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Perception of airborne odors by loggerhead sea turtles

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SUMMARY

Sea turtles are known to detect chemical cues, but in contrast to most marine animals, turtles surface to breathe and thus potentially have access to olfactory cues both in air and in water. To determine whether sea turtles can detect airborne chemical cues, captive loggerhead turtles (*Caretta caretta*) were placed into a circular, water-filled arena in which odorants could be introduced to the air above the water surface. Air that had passed across the surface of a cup containing food elicited increased activity, diving and other behavior normally associated with feeding. By contrast, air that had passed across the surface of an identical cup containing distilled water elicited no response. Increases in activity during food odor trials occurred only after turtles surfaced to breathe and peaked in the first post-breath minute, implying that the chemical cues eliciting the responses were unlikely to have been detected while the turtles were under water. These results provide the first direct evidence that sea turtles can detect airborne odors. Under natural conditions, this sensory ability might function in foraging, navigation or both.

Key words: orientation, navigation, olfaction, sea turtles.

INTRODUCTION

Chemoreception is ubiquitous among animals and is used for diverse purposes, including foraging (Nevitt et al., 1995; Derby et al., 2001; Clark, 2004), predator detection (Dielenberg and McGregor, 2001; Lukowiak et al., 2008), kin recognition (Todrank et al., 1998; Mateo, 2003), communication (Waldman and Bishop, 2004) and navigation (Hasler et al., 1978; Vickers, 2000; Lohmann et al., 2008a). Chemical cues may be particularly important to aquatic species, which often inhabit environments where visibility is poor and the availability of other sensory cues is limited (Wisenden, 2000; Lohmann et al., 2008a).

Most fish and many aquatic invertebrates spend their lives submerged in water and are rarely, if ever, above the air–water interface. As a consequence, the chemical senses of these animals have evolved to detect chemicals in water, the only medium that they normally encounter. By contrast, some aquatic and semi-aquatic animals surface to breathe and thus have access to chemical cues that exist not only in water but also in air.

At least a few species are known to detect chemical cues both in water and air. For example, American alligators (*Alligator mississippiensis*) can detect chemical cues while swimming under water (Weldon et al., 1990; Hansen, 2007) and can also perceive airborne odors from meat (Weldon et al., 1990; Weldon et al., 1992). Similarly, harbour seals (*Phoca vitulina*) can detect chemical cues related to salinity while submerged (Sticken and Dehnhardt, 2000), and can also detect airborne odorants potentially useful in foraging (Kowalewsky et al., 2006).

Sea turtles are another group of air-breathing aquatic animals that might, in principle, detect chemical cues both in water and in air. Several lines of evidence indicate that aquatic turtles in general, and sea turtles in particular, have good olfactory abilities (reviews by Bartol and Musick, 2003; Southwood et al., 2008; Schwenk, 2008). For example, electrophysiological recordings from cells in the olfactory and vomeronasal epithelia of several turtle species have revealed cells that respond to chemical cues (Shoji et al., 1993; Hatanaka and Matsuzaki, 1993; Brann and Fadool, 2006). Anatomical studies have indicated that aquatic turtles, including the loggerhead sea turtle (*Caretta caretta* L.), have well developed olfactory and vomeronasal organs (Parsons, 1971; Saito et al., 2001). Sea turtles are also known to open their nostrils and engage in a rhythmic ‘throat-pumping’ behavior while underwater, a process that floods the nasal cavities and may move water over the chemoreceptive organs (Walker, 1959; Manton, 1979; Schwenk, 2008). Several behavioral studies have provided evidence that sea turtles can perceive chemical cues (Manton et al., 1972; Grassman and Owens, 1982; Grassman et al., 1984; Constantino and Salmon 2003; Piovano et al., 2004).

Despite this considerable body of work, an unanswered question is whether sea turtles detect chemical signals carried by water, air or both. The behavioral experiments conducted so far have all involved presenting chemical cues to turtles while they were swimming in water but such studies do not resolve the matter because turtles were free to surface and some or all of the chemicals might have partitioned into air.

The question is important because the ability to detect airborne odorants might be useful to sea turtles in at least two naturally occurring situations. First, turtles navigating into the vicinity of remote islands, used as nesting sites, might be able to perceive the targets from considerable distances downwind if they are able to detect volatile chemicals associated with the island (Luschi et al., 2001; Hays et al., 2003; Lohmann et al., 2008b). Second, volatile chemicals such as dimethyl sulfide (DMS) emanate from oceanic regions in which productivity is high (Andreae and Raemdonck, 1983). Some seabirds use DMS to identify areas favorable for foraging (Nevitt et al., 1995); thus, turtles might also be able to exploit such cues as markers of promising foraging grounds. At present, however, whether sea turtles are able to exploit chemical signals transmitted through air has not been studied. In the present study we report the first direct experimental evidence that sea turtles can detect airborne odors. Under natural conditions, this ability may play a role in navigation, foraging or both.

