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Responses of hatchling sea turtles to rotational displacements

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Abstract

After emerging from underground nests, sea turtle hatchlings migrate through the surf zone and out to the open ocean. During this migration, both waves and water currents can disrupt hatchling orientation by unpredictably rotating the turtles away from their migratory headings. In addition, waves cause turtles to roll and pitch, temporarily impeding forward swimming by forcing the hatchlings into steeply inclined positions. To maintain seaward orientation and remain upright in the water column, hatchlings must continuously compensate for such displacements. As a first step toward determining how this is achieved, we studied the responses of loggerhead (*Caretta caretta* L.) sea turtle hatchlings to rotational displacements involving yaw, roll, and pitch. Hatchlings responded to rotations in the horizontal plane (yaw) by extending the rear flipper on the side opposite the direction of rotation. Thus, the flipper presumably acts as a rudder to help turn the turtle back toward its original heading. Turtles responded to rotations in the roll plane with stereotypic movements of the front flippers that act to right the hatchlings with respect to gravity. Finally, hatchlings responded to rotations in the pitch plane with movements of the hind flippers that appear likely to curtail or counteract the pitching motion. Thus, the results of these experiments imply that young sea turtles emerge from their nests possessing a suite of stereotypic behavioral responses that function to counteract rotational displacements, enable the animals to maintain equilibrium, and facilitate efficient movement toward the open sea.

Keywords: *Caretta caretta*; Equilibrium; Orientation; Navigation; Sea turtle; Waves

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1. Introduction

After emerging from their nests, hatchling sea turtles from the east coast of Florida, USA, immediately crawl to the sea and swim toward the open ocean (Salmon and Wyneken, 1987). Hatchlings near shore establish a seaward heading by swimming into waves (Salmon and Lohmann, 1989; Lohmann et al., 1990; Lohmann and Lohmann, 1992). Turtles can determine wave direction by detecting either the horizontal movement of water that occurs near the substrate in shallow coastal areas (Wang et al., 1998) or the orbital pattern of water movement that occurs as waves propagate through deeper water (Lohmann et al., 1995). Because waves are refracted in shallow coastal areas until they approach the beach directly (Denny, 1988), swimming into waves reliably leads the turtles toward the open sea.

Waves are not the only source of directional information used by hatchlings as they migrate offshore. Turtles can also maintain headings using the earth's magnetic field (Lohmann, 1991; Lohmann and Lohmann, 1994; Goff et al., 1998). This ability might be particularly important in deeper water beyond the wave refraction zone, where the direction of wave movement no longer provides a reliable indicator of the offshore direction (reviewed by Lohmann et al., 1997; Lohmann and Lohmann, 1998).

Despite the presence of multiple orientation cues, turbulent wave action can deflect a hatchling from its chosen course. Such displacements presumably impair the ability of turtles to maintain consistent headings and thus impede their progress as they migrate offshore. To determine whether sea turtle hatchlings possess any compensatory behavioral mechanisms to counteract rotational displacements imposed on them by waves and currents, we studied the responses of loggerhead hatchlings to rotations involving yaw, roll, and pitch. Our results indicate that sea turtle hatchlings possess a suite of stereotypic behavioral responses that allows them to counteract displacements from their migratory course and maintain equilibrium as they swim through waves on their way to the open ocean.

2. Materials and methods

2.1. Animal collection and handling

Hatchling loggerhead sea turtles (*Caretta caretta*) were collected during July and August, from 1995 to 1997. Hatchlings were obtained from 26 different nests deposited on beaches in Boca Raton, FL, USA, as well as from a nearby hatchery in Hillsboro, FL. Since the sex ratios of sea turtle hatchlings from nests on Florida beaches are highly skewed toward females (Hanson et al., 1998), the majority of the hatchlings used in this study were likely female. However, because both male and female hatchlings confront identical conditions while migrating offshore, it appears unlikely that the behavioral patterns studied vary between sexes.

Nests containing hatchlings due to emerge were identified by their date of deposition and incubation time relative to nearby nests that had already hatched. On the evening when emergence was expected, we gently dug into the nest using our hands and removed between 15 and 45 hatchlings. The turtles were immediately placed into lightproof Styrofoam coolers and transported to a nearby laboratory, where they were kept in darkness until they were used in experiments later that evening. All hatchlings were released on the beach after the completion of that night's experiments.

