

THREE-DIMENSIONAL ODOR TRACKING BY *NAUTILUS POMPILIUS*

JENNIFER A. BASIL^{1,*}, ROGER T. HANLON^{1,2,‡}, SARAH I. SHEIKH² AND JELLE ATEMA¹

¹*Boston University Marine Program, Marine Biological Laboratory, Woods Hole, MA 02543, USA* and ²*Marine Resources Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA*

*Present address: Biology Department, Brooklyn College, Brooklyn, NY 11210, USA

‡Author for correspondence at address 2 (e-mail: rhanlon@mbl.edu)

Accepted 17 February; published on WWW 6 April 2000

Summary

The ‘living fossil’ *Nautilus pompilius* is thought to use olfaction as its primary sensory system during foraging, yet neither the organs responsible for olfaction nor the mechanisms or behaviors associated with odor tracking have been subjected to experimentation. Flume testing under dark conditions revealed that *Nautilus* could consistently detect and follow turbulent odor plumes to the source over distances up to 10 m, exhibiting two types of orientation behavior while sampling in three dimensions. The paired rhinophores were necessary for orientation behavior: when they were temporarily blocked either uni- or bilaterally, *Nautilus* detected odor but could not track

the plume and locate the source. Animals that were tested post-blockage were able to track and locate the source. The role of the 90 thin tentacles remains enigmatic; they seemed to be able to detect odor, but they were not capable of guiding orientation behavior towards a distant odor source. Bilateral chemical sensing by rhinophores in three dimensions may have been the *Umwelt* of ammonites and belemnites before the evolution of complex eyes and fast locomotion in modern coleoids.

Key words: *Nautilus pompilius*, olfaction, odour tracking, behaviour, orientation, rhinophore.

Introduction

The few species of living *Nautilus* are the only representatives of the externally shelled cephalopod molluscs that flourished in the seas between 20 and 495 million years ago. Modern coleoid cephalopods, squid, cuttlefish and octopus, show greatly modified morphology and brain development that support a fast, predatory lifestyle. The behavior and neurobiology of living *Nautilus* may therefore provide insight into the sensory capabilities and behavioral ecology of similar inhabitants of ancient oceans.

Nautilus pompilius lives in dimly lit waters for most of its life, remaining in deep waters during the day (approximately 300 m) then migrating vertically up tropical coral-reef slopes at night to forage in waters as shallow as 75 m (Carlson et al., 1984; Ward et al., 1984; Ward, 1987; O’Dor et al., 1993). *Nautilus* appears to be primarily a scavenger on crustaceans, nematodes and echinoids; there is also some evidence that it preys on hermit crabs and may dig in soft sediment for small prey items (Ward and Wicksten, 1980; Saunders and Ward, 1987; Hanlon and Messenger, 1996). The anatomy of its primitive pinhole eye suggests that vision is not the most essential sensory system for foraging, as it is for most modern coleoids (Barber, 1987; Muntz, 1987, 1991; Messenger, 1991; O’Dor et al., 1993).

Behavioral descriptions of *Nautilus* have referred to them as ‘smellers and gropers’ that use far-field and near-field chemical detection to locate prey items (Bidder, 1962; Young, 1965; Barber and Wright, 1969; Hamada et al., 1980; Ward and

Wicksten, 1980; Saunders and Ward, 1987). *Nautilus* has approximately 90 thin tentacles and will extend them and swim forward when a dead fish or crustacean is brought within close proximity (Bidder, 1962; Saunders, 1984). Although these tentacles possess cells that, under a scanning electron microscope, resemble tastebuds (Hamada et al., 1980; Fukada, 1987), there has yet to be physiological or behavioral research demonstrating sensory function. *Nautilus* are also equipped with a pair of rhinophores, each one a fleshy papilla approximately 4 mm long located below each eye and open to the exterior by a narrow pore (Barber and Wright, 1969; Barber, 1987). The epithelium at the base of each papilla has flask-shaped, ciliated cells that are similar in ultrastructure to chemoreceptors located in the suckers of *Octopus* spp., the olfactory organs of squids and the lips of *Sepia* spp. (Graziadei, 1964, 1965; Emery, 1975, 1976; Barber, 1987). These organs, and the large central nervous system lobes to which they are connected neurally, are similar in structure to the olfactory organs in *Octopus* and other cephalopods (Young, 1965). Nevertheless, there is little experimental evidence concerning the function of olfactory organs in cephalopods (Lucero et al., 1992; Danaceau and Lucero, 1998; Boal and Marsh, 1998) and none in *Nautilus*. The behavioral function of these organs may differ substantially between *Nautilus* and coleoids considering their differences in morphology, physiology, ecology and phylogeny. Specifically, several researchers have hypothesized that *Nautilus* locates food through a combination of smell and

