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Additional Navigational Strategies Can Augment Odor-Gated Rheotaxis for Navigation under Conditions of Variable Flow

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Synopsis The navigation strategies animals use to find sources of odor depend on the olfactory stimuli, the properties of flowing fluids, and the locomotory capabilities of the animal. In high Reynolds number environments, animals typically use odor-gated rheotaxis to find the source of turbulent odor plumes. This strategy succeeds because, although turbulence creates an intermittent chemical cue, the animal follows the (continuous) directional cue created by the flow that is transporting the chemical. However, in nature, animals may lose all contact with an odor plume as variations in the direction of bulk flow cause the plume to be rotated away before the animal reaches the source of the odor. Our goal was to use a mathematical model to test the hypothesis that strategies that augment odor-gated rheotaxis would be beneficial for finding the source of an odor plume in such variable flow. The model links a stochastic variable-direction odor plume with a turbulence-based intermittent chemical signal and four different movement strategies, including: odor-gated rheotaxis alone (as a control), odor-gated rheotaxis augmented by further rheotaxis in the absence of odor, odor-gated rheotaxis augmented by a random walk, and odor-gated rheotaxis augmented by movement actively guided by the heading of the flow when the odor was still present. We found that any of the three augmented strategies could improve on strict odor-gated rheotaxis. Moreover, variations in performance caused the best strategy to depend on the speed of movement of the animal and the magnitude of the variation in flow, and more subtly on the duration over which the augmented strategy was performed. For most combinations of parameters in the model, either augmenting with a random walk or following the last-known heading were the best-performing strategies. Overall, our results suggest that marine animals that rely on odor cues to navigate in turbulent environments may augment odor-gated rheotaxis with additional movements that will increase the probability of finding the sources of odors. Moreover, we believe our approach to modeling odor plumes in variable flows is a valuable step toward mathematically capturing the key conditions experienced by animals navigating on the basis of odors carried by flows.

Introduction

Many animals navigate using odors and flow. The strategies used to find and avoid sources of odor will depend on the olfactory stimuli, physical characteristics of the flow, and the locomotory capabilities of the animal. In high Reynolds number environments, where inertial forces and turbulence dominate, animals must contend with turbulent odor plumes. Numerous studies, both theoretical and experimental, have considered how animals

find the sources of odors in attractive odor plumes generated by unidirectional bulk flow with turbulence, but without changes in the long-term average direction of flow (Murlis et al. 1992; Webster and Weissburg 2001, 2009; Grasso and Basil 2002; Lo Iacono 2010). However, navigation strategies in nature must involve more than just how to find the source of an odor while in an odor plume. To date, consideration of strategies beyond navigation inside an attractive plume has been largely

theoretical, and focused particularly on initially locating plumes in flows (Sabelis and Schippers 1984; Balkovsky and Shraiman 2002). Other recent studies have considered strategies for relocating an odor plume (but not its source) after a change in the direction of a bulk flow (Harvey et al. 2008) and for finding a plume with simulated variations in turbulence but no changes in bulk flow (Vergassola et al. 2007; Pasternak et al. 2009). However, to our knowledge, only one study (limited in scope to a single species) has considered strategic options for finding the source of an odor plume after animals lose contact with the plume due to a change in direction of bulk flow (Wyeth 2010). Our goal here was to continue exploration of how animals with differing locomotory abilities and experiencing different conditions of flow in marine habitats might improve their success in navigating in the face of directional changes in bulk flow.

The direction of bulk flow will change substantially over time in many marine habitats (Lentz and Fewings 2012). Tidal flow changes direction over time. Moreover, even within a single tidal period, turbulence at varying scales created by uneven topography, including islands, underwater ridges, ravines, boulders, and changes in the composition of the substrate can all lead to highly variable directions of flow in most near-shore habitats. Add to this complexity other induced flows (from wind, waves, or other sources), and there appears to be a low probability that marine animals in natural

habitats will experience solely unidirectional bulk flow as has been used to generate plumes in laboratory flumes and which formed the basis for models in theoretical studies. Indeed, although empirical data directly linked to a location with animals navigating in plumes is scarce, the information that is available from sensors at fixed locations and that measure the velocity of currents on time scales appropriate to animal navigation (minutes or hours) indicates that there is considerable variation in the direction of flow (e.g., Lavelle et al. 1978; Butman et al. 1979; Forbes and Drapeau 1989; Kulikov et al. 1998; Wyeth et al. 2006; Wilson et al. 2013).

Animals navigating inside turbulent odor plumes primarily use odor-gated rheotaxis to reach the source (Vickers 2000; Weissburg 2000). By following the direction of flow, the animals can compensate for the intermittency in an odor signal created by turbulent mixing. However, if the direction of bulk flow changes before the animal reaches the source of the odor plume, the plume will be rotated away from the animal, eliminating the trigger for moving upstream. Moreover, if the animal continues to follow the flow, it will no longer be moving toward the source (Fig. 1). Thus, if the direction of bulk flow changes, it is intuitively sensible for the navigating animal to continue to follow the direction of flow measured at the time the odor was last detected (i.e., following the last-known heading). The success of this strategy presumably depends on the variability of flow and the animal's locomotory speed. There are several

