

Use of multiple orientation cues by juvenile loggerhead sea turtles *Caretta caretta*

Larisa Avens^{1,2,*} and Kenneth J. Lohmann¹

¹Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599-3280, USA and ²National Oceanic and Atmospheric Administration, Beaufort Laboratory, National Marine Fisheries Service, Beaufort, North Carolina 28516, USA

*Author for correspondence at address 2: (e-mail: Larisa.Avens@noaa.gov)

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Summary

Although the orientation cues used by hatchling sea turtles have been studied extensively, little is known about the mechanisms of orientation and navigation that guide older turtles. To investigate the orientation cues used by juvenile loggerheads *Caretta caretta* L., captured turtles were tethered in a water-filled arena located outdoors. Turtles tested under these conditions established and maintained headings in specific directions in the absence of wave cues, familiar landmarks and chemical gradients. Distorting the magnetic field around the anterior part of a turtle's body did not disrupt orientation if vision remained

unimpaired. Similarly, eliminating visual cues by attaching frosted goggles did not disrupt orientation if the magnetic environment was undisturbed. However, when turtles experienced a simultaneous disruption of magnetic and visual cues, their orientation was altered. These results imply that sea turtles, like migratory birds and homing pigeons, are able to maintain headings using multiple sources of directional information.

Key words: Sea turtle, loggerhead, *Caretta caretta*, orientation, cue, magnetic, visual.

Introduction

Sea turtles migrate extensively throughout their lives (Carr, 1987; Bowen et al., 1995; Meylan, 1995; Bolten et al., 1998). Although the orientation cues used by hatchling sea turtles have been investigated in considerable detail (see reviews by Lohmann et al., 1997; Lohmann and Lohmann, in press), little is known about the guidance mechanisms used by older turtles. In many animals, the strategies and mechanisms used in orientation and navigation change as individuals mature, gain experience and take up residence in new habitats (Wiltschko, 1983; Baker, 1984; Able and Bingman, 1987; Rodda and Phillips, 1992; Able and Able, 1996). Thus, directional and positional cues used by juvenile and adult turtles might differ significantly from those used by hatchlings.

Numerous cues are potentially available to juvenile and adult sea turtles during their extensive migrations and movements. Given that hatchlings are able to set and maintain headings based on wave direction (Salmon and Lohmann, 1989; Lohmann et al., 1990; Lohmann and Lohmann, 1992), the Earth's magnetic field (Lohmann, 1991), and interactions between the two (Goff et al., 1998), similar abilities may persist in older turtles. Other cues that might provide directional information under at least some conditions include chemical gradients (Koch et al., 1969), celestial features such as the sun or polarized light (DeRosa and Taylor, 1980; Hawryshyn et al., 1990) and familiar landmarks (Luschi et al., 1996). Whether any of these cues are actually used by juvenile and adult turtles, however, is not known.

To investigate the directional cues used by older turtles, we studied juvenile loggerheads (*Caretta caretta* L.) to determine whether they were able to maintain consistent directional headings in the absence of wave cues, familiar landmarks and chemical gradients. The turtles were also tested under conditions in which magnetic cues were disrupted, visual cues were disrupted, or both were disrupted together. The results demonstrate that juvenile loggerheads can use either magnetic or visual information to orient, depending on which is available.

Materials and methods

Animals

Juvenile loggerheads were captured using pound nets in Core Sound, North Carolina, USA (latitude: 34°50'N; longitude: -76°22'W). Loggerheads ranging from 42.3 to 67.4 cm standard straight-line carapace length were retained for experiments. They were then transported to the National Oceanic and Atmospheric Administration (NOAA) Laboratory in Beaufort, North Carolina, approximately 30 km southwest of the capture area. At the facility, each turtle was placed into an outdoor, circular tank measuring 2 m in diameter. Seawater was continuously circulated through the tanks and water depth was maintained at 0.75 m. Turtles were allowed to acclimate to captive conditions for about 24 h before being used in experiments. Each turtle was used for only one set of

