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Odor-conditioned rheotaxis of the sea lamprey: modeling, analysis and validation

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Abstract

Mechanisms for orienting toward and locating an odor source are sought in both biology and engineering. Chemical ecology studies have demonstrated that adult female sea lamprey show rheotaxis in response to a male pheromone with dichotomous outcomes: sexually mature females locate the source of the pheromone whereas immature females swim by the source and continue moving upstream. Here we introduce a simple switching mechanism modeled after odor-conditioned rheotaxis for the sea lamprey as they search for the source of a pheromone in a one-dimensional riverine environment. In this strategy, the females move upstream only if they detect that the pheromone concentration is higher than a threshold value and drifts down (by turning off control action to save energy) otherwise. In addition, we propose various uncertainty models such as measurement noise, actuator disturbance, and a probabilistic model of a concentration field in turbulent flow. Based on the proposed model with uncertainties, a convergence analysis showed that with this simplistic switching mechanism, the lamprey converges to the source location on average in spite of all such uncertainties. Furthermore, a slightly modified model and its extensive simulation results explain the behaviors of immature female lamprey near the source location.

(Some figures may appear in colour only in the online journal)

1. Introduction

Animal movements are often guided by environmental stimuli such as chemicals, light, heat or fluid flow. In particular, orienting toward an odorant source is widespread in many animals and of considerable interest to ecologists due to its substantial fitness consequences. Several chemo-orientation mechanisms have been proposed to explain how organisms arrive at an odorant source in diverse environmental contexts including microscale environments where molecular diffusion dominates [6], atmospheric environments where turbulent plumes exist in three-dimensional space [11], and aquatic environments with unidirectional current where plumes exist in essentially one-dimension as they are confided by the depth and width of the channel [8, 16, 17].

The engineering problem of locating an odorant source is also widespread and has important consequences for humanity and the environment. Therefore, engineers and mathematicians

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have proposed numerous solutions for convergence to the odorant source in different environments [2–5, 7, 14, 15, 19]. Engineered infotactic trajectories show biological patterns such as zigzagging and casting paths similar to those observed in the flight of moths [19]. The pheromone-oriented behavior of silkworm moths was reproduced by a mobile robot with moth antennae as pheromone sensors [14]. Olfactory-based algorithms were proposed and validated empirically using an autonomous underwater vehicle to find a chemical plume and trace the chemical plume to its source in a turbulent and oceanic fluid flow [7]. For source seeking, extremum seeking control was used to produce fish-like locomotion that is similar to the way a fish moves [5].

Using control algorithms to characterize high efficiency biological solutions for locating an odorant source is an emerging strategy aimed to mutually advance understanding of biological mechanisms and developing novel engineering solutions [22]. In particular, two bio-inspired algorithms have recently been modeled after biological solutions for odorant source location in turbulent riverine environments [8, 21]. Blue crab (Callinectes sapidus) chemo-orientation was modeled with an 80% success rate using a complex algorithm based on time-averaged measurements of the odorant plume [21]. Sea lamprey (Petromyzon marinus) chemo-orientation was modeled over 100 m with similar success rate using a simple algorithm based on a single measurement of the odorant plume [8]. In the case of the sea lamprey, in spite of various uncertainties due to measurement noise, actuation disturbance, and turbulent flow, a simple algorithm based on a single measurement consistently converged to the odorant source and remained there for several minutes. Such simulation results correlate well with the field data observed in natural streams where the synthesized pheromone 3kPZS (7 α , 12 α , 24trihydroxy- 5α -cholan-3-one-24-sulfate) is used as an odorant source [9].

Recently, to select an appropriate model of lamprey behavior to the odorant source and its related parameters, in-stream behavioral observations of female sea lampreys orienting to plumes of a synthesized mating pheromone, 3kPZS, were coupled with computer algorithms to systematically test chemo-orientation hypotheses [8]. Most of the parameters, such as noise level, average speed, and sampling time, were obtained by considering physiology of the sea lamprey. Other unobservable internal parameters for each hypothesis were obtained by maximizing the goodness of fit of each hypothesis model with respect to observations. Comparison of results between in-stream field observations and simulated movements of female sea lampreys according to different hypotheses strongly support that odor-conditioned rheotaxis is a main component of the mechanism used to track plumes of 3kPZS over hundreds of meters in flowing water. However, findings in [8] were based on computer simulation results from different hypothetical models, which is not analytically tractable due to the complexity of the model in a two-dimensional space.