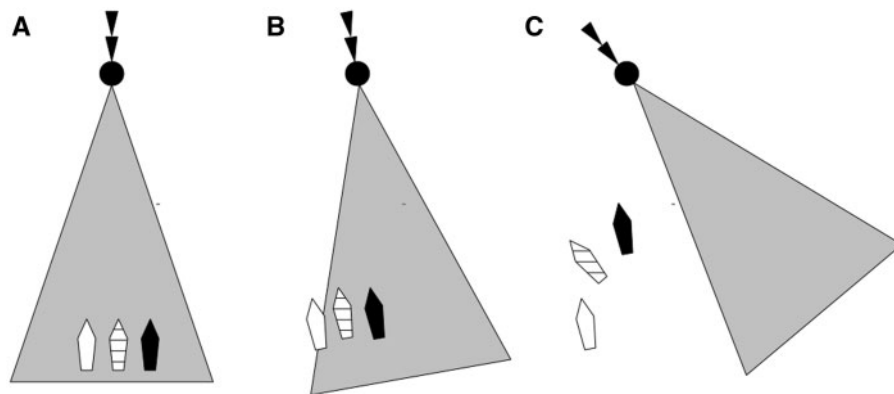


Fig. 1 Schematic of the navigational problem and a potential solution for an animal using odor-gated rheotaxis in variable flow. Three different navigational strategies (pentagons) are presented: odor-gated rheotaxis with no further movement if the odor is lost (white), further rheotaxis after odor-gated rheotaxis ends (hatched), and following the last-known heading (continued movement in the upstream direction detected when odors were last detected; black). (A) All three strategies initially use odor-gated rheotaxis when inside an odor plume (gray) generated by a source of odor (closed circle) and turbulent flow (mean heading shown by double arrowhead). (B) When the direction of flow shifts, odor-gated rheotaxis ceases movement in the absence of the odor plume, while the two other strategies lead to continued movement. (C) When the direction of flow shifts further, only the animals employing the strategy of following the last-known heading continue movement toward the source of the odor, with animals employing strict odor-gated rheotaxis remaining stationary outside the plume, and those employing further rheotaxis continuing to move, but in the wrong direction.

theoretical extremes: a very slow animal would always need to follow some previous direction of flow since flow will always change before the animal reaches the source. In contrast, a very fast animal would never need the additional strategy since it would always reach the target using odor-gated rheotaxis before the direction of flow changes. Similarly, if the direction of flow never changes, odor-gated rheotaxis alone will always work, while if the variability of the direction of flow is very high, then orienting to flow will rarely direct an animal toward the source of odor carried in that flow. Thus, there is likely to be a set of conditions between these extremes for which it will be valuable to combine odor-gated rheotaxis with an additional strategy to continue navigation following the last direction of flow detected while the animal was still receiving the olfactory stimulus.

Our objectives here were two-fold. (1) To test the hypothesis that augmenting strict odor-gated rheotaxis with additional movement after a directional change in flow has occurred can increase navigational success. (2) To survey the potential benefits of three alternative strategies to better understand how animals might best augment odor-gated rheotaxis after a change in the direction of a flow swings an odor plume away from the animal. The three strategies include (1) further rheotaxis, (2) a random walk initiated in the upstream direction when odors were last detected, and (3) following that last-known heading (using some unspecified alternative sensory system). We use a mathematical model with parameters set to encompass a wide range of crawling and swimming capabilities of marine animals (including echinoderms, gastropods, crustaceans, and fish) and the conditions of flow experienced by those animals. In addition, we vary the duration of any memory for implementing an augmented strategy and the initial distance of the animal from the source of the odor, two further parameters that could affect navigational performance. By assessing navigational performance based on the minimum distance from the source of the odor achieved by the different strategies, the results of our model support the hypothesis that odor-gated rheotaxis alone has relatively low performance, and we find subtle differences among the additional benefits of the three augmented strategies.

Methods

Our model involves three interconnected components: a variable-direction odor plume, a stochastic approximation of the odor's concentrations driven

by turbulence inside the plume, and the dynamics of various navigational strategies potentially used by animals to find the source of the odor plume. Importantly, the model is based largely on an experimentally verified approximation of a turbulent odor plume (Du et al. 1999; Hilderman and Wilson 1999; Wilson 2010), with necessary parameters also based on measurements of real odor plumes (Fackrell and Robins 1982; Mylne and Mason 1991; Webster and Weissburg 2001). Full details of the model's construction are provided in the Supplementary Material.

Briefly, the odor plume is first modeled based on an approximation of the time-averaged concentration profiles observed in real plumes. This accounts for decreasing concentrations of odor found both downstream and away from the center-line of the odor plume. To our knowledge, variation in the direction of flow has not been characterized effectively across aquatic habitats, with the focus primarily on rotary spectra to extract dominant periodic signals from variable directions in some locations (e.g., Gonella 1972; Lavelle et al. 1978; Kulikov et al. 1998; Shay et al. 1998). Consequently, as a simple approach to model a broad range of variable directions of flow, we use a Gaussian random walk to control the plume's direction, with standard deviation spanning values that approximate protected and narrow tidal channels (low variability) and a wave-swept shore with complex topography (high variability). The center-line of the odor plume is advected based on this angular input, and thus follows a meandering path over its length with greater or lesser variability, dependent on the standard deviation of the direction of flow (key parameter 1). At any point inside the plume, the instantaneous concentration of odor is determined by the time-averaged concentration profile of an odor plume mapped onto the meandering center-line. This average concentration is used as input to a first-order Markov process modeling the intermittency created by turbulence (Hilderman and Wilson 1999). This results in an intermittent and continuously variable signal that interacts with the minimum detection threshold of the animals, creating a meandering detectable odor plume with both time-averaged and instantaneous structure similar to real odor plumes.

The navigating animals move in a two-dimensional space also occupied by the odor plume. For simplicity, animals can either be stationary or moving with a fixed speed (key parameter 2). The range of speeds was chosen based on a literature survey spanning several marine taxa, including molluscs, echinoderms, crustaceans, and vertebrates

(Moore and Lepper 1997; Basil et al. 2000; Bernal et al. 2001; Baker et al. 2002; Carton and Montgomery 2003; Drolet and Himmelman 2004; Ferner and Weissburg 2005; Wyeth and Willows 2006; Fernö et al. 2011). The direction of movement was determined by four different navigational strategies: odor-gated rheotaxis alone, odor-gated rheotaxis augmented with further rheotaxis after odors are no longer detected, odor-gated rheotaxis augmented by continuing to follow the upstream heading when odor was last detected (i.e., following the last-known heading), or odor-gated rheotaxis augmented with an angular random-walk initiated at the upstream heading when odors were last detected. All of the augmented strategies continue movement after odor was last detected, and thus require a duration of memory (key parameter 3) to set the period over which that movement continues. Unlike the other parameters, we cannot draw on prior studies to set a realistic range for this parameter of memory, since, to our knowledge, this information is not available. Instead, we explored all possible durations within the constraints of the model, by allowing the parameter to range across different proportions of the model run (between zero, corresponding to no memory, and one, corresponding to memory lasting the full length of the model run). Finally, we anticipated that different strategies might perform differently at different distances from an odor source, and thus we systematically varied the initial distance (key parameter 4) of animals relative to the source of the odor.