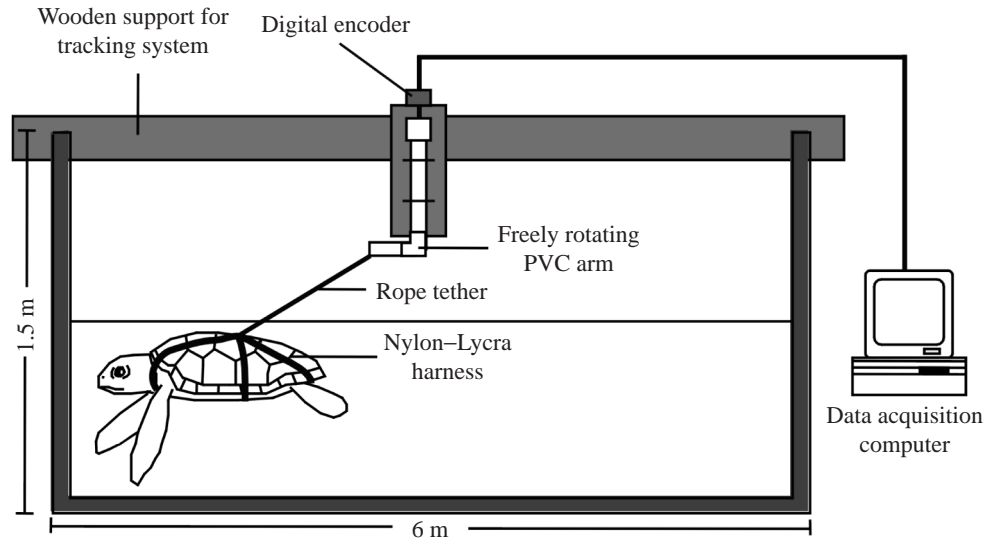


Fig. 1. Diagram of the experimental arena and the data acquisition system used to monitor the orientation of juvenile loggerhead sea turtles (not to scale). Each turtle was fitted with a Nylon-Lycra harness and tethered to a freely rotating arm in the center of the arena. Data were acquired by a computer located approximately 5 m to the south of the arena. See text for details of testing procedure.

experimental trials (see General experimental protocol) before being released at locations 15–20 km distant from their original capture site as part of a homing study (Avens et al., 2003).

Orientation arena and data acquisition

Juvenile loggerheads were tested in a circular, fiberglass tank, 6.1 m in diameter and 1.8 m high (Fig. 1; Red Ewald, Karnes City, TX, USA). The tank, which was filled with seawater to a depth of 0.75 m, was located outdoors and was uncovered, allowing the turtles a view of the sky. However, the walls of the tank blocked the turtles' view of the natural horizon and surroundings.

During testing each loggerhead was outfitted with a Nylon-Lycra harness that encircled its carapace. The turtle was then tethered to a rotatable arm mounted at the center of the tank (Fig. 1). As each turtle swam, the tether pulled the arm so that the arm tracked the turtle's swimming direction continuously. A digital encoder coupled to the arm was wired to a nearby computer so that headings could be recorded to the nearest 1.4° at intervals of 30 s.

Immediately before and after each trial, the system was checked to ensure that data were recorded accurately relative to magnetic north (0°). In addition, the water was stirred prior to each trial to ensure that no chemical gradients existed in the tank.

General experimental protocol

All experiments were conducted between May and November, months when turtles inhabit or migrate through the sounds of North Carolina (Epperly et al., 1995). Trials were carried out during daylight hours between 12:30 h and 17:00 h.

To minimize the possibility that the starting orientation of a turtle influenced the direction in which it subsequently swam, each turtle was placed into the tank facing east or west, with successive turtles started facing in opposite directions. After a turtle had been tethered and released, it was allowed a 5 min acclimation period before the trial was initiated. Following this

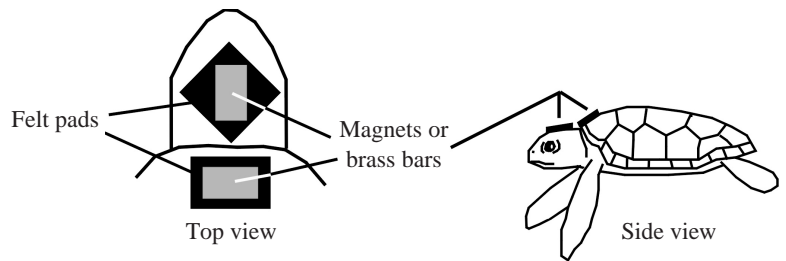
5 min period, a data acquisition computer recorded the turtle's directional heading for the next 10 min. At the end of the 10 min trial, the computer calculated a mean angle representing the average direction that the turtle swam.