MATERIALS AND METHODS

Animals

The eight loggerhead turtles used in the present study were obtained as hatchlings from nests deposited on beaches at Bald Head Island and Cape Lookout, NC, USA. Turtles were taken to the North Carolina Aquarium at Pine Knoll Shores, where they were raised for four months before being transferred to the University of North Carolina at Chapel Hill. In Chapel Hill, each turtle was maintained in a separate tank in re-circulating artificial seawater maintained at a temperature of 26–30°C. Lights in the facility were on for 12 h and off for 12 h each day. At the time of the experiment, turtles were between 25.3 cm and 31.6 cm curved carapace length (ccl) and approximately 1.5 years of age.

At both locations where the turtles were raised, they were fed the Mazuri Omnivore Aquatic Gel-based diet (www.mazuri.com). During the time of the experiments, turtles were fed every other day. Experiments were conducted on days when the turtles were not fed.

Preliminary observations

Preliminary observations of the turtles in their home aquaria during feeding revealed a characteristic pattern of behavior that provided the foundation for this study. We observed that within about 60 s after food was dropped into the aquarium, the turtles typically began to dive and crisscross the bottom of the tank repeatedly. When a piece of food was encountered, a turtle paused briefly to eat it, then quickly resumed crisscrossing the tank. This elevated level of activity often continued for a period of minutes even after all food in the aquarium had been consumed. Although little is known about this behavior, it seems likely that chemical cues from the food (dissolved in water under these conditions) elicited increased activity and searching behavior in the turtles.

We reasoned that if loggerhead turtles detect airborne food odors, then such odors might elicit searching behavior similar to that which normally occurs when food is introduced into the home aquarium. Our experiment was designed to investigate this possibility.

Experimental set-up

Experiments were conducted at the University of North Carolina in a laboratory located near to where the turtles were housed. The testing apparatus was a circular arena (48 cm in diameter) filled with artificial seawater to a depth of 28 cm. An opening in the side of the arena above the water line provided a portal through which airborne food odors could be delivered (Fig. 1). The portal was connected to a length of PVC pipe (74 cm in length and 5 cm in diameter), which extended through the wall of the room to an adjacent room from which the experiments could be monitored. A small fan at the far end of the pipe continuously moved air through the pipe and into the arena (Fig. 1). A t-joint at the end of the PVC pipe was arranged so that one opening was directed downward into a plastic cup and one opening was located 2 cm from the fan (Fig. 1). During experiments, the cup held either distilled water (as a control) or distilled water and a small amount (2 g) of gel food. When the fan was on, a gentle stream of air moved steadily into the t-joint, past the top of the cup and into the arena, presumably picking up airborne odors from the contents of the cup along the way.

The top of the arena was covered with a transparent Plexiglas lid. A small gap was left between the Plexiglas and the top of the arena on the side away from the odor portal. Thus, air entered the arena on one side, flowed across the surface of the water and escaped on the opposite side. A video camera was mounted on the ceiling and positioned above the arena, permitting the behavior of the turtle to be observed and videotaped from the adjacent room.

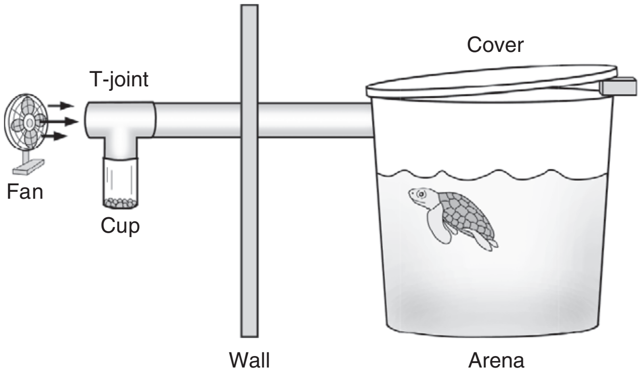

Fig. 1. Diagram of the experimental set-up (not to scale). The fan gently moved air through the PVC pipe, across the t-joint and opening of the cup, and into the arena where the turtle was tested. On the far side of the arena, a small opening between the cover and the top of the arena permitted air to escape (see text for details).