New observations on the behavior of sexually immature female sea lamprey show that they orient toward the pheromone source similarly to mature females, but do not locate the exact source of the pheromone [1, 9]. Immature females swim far beyond the source, while mature females converge at the source. Motivated by this observation, we hypothesize that differences in convergent behaviors between immature and mature females can be explained by the combined effect of detection threshold and the dynamics of olfactory perception. Using control algorithms to characterize how immature and mature females differ in olfactory sensitivity and behavior would mutually advance biology and engineering by producing a set of theoretical solutions worthy of empirical tests.

The main objective of this study is to understand convergent behaviors of odor-conditioned rheotaxis of immature and mature sea lampreys through mathematical modeling of dynamic systems. We analyze the convergent behavior of sea lampreys to the odorant source in the presence of various uncertainties. The results support the evidence obtained from experimental tests and the computational simulation studied in [8] as well as the recent findings on the behavior of immature female lamprey [1].

Note that lampreys' unique mode of locomotion has been extensively analyzed and applied to bioinspired swimming robots [18, 23]. However, engineering analysis of excellent convergent behavior of the mature lamprey and intriguing (recently discovered in [1]) behavior of the immature lamprey toward the source of the pheromone (at a level which can be beneficial to biomimetics) is scant to date [8]. Our paper will provide such analysis and insight for reasonably constructed dynamical models that will be useful in implementing the convergent behavior of the lamprey as a realization of bioinspiration and biomimetics. To obtain analytically tractable results for the case of mature sea lampreys, we first consider a one-dimensional version of the model and the parameters obtained from [8]. A simplified one-dimensional configuration used in the analysis and simulations allows modeling with various uncertainties and unveiling important insights regarding the fundamental convergent properties for both mature and immature lampreys.

Standard notation will be used throughout the paper. Let \mathbb{R} be the set of real numbers. The operator of expectation is denoted by \mathbb{E} . $\mathbb{E}(x | y)$ denotes the conditional expectation of a random variable *x* for a given *y*. A random variable *x*, which has a normal distribution of its mean μ and variance σ , is denoted by $x \sim \mathcal{N}(\mu, \sigma)$. Other notation will be explained in due course.

2. Main approach

We modeled the locomotion of the sea lamprey as a simple stochastic kinematic equation to accomplish our objective. For convergence analysis, we first assumed that the olfactory perception is instantaneous, meaning that the odorant sensing has an insignificant memory effect. Using the stochastic Lyapunov theory, its convergent behavior toward the source can then be analyzed in section 3. This can mainly explain the time-averaged behavior of mature lampreys who are observed to mostly stay near the source after convergence. Compared to mature female lampreys, however, immature female lampreys are observed to be overly rheotactic in that they swim against the flow far beyond the pheromone source. To explain such a behavioral difference in immature lampreys, we propose a combination of two hypotheses. The first hypothesis is that the olfactory systems of immature lampreys have not yet been developed to be as efficient as those of mature lampreys, i.e., immature lampreys are slow in perceiving concentration of the pheromone, due to slow olfactory dynamics as introduced in section 4. The second hypothesis is that immature lampreys are possibly more sensitive (or responsive) to environmental stimuli because of their vulnerability to environmental changes or ecological threats. Using dynamic analysis and computational results, we illustrated how these hypotheses explain the observed behaviors of immature and mature female lampreys.