Trials were observed from a raised platform located approximately 5 m from the perimeter of the tank. Preliminary tests demonstrated that the presence of observers on the platform did not influence the orientation of turtles swimming in the tank. These observations are consistent with similar findings involving hatchling turtles (Salmon and Lohmann, 1989; Witherington, 1991) and are also not surprising because sea turtles are myopic in air (Ehrenfeld and Koch, 1967). Animals were monitored to ensure that they swam consistently at the end of the tether. Turtles were eliminated from the study if, during three or more computer readings, they either did not swim (i.e. they floated motionless or sat on the bottom of the tank) or they moved backwards or otherwise swam erratically so that the direction of the rotatable arm did not accurately reflect the turtle's orientation.

Preliminary experiments indicated that different turtles swam in different directions when initially tested in the tank, but that each individual usually oriented consistently toward the same direction over a period of several days. Thus, a turtle that swam east during its first trial was likely to swim approximately east when tested again the next day, whereas a turtle that swam north the first time usually also swam approximately north when tested again. This observation formed the basis of the procedures we used in subsequent experiments.

During experiments, each turtle was tested in the arena at the same time of day on two consecutive days. On the first day, the turtle swam in the unaltered local magnetic field with a full view of the sky; these results were used to determine the individual's preferred direction of orientation under the test conditions. On the second day, each turtle was randomly assigned to one of several treatment groups and tested again, either under the same conditions or under new conditions in

Fig. 2. Magnet and brass bar attachment to loggerhead turtles. Felt pads were attached to the dorsal surface of the head and the anterior margin of the carapace; magnets or brass bars sewn into felt pouches were attached to the felt pads. See text for details.



which one or more orientation cues were manipulated (see below). This approach enabled us to determine which treatments affected the turtles' orientation, and thus to infer which cues were used to maintain consistent headings.

Magnetic impairment experiments

Experiments were conducted to determine whether disrupting the magnetic field around the turtles affected orientation if visual cues remained available. Ceramic magnets (8 cm long \times 6 cm wide \times 1 cm high; Magnet Sales & Manufacturing, Inc., California, USA) with fields measuring 4000 μ T at 1 cm from the magnet's surface, were attached to both the dorsal surface of the head and to the anterior margin of the carapace (Fig. 2). Pads of felt material were affixed to the head and carapace using cyanoacrylate adhesive. Magnets were then attached to the felt pads using plastic electrician's ties. This arrangement allowed the magnets to shift position slightly as the turtles swam, producing a strong but constantly changing magnetic field. The magnets were attached to the anterior part of the body because evidence suggests that, in vertebrates, magnetoreceptors are probably located in the head (Walker et al., 1997; Deutschlander et al., 1999; Phillips et al., 2001).

All trials were conducted under clear or partly cloudy skies when the sun was visible. Turtles were divided into four treatment groups for Day 2 trials. One group was tested in the same way as on Day 1. Turtles in two additional groups were tested with magnets attached to them. In the south-up group, both magnets were arranged so that the field lines leaving the magnet were directed downward and the south pole of the magnet was up. In the north-up group, both magnets were arranged in the opposite way so that the north pole of each magnet was up. Turtles in the fourth group served as controls and were equipped with two brass bars (6 cm long \times 4 cm wide \times 1.5 cm high) that were the same mass as the magnets, but did not disrupt the magnetic field. In all cases, magnets or brass bars were attached to the turtles immediately prior to testing on the second day.

Visual impairment experiments

A second experiment was carried out to determine whether altering visual cues disrupted orientation if magnetic cues remained undisturbed. To block visual cues, turtles were fitted with goggles (Fig. 3) that were attached using cyanoacrylate adhesive and were easily removed after completion of a trial.

Turtles were divided into three treatment groups on Day 2.



Fig. 3. Juvenile loggerhead turtle fitted with goggles containing frosted lenses. The goggle frames were attached to the turtle using cyanoacrylate adhesive and fit snugly to the contours of the turtle's head, so that turtles were unable to view the sky or surroundings.

One group was tested in the same way as during Day 1 (no treatment). A second group was fitted with goggles containing frosted, plastic lenses that blocked the turtles' view of their surroundings and the sky and also depolarized the light passing through the lenses (Fig. 3). Although some light still penetrated the frosted lenses, a human observer looking through the lenses on sunny days was unable to locate the sun's position. To control for possible effects of goggle attachment, a third group was fitted with goggle frames containing no lenses. Goggles or goggle frames were attached to the turtles immediately prior to testing on Day 2.

