

## Sharks need the lateral line to locate odor sources: rheotaxis and eddy chemotaxis

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### Summary

Odor plumes are complex, dynamic, three-dimensional structures used by many animals to locate food, mates, home sites, etc. Yet odor itself has no directional properties. Animals use a variety of different senses to obtain directional information. Since most odor plumes are composed of dispersing odor patches and dissipating vorticity eddies, aquatic animals may localize odor sources by simultaneous analysis of chemical and hydrodynamic dispersal fields, a process referred to as eddy chemotaxis. This study examines the contributions of olfaction, mechanoreception and vision to odor source localization in a shark, the smooth dogfish *Mustelus canis*. Two parallel, turbulent plumes were created in an 8 m flume: squid rinse odor and seawater control. Minimally turbulent ‘oozing’ sources of odor and seawater control were physically separated from sources of major turbulence by placing a brick downstream from each oozing source, creating two turbulent wakes, one or the other flavored with food odor. This created four separate targets for the sharks to locate. Animals were tested under two light conditions (fluorescent and infrared) and in two sensory conditions (lateral line intact and lateral line lesioned by streptomycin). Intact animals demonstrated a preference for the odor plume over the seawater plume and for the source of odor/turbulence (the brick on the odor side) over

the source of the odor alone (the odor-oozing nozzle). Plume and target preference and search time were not significantly affected by light condition. In the light, lesioning the lateral line increased search time but did not affect success rate or plume preference. However, lesioned animals no longer discriminated between sources of turbulent and oozing odor. In the dark, search time of lesioned animals further increased, and the few animals that located any of the targets did not discriminate between odor and seawater plumes, let alone targets. These results demonstrate for the first time that sharks require both olfactory and lateral line input for efficient and precise tracking of odor-flavored wakes and that visual input can improve food-finding performance when lateral line information is not available. We distinguish between rheotaxis: orientation to the large-scale flow field (olfaction, vision and superficial lateral line), eddy chemotaxis: tracking the trail of small-scale, odor-flavored turbulence (olfaction and lateral line canals), and pinpointing the source of the plume (lateral line canals and olfaction).

Key words: *Mustelus canis*, lateral line, olfaction, plume tracking, rheotaxis, chemotaxis.

### Introduction

Sharks have a keen sense of smell, which in many species is critical for locating their food (Bateson, 1890; Sheldon, 1909; Sheldon, 1911; Parker and Sheldon, 1913; Parker, 1914). They can find food sources without visual cues, while animals with their nostrils blocked show no interest in prey; blocking one nostril causes turning behavior to the intact side [‘circuit movements’ (Sheldon, 1911)], suggesting that these animals steer by comparing odor concentration bilaterally [‘chemotropotaxis’ (Fraenkel and Gunn, 1940)]. When presented with an attractive odor stimulus, the lemon shark *Negaprion brevirostris*, a pelagic species, swims upstream into

the strongest current, regardless of where the odor source was actually located (Hodgson and Mathewson, 1971), suggesting that this species’ reaction to an odor stimulus is to swim in the mean up-current direction, a process referred to as ‘chemically stimulated rheotaxis’. How they determine the up-current direction was not studied. This response would presumably bring them in proximity of the odor source where other senses, such as vision, would then allow the animal to precisely pinpoint the source (Mathewson and Hodgson, 1972). In contrast, the nurse shark *Ginglymostoma cirratum*, a benthic species, moves up the odor corridor to the source (Hodgson and Mathewson, 1971; Mathewson and Hodgson, 1972),

suggesting that for this species, a chemical stimulus triggers true concentration gradient searching ('chemo-klinotaxis'). However, these animals are unable to precisely locate an odor source in stagnant water (Kleerekoper et al., 1975), suggesting that flowing water provides a directional vector for localization. In none of these studies was the eddy fine structure of the odor dispersal process characterized or even considered. However, the chemical and momentum dispersal fields typically associated with odor sources in nature contain spatial gradients (of diluting odor peaks and decaying vorticity eddies respectively) that can provide information about the direction and distance to the source.

Analysis of the fine structure of odor plumes guiding animal behavior indicated that they consist of highly dynamic and intermittent patterns of odor patches and filaments, caused by turbulent mixing (Murliss and Jones, 1981; Elkinton and Cardé, 1984; Atema, 1985; Moore and Atema, 1991; Webster, 2007). As the time-averaged concentration of these peaks converges too slowly to be useful to an animal tracking an odor plume (Elkinton and Cardé, 1984; Webster and Weissburg, 2001), it is unlikely that a shark could locate an odor source based solely on mean concentration gradients as previously implicated (Hodgson and Mathewson, 1971; Mathewson and Hodgson, 1972). However, the eddies of the turbulent wake left behind by moving prey or by a dead food item lying in moving water are flavored with the odor of the prey or food. In complete darkness, catfish track the odorous vortex trail left behind live prey, relying heavily on their lateral line (Pohlmann et al., 2004). Simultaneous detection of these flavored eddies by chemo- and mechanoreceptors could provide animals both with detailed information about the chemical identity of the source and with directionality in the decaying wake for tracking it to the source, a process referred to as eddy chemotaxis (Atema, 1996). Many animals have chemo- and mechanoreceptor senses located in close proximity and one might predict that their input converges in the brain. In the crayfish brain, chemo-mechano receptive coincidence detector cells have since been described (Mellon, 2005).

In fish, the lateral line, in particular the superficial neuromast system, has been shown to function in the detection of large-scale turbulence (much larger than the animal), allowing animals to orient to the mean flow (Montgomery et al., 1997; Baker and Montgomery, 1999a). While aquatic animals are also known to use vision to orient to currents (Lyon, 1904; Lyon, 1909; Arnold, 1974), mean flow detection by the lateral line plays an important role during the localization of stationary odor sources in flowing water, particularly in the absence of visual information. Fish can use rheotaxis triggered by an olfactory stimulus to find the source of the odor (Baker et al., 2002; Carton and Montgomery, 2003). Other evidence suggests that specifically the superficial neuromasts of the lateral line system may be involved in rheotaxis behavior in shark species that face the current while resting on the bottom (Peach and Marshall, 2000).

The lateral line, in particular the canal neuromast system, has been shown to function in the detection of small-scale

turbulence (smaller than the animal), where in teleost fishes it makes a major contribution to feeding and prey capture behaviors (Coombs et al., 2001). Fish use their lateral line to locate stationary sources of small-scale turbulence (Janssen et al., 1995) and track wakes of moving prey (Pohlmann et al., 2001; Pohlmann et al., 2004). Within the elasmobranchs, the short-tailed stingray *Dasyatis brevicaudata* can locate water jets, similar to those produced by the bivalves in their diet (Montgomery and Skipworth, 1997). Although it has been suggested that the lateral line could play a role in prey detection in sharks (Tester and Nelson, 1967), its contribution to odor plume tracking and food source localization in sharks remains unknown.