3. Basic analysis

3.1. Proposed lamprey model for odor-conditioned rheotaxis

We consider the following one-dimensional kinematic model for the navigation of the female lamprey.

$$y(k+1) = y(k) + T_s v_{\lambda(k)} + \epsilon(k), \tag{1}$$

where $y(k) \in \mathbb{R}$ is the coordinate of the track parameterized by a length with respect to a reference position at discrete time index k, and $T_s \in \mathbb{R}_{>0}$ is the sampling time of the lamprey. $\epsilon(k) \in \mathbb{R}$ denotes the random perturbation due to the lamprey's actuation and the environment. $\{\epsilon(k)\}\$ are assumed to be the independent and identically distributed (i.i.d.) Gaussian random variables with a zero mean and a standard deviation of σ_{ϵ} , i.e., $\epsilon(k) \sim \mathcal{N}(0, \sigma_{\epsilon}^2)$. $v_{\lambda(k)} \in \mathbb{R}$ is the velocity of the lamprey, which depends on the response characteristics of the olfactory perception. We consider a simple on/off switching rule at time k. More specifically, the binary state of $\lambda(k) = 1$ represents when the lamprey detects the trace of the noisy synthesized pheromone 3kPZS with a threshold $\delta(k)$ at time k. Otherwise, the lamprey model (1) sets $\lambda(k) = 0$. Consequently, the detection mechanism of the lamprey can be described as follows.

$$\lambda(k) := \begin{cases} 1, & \text{if } \bar{c}(k) \ge \delta(k) ;\\ 0, & \text{if } \bar{c}(k) < \delta(k), \end{cases}$$
(2)

where $\bar{c}(k)$ represents the *perceived* and *processed* concentration of the pheromone for decision making. The base-line (or true) concentration c(k) is first corrupted by the aquatic measurement noise and then processed through the odorant receptor neurons to result in $\bar{c}(k)$.

Based on the detection rule in (2), the lamprey will move upstream with a velocity $v_+ > 0$ when $\lambda = 1$ or turn off control action and simply drift with a velocity $v_- < 0$, i.e.,

$$v_{\lambda(k)} := \begin{cases} v_+, & \text{if } \lambda(k) = 1; \\ v_-, & \text{if } \lambda(k) = 0. \end{cases}$$
(3)

From the dynamics model in (1), the switching rule in (2), and the control action in (3), we obtain the closed-loop switching system.

$$y(k+1) = y(k) + T_s[\lambda(k)v_+ + \lambda^{\operatorname{com}}(k)v_-] + \epsilon(k), \quad (4)$$

where the complement of the switch function is given by

$$\lambda^{\rm com}(k) := 1 - \lambda(k). \tag{5}$$

From (4), it is straightforward to show that the location of the lamprey at time n > k is given by

$$y(n) = \sum_{j=1}^{n-1} T_s[\lambda(j)v_+ + \lambda^{\rm com}(j)v_-] + \sum_{j=1}^{n-1} \epsilon(j).$$

3.2. Locating the source: convergence analysis

In this subsection, we assume that the perceived concentration can be represented as

$$\bar{c}(k) = c(k) + w(k) \tag{6}$$

where w(k) is the noise due to the measurement and turbulence. We model w(k) as a realization of the i.i.d. Gaussian random variables with a zero mean and a standard deviation of σ , i.e.,

$$w(k) \sim \mathcal{N}(0, \sigma^2).$$

The detection mechanism hypothesized in (6) presumes that the response time for decision making is fast enough to detect the change in the concentration of the pheromone within the time scale smaller than the sampling period. Later, we will show how the behavioral differences between the adult and the immature lampreys can be explained in terms of differences in their olfactory system dynamics.

Dynamics of turbulent flow may create some uncertainties in the concentration field of synthesized pheromone. Hence, we consider a probabilistic model for a concentration in turbulent flow where c(k) takes either a non-zero concentration value with probability P_1 or 0 with probability P_0 .

Considering that the lamprey is close to the source location, we move the origin of the *y* coordinate to the source location of the pheromone. Hence, the lamprey takes a negative initial value, i.e., $y(1) = y_1 < 0$. We assumed that after the source location, i.e., y(k) > 0, there is no pheromone trace due to the flow direction, i.e., $P_1(y > 0) \simeq 0$. On the other hand, it may be assumed that the probability of the existence of the concentration in the region immediately below the source is almost one, i.e., $P_1(y \le 0) \simeq 1$.