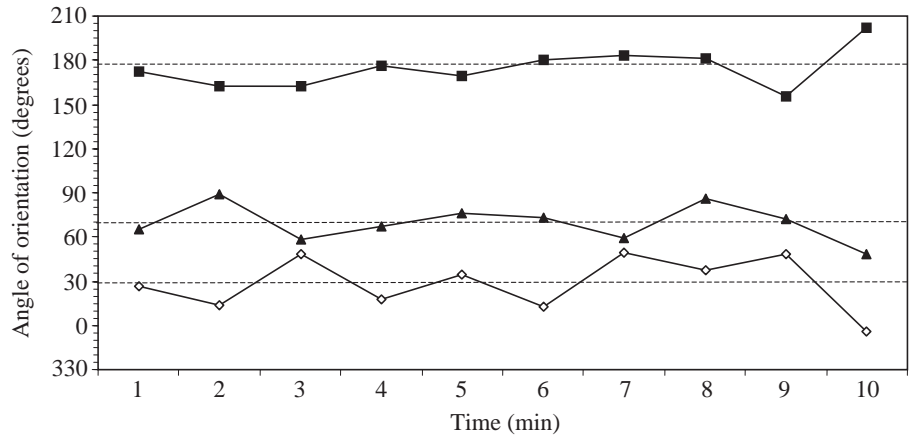
Combined magnetic and visual impairment experiments

A final experiment was conducted to determine if simultaneously disrupting magnetic and visual cues affected orientation. Turtles were divided into three treatment groups on Day 2. Turtles in all three groups were equipped with goggles containing frosted lenses. In addition, turtles in the first group were fitted with south-up magnets, turtles in the second group carried north-up magnets, and turtles in the third group were fitted with brass bars.

Data analysis

A mean heading and *r*-value were calculated for each trial

Fig. 4. Representative orientations of three juvenile loggerhead turtles tethered in the experimental arena. Each turtle is denoted by a different symbol. Time is indicated along the horizontal axis and the angle of orientation is indicated along the vertical axis. Each dotted line represents the mean heading of the turtle over its 10 min trial. Once a turtle established a course, it typically maintained relatively consistent headings for the duration of the trial.



using standard procedures for circular statistics (Batschelet, 1981). Because preliminary trials indicated that different turtles swam in different directions during Day 1 trials, each turtle's mean angle during its first trial was normalized to 0°. The angular difference between each turtle's heading on Day 2 *versus* that on Day 1 was then plotted relative to 0° (Lohmann et al., 1995). Thus, for example, a turtle that had a mean angle of 90° during its first trial and a mean angle of 110° during its second would be scored as an angle of 20°. This procedure enabled us to easily compare the responses of turtles to the different treatments by determining whether animals in each group maintained their original Day 1 courses (toward 0°) or changed direction.

For each treatment, distributions were analyzed using the V-test with an expected direction of 0° (the direction that turtles would be expected to swim if they did not change headings between Day 1 and Day 2). For distributions in which the V-test indicated statistically significant orientation, a 95% confidence interval was calculated for the mean heading to determine if the direction of orientation was consistent with the expected direction (Zar, 1996). The Mardia–Watson–Wheeler test (Batschelet, 1981) was used to determine if differences existed among the results obtained from the various treatment groups in each experiment.

Results

Behavior of tethered turtles

Most turtles swam steadily while tethered, sometimes switching gaits among powerstroking (which involves moving both front flippers synchronously) in mid-water, using alternating flipper strokes while moving along the bottom of the tank, and dogpaddling (Wyneken, 1997) when surfacing to breathe. Although the turtles spent most of their time swimming actively, they occasionally sat motionless at the end of the tether for short periods before resuming activity.

Some turtles adopted consistent headings almost immediately after being introduced to the tank, whereas others circled for several minutes before doing so. Once a course had been established, however, the orientation of the turtle was typically consistent for the duration of the trial (Fig. 4).

An analysis of orientation during first day trials (when turtles were allowed to swim while tethered but otherwise experienced no treatment) suggested that the headings of many turtles corresponded approximately with the direction of the capture area from the test site (74°). While only 3 of the 10 groups ($N=8-14$ turtles per group) reached significance at $P<0.05$ using the V-test and a fourth group approached significance ($P<0.10$), all 10 groups had mean orientation angles ranging from 21° to 167°, so that no group mean was farther than 93° from the 'homeward' direction. However, because different individual turtles generally swam in different directions, orientation data for the various experimental treatments were analyzed relative to each turtle's orientation during its Day 1 trial (see Materials and methods).