In this study we assess the role of the lateral line in conjunction with olfaction in the localization of sources of small-scale odorous turbulence; in addition, we evaluate the role of the lateral line and vision in orientation to large-scale ('mean') flow and small-scale object detection. The smooth dogfish *Mustelus canis* (Mitchell 1815), was chosen for this study as it is a small, benthic shark, 150 cm maximum length, suitable for laboratory flume testing. The food search behavior of this species has been well described (Parker, 1922), as has the anatomy of its lateral line (Johnson, 1917) and olfactory structures (Sheldon, 1909; Northcutt, 1978). With a diet consisting primarily of lobster, crabs, shrimp and small fish, these opportunistic feeders attack mainly sick and injured prey (Field, 1907; Bigelow and Schroeder, 1953; Rountree and Able, 1996; Gelslechter et al., 1999). This species is commonly found in New England bays and shallow inshore waters and, being primarily a crepuscular/nocturnal hunter, it has been described as finding its prey chiefly by olfaction (Sheldon, 1909; Parker, 1922; Bigelow and Schroeder, 1953).

## Materials and methods

### *Experimental animals*

Ten smooth dogfish *Mustelus canis* (Mitchell 1815), six male and four female, 64–100 cm total length (TL), were captured in trawl nets in the waters off Woods Hole, MA, USA. The sharks were housed in running seawater in the tank facility of the Marine Biological Laboratory (MBL) in 3 m and 4 m diameter circular tanks. They were fed small pieces of squid and various fish species, supplemented with Mazuri Vita-Zu Sharks/Rays Vitamin Supplement Tablets (PMI Nutrition International, St Louis, MO, USA) to satiation three times per week, except during periods of experimentation, when they were fed a small amount of squid daily in the flume tank as part of the experimental procedure. During periods of experimentation, animals were moved from the tank facility to our MBL flume facility at least 48 h prior to any behavioral experiments, where they were held in rectangular tanks 6 m × 1.1 m length × width, filled to a depth of 60 cm. All tanks were supplied with flow-through ambient seawater during the warm months and with re-circulated, heated, carbon filtered, aerated and buffered seawater during the winter months. Summer temperatures ranged from 16°C to 22°C; winter

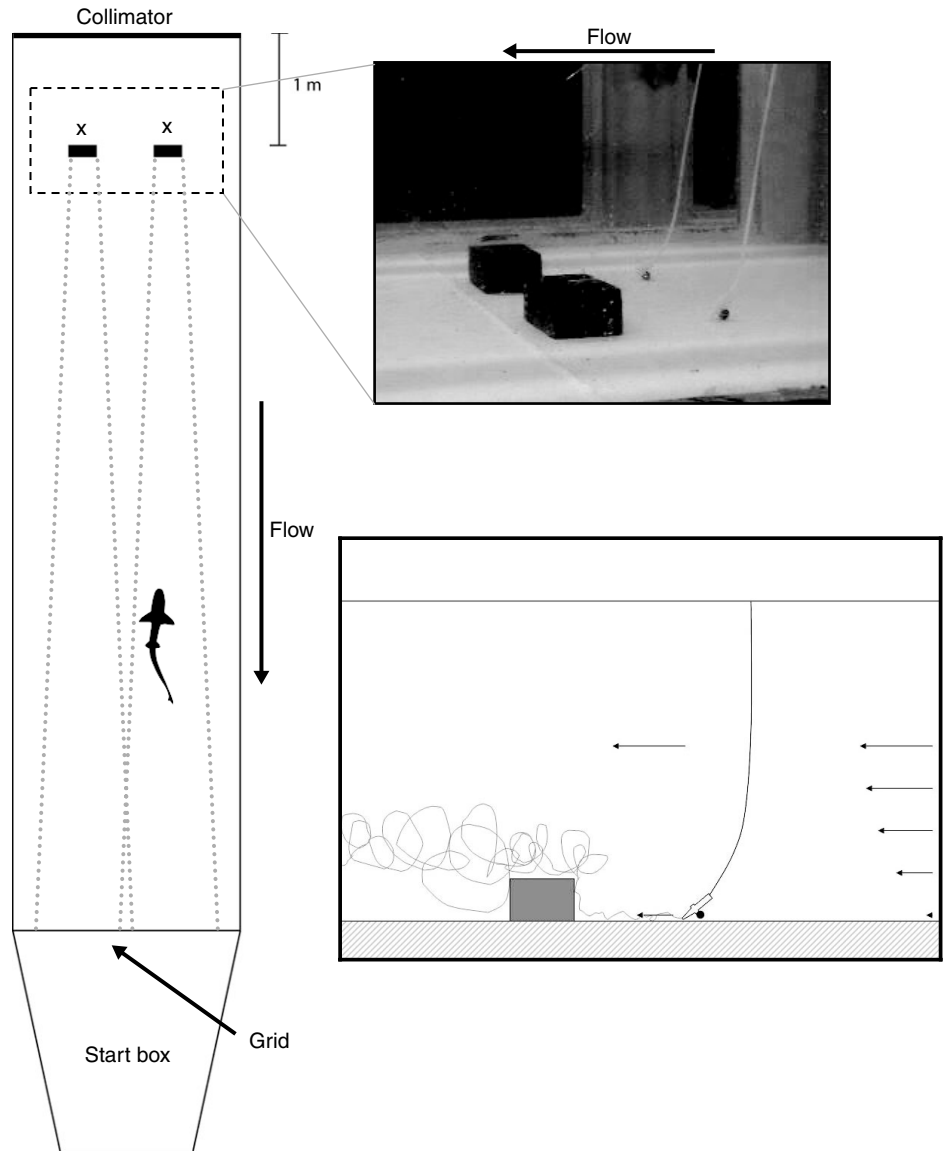


Fig. 1. Experimental flume. (A) Top view diagram, to scale; with upstream targets (x denotes nozzle locations), downstream start box and dogfish swimming up one of the plumes (indicated by the dotted lines). (B) Photograph of upstream targets: two bricks and two nozzles dispensing odor or seawater. (C) Side view diagram of targets, to scale; arrows show relative flow velocity (flume center flow  $3.5 \text{ cm s}^{-1}$ ); nozzle and weight hang down 15 cm upstream of brick ( $9 \times 6 \text{ cm}$ ); turbulent odor dispersal sketched from dye trace.

temperatures were maintained at  $16\text{--}18^\circ\text{C}$ . The pH was maintained at  $7.4\text{--}7.8$  (within 0.1 of the natural incoming seawater) and the dissolved oxygen at  $7\text{--}13 \text{ mg l}^{-1}$  (temperature dependent) year round. The lighting was on a 12 h:12 h light:dark cycle. Protocols for animal handling and use are on file and were approved by the Institutional Animal Care and Use Committees at the Marine Biological Laboratory and at Boston University (protocol number 2004-17).

#### *Test flume and stimulus sources*

All experiments were conducted in a  $\sim 10\,000$  liter near-laminar flow flume, with a working area of  $8.0 \text{ m} \times 2.0 \text{ m}$  length  $\times$  width and filled to a depth of 45 cm (Fig. 1). At the downstream end, a start box of  $2.0 \text{ m} \times 2.0 \text{ m}$  was created by a removable grid made of a plastic egg crate material. The mean current velocity, measured visually with Rhodamine B dye in the cross sectional center of the flume, was  $\sim 3.5 \text{ cm s}^{-1}$ .