Therefore, we may have

$$\mathbb{E}[\lambda_{\leq 0}(k)] > \mathbb{E}[\lambda_{>0}(k)],$$

where $\lambda_{\leq 0}$ and $\lambda_{>0}$ denote the switch functions λ when $y \leq 0$ and y > 0, respectively. Similarly to (5), the complement of the switch functions $\lambda_{\leq 0}^{\text{com}}$ and $\lambda_{>0}^{\text{com}}$ are defined accordingly.

This situation under the aforementioned assumptions leads to the following model:

$$y(k+1) = y(k) + T_s \{ 1_{\leq 0}(y(k)) [\lambda_{\leq 0}(k)v_+ + \lambda_{\leq 0}^{com}(k)v_-] + 1_{>0}(y(k)) [\lambda_{>0}(k)v_+ + \lambda_{>0}^{com}(k)v_-] \} + \epsilon(k)$$

= y(k) + u(k) + \epsilon(k), (7)

where the term inside the braces is denoted by u(k). The indicator function of a subset *A* of \mathbb{R} is a function $1_A : \mathbb{R} \to \{0, 1\}$, and is defined as

$$1_A(y) := \begin{cases} 1, & \text{if } y \in A; \\ 0, & \text{if } y \notin A. \end{cases}$$

A short notation was used such that $1_{\leq 0}(y) := 1_B(y)$, where $B = \{x : x \leq 0\}$ and $1_{>0}(y) := 1_C(y)$, where $C = \{x : x > 0\}$. We have $1_{\leq 0}(y) \times 1_{>0}(y) = 0$, since $\{x : x \leq 0\} \cap \{x : x > 0\} = \emptyset$.

Before applying stochastic Lyapunov stability theory, we first discuss a deterministic version. Consider a discrete-time, dynamical system without uncertainties given by

$$x(k+1) = f(x(k)) \in \mathbb{R}.$$

Let $V_k = x^2(k)$ be a Lyapunov function candidate. Let the energy decrease (or forward difference function) along the trajectory be expressed by

$$V_{k+1} - V_k = -k(x(k)).$$
 (8)

If k(x(k)) is a positive definite function, then the equilibrium 0 is globally uniformly asymptotically stable [20]. This implies that x will converge to the origin as $k \to \infty$. However, a dynamical system driven by a stochastic process shall be treated somewhat differently since V_{k+1} becomes a random variable for a given x(k). In this case, one may guess that the convergence properties could be analyzed by looking at how V_{k+1} behaves on the average from V_k . It turns out that the energy decrease over the trajectory should be measured by $\mathbb{E}[V_{k+1} | x(k)] - V_k$ [13]. Note that V_k is a function of x(k), (e.g., $V_k = x^2(k)$ and V_{k+1} in (8) was replaced with the conditional expectation of V_{k+1} for a given x(k) over any associated random variables for the case of a stochastic system. In fact, this is the best prediction of the forward difference function for a given x(k). For further details on stability theory for stochastic systems, the reader is referred to [13].

We are now ready to analyze the convergence properties of our stochastic system in (7) with respect to the odorant source location (y = 0). With a Lyapunov function candidate V_k given by $V_k := y^2(k)$, we first compute the following (stochastic) forward difference for the stochastic system given in (7).

$$\mathbb{E}[V_{k+1}|y(k)] - V_k = \mathbb{E}[(y(k) + u(k) + \epsilon(k))^2|y(k)] - y^2(k)$$