Magnetic impairment experiments

In magnetic impairment tests, turtles in all four groups (north-up magnets, south-up magnets, brass bars and no treatment) maintained approximately the same headings on Day 2 that they had maintained on Day 1, regardless of whether they carried magnets, brass bars or neither (Fig. 5A–D). No significant differences existed between the various treatment groups ($W=2.18$, $P>0.81$; Mardia–Watson–Wheeler test).

Visual impairment experiments

In visual impairment tests, none of the three groups (no treatment, turtles wearing goggles without lenses, or turtles with goggles containing frosted lenses) deviated significantly from their Day 1 headings when tested on Day 2 (Fig. 6A–C). No significant differences existed among the three distributions ($W=2.18$, $P=0.56$; Mardia–Watson–Wheeler test). Turtles wearing goggles with frosted lenses appeared to swim normally and their behavior did not differ in any obvious way from that of the other groups.

Combined magnetic and visual impairment experiments

Turtles fitted with frosted goggles and brass bars oriented in approximately the same direction on both Day 1 and Day 2 (Fig. 7A). In contrast, turtles fitted with frosted goggles and magnets in either the North-up or South-up position did not do

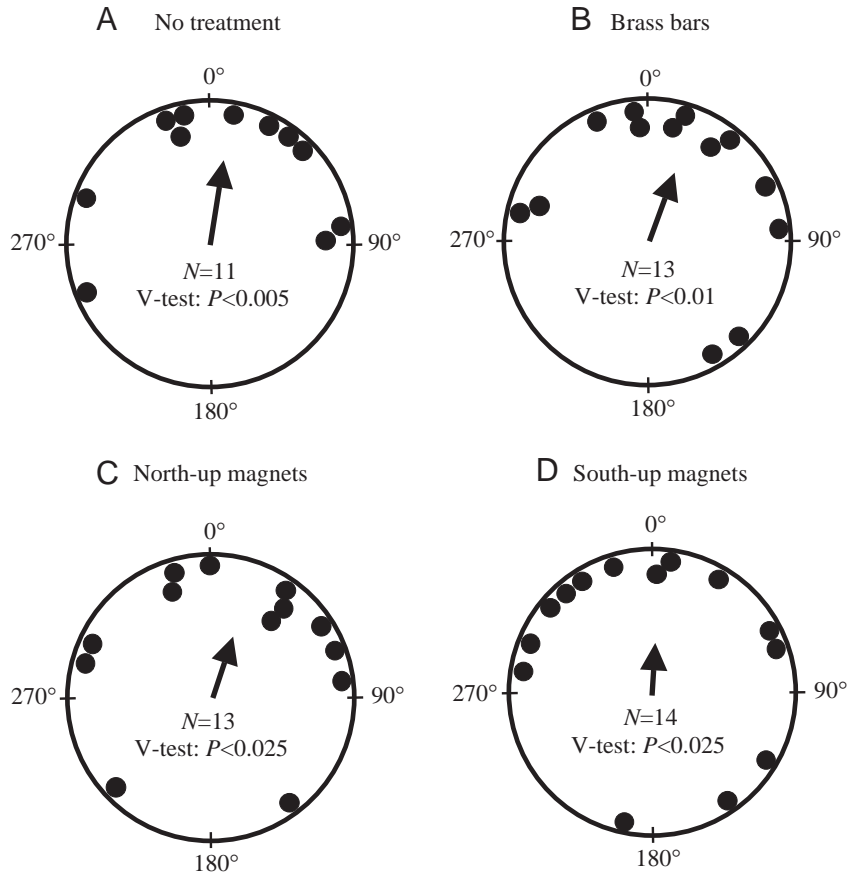


Fig. 5. Results of magnetic impairment experiment. Each dot represents the angular difference between an individual turtle's mean heading on Day 2 versus Day 1. All four groups of turtles oriented in the expected direction of 0° . (A) No treatment; mean angle = 11° , $r=0.50$, $P<0.005$ V-test, 95% confidence interval $\pm 49^\circ$; (B) Brass bars; mean angle = 26° , $r=0.35$, $P<0.01$ V-test, 95% confidence interval $\pm 90^\circ$; (C) North-up magnets; mean angle = 12° , $r=0.46$, $P<0.025$ V-test, 95% confidence interval $\pm 56^\circ$; (D) South-up magnets; mean angle = 357° , $r=0.34$, $P<0.025$ V-test, 95% confidence interval $\pm 90^\circ$. See text for statistical comparison of distributions.

disrupted, the turtles could rely on magnetic information. When both cues were simultaneously disrupted, however, then the turtles' orientation was altered.