The odor source in all experiments was squid rinse, prepared

by soaking 100 g wet mass of freshly thawed squid in 1 l of seawater at room temperature for 1 h. The seawater control source was seawater taken directly from the flume. These stimuli were delivered through soft PVC tubing (3.16 mm i.d.) at a rate of  $0.4 \text{ ml s}^{-1}$ , controlled by a Gilson Minipuls 3 peristaltic pump with a 2 channel pump head (Gilson, Inc., Middletown, WI, USA). A small lead weight kept the tubing hanging straight down even after being pushed by the sharks. The tubing of both channels was connected to a nozzle made of hard PVC connectors (5 cm long, 5 mm i.d.) delivering a mean flow velocity of  $\sim 2 \text{ cm s}^{-1}$ , or about half the velocity of the flume's mean flow, directed into the bottom boundary layer, parallel to the mean flow of the flume. The Reynolds number of the nozzle ( $Re=100$ ) indicates mild jet turbulence; the physical object of the nozzle itself (and the small attached lead weight) created an additional, small turbulent wake. Both sources of nozzle turbulence, momentum surplus (jet) and momentum deficit (wake), respectively, made small local

additions to the major uniform turbulence of the flume boundary layer. Given these conditions, we considered the nozzles to be 'oozing' odor sources, i.e. delivering odor (or seawater) but not greatly changing the turbulent flow of the flume. The two nozzles were placed symmetrically, 62 cm from each other (center to center) and 1 m from the upstream flume collimator. Major wake turbulence was created by placing a brick (20 cm×9 cm×6 cm) across the mean flow, 15 cm downstream from each nozzle (Fig. 1). The spacing between the upstream barrier and the stimulus targets was chosen so as to not restrict the turning behavior of the animals. *Mustelus canis* demonstrates great flexibility and is capable of performing tight snout-to-tail turns.

This arrangement resulted in two parallel turbulent wakes, one composed of seawater flavored with squid odor (i.e. the typical odor plume), the other unflavored seawater (control seawater plume). The odor side was alternated regularly to account for possible side bias. Prior to any experiments, these plumes were visualized and photographed with 0.1 g l<sup>-1</sup> of Rhodamine B dye dissolved in ambient seawater. The plumes remained spatially separate along the entire length of the flume. In sum, the nozzles generated two oozing plumes with minor turbulent wakes, carried downstream by the mean flow of the water in the flume tank where the two bricks generated additional major turbulent wakes. This gave the sharks four targets to locate, referred to as: odor alone (the odor nozzle), odor/turbulence (the brick on the odor side), seawater alone (the seawater nozzle), and seawater/turbulence (the brick on the seawater side).

#### *Behavioral procedures*

Prior to each trial, a shark was placed in the flume and allowed to acclimate for at least 30 min, then offered a small piece of squid to confirm its feeding motivation. If the animal would not feed, it was rejected from the experiment. If the food was accepted, the animal was then herded into the start box where it was held for 5 min while the plumes were allowed to establish. The downstream grid was then briefly lifted and replaced, allowing the animal to enter the test arena; this started the trial. Each trial lasted 10 min, during which time a characteristic push with the tip of the snout or bite on a target was scored as a strike. Other target contact, such as brushing a brick or nozzle with a fin, the tail, or the side of the snout was disregarded as accidental contact. We scored the following three measures for analysis of behavior. (1) 'Success rate' defined as the proportion of trials in which at least one strike occurred on any of the four targets. (2) 'Search time' from the beginning of the trial to the first strike on any target. (3) 'Number of strikes' on each of the four targets. In order to assess the feeding motivation of each animal at the conclusion of each trial, a small piece of squid was again offered. If this was not consumed within 10 min, we considered the animal to lack the proper motivation to track and the prior trial was rejected.

#### *Light conditions*

During trials, the room was normally illuminated by two overhead rows of fluorescent lights, referred to as the light

condition; a Sony Digital Handycam camcorder (Sony Corporation of America, New York, NY, USA) was used to record in detail the activities of the animal in the horizontal plane near the targets. To test for the effect of visual information, animals were deprived of visual cues by conducting experiments under infrared light (IR), which is outside the known range of absorption of the visual pigments of teleost fishes (Dartnall, 1975), as well as that of many sharks whose absorption peaks at an average of 500 nm (Gruber and Cohen, 1978). The retinal ganglion cells of smooth dogfish, *M. canis*, demonstrate a peak response at 505 nm and four logs of attenuation by 700 nm (Stell et al., 1975). During these tests, the overhead fluorescent lights were turned off, any point sources of light in the windowless room were blocked and the upstream end of the flume illuminated with a Tracksys IR LED Illuminator (Noldus Information Technology, Leesburg, VA, USA) with mean output at 880 nm. A Cohu 2700 Series ½ inch monochrome camera (Noldus Information Technology) was used to film the animal's activities in the horizontal plane at the upstream end; behavior was simultaneously recorded to VHS tape and played on a monitor in an adjacent room for manual scoring of any strike activities as described above. IR illumination is referred to as the dark condition.

#### *Streptomycin treatment*

Streptomycin has been shown to lesion both the surface neuromasts and canal neuromasts in teleosts (Wersall and Flock, 1964; Kaus, 1987; Montgomery et al., 1997). In amphibians, treatment with this drug results in an increase in spontaneous firing of the afferent nerves, which is linked to direct effects on the membrane of the hair cell, and a large lag phase in the receptor potentials, which may be caused by interference with the motion of the sensory hairs (Kroese and van den Bercken, 1982). Streptomycin administered externally has been demonstrated not to affect inner ear function, which is based on similar hair cells, unless applied intraluminally (Matsuura et al., 1971).

We used streptomycin to treat eight of the animals (six males and two females). Each shark was held in a heavily aerated 10 mmol l<sup>-1</sup> solution of streptomycin sulfate salt (Blaxter and Fuiman, 1987) for 3 h (Montgomery et al., 1997). Based on the evidence in teleosts and amphibians, we refer to streptomycin treated animals as lateral line lesioned. Since teleosts treated with this drug return to normal behavior in 20–24 h (Blaxter and Fuiman, 1987), the sharks were placed in the flume immediately after treatment, allowed to acclimate, then tested in the light and in the dark as described above. Since treatment with high concentrations of streptomycin results in effects in amphibians that are only partially reversible (Kroese and van den Bercken, 1982), all streptomycin lesion trials were done after completing untreated trials. The light condition was randomized during all trials.

To test for effects of the treatment procedure itself, all eight animals were subjected to a sham treatment prior to streptomycin treatment by holding them in heavily aerated seawater for 3 h, followed by immediate acclimation and

testing in the light as described above. Streptomycin-treated animals were offered a piece of squid following the trial; they were given 10 min to locate and consume the food, as with the untreated animals. However, if they were unable to locate the food in the dark, the lights were turned on and they were allowed an additional 10 min of food search time. If the food was not consumed during these additional 10 min, the prior trial was rejected.

#### Experimental design and data analysis

As we are working with large and complex animals we made every effort to use as few animals as the statistical results would allow. With a small sample size, individual differences among animals can have a large impact on the results. We thus compared each animal to itself, pre- and post-treatment, to minimize the impacts of individual differences.

For each of the four experimental conditions (intact in the light; intact in the dark; lateral line lesioned in the light; lateral line lesioned in the dark) and the sham treatment, behavioral performance was assessed by examining the parameters 'success rate', 'search time' and 'number of strikes' on the four targets to analyze plume preference and target preference within the odor plume. Given the sequential measures of behavior of individual animals, we used non-parametric Wilcoxon Sign-Rank tests (WSR; SAS Institute Inc. 1995, #4090) to compare the response of individuals in the four experimental conditions as well as the sham control condition. For each animal, we calculated the 'total number of strikes' per 10-min trial summed for all four targets. We then calculated the difference between the number of strikes on targets on the odor side and the seawater side, and tested whether that difference was significantly different from zero using a Wilcoxon Sign Rank test (two-tailed) in the Program JMP (SAS Institute Inc. 1995, #4090). A random distribution across the two sides (zero difference) is expected if a fish does not express a preference for the odor side or is unable to detect a difference between them. Finally, we tested for preference between the two targets on the odor side using the same Wilcoxon analysis.

