Report

The Function of Bilateral Odor Arrival Time Differences in Olfactory Orientation of Sharks

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Summary

The direction of an odor signal source can be estimated from bilateral differences in signal intensity and/or arrival time. The best-known examples of the use of arrival time differences are in acoustic orientation [1]. For chemoreception, animals are believed to orient by comparing bilateral odor concentration differences, turning toward higher concentrations [2–4]. However, time differences should not be ignored, because odor plumes show chaotic intermittency, with the concentration variance several orders of magnitude greater than the concentration mean (e.g., [5]). We presented a small shark species, *Mustelus canis*, with carefully timed and measured odor pulses directly into their nares. They turned toward the side stimulated first, even with delayed pulses of higher concentration. This is the first conclusive evidence that under seminatural conditions and without training, bilateral time differences trump odor concentration differences. This response would steer the shark into an odor patch each time and thereby enhance its contact with the plume, i.e., a stream of patches. Animals with more widely spaced nares would be able to resolve smaller angles of attack at higher swimming speeds, a feature that may have contributed to the evolution of hammerhead sharks. This constitutes a novel steering algorithm for tracking odor plumes.

Results and Discussion

The notion that animals respond to bilateral odor concentration differences is based on the fact that odor dilutes and diffuses gradually away from the source and on the commonly held but erroneous idea that this causes a measurable concentration gradient. This idea does not take into account the chaotic nature of most odor dispersal processes. In freely moving fluids, turbulent mixing generates a cascade of ever-smaller eddies, resulting in an odor dispersal field, or plume. An odor plume, often an odorous wake left behind another animal or object, is essentially a stream of mixing eddies (or patches, filaments) with and without odor. These spatial patches appear as temporal pulses to typically fast-adapting olfactory receptor cells, resulting in strong responses to pulse onset and sudden

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concentration increase, followed by response cessation [6]. Odor plumes show chaotic intermittency, with the concentration variance several orders of magnitude greater than the concentration mean (e.g., [5]). Therefore, a spatial concentration gradient can be obtained only by averaging. However, it typically requires many minutes for the concentration averaging process to reach a stable mean. For most animals, this is much too slow to be useful for tracking prey or mates [5, 7–9]. Steering algorithms based on odor concentration differences implemented in an underwater robot were useful only near the source under coherent plume conditions [10].

Sharks are classically believed to respond to differences in odor concentration at the nares [2, 11–16]. Previously, Johnsen and Teeter [2] fitted bonnetheads, *Sphyrna tiburo*, with a stereo headstage to control the delivery of (food) odor stimuli directly in front of the nares (nostrils). When one naris received a (2×) stronger odor pulse, the animals turned toward the side receiving the stronger stimulus. However, it is likely that concentration and timing differences were confounded. The odors in their experiment were preloaded as a discrete bolus into long tubing, with seawater both ahead of and behind the odor. This caused dilution of the leading and trailing edges of the odor bolus: it reached 50% of the applied concentration 7 s after initiation of odor delivery. Thus, the high concentration side would have reached response threshold before the low concentration side, and the animals received bilateral differences not only in the concentration but also—unintentionally—in the arrival time of detectable levels of odor at each naris.

To evaluate their contributions to steering behavior, both odor arrival time and concentration must be known. This requires accurate control of odor pulse shape, i.e., the concentration-time profile of the stimulus [7, 8]. To accomplish this goal, we fitted a small shark species, *Mustelus canis*, with a headstage apparatus designed to separately control the concentration of odor and the timing of its arrival at the nares via computer-controlled syringe pumps (Figures 1A and 1B). All odor pulses were standardized to concentration, volume 0.5 ml, duration 5.22 s, and flow speed 1.5 cm/s. The latter is less than 10% of the estimated natural flow through the shark nose (see Supplemental Experimental Procedures available online) that is driven by pressure differences between inflow and outflow nares resulting from forward swimming motion [17–20]. Six different patterns of odor pulses were used. Four involved timing differences between the nares, such that one naris received an odor pulse (1) 0.1 s, (2) 0.2 s, (3) 0.5 s, or (4) 1.0 s ahead of the other naris. Two odor stimulus patterns involved concentration differences. A 100-fold dilution of squid odor was delivered to one naris and full-strength squid odor to the other naris either (5) simultaneously to the two nares (0 s delay) or (6) with a 0.5 s delay such that the naris receiving the weak stimulus received it 0.5 s ahead of the naris receiving the full-strength squid odor. To confirm that responses were to the odor component of the pulse, we also tested each animal as above (7) with ambient seawater pulses, delivered with a 0.5 s time delay between the nares.