2.1.1. Eliciting swimming in air

When their ventral surface is no longer in contact with solid substrate, hatchlings initiate a swimming motor program in which the front flippers move synchronously up and down in a motion known as powerstroking (Salmon and Wyneken, 1987). At the same time, the rear flippers are usually held straight out behind the shell (Wyneken, 1997). When the hatchlings surface to breathe, they move all four flippers asynchronously in a "dogpaddling" motion (Wyneken, 1997).

Our experiments were based on the finding that hatchlings exhibit this same swimming behavior when suspended in air. Under these conditions, turtles alternate between powerstroking and dogpaddling and even lift their heads to breathe, just as they do when swimming in water (Lohmann et al., 1995; Manning et al., 1997; Wang et al., 1998). This behavior made it possible for us to examine hatchlings' responses to rotational displacements in air.

2.2. Simulation of rotational displacements

A machine was constructed to simulate three types of rotational displacements similar to those presumably experienced by hatchlings as they migrate offshore (Figs. 1–3). One end of a metal bar was attached to the shaft of a variable-speed motor. The other end was modified with an attachment device so that a hatchling in a harness (see Testing procedure) could be fastened securely to it. When the motor was turned on, the bar was rotated so that hatchlings experienced rotational displacements. The rotation ceased when the bar contacted padded stops that were placed in various locations to gently terminate the motion (see below).

The machine was configured to allow for rotational displacements in the yaw, roll, and pitch planes. At the start of each trial, hatchlings were harnessed to the bar in a normal, horizontal swimming position with the ventral surface of the turtle parallel to the floor. During rotations in the yaw plane, hatchlings were moved through horizontal arc of 90° in either a clockwise or anti-clockwise direction (Fig. 1). To simulate roll and pitch, the machine was arranged so that the bar was aligned vertically at the start of each trial while the hatchling remained in a normal swimming position (Figs. 2 and 3). During rotations in the roll plane, hatchlings were moved laterally and upward through an arc of 45° in either a clockwise or anti-clockwise direction (Fig. 2). Rotations in the pitch plane were accomplished in the same way, except that the turtle's starting position within the horizontal plane was perpendicular to that in the roll trials. Thus, the 45° displacement resulted in final positions in which the anterior of the turtle was higher than the posterior, or vice versa (Fig. 3).

The rotations that we used differ slightly from pure yaw, roll, and pitch in that the rotational axis was outside the body of the turtle. However, preliminary experiments suggested that the responses of hatchlings were identical regardless of whether the axis of

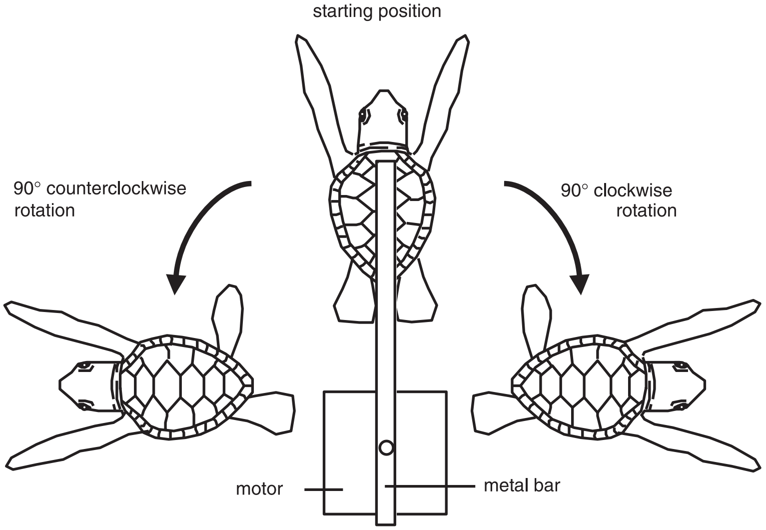

Fig. 1. Apparatus used to produce rotations involving yaw as seen when looking directly from above. Hatchlings used their rear flippers as rudders when attempting to turn. Extending the right flipper while swimming will result in a right turn, whereas extending the left flipper while swimming will cause the hatchling to turn left.