Since each animal was tested more than once under each experimental condition, the total number of strikes, search time, and target preference of the animals were examined using block-wise analysis by Cochran–Mantel–Haenszel Statistics in the program JMP.

## Results

### Lateral line intact

In the light and in the dark, all intact animals struck targets in the upstream end of the flume during every trial; thus, light had no significant effect on their success rate (WSR=0,  $N=10$ ,  $P=1$ ; Fig. 2A). There was also no significant effect of light on search time, as the animals searched for  $70 \pm 10$  s (mean  $\pm$  s.e.m.) in the light and  $63 \pm 14$  s in the dark (WSR=1.5,  $N=10$ ,  $P=0.9$ ; Fig. 2B).

Strike frequency (Fig. 3A,B) was significantly greater on the

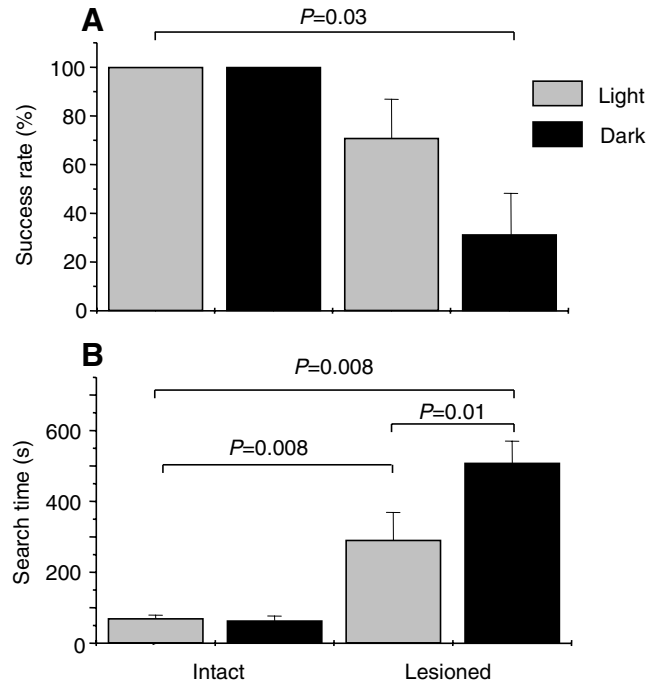


Fig. 2. Success rate (%) and mean search time (s) of *M. canis* under four experimental conditions: intact and lateral line lesioned with streptomycin in the light and in the dark. (A) Lateral line lesion reduced success rate: non-significant in the light (WSR=3.0,  $N=8$ ,  $P=0.2$ ) and significant in the dark (WSR=10.5,  $P=0.03$ ,  $N=8$ ). Lighting alone did not affect success rate (WSR=0,  $N=10$ ,  $P=1$ ). (B) Lateral line lesion significantly increased search time in the light (WSR=18.0,  $P=0.008$ ,  $N=8$ ) and even more so in the dark (WSR=14.0,  $P=0.01$ ,  $N=8$ ). Lighting alone did not affect search time (WSR=0,  $N=10$ ,  $P=1$ ). Gray bars, fluorescent light (light); black bars, infrared light (dark).

odor targets (nozzle and brick combined) than on the seawater targets both in the light (odor  $29 \pm 4$  strikes; seawater  $1 \pm 0.4$  strike; WSR=27.5,  $N=10$ ,  $P=0.002$ ) and in the dark (odor  $23 \pm 4$  strikes; seawater  $0.6 \pm 0.2$  strikes; WSR=27.5,  $N=10$ ,  $P=0.002$ ). Lighting did not significantly affect this side preference (WSR=13,  $N=10$ ,  $P=0.2$ ). Of the odor targets, the sharks struck more frequently on the source of odor/turbulence than on the source of odor alone, both in the light (odor/turbulence  $18 \pm 2$  strikes; odor alone  $11 \pm 3$  strikes; WSR=23.5,  $N=10$ ,  $P=0.01$ ; Fig. 3A) and in the dark (odor/turbulence  $15 \pm 2$  strikes; odor alone  $7 \pm 2$  strikes; WSR=27.5,  $N=10$ ,  $P=0.002$ ; Fig. 3B). Lighting did not significantly affect this target preference either (WSR=4.5,  $N=10$ ,  $P=0.6$ ). These results show that *M. canis* normally finds a source of food by tracking both odor and turbulence, regardless of vision.

### Lateral line lesioned

After streptomycin treatment the intact success rate (which was 100% in both lighting conditions) decreased somewhat in the light (to 71%, WSR=3.0,  $N=8$ ,  $P=0.2$ ) and significantly in the dark (to 31%, WSR=10.5,  $N=8$ ,  $P=0.03$ ; Fig. 2A). After streptomycin treatment five of the eight animals were also unable

to locate the piece of food in the dark, but then successfully picked it up in less than 2 min once the lights were turned on.

In the light, streptomycin treatment resulted in longer search time:  $291 \pm 78$  s compared to  $70 \pm 10$  s ( $WSR = -18.0$ ,  $N = 8$ ,  $P = 0.008$ ; Fig. 2B). Search time increased even further in the dark, to  $508 \pm 59$  s; this is significantly different both from the intact condition ( $WSR = -18.0$ ,  $N = 8$ ,  $P = 0.008$ ) and from the condition with lateral line lesion in the light ( $WSR = -14.0$ ,  $N = 8$ ,  $P = 0.01$ ; Fig. 2B).

In the light, the six out of eight animals that successfully located targets in the upstream end, demonstrated a significant strike preference for the odor targets over the seawater targets (odor,  $12 \pm 7$  strikes; seawater,  $0.6 \pm 0.3$  strikes;  $WSR = 10.5$ ,  $N = 6$ ,  $P = 0.03$ ), but they did not discriminate between the source of odor/turbulence and the source of odor alone (odor/turbulence,  $8 \pm 5$  strikes; odor alone,  $4 \pm 2$  strikes;  $WSR = 5.5$ ,  $N = 6$ ,  $P = 0.1$ ; Fig. 3C). In the dark, few animals successfully located targets in the upstream end ( $N = 3$ ); these few did not show a significant preference for the odor or seawater side (odor,  $12 \pm 4$  strikes; seawater  $7 \pm 4$  strikes;  $WSR = 3.0$ ,  $N = 3$ ,  $P = 0.2$ ; Fig. 3D).

These results indicate that lesioning the lateral line has serious effects on success rate, search time, target localization

and target discrimination, and that visual information partially mitigates some of these effects. Two of the lesioned animals did not locate any targets even in the light.