touch (Bidder, 1962; Ward and Wicksten, 1980; Saunders, 1984; Ward, 1987; O'Dor et al., 1993), moving up the 'concentration gradient' (O'Dor et al., 1993) produced by a distant odor source until it makes contact with the item with its tentacles.

Odor plumes, however, do not produce simple concentration gradients; they are turbulent and patchy by nature (Murlis and Jones, 1981; Bell and Cardé, 1984; Moore and Atema, 1991; Basil and Atema, 1994; Atema, 1996). Most animals use a combination of flow and chemical information to locate a distant odor source such as a food item or a mate. Neither the chemo-orientation behavior of *Nautilus* nor the attendant odor dispersal conditions guiding it have been investigated experimentally. Here, we demonstrate through controlled manipulation of the odor environment, and by selective and reversible olfactory blockage, that *Nautilus* (i) detects odor at a distance of up to 10 m, (ii) uses odor-plume information to locate the odor source, and (iii) relies primarily upon its rhinophores for this localization behavior.

Materials and methods

Twelve *Nautilus pompilius*, captured in the Philippines and maintained at the Marine Biological Laboratory, Woods Hole, MA, USA, were tested in dark conditions for their ability to find, within 20 min, an odor source located 2.0–10 m upstream from their start position in a 14.5 m × 2 m × 1.5 m recirculating flume with near-laminar flow at 7 cm s⁻¹. The odor source was a 30 g l⁻¹ homogenate of shrimp diluted in sea water to 1.5 % and dyed with inert Rhodamine for visualization. In the 'odor' condition, this solution was injected as a constant jet into the background flow of the flume by a gravity-fed pipette placed half-way up the 24 cm deep water column. In the 'no odor' condition, a similar volume of sea water and dye alone was injected. The Reynolds number of the jet at its source was always approximately 1000, resulting in a long turbulent plume increasing in diameter from 1 cm near the source to approximately 15 cm at a distance of 2.0 m. Each animal was tested once in the odor and once in the no odor condition on separate days and in random order. Because flume temperature (18 °C) was close to their upper temperature tolerance (approx. 21 °C), animals were never kept in the flume for longer than 2 h. Their health in this recirculating flume system during the summer thus constrained the duration of our experiments. The orientation paths of animals were videotaped (at 30 frames s⁻¹) from above and from the side, with image-intensifying cameras, and then digitized off-line. Trials were digitized at 1 s, beginning at the moment the dyed plume contacted the resting animal until the animal reached the source or until 20 min had elapsed, whichever came first.

To identify the primary chemoreceptors, we performed selective and reversible blockage of the rhinophores to determine their role in chemical detection and tracking behavior. Before the rhinophores were blocked, each animal was first tested intact to ensure receptivity to the odor stimulus. The 12 animals were tested twice each, a month apart, and each

was lesioned (blocked) in two randomly chosen ways. We blocked the rhinophores of three groups of animals ($N=24$; eight animals in each group): (i) bilaterally blocked animals had both their rhinophores filled with 1 ml of Vaseline, (ii) unilaterally blocked animals had either the right or the left rhinophore filled with Vaseline, and (iii) sham-blocked animals were handled in an identical manner but their rhinophores were not filled with Vaseline. Inert Rhodamine in the Vaseline allowed us to verify the presence or absence of the Vaseline plug in the rhinophore. For these procedures, all animals were removed from the water for 5 min, and all were touched by the syringe filled with Vaseline for the same amount of time. To determine how soon these blockages were reversible (i.e. when the *Nautilus* ejected the Vaseline from the rhinophore pit), some blocked animals were retested 2 h after Vaseline injection ($N=4$ due to temperature constraints, see above). Of the sham-blocked animals, six oriented towards and reached the source while two did not, showing an effect of handling on the animals. Therefore, the sham condition was used for the expected value in evaluating results of blockage experiments.