The four key parameters noted above, in combination with the four different navigational strategies, define the primary five-dimensional space we used to explore the outputs of the model (Table 1). All other parameters (the full list is provided in the Supplementary Material) were fixed to prevent combinatorial proliferation of parameter space. Importantly, the additional parameters were set

such that they created a realistic approximation of a turbulent odor plume and were also specifically varied in additional tests so as to confirm that they had little effect on the conclusions from the model's output. Thus, we chose to fix the two parameters (γ and i_p^2 , see Model Details in the Supplementary Material) governing the random fluctuations of odors inside the plume to values consistent with data from experimental fluid-channel plumes (Fackrell and Robins 1982; Mylne and Mason 1991; Webster and Weissburg 2001). Varying either parameter had little effect on the model's output, except that at particularly low values for which the low probability of odors exceeding the threshold for detection resulted in very little movement by any animals. The primary effects on the animals were the same for the remaining parameter k (see Model Details in the Supplementary Material) and also the threshold for detection of odors: both set the spread of the effective width of the plume. Specifically varying either of these parameters had little effect on the relative performance of the strategies, and, in particular, little variation was observed in performance (<2% difference) among the strategies augmenting odor-gated rheotaxis for almost all values for these two parameters.

Due to the random nature of the variation in flow, consistent trends in the output of the model required repeated runs. We found that 200 runs with random directions of the initial flow and animals systematically arrayed at 90-degree intervals and at the three initial distances was sufficient for the major trends to be apparent (i.e., no further substantial changes occurred when performance was averaged across more than 200 runs of the model), and model's output converged such that mean performance showed no further changes after 1000 runs.

We made several key decisions in the formulation of the model and in analyses to keep the durations of the runs reasonable and allow effective comparison of the different strategies across the parameter space. (1) We use scaled time-stepping in order to standardize the comparison of strategies across multiple speeds of the animals. Without this scaling, the success in navigation would be biased toward animals with higher speeds in our spatially explicit model. Thus, we fixed the number of intervals of time for each run of the model, and adjusted the duration of each step (and thus also the total duration of the run). The result is that if all animals moved constantly in a straight line they would travel the same distance, regardless of their speed. Provided we assume that animals of different speeds have similar locomotive efficiency, we can then compare the

Table 1 Key parameters and navigational strategies defining the primary five-dimensional output space of the model

Dimension	Typical values
1. Variation in flow	5–50 degree s ⁻¹
2. Animal's speed	0.001–1 m s ⁻¹
3. Duration of memory	0.0–1.0 (proportion of model run)
4. Initial distance	1, 2, 3 m
5. Strategy	Odor-gated rheotaxis (OGR) alone OGR + rheotaxis OGR + random walk OGR + last known heading

navigational success across different animals' speeds for the standardized distance. (2) We set the duration of the model's steps so that animals would cover 3 m over the full duration of the run. Since animals started at distances of 1, 2, or 3 m from the source of the odor, this allows a mixed assessment of navigation that includes potential errors. Those starting 1 m away from the source of the odor will be strongly affected by any errors that result in movement not directed toward the source, while the proportionate cost of errors for those 3 m away will be substantially lower and thus their results will primarily measure the benefits of the strategy. (3) We allowed the plume to develop in two-dimensions first, such that animals at all initial distances could potentially be inside the odor plume before initiating navigational responses. This approach is equivalent to animals instantaneously initiating a search for an odor's source (as opposed to a source of odor instantaneously appearing, which would be the case if animals navigated as the plume developed). Both possibilities can occur in nature, but we chose to keep the model based solely on the navigator's behavioral parameters and not to model the behavior of sources of odor. (4) At the start of each run, we arrayed animals at four equidistant angles (for each of the three initial distances) around the source. This, combined with a random initiation for the direction of flow, ensured that there was no bias based on initial locations. Moreover, this choice is a compromise between two factors affecting the relative performances of strategies. Arraying animals at more angles both increases the absolute numbers of animals detecting odors at some point in a run, thereby improving our ability to measure the effects of the different strategies, and also dilutes the effects different strategies have on recapturing a plume after it is lost (because more animals will be solely inside the plume). (5) We include all animals in our analyses, including those that never encounter a plume. Although this does create some negative bias in the effectiveness of strategies when variations of flow are low (since higher proportions of animals never encounter the plume than when the variation in flow is higher), all strategies were tested under the same conditions, thereby allowing comparison of overall navigational success for each strategy over a range of variations in flow (and alternatively excluding animals that have not detected the odor plume also biases measures of performance when variability of flow is low relative to the variability when flow is high).

We used several metrics to assess navigational performance of the different strategies relative to the

various combinations of parameters. Our primary measure of navigational success was the minimum distance from the odor's source. This eliminated the effect of any overshoot by a strategy that came close to the odor in a relatively short time. We prefer to use minimum distance rather than scoring whether or not animals reached the source since the latter approach adds complexity to the model by requiring an additional parameter for the size of the source (a point source will never be reached). Moreover, the range for this additional parameter would need to be expanded to account for alternate cues that will supplement navigation relative to the source of the odor plume as animals approach the source. This will further increase the region around the source that could be defined as the goal of successful navigation. In contrast, by avoiding the proliferation of parameters, and using the minimum distance as a performance metric captures successful navigation that either directly finds the source or sets the stage for short-distance navigation using other cues. In addition, we used two further metrics to cross-check the measures of minimum distance. First, assessing the maximum distance from the odor's source provided a measure of how many mistakes a strategy made. Second, measuring the time at which the minimum distance occurs and the total distance that is covered helped to assess how efficient a strategy is (with respect to time and energy, respectively).