#### Sham treatment

Sham treatment did not affect success rate (all animals located and struck the objects in the upstream end during every trial,  $WSR = 0$ ,  $N = 8$ ,  $P = 1$ ) or search time (pre-treatment,  $69 \pm 8$  s; post-treatment  $86 \pm 19$  s,  $WSR = -6$ ,  $N = 8$ ,  $P = 0.4$ ). Sham treated individuals continued to demonstrate a robust preference for the odor targets over the seawater targets ( $WSR = 18.0$ ,  $N = 8$ ,  $P = 0.008$ ) and for the source of odorous turbulence over odor alone ( $WSR = 17.0$ ,  $N = 8$ ,  $P = 0.02$ ). These preferences were not significantly different before and after sham treatment (odor-seawater, before *vs* after,  $WSR = 11$ ,  $N = 8$ ,  $P = 0.06$ ; odor/turbulence-odor alone before *vs* after,  $WSR = 10$ ,  $N = 8$ ,  $P = 0.1$ ). These results indicate that the subsequently observed lesion and lighting effects were not caused by the handling procedures.

#### Effect of repeated trials

Since the animals were tested more than once in each experimental condition and since lighting alone did not have a

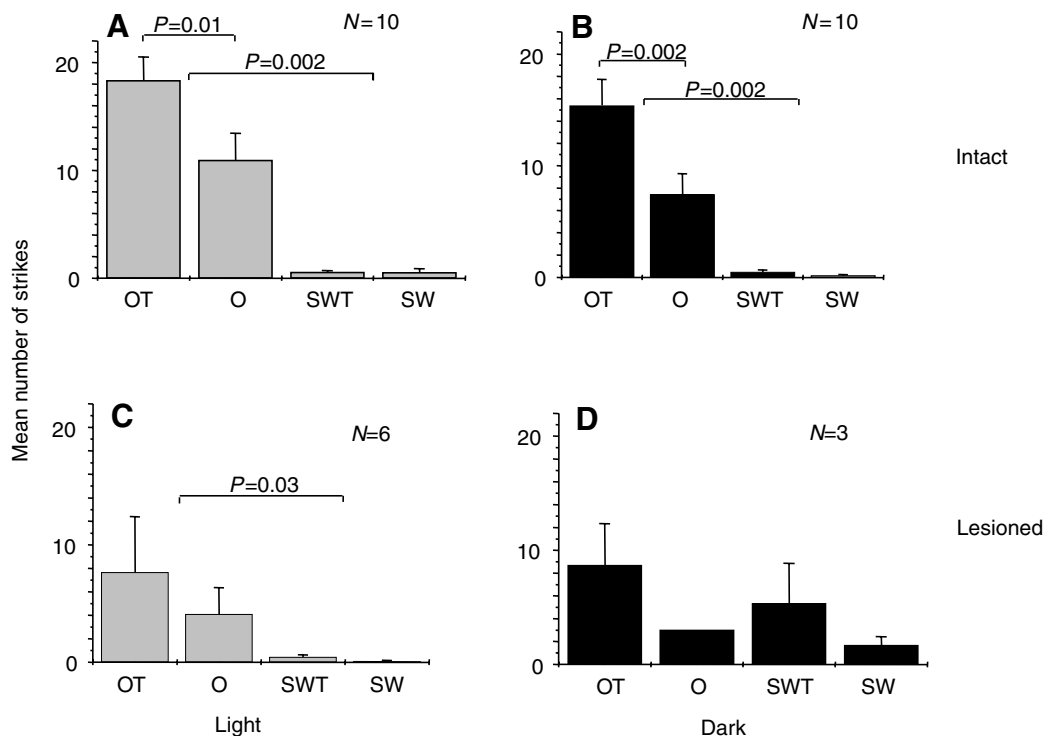


Fig. 3. Mean number of strikes by untreated *M. canis* on the four targets: odor/turbulence (OT), odor alone (O), seawater/turbulence (SWT) and seawater alone (SW). (A) Intact, in the light, the animals preferred the odor side (OT+O) over the seawater side (SWT+SW;  $WSR = 27.5$ ,  $P = 0.002$ ,  $N = 10$ ) and the odor/turbulence over the odor alone ( $WSR = 23.5$ ,  $P = 0.01$ ,  $N = 10$ ). (B) Intact, in the dark, the animals preferred the odor side over the seawater side ( $WSR = 27.5$ ,  $P = 0.002$ ,  $N = 10$ ) and the source of odor/turbulence over the source of odor alone ( $WSR = 27.5$ ,  $P = 0.002$ ,  $N = 10$ ). (C) Lateral line lesioned, in the light, the animals preferred the odor side over the seawater side ( $WSR = 10.5$ ,  $P = 0.03$ ,  $N = 6$ ) but did not discriminate between odor/turbulence and odor alone ( $WSR = 5.5$ ,  $P = 0.1$ ,  $N = 6$ ). (D) Lateral line lesioned, in the dark, the animals no longer displayed a preference for the odor side over the seawater side ( $WSR = 3.0$ ,  $P = 0.2$ ,  $N = 3$ ). Gray bars, fluorescent light (light); black bars, infrared light (dark).

significant effect on the success rate, target preferences, or search time when the lateral line was intact, these parameters, along with the total number of strikes, were screened for order effects across the trials with intact lateral line. Success rate was not affected by increasing number of trials: all animals were successful in all trials. Similarly, preference for the odor side over the seawater side was unaffected by trial order: all animals preferred the odor side over the seawater side in all trials. Preference for the odor/turbulence target over the odor target was unaffected by increasing number of trials (block-wise analysis by Cochran–Mantel–Haenszel Statistics,  $z=4.33$ ,  $d.f.=5$ ,  $P=0.5$ ) as was search time (Cochran–Mantel–Haenszel Statistics,  $z=13.71$ ,  $d.f.=16$ ,  $P=0.6$ ). Only the number of strikes decreased with increasing numbers of trials (Cochran–Mantel–Haenszel Statistics,  $z=42.78$ ,  $d.f.=25$ ,  $P=0.01$ ).

### Discussion

The results of this study show that the smooth dogfish *Mustelus canis* is severely handicapped in its ability to locate an odor source when deprived of information from its lateral line, particularly in the dark. We conclude that this shark uses not only odor, but also the hydrodynamic and visual flow fields for upstream orientation and the trail of flavored eddies when tracking a turbulent odor plume and locating its source. Since dogfish are primarily crepuscular and nocturnal hunters, their reliance on lateral line information is essential.

#### *General behavioral description and motivational state of the animals*

In the light and intact, the sharks exhibited rather stereotyped search behavior upon encountering food odor: they quickly turned upstream and swam directly up the odor plume to its source; near the source they executed an immediate and precisely directed strike from above upon one of the source objects. This is similar to previous descriptions (Parker, 1922). The majority of the first strikes occurred on the source of odor/turbulence (96%). It could be argued that this is because it is the first target encountered while swimming up the odor plume. However, we examined not only the first strike, but all strikes that occurred over a 10-min period. After the first strike, a bout of tight circling and/or figure-eights was performed in the vicinity of the odor source, accompanied by additional strikes. These strikes occurred on both targets on the odor side and very rarely on a target on the seawater side. In typical shark fashion (Hodgson and Mathewson, 1971; Mathewson and Hodgson, 1972), when no food was found, the animals swam back downstream for some distance, ignoring both plumes, and then retraced the odor plume as described above to execute another bout of strikes. This pattern was often repeated several times. Given that there were several bouts over the course of a 10-min trial in which the animals displayed a mix of strikes on both targets on the odor side, we are confident that the greatest overall number of strikes on the source of odor/turbulence reflects the animal's greater interest in this target rather than a first encounter advantage. In the dark, we could observe their

behavior only in the IR-illuminated vicinity of the source; however, the final approach to the source did not appear to be different from that in the light. Apparently, intact animals do not need vision for the final localization of the target to be struck and the preferred target is the odor/turbulence source.