Experimental protocol

The behavioral responses of each turtle were monitored under two different conditions: (1) following exposure to airborne food odors; (2) following exposure to air that had passed over a cup of distilled water (as a control). The two test conditions were presented one after the other, separated by an interval in which airborne odors presented in the first trial were allowed to dissipate from the arena. To ensure that the order in which the odorants were presented did not affect the outcome, half of the turtles were subjected to the food odor first, while the other half were subjected first to distilled water trials.

At the start of experiments each day, the arena was filled with artificial seawater. An empty plastic cup was attached to the PVC pipe (Fig. 1) and the fan was turned on. After air had blown through the PVC pipe for several minutes, the turtle to be tested was placed into the arena. Upon release, each turtle typically circled the arena rapidly for several minutes, sometimes splashing vigorously. Within 10 min, however, these rapid movements subsided and the turtle instead began to swim steadily in one or another part of the arena. At this time, the video recording system was turned on and either the stimulus or control cup was affixed to the PVC pipe by gently pressing it onto the downward opening of the t-joint.

Once the cup had been put in place, observers recorded when the turtle surfaced and took its first breath; this moment presumably represented the point at which the turtle first had an opportunity to detect airborne odorants. For all turtles tested, this occurred between 3 s and 202 s after a stimulus cup was presented (mean=104 s). Videotaping continued for an additional 5 min after the time when a turtle took its first breath.

At the conclusion of the trial, the turtle remained in the arena while the stimulus cup was replaced with the empty cup. To disperse lingering odorants from the arena, the fan was left on to blow air continuously through the PVC pipe over the empty cup and into the arena. To further facilitate odor dispersal, the Plexiglas cover was removed from the arena and the door to the room was opened for at least 10 min to allow the test area to air out. A fan in the ceiling of the room connected to vents further enhanced air exchange.

After the arena and room were aired out for at least 10 min, the Plexiglas cover was replaced, all observers left the room and the turtle was given several minutes to resume its normal swimming behavior. Once it did, videotaping resumed and the turtle was presented with the second stimulus.

Measurement of activity

Videotapes of the 16 trials (eight with the food odor, eight with distilled water) were analyzed blindly by two observers who were unaware of the purpose of the study and did not know what stimuli had been presented to the turtles. To provide a simple, objective measure of activity, the circular arena was divided into four equal quadrants on the video screen. When the turtle surfaced to breathe for the first time at the start of the trial, observers recorded the quadrant in which the turtle's nose broke the surface of the water. Activity was measured in terms of traversals of the arena (i.e. the number of times that a turtle moved from one side of the circular arena to the other). Thus, when the turtle moved around the arena so that its nose reached the quadrant opposite the one in which it had surfaced, this was considered one traversal. Every subsequent time the location of the turtle's nose moved from one of these two quadrants to the other, an additional traversal was counted. Each traversal signified that the turtle had actively moved a considerable distance around the arena, an action consistent with the increased movement previously observed when turtles are searching for food (see 'Preliminary observations').

We also analyzed, in the same way, the behavior of the turtle during the interval that began when the airborne stimulus was introduced to the arena and ended when the turtle took its first breath. During this time, turtles were submerged and presumably did not have access to airborne cues. For the purpose of these measurements, the starting quadrant of the turtle was considered to be the quadrant in which the turtle's nose was located (below water surface) when the cup was put in place and the airborne odor was first introduced to the tank. Because it was impossible to predict when a turtle would surface to breathe, pre-breath intervals were of different durations for different turtles, (mean=104 s). For each of the 16 trials, a rate of traversals (traversals min^{-1}) was calculated for the period preceding the first breath and for the 5-min period after the first breath. This permitted a direct comparison of behavior immediately before and after the turtle gained access to airborne odors.

Statistical analysis

For each turtle, the total number of traversals that occurred during the control and food odor trials was determined. Results in the two treatments were compared using the Wilcoxon signed-ranks test.

To determine whether traversal rates changed after turtles took their first breath (as would be expected if turtles detected airborne odors), traversal rates (traversals per min) were calculated for the control and food odor trials and for the corresponding pre-breath intervals. The traversal rates for pre-breath and post-breath intervals for food odor trials were then compared using the Wilcoxon signed-ranks test. The same analysis was done for pre-breath and post-breath intervals in control trials.