= $\mathbb{E}[u^2(k)|y(k)] + 2y(k)\mathbb{E}[u(k)|y(k)] + \sigma_{\epsilon}^2,$

where $\mathbb{E}[u(k) | y(k)]$ is given by

$$\mathbb{E}[u(k)|y(k)] = T_s \mathbb{E}\Big[1_{\leq 0}(y(k)) \big(\lambda_{\leq 0}(k)v_+ + \lambda_{\leq 0}^{\rm com}(k)v_-\big) \\ + 1_{>0}(y(k)) (\lambda_{>0}(k)v_+ + \lambda_{>0}^{\rm com}(k)v_-)\Big] \\ = T_s \{1_{\leq 0}(y(k)) [P_{\leq 0}^{\star}v_+ + (1 - P_{\leq 0}^{\star})v_-] \\ + 1_{>0}(y(k)) [P_{>0}^{\star}v_+ + (1 - P_{>0}^{\star})v_-]\}.$$

 $P_{\leq 0}^{\star}$ and $P_{>0}^{\star}$ denote $\mathbb{E}[\lambda_{\leq 0}]$ and $\mathbb{E}[\lambda_{>0}]$, respectively, and are given by

$$P_{\leq 0}^{\star} := P_1(y \leq 0)[1 - \Phi(\delta - c, \sigma)] +P_0(y \leq 0)[1 - \Phi(\delta, \sigma)], P_{>0}^{\star} := P_1(y > 0)[1 - \Phi(\delta - c, \sigma)] +P_0(y > 0)[1 - \Phi(\delta, \sigma)],$$

where $\Phi(x, \sigma)$ denotes the Gaussian cumulative distribution function defined by

$$\Phi(x,\sigma) := \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{x} \exp\left(-\frac{t^2}{2\sigma^2}\right) \mathrm{d}t.$$

Now we can obtain $\mathbb{E}[u^2(k) | y(k)]$ as follows.

$$\begin{split} \mathbb{E}[u^{2}(k)|y(k)] &= T_{s}^{2} \mathbb{E}\Big[1_{\leq 0}(y(k)) \big(\lambda_{\leq 0}(k)v_{+} + \lambda_{\leq 0}^{\text{com}}(k)v_{-}\big)^{2} \\ &+ 1_{>0}(y(k)) \big(\lambda_{>0}(k)v_{+} + \lambda_{>0}^{\text{com}}(k)v_{-}\big)^{2}\Big] \\ &= T_{s}^{2} \{1_{\leq 0}(y(k)) [P_{\leq 0}^{\star}v_{+}^{2} + (1 - P_{\leq 0}^{\star})v_{-}^{2}] \\ &+ 1_{>0}(y(k)) [P_{>0}^{\star}v_{+}^{2} + (1 - P_{>0}^{\star})v_{-}^{2}] \}, \end{split}$$

where $1_{\leq 0}(y)1_{>0}(y) = 0$ and $\lambda(k)\lambda^{com}(k) = 0$ have been exploited.

The quantity of interest can be shown further in detail.

$$\begin{split} \mathbb{E}[V_{k+1}|y(k)] - V_k &=: -k(y(k)) = \\ \begin{cases} T_s^2 [P_{\leq 0}^{\star} v_+^2 + (1 - P_{\leq 0}^{\star}) v_-^2] + T_s 2y(k) [P_{\leq 0}^{\star} v_+ + (1 - P_{\leq 0}^{\star}) v_-] + \sigma_{\epsilon}^2, \\ \text{if } y(k) &\leq 0; \\ T_s^2 [P_{>0}^{\star} v_+^2 + (1 - P_{>0}^{\star}) v_-^2] + T_s 2y(k) [P_{>0}^{\star} v_+ + (1 - P_{>0}^{\star}) v_-] + \sigma_{\epsilon}^2, \\ \text{if } y(k) &> 0. \end{split}$$

(9)