Results

For odor-gated rheotaxis alone, the minimum distance from the odor source that is achieved showed some variation both with the animal's speed and the variation in flow (Fig. 2A). Performance was largely uniform for intermediate speeds and variations in flow. However, at the highest variations, performance decreased in slowly moving animals as these were more likely to lose contact with the plume and stop movement. Conversely, for the lowest variations in flow, performance increased for faster-moving animals, as in this relatively constant plume, faster movement meant they were less likely to be delayed by the intermittency of the plume. This heterogeneity did not affect subsequent analyses since all strategies were based on odor-gated rheotaxis augmented by further navigational procedures. Thus, either in direct comparisons between augmented strategies, or by normalizing results from augmented strategies to the performance of odor-gated rheotaxis alone, differences in performance will be the consequence of the augmentation (which is our interest), not the

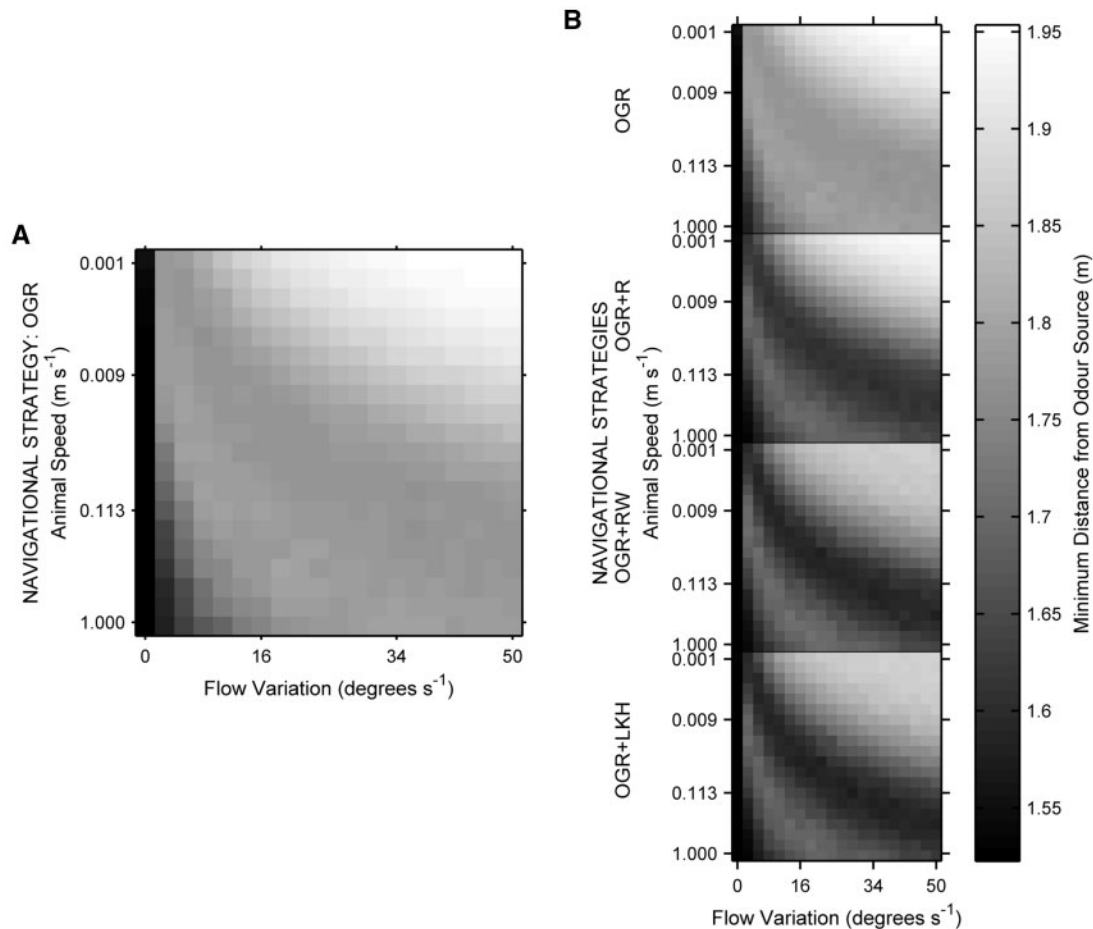


Fig. 2 Navigational performance of different strategies depend both on the speed of the animal and the variability in flow. **(A)** Intensity map showing minimum distance from the source of the odor when strict odor-gated rheotaxis is employed across a range of speeds of the animals and variabilities in flow. Subsequent figures present arrays of this basic intensity map for different strategies and combinations of parameters. **(B)** Minimum distance from the source of the odor for four navigational strategies: odor-gated rheotaxis, OGR; OGR augmented by further rheotaxis (OGR + R); OGR augmented by a random walk (OGR + RW), and OGR augmented by following the last-known heading (OGR + LKH). Intensity maps for a range of animals' speeds and of variations in flow are outlined in black for each strategy (thus, the axis of the animals' speeds is repeated four times). All data are means from 1100 runs, with all animals starting 2 m from the source of the odor, and memory (for the three augmented strategies) lasting 20% of the duration of the model run. Intensity scale identical for A and B.

underlying heterogeneity resulting from the basic odor-gated rheotaxis.

Differences among the strategies that augmented basic odor-gated rheotaxis were subtle. The basic odor-gated rheotaxis was always the poorest strategy, usually by a substantial margin (between 5% and 10% difference on average, and greater than 20% in some cases) (Fig. 3), for all combinations of parameters (animal's speed, variation in flow, initial distance from the source of the odor, and duration of memory). Comparing across animals' speeds and across variations in flow, the three strategies augmenting odor-gated rheotaxis, i.e., with further rheotaxis, with a random walk, or by following a last-known heading, were particularly advantageous

in a non-linear swath of parameter space (Fig. 2B). This space comprised a contiguous area spanning low speeds of animals and low variation in flow, as well as high speeds of animals and high variation in flow, with benefits at intermediate speeds and variation offset by a small region with lesser benefits at very high speeds of animals and very low variation in flow and a larger region with lesser benefits at lower speeds and variation. In contrast, the differences among the three augmented strategies were small, less than 2% on average, across all combinations of parameters (Fig. 3). However, these averages belied considerable heterogeneity across the full parameter space, with differences between augmented strategies in some cases reaching between 5% and 10%