Results

All 12 animals in the odor condition successfully located the source at 2.0 m within 2 min of initial encounter with the dyed stimulus (mean 43.5 s). None of the 12 animals in the no odor control condition moved from the start position during the entire 20 min trial. Thus, any up/downstream swimming or cross-current swimming took place only when odor was present. Source-generated hydrodynamic stimuli alone did not elicit swimming behavior. A few seconds after the odor contacted an animal in the start position, the *Nautilus* became active, spread its tentacles and began to swim. The animals swam with their tentacles extended, and they moved up the odor plume close to its cross-sectional center. Individual animals swam towards the source either shell first or tentacles first; the swimming position did not affect the ability of the animal to locate the source successfully. Animals did not swim solely upstream (Fig. 1C, magenta path), but often made brief excursions downstream during a trial when odor was present. When the animals came close to the odor source (within approximately 20 cm), their behavior changed; they slowed, then approached the odor source with their tentacles spread widely, especially the ventral digital tentacles, indicating that these tentacles may be important for near-field detection of the odor source. The overall paths of animals in the plume suggested that they found the odor source by moving in all three planes: left and right; up and down; up-current and down-current (Fig. 1A–C). Subsequent analysis (Fig. 1D) of the 'heading angle' (i.e. the angle in a horizontal plane between the animal's swimming direction and a straight path to the source) demonstrated that their heading angles first decreased as they moved towards the source. Specifically, at distances greater than 120 cm from the source, their headings were on average 57° to the right or the left of the source. Between 120 and 60 cm from the source, they were oriented on average only 35° to the right or left of the