Provided that $P_{\leq 0}^{\star}v_+ + (1 - P_{\leq 0}^{\star})v_- > 0$, (9) shows that if

$$y(k) < \alpha_{1}[P_{1}(y \leq 0), \delta, \sigma, \sigma_{\epsilon}] \\ := -\frac{T_{s}^{2}[P_{\leq 0}^{\star}v_{+}^{2} + (1 - P_{\leq 0}^{\star})v_{-}^{2}] + \sigma_{\epsilon}^{2}}{2T_{s}[P_{\leq 0}^{\star}v_{+} + (1 - P_{\leq 0}^{\star})v_{-}]} < 0,$$
(10)

y(k) will approach the origin on the average. If the lamprey misses the origin, moves up further, and if

$$y(k) > \alpha_2[P_1(y > 0), \delta, \sigma, \sigma_{\epsilon}] := -\frac{T_s^2[P_{>0}^{\star}v_+^2 + (1 - P_{>0}^{\star})v_-^2] + \sigma_{\epsilon}^2}{2T_s[P_{>0}^{\star}v_+ + (1 - P_{>0}^{\star})v_-]} > 0,$$
(11)

and $P_{>0}^{\star}v_{+} + (1 - P_{>0}^{\star})v_{-} < 0$, then y(k) will approach back to the origin on the average. One the other hand, if y(k) is near the origin and $\alpha_1 < y(k) < \alpha_2$, then y(k) will move away from the origin on the average. The attraction tendency if y(k) is far away from the origin and repulsion tendency if y(k) is close to the origin make the process $\{y(k)\}$ randomly moving near the origin.

If we consider a simplified situation in which $P_{\leq 0}^* = 1$, $P_{>0}^* = 0$ and $v_+ = -v_- = v$, we then have the following. $\mathbb{E}[V_{k+1}|y(k)] - V_k = -k(y(k)) = -2T_s v|y(k)| + T_s^2 v^2 + \sigma_{\epsilon}^2$. (12)

where -k(y(k)) is then strictly negative outside of a compact set $S = \{y \mid |y| \leq \frac{1}{2}T_sv + \frac{\sigma_e^2}{2T_sv}\}$. Theorem 7 in [13], suggests that the stochastic process $\{y(k)\}$ becomes recurrent, i.e., y(k)re-visits an arbitrary point in some domain an infinite number of times. Therefore, we can consider the compact set *S* as a boundary of the lamprey's location near the source on the average. The balance between the repulsive and attractive tendencies in and out of the compact set that contains the origin is the reason for the recurrent process $\{y(t)\}$.

We conducted numerical simulations for the recurrent sequence $\{y(k)\}$ in (7) using parameters listed in table 1. The 0.5 s sampling time was chosen based on the inhalation period of sea lampreys [12]. Other parameters are selected from experimental conditions given in [8].

Figure 1 shows two sample sequences of y(k) that are different by the value of the detection threshold δ . Both plots show the lamprey approaches the vicinity of the source location of the pheromone in spite of the uncertainties in the actuation



Figure 1. Simulations of the recurrent sequence $\{y(k)\}$ for different detection threshold δ under $T_s = 0.5$, $\sigma_{\epsilon} = 0.1$, $v_+ = 0.5$, and $v_- = -0.75$. (a) $\delta = 0.6$ (b) $\delta = 0.2$.

	Table	1.	Simu	lation	parameters
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Description	Parameter	Value	Unit
Sampling time	T_s	0.5	(s)
Upstream lamprey speed	v_+	0.50	$(m s^{-1})$
Downstream lamprey speed	v_{-}	-0.75	$(m s^{-1})$
Kinematic randomness	σ_{ϵ}	0.1	(m)
Concentration of 3kPZS	С	$\begin{cases} 5, \ y \leq 0\\ 0, \ y > 0 \end{cases}$	(10 ⁻¹³ M)
Odor sensing noise level	σ	Ò.6	(10^{-13} M)
Probability of plume when $y \leq 0$	$P_1(y \leq 0)$	0.9	
Probability of plume when $y > 0$	$P_1(y>0)$	0.1	

and perturbation. The dotted straight lines above and below the source location (y = 0) indicate the statistical bounds of the lamprey given by (10) and (11), outside which the lamprey become reentrant on the average. Comparing two plots in figure 1, we can see that, as the detection threshold increases, the reentrant bound gets tighter. Such a mechanism may explain one aspect of the behavioral change of lampreys in relation to the odor-conditioned rheotaxis. As they mature, lampreys may refine their detection threshold to be more reliable and thus enhance their probability of locating the source. In the next subsection, we investigate in more detail why the immature female lampreys show different convergent behaviors from those of adults.