rotation passed through the turtle's body. Also, turtles swimming offshore rarely experience pure yaw, roll, or pitch because waves and water currents usually result in more complex rotations involving simultaneous movement along more than one axis. Thus, neither the rotations we used, nor pure yaw, roll, and pitch are likely to simulate in all details the complex wave-induced movements of the ocean surface. Nevertheless, we consider the

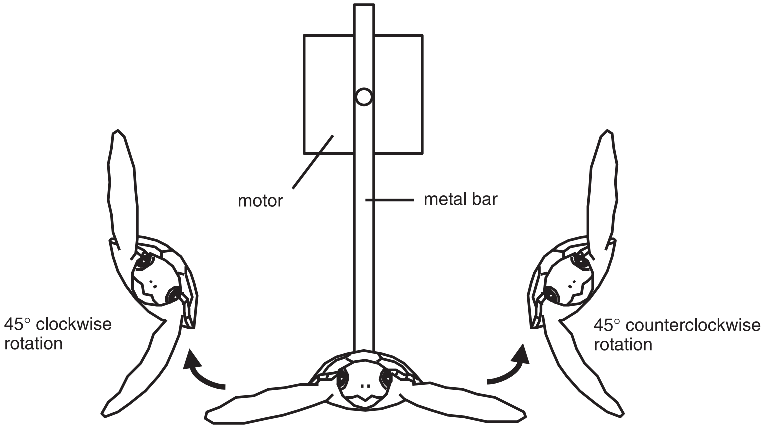

Fig. 2. Apparatus used to produce rotations involving roll as seen from the front. Hatchlings attempting to right themselves will continue to stroke with their front flippers while positioning one front flipper lower than the other, to return to an upright position. Hatchlings rotated clockwise maintained the left front flipper in a lower position while hatchlings rotated anti-clockwise maintained a lower position for the right front flipper.

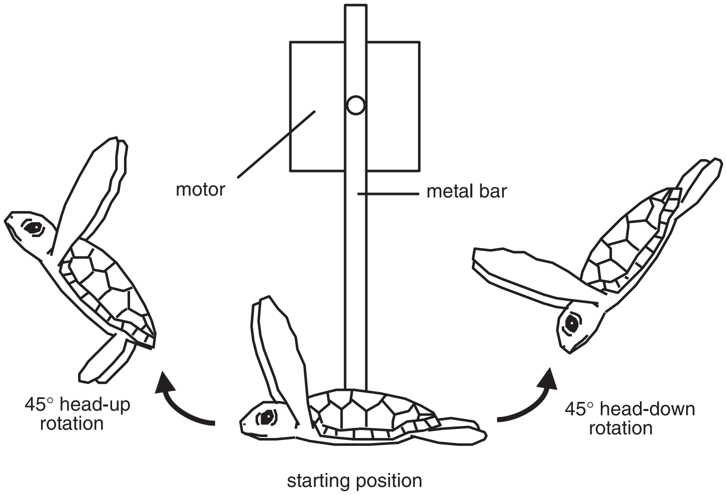

Fig. 3. Apparatus used to produce rotations involving pitch as seen from the front. Hatchlings experiencing the head-up displacement oriented their rear flippers perpendicular to the body, broadside to the direction of movement, in an attempt to slow the displacement. Hatchlings experiencing the head-down displacement did not position their flippers in this manner.

stimuli used to be reasonable approximations of the simplest rotations that hatchlings experience and therefore a good starting point for investigating the responses to such displacements.

2.3. Testing procedure

All experiments were conducted between 2030 and 0200 h, the time when most hatchlings emerge from their nests and enter the sea (Witherington et al., 1990). To ensure that visual cues did not influence the responses of the turtles to rotational displacements, all trials were carried out in darkness inside a lightproof room. Trials were recorded for later analysis using a video camera with an infrared filter in conjunction with an infrared light. The camera was wired to a monitor in an adjacent room so that each turtle could be observed during experiments.