The seawater control caused a greater proportion of null responses—i.e., no turns—than turns (t test, p = 0.0008), and
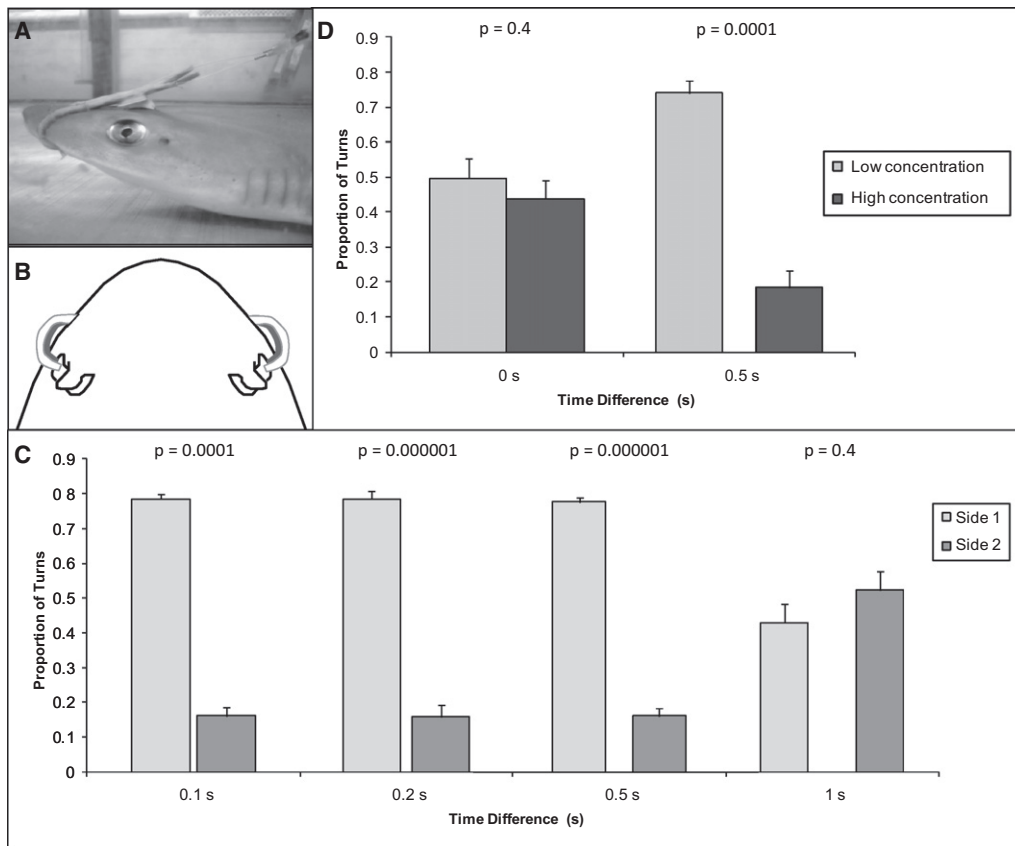
Figure 1. Proportion of Turns in Response to Different Stimulus Patterns

(A) Photograph of a resting smooth dogfish, *Mustelus canis*, wearing the headstage apparatus.