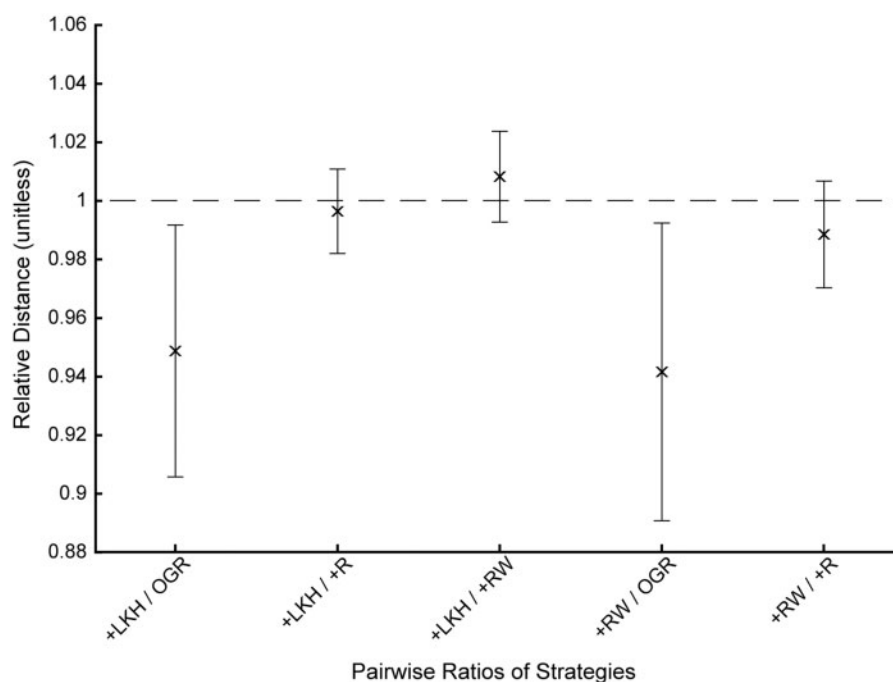


Fig. 3 Key pairwise comparisons of overall performance for four navigational strategies. Strategies (odor-gated rheotaxis, OGR; OGR augmented with further rheotaxis, +R; OGR augmented with a random walk, +RW; and OGR augmented with following the last-known heading, +LKH). Means and standard deviations for pairwise ratios for the minimum distance from the odor's source, calculated across all combinations of parameters. Values < 1 (dashed line) indicate that the strategy in the numerator moves closer to the source. All data are means from 1000 runs of the model, with animals starting at 1, 2, and 3 m from the source.

(Fig. 4). In the majority of cases, the two strategies augmented by either the last-known heading or a random walk were better than augmenting with further rheotaxis. The relative performance of following the last-known heading was best in some cases, usually by a very small margin (on the order of 1% or less). Alternatively, in those cases in which a random walk was better, the performance was often substantially greater (and thus biased the overall difference in average performance of the two strategies) (Fig. 3). Exploration of the full parameter space showed that the heterogeneity in performances of the various strategies depended on all four major parameters.

Speed of the animals and variability of flow

The basic pattern of results is that the two-dimensional parameter space (for animal's speed and the variability in flow) is split between two regions (Fig. 5). Last-known heading was the best option if the animals are fast and the variation in flow is low. Conversely, a random walk was the better option if speed is low and variation is high. The advantage of the random walk over following the last-known heading is presumably because errors made in relatively variable flow (falsely predicting the direction to

the upstream source) can only be compensated by speedy movement of the animals to the target before the high variation in flow leads them astray. Moreover, at lower speeds a random walk will be better at recapturing the plume when variation in flow is high. However, at high speeds and low variability, the reduced drift of following the last-known heading outweighs the costs of errors, which was also the case for lower speeds coupled with low variability. The only consistent exception to the supremacy either of augmenting with a random walk or of following the last-known heading was at the shortest initial distance from the source, in a narrow band of parameter space where augmenting with rheotaxis was better than augmenting with a random walk (for slower animals spanning all levels of variation in flow) (Fig. 5). Overall, these results indicate that continued movement is highly beneficial, and that subtle variations in flow and locomotory conditions will have an effect on whether a random walk, following a last-known heading, or, occasionally, further rheotaxis is the best option.

The relative performances of the random-walk strategy and the last-known-heading strategy depended on the weighting of the random component. The two strategies are the same when random