Prior to testing, all turtles were placed into buckets of seawater for at least 10 min to activate swimming behavior (Lohmann and Lohmann, 1992; Lohmann et al., 1995). At the beginning of each trial, a hatchling was placed into a nylon-lycra harness that encircled its carapace without impeding swimming (Salmon and Wyneken, 1987; Lohmann et al., 1995; Manning et al., 1997). Under illumination from a dim flashlight, we fastened the turtle to the end of the metal bar. To ensure that each hatchling was swimming steadily, we then briefly held the light directly in front of the turtle. Because hatchlings normally swim toward bright lights (Salmon and Wyneken, 1987; Lohmann and Lohmann, 1994), this stimulus usually elicited vigorous swimming. Once a turtle was swimming continuously, we turned off the flashlight so that the room was completely dark. An observer in the adjacent room then monitored the activity of the turtle for an additional 20–60 s. If the turtle continued to swim vigorously, then the machine was activated using a remote switch. All hatchlings underwent only one type of rotational displacement and those few turtles that ceased swimming after the flashlight was turned off were replaced with other, more active, hatchlings.

2.3.1. Rotations involving yaw

Each hatchling was rotated either clockwise or anti-clockwise at one of three different speeds termed slow, medium, or fast. The speeds and accelerations for each treatment group were determined by filming the motion of the bar (without a hatchling attached) at all three speeds using a high-speed (1000 frames/s) video camera and then digitizing the frames. The data were plotted and a second-order regression line was fitted to the acceleration region to determine maximum accelerations. A linear regression was fitted to the constant velocity region to determine maximum velocity. At the slow speed, hatchlings experienced a maximum velocity of 0.046 m/s with a maximum tangential acceleration of 0.048 m/s^2. Hatchlings tested at the medium speed were rotated at a maximum velocity of 0.175 m/s and a maximum tangential acceleration of 1.99 m/s^2. The fast speed had a maximum velocity of 0.35 m/s and a maximum tangential acceleration of 5.9 m/s^2. These values fall toward the low end of the range of measurements taken for breaking waves in the surf zone, where it is possible for velocities to regularly exceed 5 m/s^2 and accelerations up to 400 m/s^2 are not unusual (Gaylord, 1999).

In principle, hatchlings under our experimental conditions might detect rotational displacements either by relying on vestibular organs or by detecting air motion at the surface of their bodies. To assess the potential influence of wind drag on the hatchlings' behavior, the two treatments at the fast speed were repeated with the turtles partially enclosed in a transparent box made of thin plastic. The box eliminated wind drag without disrupting swimming activity.

The videotape of each trial involving yaw was examined to determine whether hatchlings exhibit turning behavior in response to rotational displacements in the horizontal plane. Hatchling sea turtles turn by using their rear flippers as rudders (Walker, 1971). Turtles turning left extend their left rear flipper almost perpendicular to their body, whereas turtles turning right extend their right rear flippers in the same manner (Fig. 1). Therefore, during analysis, each hatchling was scored as to whether the right or left rear flipper was extended following displacement. Responses in each case were unambiguous and independent assessments by different researchers yielded identical results.

2.3.2. Rotations involving roll and pitch

Preliminary observations indicated that turtles exposed to displacements involving roll all responded in the same manner regardless of the acceleration at which the displacement occurred. Similarly, differences in accelerations did not appear to affect the way in which turtles responded to displacements involving pitch. Thus, these observations suggest that hatchlings undergoing rotational displacements in the roll and pitch planes react to changes in body position relative to gravity without regard to how quickly the change occurs. The trials involving roll and pitch were therefore run at an arbitrary, intermediate speed of 0.1–0.13 m/s.