(B) Illustration of the ventral side of a smooth dogfish wearing the headstage apparatus. The tubing orifice is located just inside the entrance of the inflow naris without closing it off and keeps the outflow naris unobstructed for normal function. Close observation of dye pulse delivery showed that the entire pulse is immediately drawn into the inflow naris.

(C) Proportion of turns in response to timing differences. The size of the gap between the bars on the y axis is proportional to the difference in timing of arrival of the odor stimulus at the nares. Light bars indicate turns toward the first side stimulated, darker bars indicate turns toward the second side stimulated. Odor concentration is equal in all cases. Data are represented as mean ± standard error of the mean (SEM).

(D) Proportion of turns in response to concentration differences. The gap between the bars on the y axis is proportional to the difference in arrival time of the stimulus at the nares. Dark bars indicate stronger odor stimuli (full strength), lighter bars indicate weaker odor concentration (1:100 dilution). Data are represented as mean ± SEM.

there was no significant difference between the number of turns toward and away from the water pulses (t test, $p = 0.8$); thus, the animals did not respond to seawater pulses. In contrast, each of the odor stimulus patterns caused a greater proportion of turns than null responses (see also Table S1); thus, odor and seawater stimuli were significantly different in terms of the proportion of responses observed (repeated-measures analysis of variance [RM ANOVA], $p < 0.001$, $n = 8$; Tukey test, $p < 0.001$). Among the odor stimulus patterns, the proportion of responses observed was not significantly different (Tukey test, $p = 1$). These results indicate that the animals did not respond to the tactile sensation of slightly increased flow entering the nares. Of course, one might still argue that the directional response might be caused by the tactile sensation of time-delayed bilateral flow, but only in the presence of nondirectional odor. However, in nature, odor arrival is a far more salient signal than ubiquitous flow variance, which, in our experimental condition, was estimated to be at least an order of magnitude lower than the normal flow through the nose (see Supplemental Experimental Procedures).

For the 0.1 s, 0.2 s, and 0.5 s time delays, the animals turned with a significantly greater frequency toward the side receiving the first stimulus than toward the side receiving the later stimulus. For the 1 s time delay, the animals turned to either side with equal frequency (Figure 1C). For the bilateral (0 s delay) concentration differences, the animals again turned toward either side with equal frequency. When the concentration and time differences were combined, the animals once again turned toward the side receiving the first, albeit weaker, stimulus with significantly greater frequency (Figure 1D). The results for the 0.1 s, 0.2 s, and 0.5 s delays, and for the concentration difference with 0.5 s delay, were significantly different from those for the 1 s time delay and simultaneous bilateral concentration differences (RM ANOVA, $p < 0.001$; Tukey test, $p < 0.001$), but they were not significantly different from one another (Tukey test, $p = 0.98–1$).