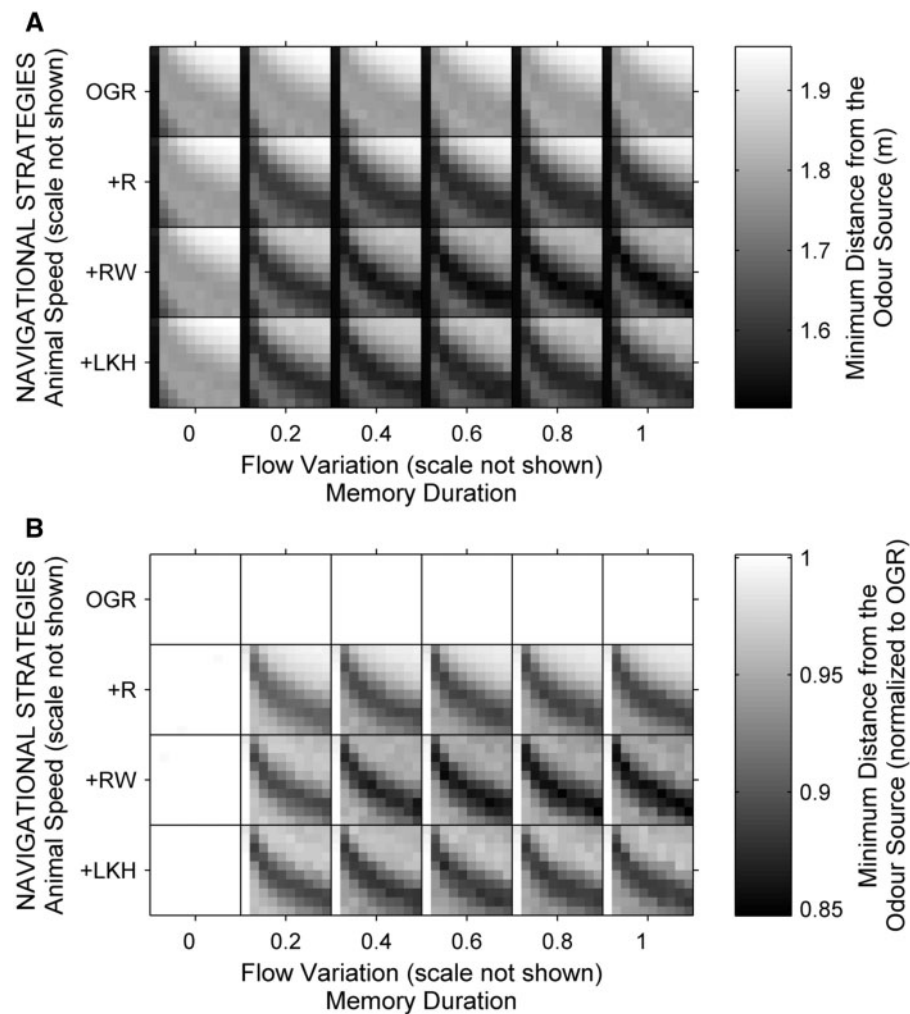


Fig. 4 Navigational performance of different strategies depends both on the animal's speed, the variability in flow, and the duration of memory. Each panel is an array of intensity maps measuring performance for four navigational strategies based on varying durations of memory (measured by proportion of the model run). Intensity maps for a range of animals' speeds and of variations in flow (see Fig. 2 for scales of the parameters) are outlined in black for each combination of strategy and duration of memory. The same data are presented on two scales: minimum distance from the source of the odor (**A**), and normalized to the data for the OGR strategy (**B**). Strategies: odor-gated rheotaxis, OGR; OGR augmented by further rheotaxis, +R; OGR augmented by a random walk, +RW, and OGR augmented by following the last-known heading, +LKH. Note that the augmented strategies with zero duration of memory and all OGR strategies (which does not involve memory) are all identical. All data are means from 1000 runs of the model, with all animals starting 2 m from the source of the odor.

orientation is weighted at zero in the random-walk strategy. Beyond that, in some combinations of parameters (see below), a relatively low weighting (<20%) of random orientation can initially increase the region in which a random walk is the best option (see Supplementary Fig. S2), presumably because it achieves a balance between correct headings that are remembered and erroneous headings that are remembered (and are better fixed by random movements that can recapture the odor plume). This is borne out by the fact that the maximum distance achieved by the various strategies (a measure of grievous errors) indicates that the last-known

heading also results in the worst navigation (data not shown). As the weighting of random orientation increases further (increasing the dispersion with respect to the last-known heading), the region of parameter space in which the random-walk strategy is best is reduced, replaced instead by the last-known heading strategy (or rheotaxis augmented by rheotaxis in cases in which the last-known-heading strategy is particularly poor).

Distance from source and the duration of memory

Increasing the initial distance from the source slightly expanded the region in which using a

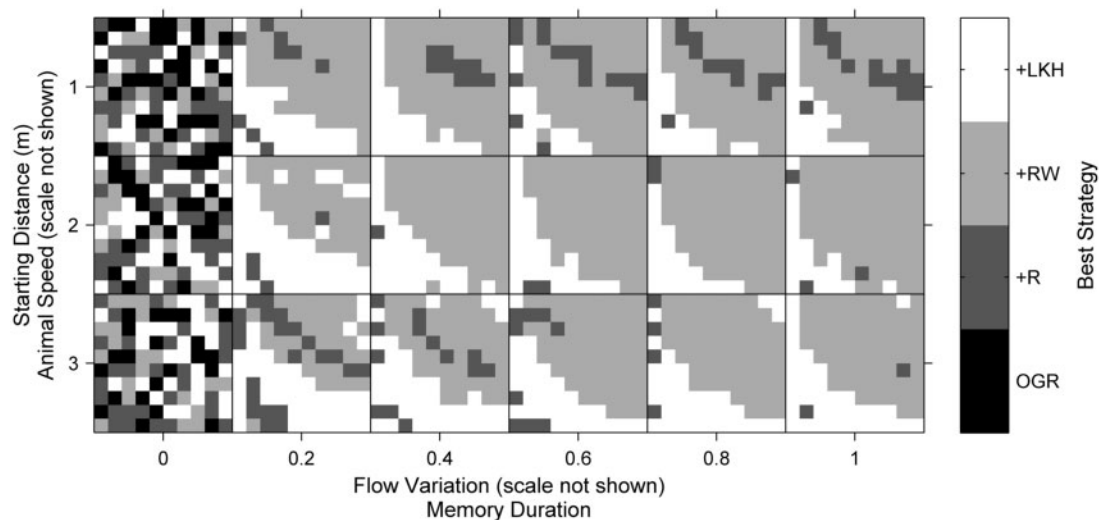


Fig. 5 The full five-dimensional results measuring relative performance of four navigational strategies with respect to the animal's speeds, the variability in flow, initial distance from the source, and the duration of memory. The best strategy (shortest minimum distance from the source) is presented in an array of intensity maps for a range of animals' speeds and variations in flow (see Fig. 2 for scales of the parameters), with each combination of initial distance and duration of memory outlined in black. Strategies: odor-gated rheotaxis, OGR; OGR augmented by further rheotaxis, +R; OGR augmented by a random walk, +RW, and OGR augmented by following the last-known heading, +LKH. Note that the strategies involving no memory are all identical to OGR and thus the random components of the model account for all differences in the first column of the array. All data are means from 1000 runs of the model.

last-known heading was the best strategy, correspondingly contracting the region in which augmenting with a random-walk was best. Thus, as animals began movement farther away from the source of the odor, the range of animals' speeds that performed best with the last-known-heading strategy increased slightly to include animals with slower locomotion. Similarly, the range of variabilities in flow that were accommodated best by the last-known-heading strategy increased to include higher variabilities. The fact that the costs of erroneous last-known headings are greater when close to the source of the plume can account for this trend. At greater distances, the relative differences of movements either toward or away from the source are arithmetically diminished and there is little or no chance of moving beyond the odor's source.

