea</i>	<i>Aurelia</i>			
18	<i>Cyanea</i>	<i>Aurelia</i>			
19	<i>Aurelia</i>	<i>Cyanea</i>			

Results

A total of 19 posthatchlings were used in 60 experiments (visual tests, $n = 18$; chemical tests, $n = 27$; visual plus chemical tests, $n = 15$; Table 1).

Response to visual stimuli

In the presence of visual stimuli, biting frequency (Wilcoxon $T+ = 95$, $p < 0.05$), diving frequency ($T+ = 52$, $p < 0.01$), and dive duration ($T+ = 55$, $p = 0.01$; Fig. 4) increased significantly over levels shown during the control period. During the test period, the turtles showed significant orientation (remained longer in the pool quarter that contained the visual stimulus; Fig. 5, top, Wilcoxon $T+ = 118.5$, $p = 0.001$).

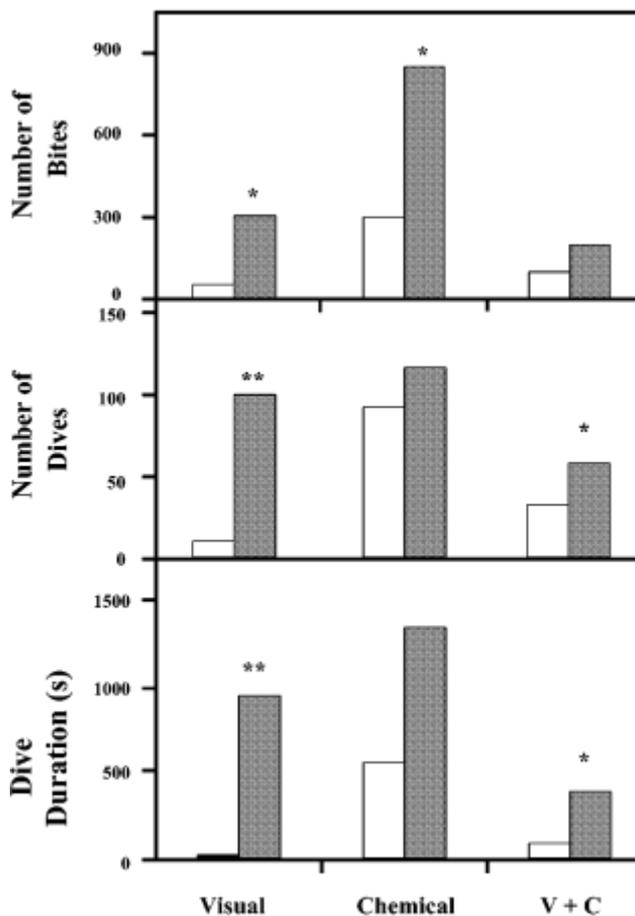


Fig. 4. Summed response to visual (18 tests), chemical (27 tests) and both stimuli presented simultaneously (15 tests). Above, biting frequencies; middle, diving frequencies; below, dive duration recorded during the control (open bars) and test (grey bars) periods. Probabilities (for comparison between control and test periods by paired Wilcoxon Signed-Rank tests) are: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

Response to chemical stimuli

Chemical stimuli elicited significant increases in biting (Fig. 4, top, Wilcoxon $T+ = 79$, $p < 0.05$), but not in diving frequency or duration. During the test period, the turtles showed significant orientation toward the filter quarter (Fig. 5, middle; Wilcoxon $T+ = 208.5$, $p < 0.01$).

Response to combined stimuli

In the presence of visual and chemical stimuli, turtles showed no significant increases in biting frequency but did so in diving frequency ($T+ = 30$, $p = 0.05$) and diving duration ($T+ = 31$, $p < 0.05$; Fig. 4). Turtles showed strong orientation (Fig. 5, bottom) but, in contrast to