Lesioned animals, in the light, again displayed food search behaviors including tight circling and figure-eights, but they swam much closer to the bottom of the tank than when intact. In the dark, few lesioned animals located the source. These few did not display a direct final approach and strike from above, but rather appeared to run accidentally into one of the source objects. The behavior that followed appeared frantic and erratic, with the animals performing wider circles and random strikes with poor direction, on all four targets in turn. Most of the animals were unsuccessful in locating any target during the 10-min trial and either did not even enter within the IR illuminated target area of the tank, or did enter but turned back downstream before reaching the targets. One might argue that after treatment they lacked the proper motivation for finding food. However, these animals eagerly consumed a piece of squid immediately following the conclusion of each trial. We conclude that they were motivated to track the odor plume during the trial but were unable to locate its source within the allotted time.

The piece of squid presents a different odor dispersal field, oozing in the boundary layer almost without any additional turbulence. Some lesioned animals were capable of tracking and locating this piece of food in the dark, presumably based on olfaction alone; however, most needed light and therefore additional visual input to locate it. These observations provide further support for the conclusion that dogfish can find food by odor alone, but that the additional presence of source turbulence provides more 'convincing' information leading to repeated strikes on the odor/turbulence source. The sense of taste is not likely to play an important role in food finding since nose-blocked dogfish cannot find food (Sheldon, 1911).

#### *Non-specific effect of streptomycin treatment*

The effects of streptomycin on the elasmobranch lateral line are thus far unknown; however, our behavioral results are consistent with known lateral line lesion effects in teleosts (Montgomery et al., 1997; Coombs et al., 2001). Streptomycin has been shown to lesion both the surface neuromasts and canal neuromasts in teleosts (Wersall and Flock, 1964; Kaus, 1987; Montgomery et al., 1997), although its effects on the two lateral line subsystems have not yet been specifically compared. Since the hair cells of the inner ear remain unaffected unless the drug is applied intralumenally (Kroese and van den Bercken, 1982), the drug exerts its effect through direct contact with hair cells that are either exposed to the environment (surface neuromasts) or to the liquid contained within the canals, which are connected to the external environment *via* pores. The electrosensory system is related to the lateral line; however, its receptor cells are buried deeply at the end of long ampullae of Lorenzini and separated from the environment by the jelly, which would likely protect them from the effects of streptomycin. More importantly, since we did not employ

electric targets in this study, we can infer that the observed target preferences are based on the use of other sensory modalities. It is well known that when the nares of *M. canis* are physically blocked to prevent odor access to the nose, they do not display any feeding behaviors, even in the presence of visible food items (Sheldon, 1911). Our animals successfully located and consumed small pieces of squid after streptomycin treatment, confirming that the olfactory sense was not affected. Based on all of this evidence, we are confident that we observed lateral line lesion effects after streptomycin treatment and not deficits in other sense organs.

#### *Effect of repeated trials*

Since the 'lateral line intact' and 'lateral line lesioned' trials occurred sequentially, it is important to evaluate if the decrease in success rate following streptomycin treatment could be an effect of repeated trials. This appears not to be the case, since search time prior to the first strike and target preferences did not change after several trials: these animals chased the odor with the same enthusiasm every time they were exposed to it. This suggests that they were not aware at the start of a trial that the odor plume was not originating from an actual food source, or that they were so motivated that they ignored any memories they may have formed in association with the overall experimental setup. Their interest in the targets began to wane only after striking the targets and receiving additional tactile (and in this case possibly gustatory) information that indicated to them that the objects in the upstream end were not food. Thus it is the frequency of returns to the targets for additional bouts of striking that decreases following repeated trials and not the initial interest in the setup or in a particular target. Additionally, following streptomycin treatment, the light and dark trials were conducted at random so the observed behavioral differences are due entirely to increased sensory deprivation.

#### *The interplay of senses in odor plume tracking*

##### *Odor stimulated rheotaxis*

While rheotaxis implies orientation to water flow, we argue that both hydrodynamic and visual flow fields can be used to orient upstream. Moths primarily use the visual flow field for anemotaxis, the air equivalent of rheotaxis (Mafra-Neto and Cardé, 1994; Vickers and Baker, 1994), while we demonstrate here that the sharks can use both but rely more on the hydrodynamic flow field than on vision. Intact animals clearly demonstrated the ability to orient to the mean flow of the flume and to navigate in an upstream direction on the odor side. Since the animals could perform this function successfully and efficiently under both light and dark conditions (Fig. 2A,B), visual information is not critical to this behavior. This is not unexpected, given that *M. canis* is primarily a nocturnal hunter (Bigelow and Schroeder, 1953). It suggests a major role of olfaction to trigger the upstream swimming with directional information provided by the lateral line, presumably the free neuromasts (Montgomery et al., 1997; Baker and Montgomery, 1999b). This part of the search

is a classic example of odor-stimulated rheotaxis (Hodgson and Mathewson, 1971; Mathewson and Hodgson, 1972).

##### *Vision*

Once the lateral line system was disabled, most of the individuals in this study could still successfully orient to the mean flow and navigate to the upstream end of the flume as long as there was visible light. Since success rate did not drop significantly after lesion (Fig. 2A), it suggests that these animals compensated for the lack of lateral line information using the visual flow field for directional information. The animals may see features of the environment drift by as they and/or the features are moved by the mean flow of the water. Orientation in this manner has been described in teleost fish (Lyon, 1904; Lyon, 1909). Needless to say, such visual input would be absent in extreme darkness and in featureless visual environments such as open ocean. However, since the search time increased significantly (Fig. 2B), it suggests that for *M. canis*, using visual orientation to the mean current is slower and less efficient than using lateral line information. The 29% failure rate after lateral line lesion in visible light, although not statistically significant with our sample size, still suggests that not all animals were always able to use vision to navigate upstream to the targets, at least within the 10 min window allowed in these trials, and that some individuals were better than others at visual navigation.

##### *Olfaction alone*

Intact animals, regardless of light, always successfully located a piece of real food. This small piece of dead meat provides an almost pure odor source: it oozes odor into the bottom boundary layer and, in contrast to live prey, generates no electric, hydrodynamic or acoustic fields. Apparently, such pure odor sources can be better located when there is no 'distraction' from a nearby turbulence source, as seen in their preference for the odor/turbulence target.

In the dark, lesioned animals did not discriminate between any of the targets or between the odor and seawater plumes. This suggests that the few strike successes (31%) appear to be by chance, such that the animals, while swimming in the flume and excited by the odor, happened to find the upstream area where perhaps tactile information triggered strikes on any or all four targets. Only three of the lesioned animals were able to locate the piece of food in the dark, though several of them were observed to swim over the food on the first pass or to miss the piece of food on the first strike. The other five animals only located the food after the lights were turned on. These results indicate that without vision and lateral line information, and despite an olfactory flow field, *M. canis* cannot efficiently navigate in the mean flow of the flume nor pinpoint a piece of food. Thus, contrary to earlier suggestions (Hodgson and Mathewson, 1971; Mathewson and Hodgson, 1972), olfaction alone cannot support efficient orientation and tracking.