The results show that odor arrival time differences, and not concentration differences, cause directional turning in the shark *M. canis*. Even 100× concentration differences were ignored in favor of arrival time differences. Although the concentration of odor is still important in that it must be high
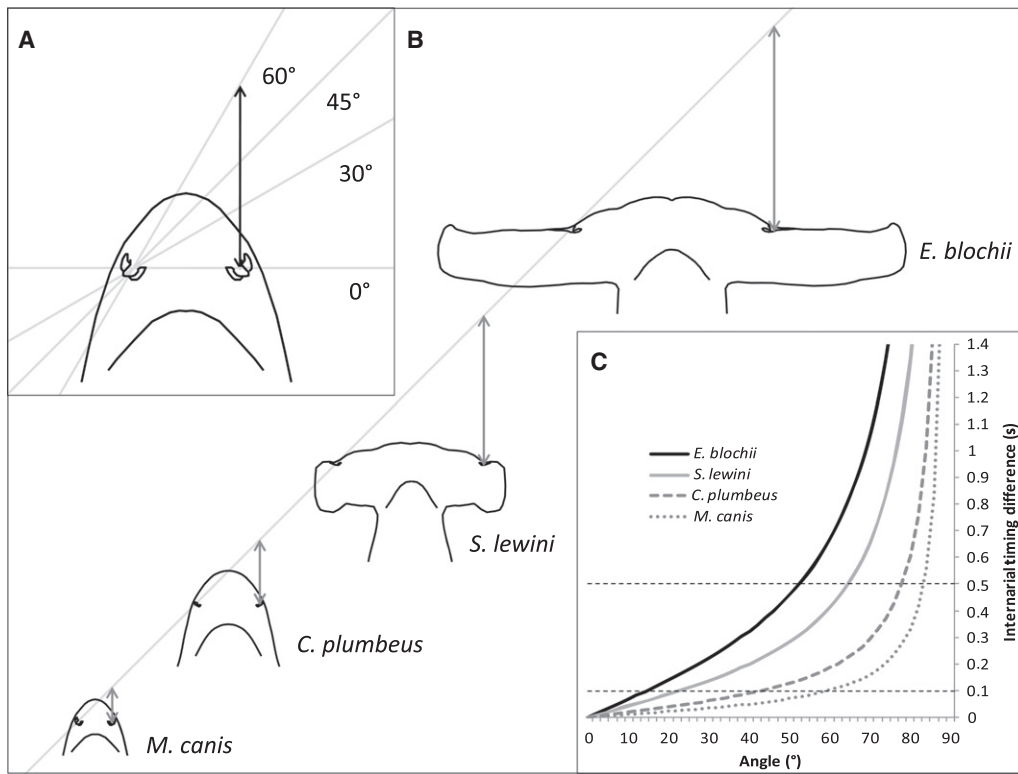
Figure 2. Differences in Odor Arrival Time

(A) Differences in odor arrival time based on angle of attack. Illustration of a smooth dogfish, *Mustelus canis*, swimming into the leading edge of an odor patch oriented at various angles to the head. Assuming a constant swim speed, the time delay of odor arrival at the second naris (arrow) increases as the angle increases.

(B) Differences in odor arrival time based on internarial spacing. Comparison of the smooth dogfish, *Mustelus canis*, with the sandbar shark, *Carcharhinus plumbeus*, and two species of hammerhead sharks, the scalloped hammerhead, *Sphyrna lewini*, and the winghead, *Eusphyra blochii*, swimming into an odor patch at a 45° angle. If the swim speed is constant across all four species, the wider spacing of the nares of the hammerheads results in an increased internarial arrival time difference (arrows). All heads are scaled to animals of 1 m total length.

(C) Comparison of internarial arrival time differences among shark species. The expected internarial timing difference (in seconds) resulting from the encounter of the leading edge of an odor patch over a range of angles for four species of sharks: *E. blochii* (black solid line), *S. lewini* (gray solid line), *C. plumbeus* (gray dashed line), and *M. canis* (gray dotted line). The horizontal dashed lines indicate the largest and smallest timing differences tested in this study, to which *M. canis* demonstrated a directional response.

enough to trigger a behavioral response, the animals did not use comparisons of odor concentration between the nostrils for orientation as previously hypothesized [2, 11–16].

The latency from delivery of the stimulus to the initiation of a turn (1.07 ± 0.1 s standard error of the mean) did not vary significantly among the different stimulus patterns (RM ANOVA, p = 0.08). Thus, directional turning was limited to a subsecond time window of arrival time differences. This suggests that sharks use a simple brain algorithm that would allow the animal to distinguish between (1) a head-on encounter with an odor patch (no time difference: respond with turning in either direction to obtain new patch encounters with directional information), (2) an oblique encounter (0.1–0.5 s time difference: respond directionally and turn into the odor patch), and (3) an encounter with two separate odor patches on either side, indicating a position likely within the plume (1 s time difference: respond with a turn in either direction to obtain new encounters with directional information). Unilateral stimulation (encounter with odor on one side and a delay of > > 1 s before the next encounter) is likely to indicate a position at the plume edge and results in a turn toward the stimulated side as shown earlier [16]. A related phenomenon is known in flying moths, which, during plume tracking, delay their turning

behavior by 300 ms after losing contact with an odor patch. Apparently this delay provides good probability of hitting a possible next patch, which leads them closer to the plume source [21, 22]. The overall result is an enhanced ability to stay connected with the chaotic dispersal field of an odor plume, reducing the real danger of losing the plume altogether. (We note that our smallest temporal resolution of 100 ms internarial delay for *M. canis*, measured with 20 ms accuracy, was the result of our technical limitation of measurable odor delivery and did not establish the actual lower limit of the animal.)