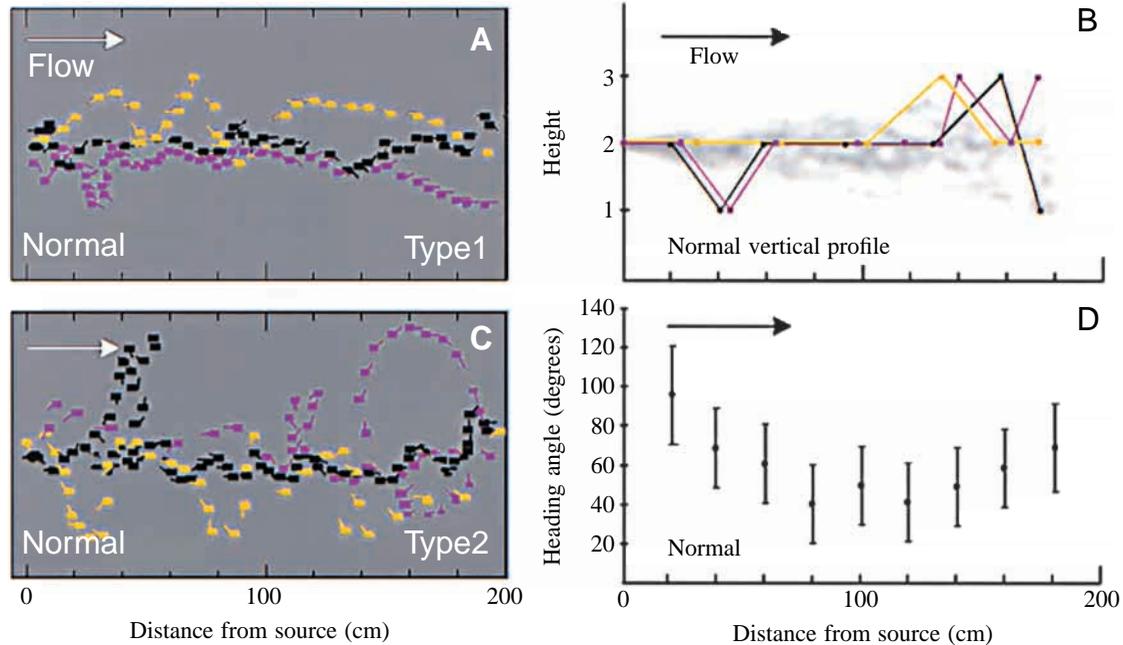


Fig. 1. Chemosensory behavior in *Nautilus pompilius*. (A) Source-directed tracks (type 1) of three *Nautilus* (in the x,y horizontal plane) to a distant odor source (black-filled circle on the left). Each rectangle symbolizes the position of an individual animal at each second. The projections on *Nautilus* rectangles indicate whether the tentacles are facing forwards or backwards. Water flow is from left to right (arrow); paths are digitized at 1 s intervals. (B) Vertical excursions of the three *Nautilus* in A as they tracked a distant odor. Height was scored as below the odor plume (1), in the plume (2) or above the plume (3). The shaded area represents the approximate dimensions of the turbulent odor plume. (C) Cross-current tracks (type 2) of three *Nautilus* (in the x,y horizontal plane) to the odor source. Animals using type 1 tracks took significantly less time to reach the source (mean 35.5 s) than those using type 2 tracks (mean 59 s; t -test, $P < 0.03$). (D) Mean absolute heading angles (mean \pm s.e.m.) for all 12 *Nautilus* orienting to a distant odor source (0 on the x -axis) in the untreated (normal) condition (including both type 1 and type 2 tracks). *Nautilus* showed an initial decrease in heading angle, followed by a stable heading angle, and heading angle then increased as the animals approached the source.

source. However, heading angles increased again to 65° when the animals were within approximately 60 cm of the source (Fig. 1D), perhaps indicating that there is a gradual switch to a different behavior, possibly involving the tentacles.

Successful foragers exhibited at least two types of orientation behavior. Eight animals became more source-directed (type 1) as they approached the source (Fig. 1A, three paths) and four swam back and forth across the current (type 2) until they reached the source (Fig. 1C, three paths). More specifically, the time taken to complete a trial was bimodally distributed: the source-directed group (type 1) took on average 35.5 s to complete a trial, while the other group took on average 59 s (t -test, $P < 0.03$). The *Nautilus* maintained a steady average ground speed of 5 cm s^{-1} regardless of their orientation with respect to the flow, demonstrating that they were able to compensate for background flow under a variety of conditions.

Vertical sensing (Fig. 1B) was revealed as animals swam above and below the odor plume during approaches to the source. Although *Nautilus* spent the greatest proportion of time within the plume, 10 of the 12 animals coursed through the plume in the vertical plane. *Nautilus* tended to vertically swim above the plume (Fig. 1B) at distances greater than 100 cm from the source, while they swam vertically below the plume when nearer the source. Each vertical excursion either above

or below the plume lasted on average less than 5 s, indicating that the animals rapidly detected a loss of odor and then compensated their swimming height. Using the video recordings filmed through the Plexiglas side of the flume, we were able to describe the behavior of the tentacles as the animals approached the source. In general, *Nautilus* extended their tentacles in the start location when they first came into contact with the odor plume. As they swam towards the odor source, they gradually extended their tentacles farther, up to a full body length in extension, once they reached the source.

We also tested three animals for their ability to find an odor source located 6 or 10 m upstream (approximately 1000 body lengths) from the start position. Each animal was successful within approximately 10 min when the odor was 6 m upstream, and two of the three found the source when it was located 10 m upstream. In addition, when we moved the odor source slowly vertically and horizontally during a trial with one of these animals, the *Nautilus* was capable of tracking this plume emanating from the moving source.

None of the eight unilaterally blocked animals and one of the eight bilaterally blocked animals found the odor source (Fisher's exact test, $P < 0.02$ for bilaterally blocked animals compared with sham-blocked, and $P < 0.003$ for unilaterally blocked animals compared with sham-blocked; Fig. 2C–F).