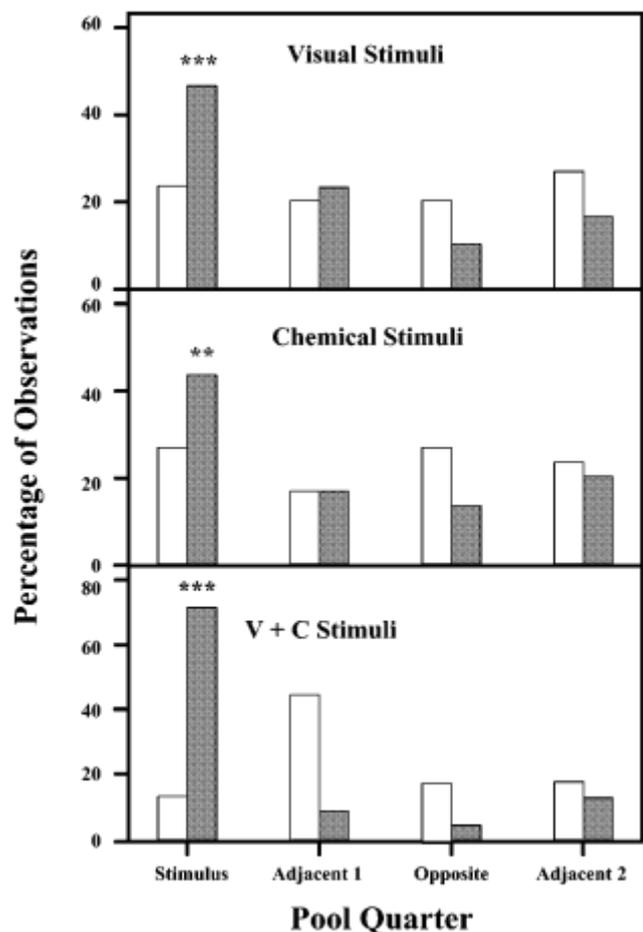


Fig. 5. "Orientation" during the control (open bars) and test (grey bars) periods. Responses are shown to visual (top), chemical (middle) and combined visual plus chemical (lower graph) stimuli. Stimulus quarter was the site for presentation of the visual (upper and lower graphs) or the chemical (middle graph) stimulus. Adjacent quarters are to the right or left of the stimulus quarter. Asterisks as in Fig. 4.

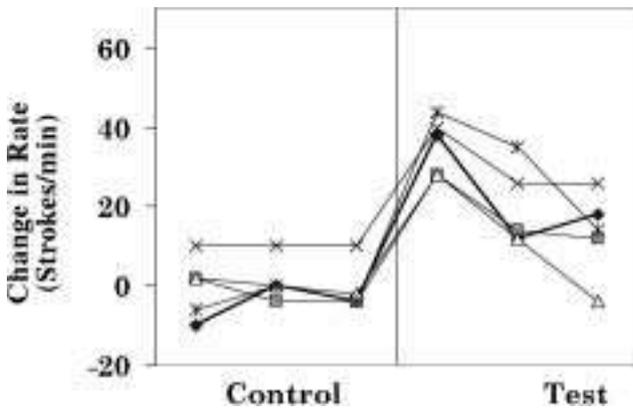


Fig. 6. Relative change in stroke rate of five turtles during min 5, 10, and 15 of the control period (left) and the test period (right). Values are compared to the rate observed for each turtle during min 1 of the control period. Test stimulus was a jellyfish model.

tests involving chemical stimuli only, spent their time in the quarter containing the visual stimulus, not the filter quarter (Wilcoxon $T^+ = 134.5$, $p < 0.001$).

Changes in stroke rate

Stroke rates typically showed little relative change during min 5, 10 and 15 of the control period, compared to an initial measurement (min 1 of the control period; Fig. 6). When turtles responded positively during the test period, stroke rates initially increased, then rapidly declined (Fig. 6).

When exposed to either *Aurelia* ($n = 9$ turtles; $T^+ = 26.5$, $p = 0.15$) or *Cyanea* ($n = 15$ turtles; $T^+ = 80$, $p = 0.14$) homogenate, posthatchlings showed no significant increase in stroke rate. Too few tests ($n = 3$ turtles, Table 1) were done with *Ocyropsis* homogenate to obtain meaningful results.

Turtles exposed to either the model (Fig. 7, top left; $T^+ = 15$, $p = 0.03$) or to the shapes (Fig. 7, lower left; $T^+ = 88$, $p = 0.001$) showed significant increases in stroke rate during the test period. When exposed to combined chemical and visual stimuli, stroke rates again increased significantly (Fig. 7, right graphs; jellyfish model, $T^+ = 15$, $p = 0.03$; shapes, $T^+ = 45$, $p = 0.002$).