Magnetic cues

The results imply that juvenile loggerheads used a magnetic compass to orient when visual cues were not available. A magnetic compass has been previously demonstrated to exist in both loggerhead (Lohmann, 1991; Light et al., 1993) and leatherback *Dermochelys coriacea* turtle hatchlings (Lohmann and Lohmann, 1993). In these young turtles, the magnetic compass presumably helps hatchlings maintain

an offshore heading during their migration from their natal beaches to the open ocean (for a review, see Lohmann and Lohmann, in press). The results of the present study provide strong evidence that juvenile loggerheads are able to maintain consistent headings using the Earth's magnetic field in a manner similar to that observed in hatchlings.

Visual cues

Although depriving turtles of both visual and magnetic information evidently affected their orientation (Fig. 7), the orientation of turtles with access to visual information alone did not differ from that of control turtles (Fig. 6). These data imply that swimming turtles can exploit visual cues to maintain headings. Although the results do not enable us to determine the precise type of visual information that was used, two types of celestial cues appear to be good candidates. One possibility is that juvenile loggerheads possess a time-compensated sun compass, as is present in numerous animals including pigeons (Schmidt-Koenig, 1960; Schmidt-Koenig et al., 1991), freshwater and terrestrial turtles (DeRosa and Taylor, 1980), fish (Hasler et al., 1958; Winn et al., 1964; Levin et al., 1992), and various invertebrates (Mouritsen and Frost, 2002; Scapini et al., 1999; von Frisch, 1967). Alternatively or additionally, turtles might exploit patterns of skylight polarization. This cue is used by desert ants during path integration (Wehner et al., 1996), by birds during migratory movements (Able and Able,

so (Fig. 7B,C). The Mardia-Watson-Wheeler test indicated that significant differences existed among the three groups ($W=11.89$, $P=0.02$).

Discussion

Juvenile loggerheads tethered in an experimental tank established and maintained directional headings in the absence of wave cues, familiar landmarks and chemical gradients (Figs 4, 5A, 6A, 7A). Although the results do not eliminate the possibility that turtles use some or all of these cues under other conditions, they imply that turtles under the test conditions relied on different cues to maintain orientation.

Turtles with unimpaired vision that swam in a distorted magnetic field did not orient differently from those in control groups (Fig. 5A–D). Similarly, turtles wearing goggles that deprived them of visual cues did not orient differently from control turtles if the magnetic environment around them was undisturbed (Fig. 6A–C). However, turtles that were simultaneously deprived of both magnetic and visual cues exhibited orientation that was significantly different from that of the control group (Fig. 7A–C). Taken together, these results imply that juvenile loggerheads possess at least two different means of maintaining a heading. When only magnetic cues were disrupted, the turtles could apparently compensate by using visual information; when only visual cues were