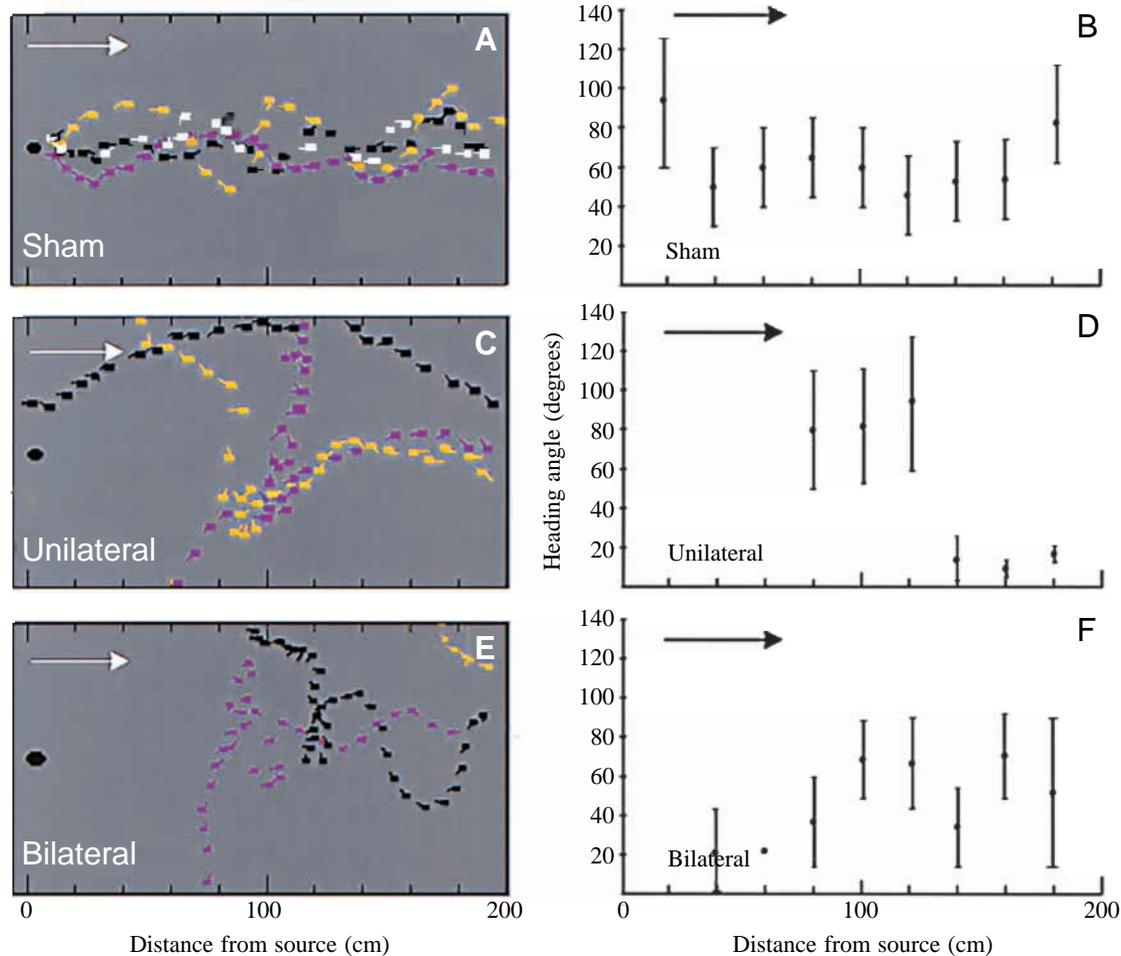


Fig. 2. Paths of *Nautilus pompilius* that had been (A) sham-operated (or tested 2 h after ejection of the Vaseline plug; white symbols), (C) unilaterally blocked, and (E) bilaterally blocked. Note that most unilaterally and bilaterally blocked animals did not reach the source (as illustrated). For further details, see Fig. 1. (B,D,F) Mean absolute heading angles (mean \pm S.E.M.) for all *Nautilus* ($N=8$ for each group) orienting to a distant odor source (0 on the x -axis) in the sham-blocked, unilaterally blocked and bilaterally blocked conditions, respectively. The x -axes are identical to those in A, C and E. Each point represents the mean heading angle of all animals averaged over 20 cm (e.g. the point at 120 cm represents the mean value for all animals from 120 to 140 cm from the source). (B) Sham-blocked condition: animals showed a similar gradient in heading angles to those in the normal condition (see Fig. 1D) as they approached the source. (D) Unilaterally and (F) bilaterally blocked animals: heading angles varied greatly as they searched but failed to locate the source.