If turtles detect airborne odors, then traversals would be expected to increase immediately after turtles first surface to breathe; by contrast, if airborne odors slowly diffuse into water and are detected below the surface, then responses would be expected to increase over time as the concentration of odorants in the water gradually increases. To investigate the time course of the response of turtles during the period after the first breath, the number of traversals by each turtle was determined for each minute during the course of each trial.

RESULTS

All eight turtles crossed the arena more times when exposed to the food odor than they did when exposed to the odor of distilled water alone (Table 1). The difference in responses to the two treatments was significant (Wilcoxon test, $T=0$, $P=0.005$, one-tailed), implying that turtles increase activity in the presence of air that has passed across food.

For control trials in which the odor source was distilled water, the mean traversal rate was 0.26 traversals min^{-1} during the pre-breath period and 0.40 traversals min^{-1} during the post-breath period (Fig. 2). No significant difference existed between the traversal rate during pre-breath and post-breath periods (Wilcoxon test, $T=9$, not significant).

For trials involving food odors, the mean traversal rate during the pre-breath period was 0.62 traversals min^{-1} and 2.85 traversals min^{-1} for the post-breath period (Fig. 2). The traversal rate for the post-breath period of the food odor trials was significantly higher than that of the corresponding pre-breath period (Wilcoxon test, $T=0$, $P=0.005$, one-tailed).

Analysis of traversals over the course of the 5-min trials indicated that, for turtles exposed to the food odors, the number of traversals peaked in the first minute after the first breath and then subsequently declined (Fig. 3). By contrast, the traversal rates of control turtles remained relatively constant throughout the 5-min trial period (Fig. 3).

DISCUSSION

The activity of juvenile loggerhead turtles, as measured by the number of times they traversed the arena, increased significantly in the presence of air that had passed over a cup containing food submerged in distilled water (Table 1; Fig. 2). No such increases in activity occurred during control trials in which turtles were exposed to air that had passed over a cup containing distilled water alone. These results imply that loggerhead turtles can perceive food odors carried through the air and respond to them by increasing activity that is normally associated with searching for food.

In principle, chemical cues emanating from turtle food might have been detected in several different ways. One possibility is that turtles perceived airborne odorants from the food. Alternatively, chemical cues emanating from the food might have gradually dissolved into the water of the arena as the scented air passed along the water surface. In the latter case, turtles might potentially have detected

Table 1. Summary of the total number of traversals for control trials (trials with distilled water alone) and food odor trials

Turtle	Traversals during control trials	Traversals during food odor trials
1	3	10
2	1	15
3	3	22
4	3	9
5	2	8
6	1	18
7	0	16
8	5	16
Total	18	114

Each turtle was tested under both conditions (see text for details). Each trial lasted 5 min. Turtles 1, 2, 4 and 6 were exposed to the control treatment first whereas turtles 3, 5, 7 and 8 were exposed to the food odor first.

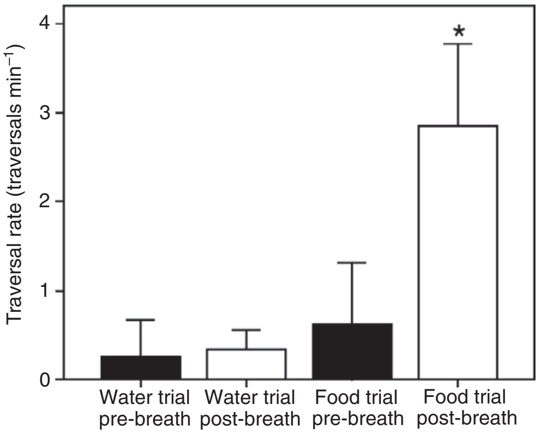

Fig. 2. Summary of turtle traversal rates. For the control trials (those involving a cup filled with distilled water alone), no difference existed between the pre-breath rate and the post-breath rate (Wilcoxon test, T=9, not significant). For trials involving food odors, the asterisk indicates that the post-breath rate was significantly higher than the pre-breath rate (Wilcoxon test, T=0, P=0.005, one-tailed). Error bars indicate the 95% confidence interval (see text for details).

chemicals using gustation or underwater olfaction without surfacing to breathe.

An analysis of behavior before and after turtles breathed provides evidence consistent with detection of airborne odors. In trials involving food odors, traversal rates did not increase until turtles first surfaced to breathe (Fig. 2), implying that turtles had to sample the air to perceive the odor. Moreover, the peak number of traversals occurred in the minute immediately after the first breath and then declined in subsequent minutes (Fig. 3). This pattern of behavior is consistent with aerial olfaction but difficult to reconcile with detection of chemical cues underwater. In the latter case, the concentration of chemicals in the water should have steadily increased over the entire trial, and the first breath (which occurred at variable times between 3 s and 202 s after the food odor was presented) should not have been followed by an immediate increase in activity.