*Eddy chemotaxis*

Intact animals, once near the four stimulus targets, were more attracted to the major source of turbulence on the odor side than to the source of the odor itself. These preferences did not change with light condition, indicating that they were not visually attracted to the largest object on the odor side, but to the turbulence that it generated. This suggests that they tracked the wake of the brick (on the odor side) and used the source of this turbulence as the most probable identifier for the source of odor and thus food. Since the animals only rarely struck targets on the seawater side and did not discriminate between the source of seawater/turbulence and seawater alone, it would appear that turbulence by itself is not particularly interesting to this species. This is reasonable, since the natural environment is full of uninteresting wakes. While wakes provide good directional information, odor is far more informative for the identity of the source (Atema, 1985). Therefore, information contained in an odor-flavored wake combines two desirable features: identity and directionality. This is the basis for the 'eddy chemotaxis' idea (Atema, 1995; Atema, 1996; Atema, 1998).

With a disabled lateral line system, target preferences changed. In the light, the animals still displayed a significant preference for the odor side over the seawater side, but they no longer discriminated between the source of odor/turbulence and the source of odor alone. This further supports the conclusion that intact animals were interested in the turbulence generated by the brick, rather than its size or visual appearance, as once this turbulence could no longer be detected, they were equally interested in both targets on the odor side. Tracking the odor plume rather than the seawater plume indicates that lesioned sharks can still roughly locate the source of a turbulent odorous wake using olfaction and vision. However, increased search time shows that they lost plume-tracking efficiency and the loss of target preference shows that they lost precision in target localization. The most coherent interpretation is that lateral line lesion not only affected orientation to the mean flow field but also to the turbulent fine structure of the plume. The pattern of decaying eddies in an odor plume can provide additional directional information and the detection of a stream of flavored eddies could further increase tracking efficiency and target discrimination and localization. As an animal approaches the source of a turbulent odor plume, both the odor peaks (Moore and Atema, 1991) and eddy velocity peaks (Webster, 2007) become stronger and more distinct. The mean hydrodynamic flow field is probably detected best by the superficial neuromast system of the lateral line, since the major stimulus is a velocity-coupled drag on the neuromasts. This corresponds to behavioral results in teleosts (Montgomery et al., 1997; Baker and Montgomery, 1999a). The turbulence fine structure provides local pressure gradients that are detected best by the canal neuromasts system, and behavioral results confirm this link (Coombs et al., 2001). For eddy chemotaxis animals would then be using a combination of olfaction and the canal

system. This distinction is not as trivial as it may seem. Turbulent jets and wakes consist of many scales with eddies ranging from much larger to much smaller than the animal. The existence of two distinct lateral line systems in many fishes seems to indicate the importance of filtering information in two different hydrodynamic band widths: large-scale flow for general upstream orientation and small-scale eddies for jet and wake tracking, including close-up target localization. Studying live prey detection, Kanter and Coombs (Kanter and Coombs, 2003) came to the same conclusion based on the detection of mean flow and small scale turbulence from prey (or a vibrating sphere). Olfaction is essential in that it allows the animal to identify the character of the source and to determine if it is worthwhile pursuing. It triggers the initial upstream orientation and the subsequent plume tracking and source localization. In addition, the vestibular inertial detection system could be involved in even larger scale motion detection.

*Olfaction and electroreception*

The use of turbulence to provide directional information in an odor field bears some resemblance to the shark's use of electroreception to pinpoint the location of living prey. Kalmijn (Kalmijn, 1982) used *M. canis* to test the use of electroreception in nature confirming his earlier laboratory results with *Scyliorhinus canicula* (Kalmijn, 1971), an animal strikingly similar to *M. canis* in terms of anatomy and feeding ecology. He attracted the sharks with an odor plume, the source of which was located on the bottom of a shallow bay between two sets of electrodes. Whenever a shark approached the source area, one or the other of the electrical stimuli, made to resemble the electrical field of a breathing flounder, was switched on. Inevitably the sharks would strike the active electrodes, bypassing the nearby odor source. Only when the electric field was off did the sharks strike the odor source. This behavior is adaptive since the electric field, although detectable only over short distances, is highly directional and exists only in the presence of the animal. In contrast, the odor field is less directional and can linger after the prey has left.

*Conclusion*

To locate food *M. canis* uses a suite of sensory information varying with the nature and distance of the food source. It detects the presence of an interesting distant source by olfaction. It then orients to the mean flow field using the superficial lateral line (odor-stimulated rheotaxis) and, when available, vision. It tracks the trail of small-scale, odor-flavored turbulence using olfaction and the canal lateral line (eddy chemotaxis), and also pinpoints the source of the plume with lateral line canals and olfaction. For live prey, particularly when no significant wake is present, it uses electroreception to direct the final strike (Kalmijn, 1971).