The one bilaterally blocked animal that found the source began swimming upstream outside the odor plume for over 1 m, and then turned into the odor stream only 20 cm from the source. It then extended its tentacles and moved straight for the source. Instead of tracking from the start position, this animal appeared to encounter the near field of the source by chance, so that the tentacles may have steered its final approach.

Orientation behavior differed substantially among the three groups of animals (Fig. 2). Sham-blocked animals (Fig. 2A) swam in a manner similar to intact animals, first decreasing their headings significantly as they approached the odor source (Fig. 2B). The overall effect of distance from the source on heading angles was significant; overall analysis of variance, ANOVA, $F_{16,772}=2.85$; $P<0.0001$. Headings decreased then increased as sham-blocked animals approached the source (*post-hoc* Tukey HSD test, $P<0.03$). Bilaterally and unilaterally blocked animals (Fig. 2C–F) swam in a strikingly

different manner: they initiated searching by swimming upstream upon first exposure to the odor stimulus with headings that were not significantly different from one another. Between 120 and 60 cm from the source, unilaterally (Fig. 2C,D) and bilaterally (Fig. 2E,F) blocked animals swam increasingly cross-current, resulting in increased heading angles. The cross-current swimming behavior of rhinophore-blocked animals continued until they swam downstream and rested in the start position or until the trial ended after 20 min. Finally, successful tracking ability returned to the four *Nautilus* that were retested 2 h later: having ejected the Vaseline block, they behaved like untreated and sham-treated animals (Fig. 2A, white symbols).

Discussion

Nautilus pompilius is clearly dependent upon its paired

rhinophores for localization of a distant odor stimulus. Under our test conditions, water current alone did not elicit swimming behavior, the presence of odor was required. None of the animals in the 'no odor' condition exhibited tracking behavior of any kind. Since at 2 m even the odor patches of highest concentration are diluted 10 000-fold, and the more common lower-concentration patches are diluted 100 000-fold (Moore and Atema, 1991; Basil and Atema, 1994), the ability of *Nautilus* to detect, track and find an odor source 10 m away demonstrates a sensitive plume-tracking system that is heavily reliant on chemical information. This spatial scale of tracking is relevant to an animal that regularly swims and migrates vertically along coral-reef slopes, where many of its potential prey items are located (e.g. crustacean molt shells, hermit crabs; Ward and Wicksten, 1980).

While *Nautilus* can detect the presence of odor without information from its rhinophores (probably using its array of tentacles), it cannot maintain a heading to locate the source successfully. The striking recovery of successful tracking in animals that had ejected their rhinophore plug of Vaseline demonstrates the essential role of the rhinophores in this behavior (Fig. 2A). It was noteworthy that the heading angles of intact *Nautilus* approaching an odor source increased to 65° when they approached within approximately 60 cm of the source (Fig. 1D). A similar increase in heading angles has been observed in the plume-tracking behavior of lobsters when they approach within 40 cm of an odor source (Moore et al., 1991); at that point, lobsters start grasping with their legs, suggesting a switch from olfactory plume-tracking to feeding behavior mediated by taste receptors in the legs. The tentacles of *Nautilus* may play a role in this gradual switch to a different behavior upon close approach to an odor source.