Differences in bilateral encounter times with a single patch are a function of three factors: the angle of attack (i.e., the angle by which the animal approaches the odor patch boundary (Figure 2A), the spacing of the nares, and the swimming speed of the animal with respect to its fluid environment. Whereas the angle of attack is a function of local plume structure and internarial spacing is a species property, swimming speed is regulated by the individual animal. This suggests control over swimming speed during plume tracking, which determines the size scale of patches that can be resolved, because both faster and slower speeds could take them out of the neural detection-time window. Our sharks track at a

typical speed of ~1 m/s, which is significantly less than what they are capable of (>3 m/s), despite the potentially competitive nature of food tracking among nearby animals. This speed (10 cm/100 ms) is well suited to resolve odor patches spaced on the order of 10 cm. Similarly, reduced walking speed during plume tracking has been observed in lobsters [7]. Also, lobsters stop tracking if patch spacing is greater than 10 cm [23]. It also suggests that in order to obtain the same information, faster swimming animals may have developed greater time resolution and/or more widely spaced nares.

For a given angle of attack, the lag time between nares is a function of internarial distance (Figure 2B). Hammerhead sharks (Carcharhiniformes, Sphyrnidae) all possess dorsoventrally compressed and laterally expanded heads, termed cephalofoils. This anatomy increased separation of the nares [12, 24–26] and may confer an olfactory advantage to these animals [2, 11, 12, 26, 27]. Their broad nares and long prenarial grooves allow hammerheads to sample a greater area of the medium, increasing the probability of detecting an odor [12, 24, 26]. However, hammerheads do not possess a greater olfactory epithelial surface area than the typical carcharhinid sharks [12, 26], nor do they appear to have a greater olfactory sensitivity, as indicated by their thresholds for detection of single amino acids, which are comparable to other fishes [28–31]. However, as a result of the wider spacing of the nares, hammerheads may be able to perceive a bilateral time difference at a smaller angle or at a greater swimming speed than an animal with a narrow head.

We compared measurements of the head and nares of *M. canis* to other elasmobranchs, as per Kajiura et al. [26]. Using a swim speed of 1 body length per second and scaling all species to a total length of 1 m reveals that the winghead, *Eusphyra blochii*, which has the widest head and the greatest narial separation, would be expected to experience the longest internarial timing delays for a given angle (Figure 2C). Assuming that both the concentration detection threshold and the threshold for detection of internarial time differences are the same across all four species, *E. blochii* would be capable of orienting to odor patches at a much smaller angle of attack as compared to the other species, followed by the scalloped hammerhead, *Sphyrna lewini*, the sandbar shark, *Carcharhinus plumbeus*, and the smooth dogfish, *Mustelus canis*. The results of our study suggest a new theory for the evolution of the "hammer": enhanced olfactory tracking capabilities as a result of increased temporal resolution for klinotaxis. To confirm this new version of the enhanced olfactory hypothesis, we need to examine the range of internarial timing differences that hammerhead sharks can actually detect.

In conclusion, this study has shown that sharks can use odor information for steering despite the scalar nature of odor. This function may be important and specific: turning into an odor patch. Superficially, steering by a scalar suggests using an intensity gradient, but the physics of odor dispersal make this difficult, and it appears to not be used except in special odor-dispersal circumstances. However, bilateral arrival time differences can give useful directional information at the spatial scale of an odor patch encounter. Because odor plumes can be seen as odor patch dispersal fields, tracking the sequence of patches may be the best way to locate the odor source (eddy chemotaxis; [32]). Insects use this approach, but they steer by local wind direction [9, 21, 22, 33]; sharks appear to do the same, but they steer by bilateral odor arrival time differences. Again, the physics of dispersal may have enforced the difference. In insects, small antennal separation distance and great flight speed may make time differences more difficult to resolve, whereas visual contact with the ground allows them to use local wind drift for steering, something not possible for many marine animals that cannot see the bottom.