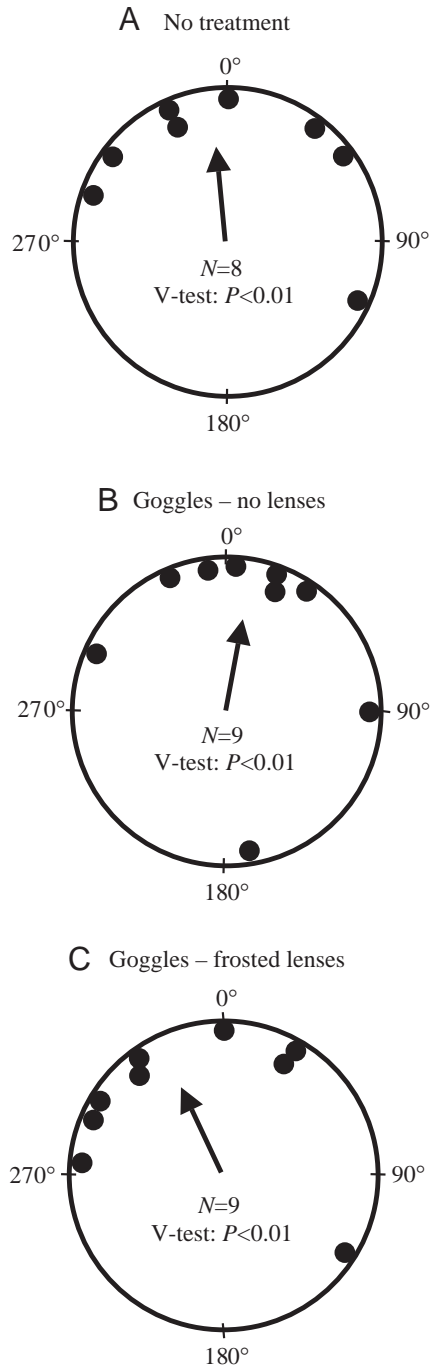


Fig. 6. Results of visual impairment experiment. Each dot represents the angular difference between an individual turtle's mean heading on Day 2 versus Day 1. Loggerheads in all three treatment groups maintained similar headings on Day 1 and Day 2. (A) No treatment; mean angle=356°, $r=0.61$, $P < 0.01$ V-test, 95% confidence interval $\pm 51^\circ$; (B) Goggles with no lenses; mean angle=9°, $r=0.58$, $P < 0.01$ V-test, 95% confidence interval $\pm 51^\circ$; (C) Goggles containing frosted lenses; mean angle=335°, $r=0.60$, $P < 0.01$ V-test, 95% confidence interval $\pm 48^\circ$. The expected direction in all cases was 0°. See text for statistical comparison of distributions.

are thought to have limited visual acuity in air (Ehrenfeld and Koch, 1967) and no obvious markings existed in the arena below water.

Use of multiple orientation cues

The finding that juvenile loggerheads can use at least two different directional cues to maintain headings closely parallels results reported for several other animals (Quinn and Brannon, 1982; Sinsch, 1990; for reviews, see R. Wiltschko and Wiltschko, 1995; Wiltschko et al., 1998). For example, young sockeye salmon *Oncorhynchus nerka* are able to orient using both celestial cues and a magnetic compass (Quinn, 1980). Similarly, young homing pigeons use a time-compensated sun compass when the sun is visible (Schmidt-Koenig, 1960; for a review, see Schmidt-Koenig et al., 1991), but rely on a magnetic compass when skies are overcast (Keeton, 1971; Ioalè, 2000). Older, more experienced pigeons appear to set headings based on compass information obtained from both the sun and the Earth's magnetic field (Wiltschko and Wiltschko, 2001).

In juvenile loggerheads, the relative importance and function of the different cues is not yet known. In principle, turtles might use solar or celestial cues when they are available but rely on magnetic cues at night, when the sky is overcast, or when water visibility is poor. Alternatively, both cues might be used simultaneously.

Orientation and homing behaviour

Under many circumstances, juvenile turtles displaced from their feeding grounds return to the areas where they were captured (Ireland, 1980; Musick and Limpus, 1997; Avens et al., 2003). Analyses of the directional headings of the 10 groups of turtles during their Day 1 trials suggested that many turtles attempted to home while tethered in the arena. For example, all groups had mean angles within 93° of the direction to the capture area. Nevertheless, some turtles swam in directions that did not lead toward the capture area, and only 3 of 10 distributions achieved statistical significance.

A likely explanation for this variability is that turtles in this study were tested during a range of seasons (late spring, summer and autumn) when the natural migratory and orientation behavior of the turtles differs. Many turtles migrate north either into or through the sounds of North Carolina in late spring, remain resident there or in feeding grounds further north during summer months, and migrate south in the fall

1993, 1996), and by several fish species (Waterman and Forward, 1970; Hawryshyn et al., 1990).

Yet another possibility is that each turtle cued in on some visual discontinuity or feature within the tank and used it as a reference to set and maintain a directional heading. Such a strategy would require that turtles, during their brief Day 1 trials, establish a heading that could be maintained using either a magnetic compass or visual markings that they have never before experienced, and then retained the ability to orient using both for at least 24 h. Although such a possibility cannot be excluded at present, we consider it unlikely because sea turtles