The behavior of the unilaterally blocked animals was particularly interesting because they had one intact rhinophore and could hypothetically detect which way was upstream (the mean direction to the source) perhaps, like moths (Murlis et al., 1992), using visual information to maintain the correct heading. The few field observations of *Nautilus* indicate that they may stay within tens of meters of coral-reef slopes as they migrate vertically, which could provide a potential visual reference for them to maintain a heading (Saunders, 1984; Zann, 1984; Carlson et al., 1984; Ward et al., 1984; O'Dor et al., 1993). Yet unilaterally blocked animals did not maintain a source-directed search pattern, despite having turbulent flow and potential visual information available in the dimly lit flume. This suggests that *Nautilus* may be heavily reliant upon chemical information to guide its search, perhaps without an external reference point, visual or otherwise. *Nautilus* did not respond to a hydrodynamic (no odor) stimulus alone. Therefore, odor must be present for *Nautilus* to be stimulated to find a distant, plume-producing source; i.e. flow information from the source jet alone is not sufficient to stimulate or guide these animals rheotactically. The concentrations and distances in these trials were, in a very general way, comparable with conditions in the natural habitat of *Nautilus*. Since *Nautilus* does not have a high rate of food intake (Ward and Wicksten, 1980; Saunders and

Ward, 1987), has a low metabolic rate (Wells et al., 1992; Boutilier et al., 1996) and may sample the water column vertically, it may be able to exploit a slowly dispersed signal such as an odor to find food rather than relying upon the energetically expensive pursuit of prey that is characteristic of coleoids guided by vision and fast locomotion (O'Dor et al., 1993; Hanlon and Messenger, 1996). This would allow *Nautilus* to occupy a unique sensory niche in nature: tracking dead-prey odor that emanates from deep coral-reef slopes during vertical migrations that take place under dark conditions.

Taken together with previous morphological and neuroanatomical evidence for an olfactory function for the rhinophore (Young, 1965; Barber and Wright, 1969; Barber, 1987), these behavioral experiments (i) illustrate the three-dimensional olfactory capabilities of *Nautilus*, (ii) provide the first demonstration that rhinophores serve a primary olfactory function, and (iii) show that the bilateral organization of the rhinophores is essential for *Nautilus* to steer along a turbulent odor plume at distances of up to 10 m (or more, not tested). This chemically guided behavior, supported by bilateral olfactory organs, is similar to that of lobsters, nocturnal animals that occupy similar benthic habitats (Moore and Atema, 1991; Basil and Atema, 1994; Atema, 1996), except that *Nautilus* samples the vertical (or third) dimension as well. Planktonic shrimps rely less heavily upon their bilateral chemoreceptors, tracking odor from a falling food item through a combination of horizontal circular casting and, once the odor is encountered, downward vertical tracking (Hamner and Hamner, 1977). Our laboratory findings corroborate telemetry data (Carlson et al., 1984; Ward et al., 1984; O'Dor et al., 1993) from *Nautilus* in nature: vertically foraging *Nautilus* could potentially detect quantities of odor from horizontal cross-currents along the coral reef slopes and sample them in all dimensions even against a moderately strong flow. The surprisingly fast initial reaction of *Nautilus* to an odor stimulus in the plume should, in retrospect, have been expected of a vertical sampler of cross-currents. In the complex environment of a coral-reef/oceanic interface, detecting and following wisps of odor from prey would be conducive to the smelling and groping mechanism of a vertical scavenger. The role of the tentacles in this tracking behavior remains enigmatic; future investigation might benefit from research on tentacular function in other molluscs (e.g. Chase and Croll, 1981; Lemaire and Chase, 1998). Our analysis of the odor-plume tracking behavior of *Nautilus*, an animal that has remained relatively unchanged for millions of years (Saunders and Landman, 1987; Ward and Saunders, 1997), suggests a mechanism and function for a rhinophore-based sensory system that may have guided the behavior of ancient cephalopods.

The authors thank Mrs Ellen Grass and the Grass Foundation for scientific and financial support of this project. We also thank Rainer Voigt for providing software for digitalization and path analysis. John Apolinski of JCA-International located and shipped us animals in healthy

condition. Robert Bullis, Janice Hanley and William Mebane of the Marine Biological Laboratory (MBL) provided excellent veterinary and animal care for the *Nautilus*. We thank Jean Boal, Frank Grasso, Elise Hugus, Arthur Humes, Alan Kamil, Ron and Janet O'Dor, Nadav Shashar, John Dowling and Grass Fellows at the MBL for thoughtful comments regarding this manuscript. Care of *Nautilus* was in accordance with institutional and NIH guidelines.

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