Experimental Procedures

Eight smooth dogfish, *Mustelus canis*, were captured in the waters surrounding Woods Hole, MA and transported to the Marine Biological Laboratory (MBL), where they were maintained according to protocols approved by the Institutional Animal Care and Use Committees at the MBL (protocol 08-26) and the University of South Florida (protocol W3211). To control the presentation of odors, we fitted the animals with headstages, attached such that the tubing sat just inside the inflow nares (Figures 1A and 1B). Tubing from the left and right sides of the headstage were attached to two syringes, each driven by a programmable syringe pump. These pumps were synchronized via a laptop computer. Squid rinse [34] was used as the odor source in all experiments. Details of this apparatus and procedures are described in the Supplemental Experimental Procedures available online.

Experiments were conducted in a flume tank filled to 60 cm and divided into 3 m long × 2 m wide pens. During trials, seawater flow in the tank was shut off, and experiments were conducted in still water. Each trial began by offering the animal a small piece of squid to confirm its hunger status. If the animal did not consume the squid, testing was delayed for another 24 hr. If the animal consumed the squid, the trial proceeded. In a trial, an animal was presented ten times with one of the seven stimulus patterns (described above), each repetition separated by a 10 s delay between the end of the previous stimulus and the onset of the next. Each trial was simultaneously observed and recorded by overhead video cameras. Each animal was given two trials for each of the six odor stimulus patterns (as well as the seawater control), once with the left naris receiving the first or strongest odor pulse and once with the right naris receiving the first or strongest odor pulse. This was to account for any possible bias on the part of the animal to turn in a particular direction.

Following each trial, the animal was again offered a piece of squid. If it was not consumed, the animal was determined to lack the proper motivation and the prior trial was rejected, resulting in rejection of 3 out of 115 trials. Between trials, the tank was placed on flow-through seawater for 30 min to flush out any lingering odors. Up to four trials per day were conducted in this manner on each animal. Each animal was tested with all six stimulus patterns, as well as the seawater control. The order of the presentation of the stimulus patterns was randomized, and the headstage tubing was flushed with fresh seawater after every trial.

The overhead video was analyzed using MaxTRAQ Standard v.1.93 software (Innovision Systems). A turn was defined as at least a 30° change in heading from the direction of travel just prior to the delivery of an odor pulse. A null response score was given to any changes in heading of less than 30° or to turns that were initiated more than 6 s after the beginning of the first odor pulse. If the animal was already in a turn when the odor pulses were delivered, the response was removed from the analysis because it could not be determined whether the animal was responding to the pattern of the odor stimulus or simply completing the turn that it had already initiated. The direction of any turn was recorded, as well as the latency, defined as the time from the start of the first odor pulse in each pair to the initiation of a turn. The researcher analyzing the video was provided with the start time for each odor pulse but was otherwise blind to the stimulus pattern being tested. A film record of a sample trial (Movie S1) and its analysis (Table S2) are available online.

The data for each stimulus pattern for each animal were pooled, sine square-root transformed, and tested for normality and equality of variance using Kolmogorov-Smirnoff and Levene Median tests [35]. Within each stimulus pattern used, responses were examined using t tests for dependent samples, with each animal weighted based on the number of data points (turns + null responses). Because the same animals were tested with each stimulus pattern, data were compared among stimulus patterns using RM ANOVA and Tukey post hoc tests. Analyses were conducted using Statistica 5.5 (StatSoft) and SigmaStat 3.05 (Systat Software).

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, two tables, and one movie and can be found with this article online at doi:10.1016/j.cub.2010.04.053.

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