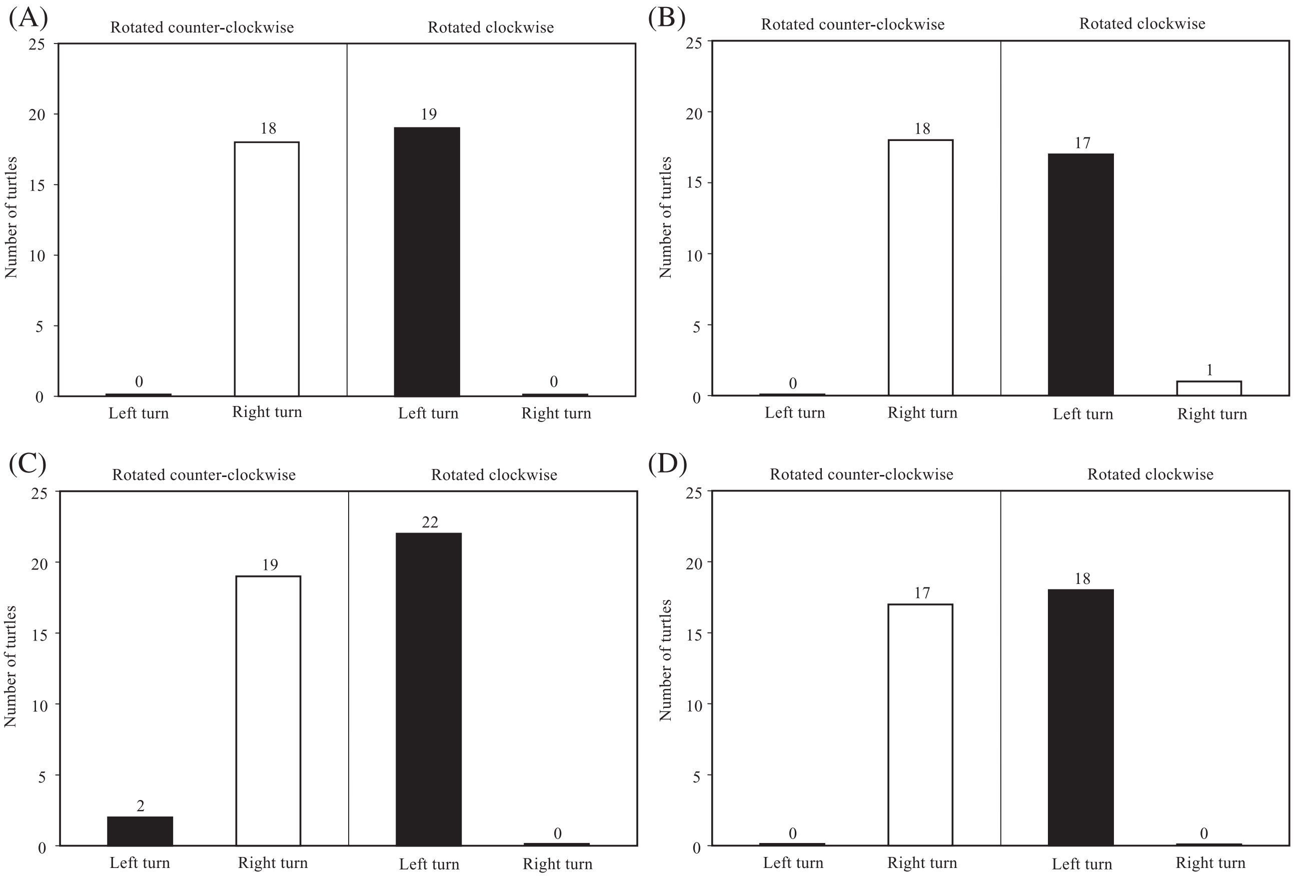

Fig. 4. Hatchling responses to rotations involving yaw. The black bars represent the number of turtles that turned to the left. The white bars represent the number of turtles that turned to the right. (A) Results from slow rotation speed. (B) Results from medium rotation speed. (C) Results from fast rotation speed. (D) Results from control trials in which wind drag was eliminated.

During analysis of the roll trials, a hatchling's videotaped trial was replayed on a monitor using a VCR that permitted the tape to be advanced one frame at a time. The tape was advanced until the rotational displacement had been completed. A circle 10 cm in diameter was then drawn on a transparent sheet of acetate. Two perpendicular lines were drawn within the circle so that it was divided into quadrants. The acetate sheet was then placed over the screen of the monitor so that the center of the circle (as defined by the intersection of the lines) coincided with the center of the hatchling's head (Fig. 5). The circle was then rotated until one of the lines was parallel to the edges of the metal bar from which the turtle was suspended and therefore parallel to the turtle's dorsal–ventral axis. Measurements of flipper positions could then be made relative to the second line, which was perpendicular to the dorsal–ventral axis of the turtle (Fig. 4). For purposes of analysis, this second line was assigned a value of 0°. Thus, at any point in time, the position of each front flipper tip could be described in terms of an angle ranging from +90° (tip directed straight up) to −90° (tip directed straight down) relative to the 0° line.