Increasing the duration of memory also had subtle effects. At short initial distances from the source of the odor, it resulted in decreasing performance of the last-known-heading strategy but had little effect on performance for either continued rheotaxis or a random walk (data not shown). In contrast, at intermediate and long initial distances, all three augmented strategies initially increased performance as the duration of memory increased to 40% of a model run, but then had relatively little change with further increase in the duration of memory (Fig. 4). Minor differences in the relative effects of duration of

memory on the different strategies resulted in the random walk being the best strategy in a slightly expanding area of parameter space as the duration of memory lengthened (i.e., as memory increased from 20% to 40% of the simulated duration, the random-walk strategy replaced the strategy of following the last-known heading at the border between their respective regions of parameter space as the best option, located at intermediate levels of variation of flow).

Efficiency

The differences among the three augmented strategies were even more subtle when considering two potential measures of locomotory efficiency. Since our primary measure of performance, minimum distance from the source, could theoretically be achieved by either a very direct (i.e., efficient) trajectory from the starting position or a very indirect (i.e., inefficient) trajectory, it was important to verify the relative efficiencies of the different navigation strategies. We found little difference in efficiency among the strategies (see Supplementary Fig. S3). Overall, the average difference between the two best strategies (as judged by minimum distance from the source of the odor) was less than 0.1% with respect to both the time at which that minimum distance was achieved and the total distance traveled prior to reaching that minimum. Focusing on the

heterogeneity underlying those averages, the time at which animals reached their minimum distance from the source was similar among all three augmented strategies, with the last-known heading typically having the slightly shorter time in regions of parameter space where the random-walk strategy resulted in slightly closer minimum distances, and vice versa. Total distance traveled before reaching the minimum distance to the source was also very similar, but with a consistent pattern. At short initial distances, the random-walk strategy produced shorter total distances for all but the shortest (20%) duration of memory (for essentially all combinations of speeds of animals and variations in flow). Conversely, at long initial distances, the last-known heading consistently produced the shorter total distances. The intermediate initial distance resulted in a balance between the two strategies, with following the last-known heading resulting in shorter distances for durations of memory of 60% or lower and random walk resulting in shorter distances for greater durations. These results for time and total distance were all consistent with relatively direct paths leading to the minimum distance to the source for the different strategies, and thus differences among the strategies with regard to their minimum distance from the source of the odor are not skewed by any substantial differences in how direct (or indirect) their paths were.

Discussion

Our primary finding is that odor-gated rheotaxis could be augmented to substantially improve navigational success in environments with variable flow. The modeling results give strong evidence supporting our original hypothesis that if odor-gated rheotaxis (strictly limited to the interior of an odor plume) is followed by additional movement it will lead animals closer to the source of an odor plume that was swept away from the animal by a change in the direction of bulk flow. Once an animal detects odors in a turbulent odor plume, it can subsequently cease to detect the odor for two potential reasons. First, the olfactory signals inside turbulent odor plumes are intermittent, and gaps between odor “filaments” occur (Weissburg 2000). Second, the direction of the bulk flow transporting the odors can change, sweeping the entire plume away from the animal. In the first case, it is well established that the best strategy (odor-gated rheotaxis) is to continue movement despite the loss of an olfactory signal (Vickers 2000; Webster and Weissburg 2009). We have now shown that continued movement is also probably

beneficial in the second case, helping animals to move closer to the sources of odor plumes despite the change in the direction of flow. Thus, we hypothesize that animals guided by chemosensory cues in turbulent odor plumes in nature will continue movement over longer times than expected, given the intermittency of the odor signal in the habitat. Such continued movement will accommodate larger-scale variations in flow that change the direction of entire plumes.

Our model does not predict a particular strategy that is best used to augment odor-gated rheotaxis. Differences were subtle among the three augmented strategies we tested, and varying the parameters that could affect a strategy's success (speed of the animal, variability in flow, initial distance from the source of the odor and length of time over which the augmented strategy was applied) could result in any of the strategies achieving the best performance, often with differences of only 2% or less. Given the necessary artificiality of our model and that factors we did not model will certainly affect the success of these strategies in nature, we cannot predict which augmented strategy will be optimal in any particular natural habitat.

Costs and benefits of augmenting odor-gated rheotaxis by additional movement

Comparison of the results between the different strategies across the model's parameter space does provide insight into the potential costs and benefits of augmenting odor-gated rheotaxis. As expected, continued rheotaxis (which continues after the change in the flow has occurred that caused loss of the odor plume in the first place) is usually the worst of the three augmented strategies we tested. Nonetheless, even this continued movement can provide substantial benefits over strict odor-gated rheotaxis as, on average, it does take the animals closer to the source of the odor. However, in the majority of parameter space we explored, either following the last-known heading when odor was detected or a random walk initiated at that last heading, were the best strategies. Again, the differences were subtle in most combinations of parameters; however, larger differences (5–10%) were also found. In these more differentiated cases, the random-walk strategy was best, driven largely by errors made by the last-known-heading strategy. Thus, particularly for (1) slower animals in (2) flows of high variability at (3) initial distances closer to the source of the odor that (1) cannot reach the source of the odor quickly, and thus (2) are likely to experience large shifts in

direction, and (3) will have greater costs from erroneous headings, there is the strongest possibility that the last-known heading could lead them astray from the source of the odor. The random-walk strategy can (partly) compensate for initial errors by the introduction of random variation in the subsequent navigational path. The optimal amount of random variation will depend on both the frequency and magnitude of the errors, which in turn will be affected by the animal's speed, the variation in flow, initial distance from the source, duration of memory (to a lesser extent), and presumably also other factors not included in the model. This result is consistent with a previous simulation comparing strategies used by navigating nudibranchs (Wyeth 2010) in which a last-known-heading strategy implemented as a biased random-walk (that presumably created the appropriate compensation for errors) was also best.

The results for all three augmented strategies suggest that there is considerable scope for augmenting odor-gated rheotaxis. First, the benefits are not limited to particular spatial scales or patterns of transience of the odor's source since neither the duration of memory nor the initial distance had widespread effects on the model's results. The benefit of seeking a source of odor that is no longer detectable will be strictly curtailed if that source is too distant, or if it can be expected to disappear before use of the augmented strategy enables the animal to reach the location of the source. Our data suggest that over a range of distances and a range of the durations of memory, the augmented strategies are beneficial, and therefore such limitations would not apply to evolution of these strategies. Second, other potential strategies (e.g., Kuenen and Carde 1994) might also be similarly effective to those we modeled. For example, our unpublished observations suggest that both casting at angles to the flow once odor is lost and a time-shifted last-known-heading strategy (i.e., following the heading of the flow that was detected some time prior to losing the odor signal) can also be effective. Both possibilities are different approaches to dealing with the problem of errors created by following the last-known heading. Overall, our data suggest a diverse set of strategies may have benefits for navigation following odor-gated rheotaxis in variable flow.