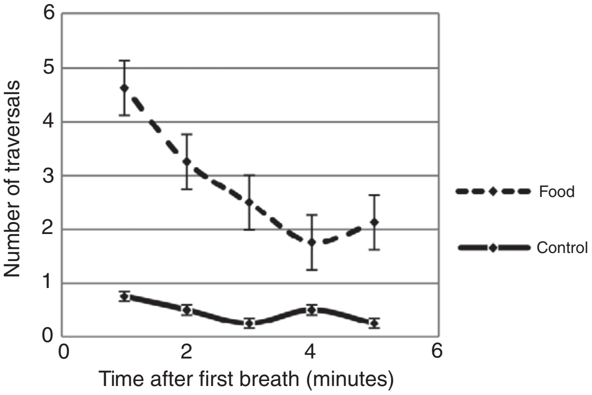

Fig. 3. Number of traversals in relation to time after first breath. Each data point indicates the mean number of traversals (for N=8 turtles) that occurred during each min of the 5-min food trials and control trials. Error bars indicate the standard error of the mean. On the horizontal axis, zero indicates the time in the trial at which each turtle took its first breath (see text for details).

The behavior elicited by the airborne food odor closely resembled behavior observed when food was added to the home aquaria of the turtles. All turtles used in this study had been raised in captivity and received the gel food at least several times a week throughout their lives. During feeding sessions, food was typically brought into the turtle facility and kept there for several minutes before it was placed in the aquaria. Thus, one possibility is that the captive turtles used in these experiments learned to associate airborne odors of their food with the experience of being fed. An alternative possibility, however, is that all loggerhead turtles respond with increased activity to the odors that emanate from the gel food, regardless of whether they have encountered the food before. Additional experiments with wild-caught turtles unfamiliar with the gel food will be needed to resolve this issue. Regardless, the results imply that sea turtles can detect airborne odorants.

The way in which this ability is used under natural conditions is not known. One interesting possibility is that the presence of certain, specific, airborne odors might signal favorable feeding areas. An odor that might be particularly useful in oceanic foraging is DMS, a scented compound that has been studied in the context of global climate change (Kettle et al., 1999). DMS is the hydrolysis product of dimethylsulfoniopropionate (DMSP), a compound produced by phytoplankton (Kirst et al., 1991; Karsten et al., 1992). High concentrations of DMS are often associated with coastal upwelling areas and other oceanic regions with high productivity (Andreae and Raemdonck, 1983; Kettle et al., 1999). Some seabirds detect DMS and use it to identify areas that are likely to be favorable for foraging (Nevitt et al., 1995; Nevitt et al., 2008). Harbour seals are also capable of detecting DMS (Kowalewsky et al., 2006). If sea turtles can perceive DMS (or any other airborne chemical associated with food), then this ability might function in helping them locate productive oceanic areas for foraging.

Additionally or alternatively, airborne odors might play a role in the navigation of sea turtles under some conditions. Sea turtles of many populations and species migrate long distances and are thought to rely at least partly on the Earth's magnetic field for guidance (e.g. Lohmann et al., 2004; Lohmann et al., 2007; Lohmann et al., 2008a; Luschi et al., 2007). Additional cues are also likely to be involved, however, especially when turtles have arrived in the general vicinity of target areas and need to pinpoint islands, nesting areas or other specific locations (Lohmann et al., 1999; Putman and Lohmann, 2008). Airborne odorants have been proposed to play a role in helping turtles locate islands at the end of long migrations (Luschi et al., 2001; Hays et al., 2003; Lohmann et al., 2008b). Our results confirm for the first time that sea turtles can indeed perceive airborne odors, suggesting that the use of airborne chemical cues in navigation might be plausible. For example, turtles migrating through open ocean might detect nearby land by perceiving odorants from coastal vegetation or soil; similarly, on a smaller spatial scale, airborne odors from decaying turtle eggs laid in previous seasons, or of other turtles nesting on land, might signal the existence of nearby nesting areas.

The finding that sea turtles can detect chemical cues in air extends the growing list of environmental cues that these animals are known to perceive but also raises many additional questions. Further studies will be needed to determine the sensitivity of sea turtles to airborne odorants, which chemical cues can be detected, the physiological mechanisms that underlie aerial olfaction, and the purpose or purposes for which this sensory ability is used under natural conditions.

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