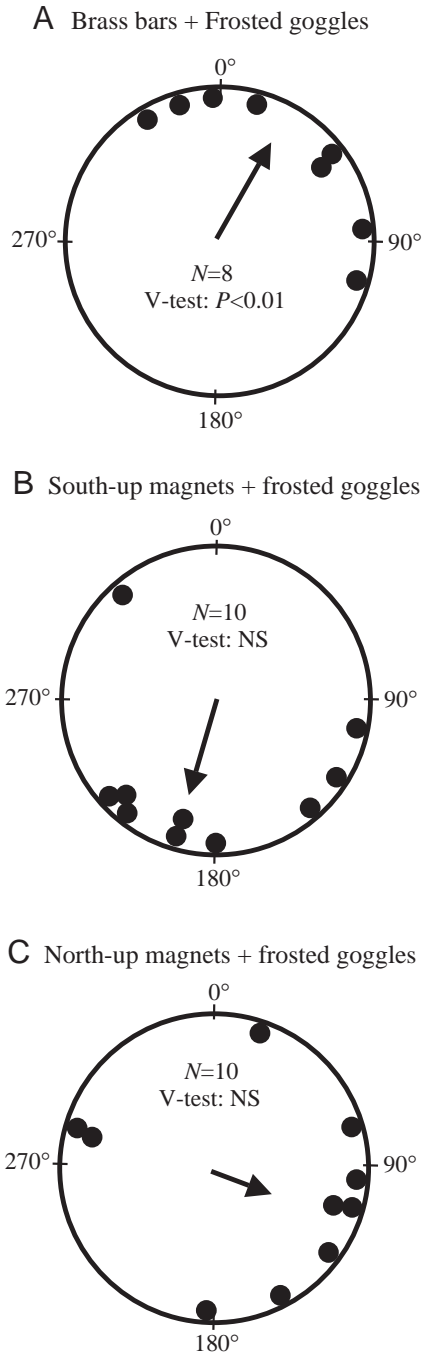


Fig. 7. Results of combined magnetic and visual impairment experiment. Each dot represents the angular difference between an individual turtle's mean heading on Day 2 versus Day 1. Turtles wearing frosted goggles and fitted with brass bars maintained an orientation direction from Day 1 to Day 2, while those bearing frosted goggles and magnets did not do so. (A) Brass bars + frosted goggles; mean angle = 31° , $r=0.69$, $P<0.01$ V-test, 95% confidence interval $\pm 41^\circ$; (B) South-up magnets + frosted goggles; mean angle = 196° , $r=0.65$, NS V-test; (C) North-up magnets + frosted goggles; mean angle = 110° , $r=0.37$, NS V-test. See text for statistical comparison of distributions. NS, not significant.

If some of the turtles were attempting to home to specific capture areas, then altered orientation might hypothetically result if an experimental treatment affected compass orientation, position-finding, or both. Although the possibility of an effect on a positional or 'map' system cannot be entirely ruled out, all turtles were kept at the test location for approximately 48 h before goggles or magnets were attached, thus providing the animals with an opportunity to determine their position long before sensory cues were disrupted during Day 2 trials. In addition, if the altered orientation (Fig. 7B,C) were due to disruption of a map system, then this would imply the existence of dual positioning systems, one based on magnetism and one based on visual cues. Although turtles (Lohmann and Lohmann, 1996; Lohmann et al., 2001) and some other animals (Phillips et al., 2002; Boles and Lohmann, 2003) are known to derive positional information from the Earth's magnetic field, no comparable positioning system based on visual cues has been demonstrated (Gould, 1998). Thus, we presently favor the interpretation that the results reflect an effect on compass orientation.

Apart from studies involving hatchlings (see reviews by Lohmann et al., 1997; Lohmann and Lohmann, 1998), most previous investigations of sea turtle orientation and navigation have been conducted in the ocean, where numerous cues are simultaneously available and the ability to control sources of directional and positional information is at best limited. The techniques developed in this study demonstrate for the first time that the orientation mechanisms of juvenile turtles can be studied under controlled conditions where cues can be manipulated with relative ease. Thus, the findings set the stage for additional investigations of the mechanisms underlying orientation and navigation in juvenile and adult sea turtles.

(Epperly et al., 1995; Musick and Limpus, 1997; NOAA Beaufort Laboratory, unpublished data). Thus, the turtles used in our experiments probably included individuals motivated to move toward different seasonally appropriate destinations rather than toward a single goal. Recent experiments have confirmed that the orientation behavior of juvenile turtles tested in arenas does indeed change seasonally; turtles tested during summer oriented toward the locations where they were captured (presumably in an effort to return to their feeding areas), whereas turtles captured during the autumn migratory season swam predominantly southward (Avens, 2003; L. Avens and K. J. Lohmann, manuscript in preparation).

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