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## References

- Arnold, G. P.** (1974). Rheotropism in fishes. *Biol. Rev.* **49**, 515-576.
- Atema, J.** (1985). Chemoreception in the sea: adaptations of chemoreceptors and behaviour to aquatic stimulus conditions. *Symp. Soc. Exp. Biol.* **39**, 386-423.
- Atema, J.** (1995). Chemical signals in the marine environment: dispersal, detection, and temporal signal analysis *Proc. Natl. Acad. Sci. USA* **92**, 62-66.
- Atema, J.** (1996). Eddy chemotaxis and odor landscapes: exploration of nature with animal sensors. *Biol. Bull.* **191**, 129-138.
- Atema, J.** (1998). Tracking turbulence: processing the bimodal signals that define an odor plume. *Biol. Bull.* **195**, 179-180.
- Baker, C. F. and Montgomery, J. C.** (1999a). Lateral line mediated rheotaxis in the Antarctic fish *Pagothenia borchgrevinkii*. *Polar Biol.* **21**, 305-309.
- Baker, C. F. and Montgomery, J. C.** (1999b). The sensory basis of rheotaxis in the blind Mexican cave fish, *Astyanax fasciatus*. *J. Comp. Physiol. A* **184**, 519-527.
- Baker, C. F., Montgomery, J. C. and Dennis, T. E.** (2002). The sensory basis of olfactory search behavior in banded kokopu (*Galaxias fasciatus*). *J. Comp. Physiol. A* **188**, 553-560.
- Bateson, W.** (1890). The sense-organs and perceptions of fishes; with some remarks on the supply of bait. *J. Mar. Biol. Assoc. U. K.* **1**, 225-256.
- Bigelow, H. B. and Schroeder, W. C.** (1953). Fishes of the Gulf of Maine. *Fish. Bull. Fish Wildl. Serv.* **74**, 561.
- Blaxter, J. H. S. and Fuiman, L. A.** (1987). Function of the free neuromasts of marine teleost larvae. In *The Mechanosensory Lateral Line: Neurobiology and Evolution* (ed. S. Coombs, P. Gorner and H. Munz), pp. 481-499. New York: Springer-Verlag.
- Carton, A. G. and Montgomery, J. C.** (2003). Evidence of a rheotactic component in the odour search behaviour of freshwater eels. *J. Fish Biol.* **62**, 501-516.
- Coombs, S., Braun, C. B. and Donovan, B.** (2001). The orienting response of Lake Michigan mottled sculpin is mediated by canal neuromasts. *J. Exp. Biol.* **204**, 337-348.
- Dartnall, H. J. A.** (1975). Assessing the fitness of visual pigments for their photic environments. In *Vision in Fishes - New Approaches in Research* (ed. M. A. Ali), pp. 543-563. New York: Plenum Press.
- Elkinton, J. S. and Cardé, R. T.** (1984). Odor dispersion. In *Chemical Ecology of Insects* (ed. W. J. Bell and R. T. Cardé), pp. 73-91. London: Chapman & Hall.
- Field, I. A.** (1907). Unutilized fishes and their relationship to the fishing industries. In *Report to the Commissioner of Fisheries for the Fiscal Year 1906 (Bureau of Fisheries Document No. 622)*. Washington: Bureau of Fisheries.
- Fraenkel, G. S. and Gunn, D. L.** (1940). *The Orientation of Animals: Kineses, Taxes, and Compass Reactions*. Oxford: Clarendon Press.
- Gelsichter, J., Musick, J. A. and Nichols, S.** (1999). Food habits of the smooth dogfish, *Mustelus canis*, dusky shark, *Rhizoprionodon terraenovae*, and the sand tiger, *Carcharias taurus*, from the northwest Atlantic Ocean. *Environ. Biol. Fishes* **54**, 205-217.
- Gruber, S. H. and Cohen, J. L.** (1978). Visual system of the elasmobranchs: state of the art 1960-1975. In *Sensory Biology of Sharks, Skates, and Rays* (ed. E. S. Hodgson and R. F. Mathewson), pp. 11-105. Arlington, VA: US Office of Naval Research.
- Hodgson, E. S. and Mathewson, R. F.** (1971). Chemosensory orientation in sharks. *Ann. N. Y. Acad. Sci.* **188**, 175-182.
- Janssen, J., Jones, W. R., Whang, A. and Oshel, P. E.** (1995). Use of the lateral line in particulate feeding in the dark by juvenile alewife (*Alosa pseudoharengus*). *Can. J. Fish. Aquat. Sci.* **52**, 358-363.
- Johnson, S. E.** (1917). Structure and development of the sense organs of the lateral canal system of selachians (*Mustelus canis* and *Squalus acanthias*). *J. Comp. Neurobiol.* **28**, 1-74.
- Kalmijn, A. J.** (1971). The electric sense of sharks and rays. *J. Exp. Biol.* **55**, 371-383.
- Kalmijn, A. J.** (1982). Electric and magnetic field detection in elasmobranch fishes. *Science* **218**, 916-918.
- Kanter, M. J. and Coombs, S.** (2003). Rheotaxis and prey detection in uniform currents by Lake Michigan mottled sculpin (*Cottus bairdi*). *J. Exp. Biol.* **206**, 59-70.
- Kaus, S.** (1987). The effect of aminoglycoside antibiotics on the lateral line organ of *Aplocheilichthys lineatus* (Cyprinodontidae). *Acta Otolaryngol.* **103**, 291-298.
- Kleerekoper, H., Gruber, D. and Matis, J.** (1975). Accuracy of localization of a chemical stimulus in flowing and stagnant water by the nurse shark *Ginglymostoma cirratum*. *J. Comp. Physiol. A* **42**, 79-84.
- Kroese, A. B. A. and van den Bercken, J.** (1982). Effects of ototoxic antibiotics on sensory hair cell functioning. *Hear. Res.* **6**, 183-197.
- Lyon, E. P.** (1904). On rheotropism. I. Rheotropism in fishes. *Am. J. Physiol.* **12**, 149-161.
- Lyon, E. P.** (1909). On rheotropism. II. Rheotropism of fish blind in one eye. *Am. J. Physiol.* **24**, 244-251.
- Mafra-Neto, A. and Cardé, R. T.** (1994). Fine-scale structure of pheromone plumes modulates upwind orientation of flying moths. *Nature* **369**, 142-144.
- Mathewson, R. F. and Hodgson, E. S.** (1972). Klinotaxis and rheotaxis in orientation of sharks toward chemical stimuli. *Comp. Biochem. Physiol.* **42A**, 79-84.
- Matsuura, S., Ikeda, K. and Furukawa, T.** (1971). Effects of streptomycin, kanamycin, quinine, and other drugs on the microphonic potentials of goldfish sacculus. *Jpn. J. Physiol.* **21**, 579-590.
- Mellon, D.** (2005). Integration of hydrodynamic and odorant inputs by local interneurons of the crayfish deutocerebrum. *J. Exp. Biol.* **208**, 3711-3720.
- Montgomery, J. C. and Skipworth, E.** (1997). Detection of weak water jets by the short-tailed stingray *Dasyatis brevicaudata* (Pisces: Dasyatidae). *Copeia* **1997**, 881-883.
- Montgomery, J. C., Baker, C. F. and Carton, A. G.** (1997). The lateral line can mediate rheotaxis in fish. *Nature* **389**, 960-963.
- Moore, P. A. and Atema, J.** (1991). Spatial information in the three-dimensional fine structure of an aquatic odor plume. *Biol. Bull.* **181**, 408-418.
- Murliss, J. and Jones, C. D.** (1981). Fine-scale structure of odour plumes in relation to insect orientation to distant pheromone and other attractant sources. *Physiol. Entomol.* **6**, 71-86.
- Northcutt, R. G.** (1978). Brain organization in the cartilaginous fishes. In *Sensory Biology of Sharks, Skates, and Rays* (ed. E. S. Hodgson and R. F. Mathewson), pp. 117-193. Arlington, VA: Office of Naval Research, Department of the Navy.
- Parker, G. H.** (1914). The directive influence of the sense of smell in the dogfish. *Bull. US Bur. Fish.* **33**, 61-68.
- Parker, G. H.** (1922). *Smell, Taste, and Allied Senses in Vertebrates*. Philadelphia, PA: J. P. Lippincott Co.
- Parker, G. H. and Sheldon, R. E.** (1913). The sense of smell in fishes. *Bull. US Bur. Fish.* **32**, 33-46.
- Peach, M. B. and Marshall, N. J.** (2000). The pit organs of elasmobranchs: a review. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **355**, 1131-1134.
- Pohlmann, K., Grasso, F. W. and Breithaupt, T.** (2001). Tracking wakes: the nocturnal predatory strategy of piscivorous catfish. *Proc. Natl. Acad. Sci. USA* **98**, 7371-7374.
- Pohlmann, K., Atema, J. and Breithaupt, T.** (2004). The importance of the lateral line in nocturnal predation of piscivorous catfish. *J. Exp. Biol.* **207**, 2971-2978.
- Rountree, R. A. and Able, K. W.** (1996). Seasonal abundance, growth and foraging habits of juvenile smooth dogfish, *Mustelus canis*, in a New Jersey Estuary. *Fish. Bull.* **94**, 522-534.
- Sheldon, R. E.** (1909). The reactions of the dogfish to chemical stimuli. *J. Comp. Neurol. Psychol.* **19**, 273-311.
- Sheldon, R. E.** (1911). The sense of smell in selachians. *J. Exp. Zool.* **10**, 51-62.
- Stell, W. K., Detweiler, P. B., Wagner, H. G. and Wolbarsht, M. L.** (1975). Giant retinal ganglion cells in dogfish (*Mustelus*): electrophysiology of single on-centre units. In *Vision in Fishes. New Approaches in Research* (ed. M. A. Ali), pp. 99-112. New York: Plenum Press.
- Tester, A. L. and Nelson, G. J.** (1967). Free neuromasts (pit organs) in sharks. In *Sharks, Skates, and Rays* (ed. P. W. Gilbert, R. F. Mathewson and D. P. Rall), pp. 503-531. Baltimore, MD: John Hopkins Press.
- Vickers, N. J. and Baker, T. C.** (1994). Reiterative responses to single strands of odor promote sustained upwind flight and odor source location by moths.