The average position of each flipper was determined by measuring the uppermost and lowermost angles for the first five flipper strokes that occurred immediately after displacement. A midway angle (representing the point halfway between the uppermost and lowermost positions) was then calculated for each of the five strokes; those angles were then averaged to obtain a final mean midway point for the left and right flippers of each turtle. The mean angle for each flipper at both its uppermost and lowermost points during the first five flipper strokes was also calculated (Fig. 5). Measurements yielded by two independent observers were not significantly different from one another and thus they were averaged. These averages were then used to compare the positions of the right and left front flippers for each treatment.

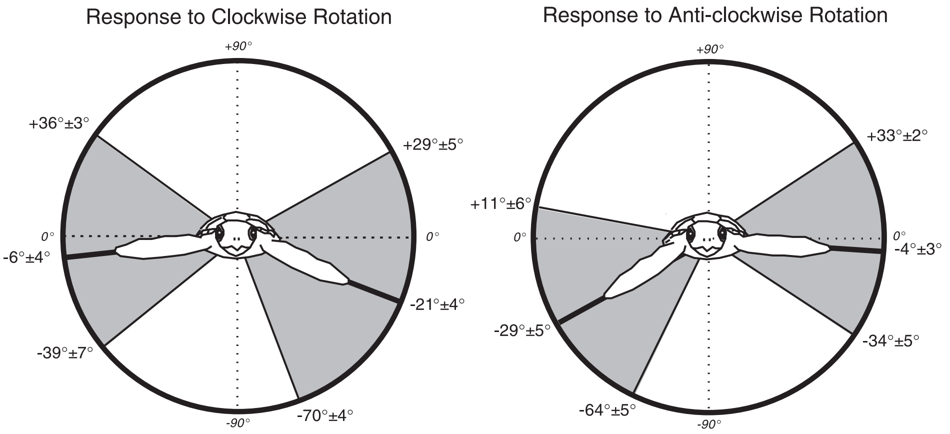

Fig. 5. Hatchling responses to rotations involving roll. All measurements are given as the mean angle ± the standard error. Hatchlings rotated clockwise positioned their left front flipper at a lower midpoint and lowest point than the right front flipper. In contrast, hatchlings rotated anti-clockwise positioned their right front flipper at lower mid-, lower, and upper points than the left front flipper.

In trials involving pitch displacements, hatchlings were rotated in one of two directions. At the completion of head-up trials, the turtle’s anterior end was inclined upward, whereas the head was inclined downward at the end of head-down trials (Fig. 3). In each case, the turtles’ rear flippers were monitored to determine if they remained trailing behind the carapace as in normal swimming, or were rotated forward until they were perpendicular to the longitudinal body axis, a movement that might counteract head-up pitching.

3. Results

3.1. Rotations involving yaw

Most loggerhead hatchlings responded to rotations in the horizontal plane by immediately extending a rear flipper (Fig. 1). Within all three rotation speeds, hatchlings that were rotated anti-clockwise extended their right rear flipper significantly more often than their left rear flipper (Fig. 4A,B,C) (χ^2: $p < 0.001$), thus demonstrating a preference for right-turning. Similarly, hatchlings subjected to clockwise rotations at all three speeds showed a significant preference for turning left (Fig. 4A,B,C) (χ^2: $p < 0.001$). Comparisons of the anti-clockwise and clockwise results for all rotation speeds indicated that the hatchlings’ turning responses were significantly different under the two directions of rotation (χ^2: $p \ll 0.001$). Hatchlings’ responses to rotations when wind drag was eliminated were not significantly different from those observed in the original fast-speed rotations ($p > 0.99$, Fisher Exact Probability Test) (Fig. 4D).

3.2. Rotations involving roll and pitch

Hatchlings responded to rotations involving roll by continuing to stroke with the front flippers. However, the midway point of the left front flipper stroke for turtles rotated clockwise was significantly lower than the midway point of the right front flipper stroke (Fig. 5) ($p < 0.001$, Wilcoxon paired-sample test). While the upper points for the left and right front flippers were not different, the lower point for the left front flipper was significantly lower than that for the right front flipper (Fig. 5) ($p < 0.001$, Wilcoxon paired-sample test). In contrast, the midway point of the right front flipper stroke for turtles rotated anti-clockwise was significantly lower than the midway point of the left front flipper stroke (Fig. 5) ($p < 0.001$, Wilcoxon paired-sample test). Also, the upper and lower points for the right front flipper were significantly lower than those for the left front flipper (Fig. 5) ($p < 0.005$ in each case, Wilcoxon paired-sample test).