Discussion

Role of visual and chemical cues

Both visual and chemical stimuli evoke responses in posthatchling leatherbacks that in other animals are associated with appetitive (orientation, increased dive duration, locomotory activity) as well as consummatory (biting) behavior. Under our testing regime, responses

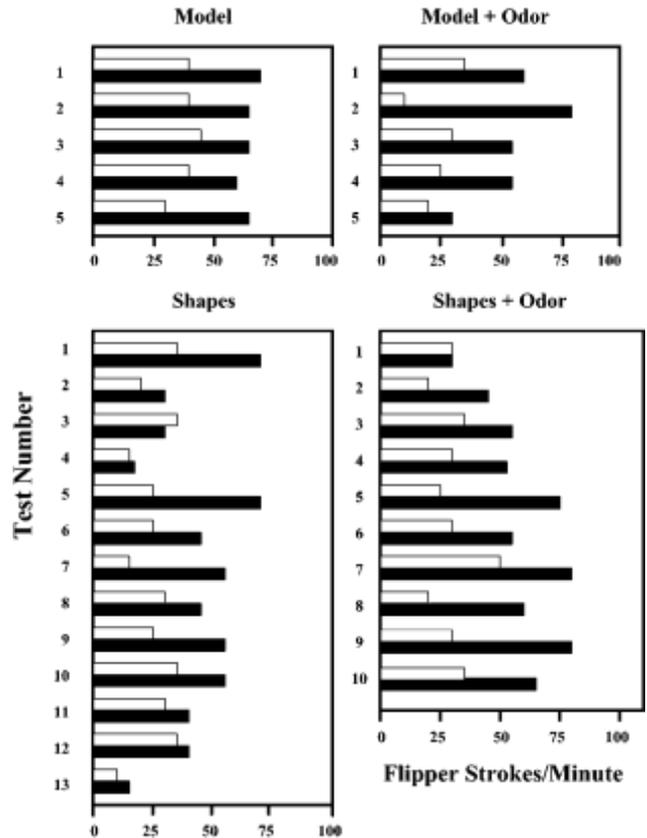


Fig. 7. Actual stroke rates shown by turtles during the last 5 min of the control period (open bars), and during the first 5 min of the test period (filled bars). Responses are shown to visual stimuli presented alone (left graphs), or combined with homogenate (right graphs). The visual stimulus was either a jellyfish model (upper graphs) or shapes (lower graphs). Shapes (lower left) were: tests 1–4, circle; 5–9, square; 10–13, diamond. Homogenates paired with the model (upper right) were: tests 1–3, *Cyanea*; 4, *Ocyropsis*; 5, *Aurelia*. Homogenates combined with shapes (lower right) were: 1–6, *Cyanea*; 7–8, *Ocyropsis*; 9–10, *Aurelia*.

to visual or chemical cues (either separately presented or combined) were generally brief in duration (Fig. 6), probably because during visual stimulus exposure there was no food reward and models were stationary. Responses to odors may also have declined over time due to sensory adaptation.

Both visual and chemical stimuli evoked an increase in biting (Fig. 4) and orientation (Fig. 5), but only visual stimuli (alone or in combination with chemical stimuli) elicited “complete” responses (increases in diving frequency and duration [Fig. 4] as well as in stroke rate [Fig. 7]). These more robust responses suggest that under natural conditions young leatherbacks may – at least during the day – rely primarily upon visual cues to detect, locate and capture prey.

Responses to chemical stimuli are probably used in food searching when prey are in the vicinity, but not directly visible. Evidence in support of this hypothesis is that the turtles (1) orient into currents when these contain chemical cues (Fig. 5), but (2) ignore currents containing chemical stimuli when visual stimuli are present and indicate food is located elsewhere (Fig. 5).