Modeling odor-based navigation

One potential limitation to our model is that the magnitude of the variation in flow is not linked to the fluctuations in concentration and intermittency

generated by turbulence in the odor plume. In nature, variation in bulk-flow and turbulence within the plume will be at least partly correlated (Vogel 1994). To our knowledge, no system has been devised to approximate this physical coupling at different scales, and thus we were faced with an insurmountable limitation of our method for combining variation in bulk flow with a realistically intermittent odor signal inside the odor plume. However, we found there was little effect on relative performance of the strategies for different approximations of within-plume turbulence (by varying γ and i_p^2 ; see Model Details in the Supplementary Material). This is because the only major effect of changing these is to change the frequency at which animals receive chemical signals, something that should affect all strategies equally since they are all based on odor-gated rheotaxis. Thus, we suggest that despite our inability to explicitly model the hierarchical nature of variation in turbulent flow, the approximation we use is adequate for our comparisons of strategies that augment odor-gated rheotaxis.

Optimal navigation requires the animals reach as close to the target as possible while expending as little energy as possible. We did not incorporate relative energetics into our model (e.g., for different speeds of the animals) because this would have led either to a proliferation of parameters or to lack of generality (Parker and Smith 1990). Instead, we used two proxy measures for energy expenditure: total distance covered prior to achieving the minimum distance from the odor source, and the time taken to reach that point. In both cases, there was little or no evidence of excessive inefficiency. Thus, in comparison, when the last-known-heading and random-walk options tended to achieve the shortest distance to the target, they also took the longest time to do so, but only by a small margin. At the same time, there were no substantial differences in total distances traveled. Thus, overall, in the absence of specific information about either expenditures of energy or rewards, we restricted our analysis to navigational performance based on spatial metrics alone.

Future modeling needs to consider the relative benefits of searching for the source of the odor versus searching for the odor plume. A number of other models have tested strategies for finding or relocating odor plumes. Cross-stream, down-stream, casting, and levy-taxes are some of the possible movements that may help animals (or robots) find odor plumes (Sabelis and Schippers 1984; Dusenbery 1989a, 1989b, 1990; Vergassola et al. 2007; Harvey et al. 2008; Pasternak et al. 2009). However, the ultimate goal of the navigation is the source of the

odor. By using source-dependent measures of performance, we have indicated the potential value of strategies used to seek out the source on an odor directly rather than first finding an odor plume before restarting odor-gated rheotaxis. To properly compare all the various options, a combined modeling exercise is required, incorporating both plume-finding and source-finding strategies, variable flow, and the intermittency of turbulence, all measured against the success of finding the source of the odor.

Biological implications

Given the potential improvements to navigation shown by our model for strategies that augment odor-gated rheotaxis, we hypothesize that such behaviors should be observable as adaptations in nature. To our knowledge, there are no reports on what animals do after a variation in the direction of flow eliminates detection of an odor plume. Thus, to test our hypothesis, future studies are needed that combine observations of animals' movements with respect to sources of odors and the direction of flow over both the odor's source and the animal. These data could establish whether during conditions of variable flow, animals continue movement after odor-gated rheotaxis, and also whether their pattern of movement fits any of the strategies modeled here. Alternatively, if evidence for further movement is lacking, additional costs for the behavior must be considered to explain why animals do not augment odor-gated rheotaxis despite the potential benefits shown in our data. These tests could be achieved over a range of speeds of locomotion and conditions of flow by working with established experimental systems for odor-based navigation, including gastropods (Ferner and Weissburg 2005; Wyeth et al. 2006; McCullagh et al. 2014), crustaceans (Weissburg and Zimmer-Faust 1994; Grasso and Basil 2002; Jackson et al. 2007), and fish (Baker et al. 2002; Johnson et al. 2012; Gardiner and Atema 2014).

If animals do indeed augment odor-gated rheotaxis, there are probably a number of different mechanisms by which it could be achieved. Importantly, the distinction between the last-known-heading and random-walk strategies, although important for our exploration of navigational performance, may not be realistic in a biological context. All navigational strategies will have some random error generated by environmental perturbations. Thus, we suggest it is more likely that animals will be adapted to have greater or lesser fidelity when following a last-known heading, depending on locomotory speed, variability in flow, and initial distance from the

odor source. Any animal following the last-known heading (with lesser or greater accuracy) will have two basic options: adjusting headings based on a memory of the past history of the change in direction of flow (a potentially difficult task in turbulent flow), or switching to a more stable cue. Visual and magnetic cues are two obvious alternatives, although other compass cues might also be used (Odling-Smee and Braithwaite 2003; Waterman 2006; Alves et al. 2007; Wyeth 2010). The neural architecture required for such a switch in cues need not be complex. A constantly updated memory of the upstream direction when odors are being detected could be based either on parallel output from rheosensory processing or an independent sensory system that is simply calibrated by the rheotactic orientation that occurs during odor-gated rheotaxis (e.g., "memorizing" a magnetic heading or azimuth of a visual cue while odor-gated rheotaxis is ongoing). Thus, given the apparent benefits of the strategies augmenting odor-gated rheotaxis, and correspondingly few constraints on their evolution, we expect such strategies will exist in nature. Given the subtle differences in performance among the strategies we tested, we suggest our understanding of adaptive navigational strategies will be best advanced by further field work to characterize both the circumstances under which odor plumes are lost and what animals do in response.

Author contributions

All authors had full access to all the data in the study and take responsibility for the integrity of the data and the accuracy of the analysis. Study concept, R.C.W.; formulation of the model, G.V., R.L.; analysis and interpretation of data, G.V., R.L., R.C.W.; drafting of the article, R.C.W.; critical revision of the article for important intellectual content, R.L., R.C.W.; funding, R.L., R.C.W.

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Supplementary data

Supplementary Data available at *ICB* online.

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