During the pitch trials, 14 of the 15 turtles tested responded to the head-up displacements by rotating their rear flippers forward so that they were perpendicular to the long axis of the body (Fig. 3); only one hatchling continued to hold its flippers in the normal swimming position (trailing behind the carapace) following the displacement. Of the 15 hatchlings that underwent head-down rotations, none rotated their rear flippers forward (Fig. 3). The responses of the two groups were significantly different ($p \ll 0.001$, Fisher Exact Probability Test).

4. Discussion

The results of this study indicate that sea turtle hatchlings possess a suite of behavioral responses that are elicited by rotational displacements. The responses appear to function in retarding or counteracting changes in direction or equilibrium that are imposed on the turtle. Under natural conditions, hatchlings migrating offshore presumably experience similar rotations as a result of the actions of waves and water currents.

An important caveat is that we have focused our attention only on several conspicuous elements of behavior that are relatively easy to quantify. Thus, although this study is the first to investigate how marine turtles counteract rotational displacements, the results are descriptive and are not intended to represent a complete kinematic analysis of the corrective behavior and all of its subcomponents. Additional studies are needed to characterize in detail the full range of movements, muscles, anatomical structures, and biomechanical principles that comprise each response.

4.1. Rotations involving yaw

Hatchlings responded to rotational displacements in the horizontal plane by paddling with their front flippers and simultaneously extending one of their two rear flippers. Nearly all hatchlings that were rotated counterclockwise extended their right rear flipper (Figs. 1 and 4), whereas most hatchlings rotated clockwise extended their left rear flipper (Figs. 1 and 4). These results indicate that the turtles detected the direction of rotation and responded by attempting to turn back toward their original alignment.

Such responses might be useful throughout the hatchlings' migration offshore to the Gulf Stream. However, counteracting rotational displacements might be particularly important in shallow, nearshore regions where hatchlings guide themselves by detecting wave surge, the horizontal movement of water that occurs near the substrate as waves propagate through shallow water (Wang et al., 1998). One limitation of using wave surge as an orientation cue is that although the surge axis can be easily detected, the onshore and offshore directions cannot readily be distinguished because the movement of water in each direction is virtually identical. Given that turtles enter the ocean oriented seaward, they begin the migration with an appropriate offshore heading. Thus, an ability to quickly counteract wave-induced rotations might assist turtles in maintaining offshore headings as they swim through water immediately adjacent to shore.

It is also possible that the ability of counteract rotational displacements in the horizontal plane might benefit turtles at other times in their lives. Juvenile and adult sea turtles undergo lengthy migrations, in some cases traversing hundreds or even thousands of kilometers (Keinath, 1993; Meylan, 1995; Nichols et al., 2000). During these movements, waves and water currents undoubtedly deflect the turtles away from their chosen direction of orientation, making it difficult for them to maintain a constant heading. By rapidly compensating for displacements from their migratory pathways, turtles could minimize the distance traveled during migrations as well as the energy expected over the course of the journey.

4.2. Equilibrium responses

Hatchlings responded to rotations in the roll plane with stereotypic movements of the front flippers that presumably act to right the turtle with respect to gravity (Figs. 2 and 5). The positioning of the front flippers closely resembles that of the paired pectoral fins during the righting responses of teleost (Lowenstein, 1971) and elasmobranch fish (Timerick et al., 1990). Turtles responded to rotations involving pitch with movements of the hind flippers that appear likely to curtail or counteract the displacement (Fig. 3). In teleost fish, similar positioning of the pelvic and/or pectoral fins creates drag and serves to slow or reverse displacements caused by pitching motions, thus helping the fish return to an upright position (Blake, 1983; Videler, 1993). For long-distance migrants such as sea turtles, rapidly correcting for changes in equilibrium presumably helps to maximize overall energetic efficiency during swimming. Maintaining a dorsal-side up position while underwater is also crucial for aquatic animals that need to surface periodically to breathe.