Such response “hierarchies” are common among aquatic predators with image-forming eyes, and for obvious reasons: visual cues provide reliable information on the spatial location of prey, whereas chemical stimuli most commonly activate responses to less reliable “directing” stimuli (such as currents). Locating food sources by orientation into currents can be difficult. Feeding attractants embedded in currents often exist as patches of varying concentration, within regions of turbulence. This environmental complexity can make detection, as well as assessment of current direction, laborious (Zimmer and Butman, 2000). This problem especially applies to any flying or swimming organisms (like leatherbacks) that detect odors while the substrate is not visible. Without a fixed reference, it is difficult for the animal to reliably distinguish between movement direction of fluid due to flow, and apparent movement due to the organism’s self-propulsion (Vickers, 2000).

Visual cues and behavior

Gelatinous prey vary in size, shape, propulsive movement, and color. Any of these attributes, alone or in combination, might be used by gelatinivores to visually locate and/or recognize suitable prey.

Little is known about the visual capacities of leatherbacks. In a recent study, Oliver et al. (2000) found that the retina of hatchling leatherbacks had an *area* (region of concentrated receptor and ganglion cells) *temporalis* that appeared specialized to detect gelatinous prey below, and slightly ahead of, a swimming turtle. Analogous retinal structures amplify prey detection in reef fishes (Collin & Pettigrew, 1988). No such *area* was present in the retinae of green turtles (*Chelonia mydas* L.) or loggerheads.

Electrical responses from the retina (ERG recordings) were used to determine the spectral sensitivity of leatherback hatchlings to light wavelengths (Gocke, Horch and Salmon, in preparation). Wavelengths from 340–660 nm (near ultraviolet to red) were detected, with peak sensitivity between 460–500 nm (blue-green). The breadth of this spectral response suggests that more than one visual pigment is involved (making color vision possible). A capacity for wavelength discrimination might enable posthatchlings to selectively discriminate between differently colored prey during the day, and to locate prey by their bioluminescent emissions either at

night, or when deep-diving (as hypothesized by Davenport, 1988). The bioluminescent light emitted by most deep-sea gelatinous organisms falls between 440–506 nm (Haddock and Case, 1999). Leatherbacks are especially sensitive to these wavelengths.

We used simple shapes and a more realistic model to determine if naïve leatherbacks were attracted to objects that resembled gelatinous prey. We expected that only the model would evoke attraction but found that the turtles not only swam vigorously toward simple shapes (Fig. 7), but that all visual stimuli evoked “hunting” behavior (Fig. 4).

One might conclude from these results that leatherbacks are unable to discriminate between objects of different shape, but retina anatomy (densities of rods and cones) and behavioral responses of other marine turtles (loggerheads; Bartol and Musick, 2001, 2003) make this explanation unlikely. We postulate that for leatherbacks, it may be advantageous to attack virtually any object, regardless of its shape, size, or color, because gelatinous prey vary enormously in all of these parameters (small ctenophores to enormous *Cyanea* and *Physalia*, several m in length; round bells of cnidarians to chains of colonial salps; species that are transparent or colored white, blue, orange or red). Both juvenile and adult leatherbacks are known to feed simultaneously on a wide variety of prey (siphonophores, tunicates, salps, and medusae; Bjorndal, 1997), at the surface as well as at great depths (Eckert et al., 1989). Among the documented prey genera are *Aurelia* (Den Hartog, 1980; Eisenburg and Frazier, 1983) and *Cyanea* (Bleakney, 1965).

Posthatchling leatherbacks, reared using methods identical to those employed here, were also nonspecific in their prey choices upon their first opportunity to interact with live prey in the open ocean (Salmon et al., in press). Turtles dove toward and fed upon *Aurelia* located 1–14 m below the surface, with the largest specimens 4 times the size (bell diameter) of the smallest. They also fed near the surface on small (2–6 cm long) ctenophores and masses of molluscan eggs (species not identified).

Chemical cues and behavior

Many aquatic predators locate food using chemical cues (Carr and Derby, 1986; Carr et al., 1996). Chemical stimuli are especially important for detection of prey at a distance because under water, particulates (and reduced light levels at greater depth) restrict visual range in even the clearest water (Lythgoe, 1988; Sorensen and Caprio, 1997; Vickers, 2000).

Chemical cues typically elicit appetitive behaviors such as “arousal”, manifested by an increase in locomotor activity. Movement into currents (odor “tracking”) is also a common response among both aquatic and ter-

restrial organisms, as odor sources are always located “upstream” (Vickers, 2000).