4.3. Detection of displacements

To monitor posture and spatial orientation, terrestrial animals are able to use proprioceptive information obtained from the limbs and body to supplement input from the visual and vestibular systems (Ott and Platt, 1988; Deliagina, 1997). However, because aquatic animals swimming in the water column are not in contact with solid substrate, proprioceptive cues do not provide positional information. Maintaining body orientation is made even more difficult by displacements imposed on the animal by the motion of the surrounding medium (Mayne, 1974). Diurnal fish utilize both visual and vestibular information to maintain a dorsal-side up position (Braemer and Braemer, 1958; Ohnishi et al., 1999) and to orient spatially. However, nocturnally active aquatic animals, such as hatchling sea turtles, rarely have access to visual cues and might therefore be more reliant upon input from the vestibular organs.

Although the specific physiological mechanism underlying the hatchlings' detection of rotational displacements are unknown, transduction most likely occurs within the otolith organs and the semicircular canals, which are located in the inner ear. In vertebrates, these vestibular organs assist in maintaining body position by detecting deviations from the normal position and then initiating reflexes involving the eyes, limbs, body, and head (Lowenstein, 1971). Small adjustments in posture occur almost continuously, but particularly dramatic or stereotypical motions, such as those we have observed in hatchlings sea turtles, may be termed "postural" or compensatory reflexes (Gernandt, 1974).

The turtle inner ear contains three otolith organs; the utricle, the saccule, and the lagena (Ramrashad et al., 1986). Otolith organs are sensitive to tilt and also to changes in straight-line velocity, or linear acceleration (Precht, 1974; Kure et al., 1999), and are therefore extremely sensitive to changes in body position which occur as a result of roll and pitch displacements. Within the turtle inner ear, there are also three semicircular canals (anterior, posterior, and horizontal), which occur at approximate right angles to one another (Ramprashad et al., 1986). The semicircular canals are sensitive to angular acceleration in the planes of the canals and are not involved in the detection of tilt (Lowenstein, 1974; Markham, 1987; Rabbitt et al., 1994; Kure et al., 1999). Electrophysiological recordings made from the cristae of the anterior and posterior canals of thornback rays (*Raja clavata*; Lowenstein and Sand, 1940) and red-eared sliders (*Trachemys scripta*; Brichta and Goldberg, 1998) have shown that these organs respond to roll, pitch, and yaw displacements. The papilla neglecta (PN), another vestibular organ found in most vertebrates, may also play a role in detection of spatial orientation (Brichta and Goldberg, 1998). Electrophysiological recordings from nerves innervating the PN of a fresh-water turtle, the red-eared slider *T. scripta*, indicated that PN units are extremely sensitive to head-up pitch displacements (Brichta and Goldberg, 1998). The PN might serve a similar function in sea turtles.

In some animals there are indications that the otolith organs and semicircular canals might interact during the detection of displacements (Precht, 1974; Timerick et al., 1990), and this could also be the case of sea turtles. The semicircular canals might be stimulated by the initial angular acceleration during a displacement, but once constant rotational velocity is attained, the canals would no longer respond and any compensatory reflex would cease. However, if the orientations of the body after displacement were incorrect, the otolith organs would be stimulated, eliciting a continuation of the compensatory response until the body position returned to normal. Thus the vestibular organs might complement one another, resulting in a system that is remarkably sensitive to displacements that could alter the posture of the body and decrease overall energetic efficiency during locomotion.

Although the compensatory responses exhibited by hatchling sea turtles in this study represent an interesting adaptation in the context of orientation behavior, they might also form the basis for a new model for the study of vestibular postural reflexes. Studies involving compensatory responses have typically focused on vestibulo-ocular responses rather than responses elicited by vestibular stimuli alone. One reason is that, in most animals, separating effects due to proprioceptive and visual information from those elicited by vestibular input is difficult or impossible (Anderson et al., 1980). Hatchling sea turtles, however, readily swim in air and respond to rotational displacements in complete darkness. Thus, the sea turtle system provides an opportunity to investigate compensatory responses under conditions in which visual, vestibular, and tactile information can potentially be manipulated independently.

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