Leatherback posthatchlings, not unexpectedly, also showed these behavior patterns. Biting is typically stimulated in predatory fishes in response to specific compounds (particular amino acids) present at concentrations well above threshold (Valenticic and Caprio, 1994; 1997). Further studies with leatherbacks will be required to determine if specific chemical substances are used by these gelatinivores to recognize their prey.

It might be argued that in our chemical tests, we should have used seawater from tanks that contained live jellyfish or ctenophores (providing “body odors”), rather than extracts made from homogenized prey, because predators in nature do not encounter extracted or homogenized prey (Rittschoff et al., 1984; Luczkovich, 1988). Actually, the use of chemical preparations in tests has experimental advantages and disadvantages, and a complete understanding of predator behavior would involve the use of body odors, homogenates, and pure compounds as test stimuli (Zimmer-Faust, 1989). We used homogenates because gelatinous prey are delicate creatures that in nature often have tears, rips and other signs of injury. The prevalence of these injuries suggests that gelatinivores will commonly encounter chemical stimuli from within, as well as upon, the body surface of their prey. Natural selection could potentially favor a response to all of these stimuli.

Adult leatherbacks are known to aggregate and feed where gelatinous prey are spatially concentrated (“blooms”; Eisenburg and Frazier, 1983; Grant and Ferrel, 1993; Grant et al., 1996). It has also been hypothesized that posthatchling marine turtles will find the highest concentrations of prey at oceanic “fronts”, or convergence zones between oceanic currents, where both flotsom and planktonic organisms (such as gelatinous zooplankton) accumulate (Carr, 1986a, 1986b; Witherington, 2001). At such sites, ocean water is likely to contain a rich array of chemical stimuli consisting of metabolic byproducts, as well as partially consumed and intact prey. Any of these compounds might be used by gelatinivores as food attractants.

Development of prey recognition

Our study is the first to demonstrate that leatherbacks respond to chemical cues emanating from gelatinous prey. Whether the turtles did so upon their first exposure to feeding stimulants is uncertain since compounds present in prey homogenate may also have been present in our artificial diet. To determine if leatherbacks have innate predispositions to respond to prey odors, experiments would have to be done with naïve subjects that are ready to feed, but have not had previous contact with feeding stimulants.

There is little information on the responses of turtles to chemical stimuli generally, and feeding stimulants in particular (reviews: Owens et al., 1986; Bartol and Musick, 2003). Manton (1979) established that juvenile green turtles would quickly associate “neutral” (non-food) chemical stimuli with food reward. After training, these associations were remembered for more than a year. Owens and coworkers (Owens et al., 1982; Steele et al., 1989) showed that posthatchling loggerheads could orient toward chemical substances (both food and non-food stimuli), and retain memories of these for several weeks. Thus marine turtles easily learn to associate chemical stimuli with food.

Our results indicate that visual and chemical cues play important roles in prey detection, and that the turtles possess visually-mediated predispositions to orient toward, and attack, a variety of objects. We hypothesize that if these encounters result in successful feeding, turtles may learn to associate chemical with visual cues from prey. Such an association could, under natural conditions, then be used to locate distant prey by chemical cues only.

Alternatively, turtles may have innate predispositions to respond to specific chemical substances from prey. These alternative hypotheses, and many other issues concerning the development of food-seeking behavior in marine turtles, remain interesting (but largely unexplored) topics for future research.

Acknowledgements

This study was completed by M. A. C. as part of the requirements for a Masters degree. We thank Profs. P. Lutz and S. Mahoney for their guidance as members of the thesis committee. B. Squillante, C. Johnson, and K. Rusenko provided the hatchlings; P. Constantino, T. T. Jones, and L. Northsea assisted with hatchling care; and D. Weyrich and B. Carson recorded data from hours of videotape. Prof. A. Nash provided statistical expertise. Funding was provided by the National-Save-the-Sea-Turtle Foundation, Ft. Lauderdale, Florida, U. S. A. Critical readings by D. Rittschof, J. Wyneken, and two referees improved the manuscript. The research was carried out under FFWCC sea turtle permit # 073, and approved by the Florida Atlantic University IACUC committee.

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