4. Behavior of immature female lampreys: dynamic model of olfactory system

The analysis described in the previous section conforms well to the observed behavior of mature lampreys [8]. However, it does not explain why immature female lampreys tend to swim past the odorant source [1]. To encompass behaviors of sexually mature and immature adult females, we raise a hypothesis that the perceived concentration of the pheromone by a lamprey is generated through a first-order dynamic system

$$\bar{c}(k) = f_s \bar{c}(k-1) + (1 - f_s)(c(k) + w(k)), \quad 0 < f_s < 1$$
(13)

where f_s is the reaction time constant of the olfactory sensory processing. If f_s is close to 1, it means that the perceived sensory image has a longer residue. On the other hand, if f_s is close to 0, then the sensory system has a small reaction time and thus the lamprey can perceive the instantaneous change of the concentration within the time scale of the inhalation period. Basically, the perceived concentration modeled in (6) is a special case of a generalized version in (13) when $f_s = 0$. Therefore, the overall kinematic model in (1) with (13) converges to the model in (1) with (6) as f_s decreases to 0.

The detection threshold δ as well as the olfactory reaction time constant f_s may contribute to the orienting mechanism toward the source of 3kPZS. To see this, we can illustrate how the concentration of the 3kPZS will be perceived by both mature and immature female lampreys, if they were to swim upward at a constant speed ($v_{+} = 0.5$ m/s) passing through the source. Let us consider that the concentration of the 3kPZS has dropped from c = 5 to c = 0 at t = 0, i.e. the lamprey passes through the source at t = 0. Then, we can analyze how δ and f_s affect the response time to the change of concentration of 3kPZS. Figure 2 shows that, if its olfactory perception is processed with $f_s = 0.61$ and the $\delta = 1$, then there is only 1.64 second of delay in realizing it has passed the source. On the other hand, if $f_s = 0.95$ and $\delta = 0.2$, then the lamprey does not realize that he has passed the source until 32.2 second has elapsed. Note that $\delta = 0.2$ is relatively small compared to the measurement noise of the base-line concentration whose standard deviation is $\sigma = 0.6$. Therefore, in order for a lamprey to increase its success of locating the pheromone source, f_s needs to be tuned small while δ is tuned large compared to the concentration noise.

The behavior of immature and mature females can be demonstrated more intuitively by the statistical simulations. Figure 3(a) shows the Monte Carlo simulation with 100 lampreys with two different sets of (f_s, δ) as chosen in



Figure 2. Illustration of the effect of δ and f_s on the response time to the perception of concentration of 3kPZS when the lamprey is assumed to swim upstream with a constant speed of $v_+ = 0.5 \text{ m s}^{-1}$.

figure 2. The thick solid lines denote the range of one standard deviation from the mean among ensemble trials (100 lampreys). Figure 3(a) suggests that most of sea lampreys will converge near the pheromone source if f_s is small and δ is relatively large compared to the noise level. Figure 3(b), on the other hand, confirms that the lamprey is likely to swim past the pheromone source if f_s and δ are tuned in opposite way, which closely resembles the actual behavior of immature female lampreys observed in the experimental tests [1].

For the case of mature female lampreys, figure 4 shows a sample trajectory selected from the Monte Carlo simulation of figure 3(a). The upper plot shows the lamprey location y(k) and the lower plot illustrates how the pheromone concentration is perceived by the adult lamprey during this motion. In the lower plot, the thin solid line is the true concentration c(k) which is contaminated by the noise w(k) to form the thin dashed line. This noisy signal is then processed by the olfactory sensory dynamics (with $f_s = 0.61$) to be perceived by the mature female lamprey as the thick solid line.

Similarly, we can plot a sample trajectory of immature female lampreys as shown in figure 5 which is selected from the Monte Carlo simulation of figure 3(b). As shown in the upper plot, we can see that the immature lamprey does not well converge to the source. The lower plot suggests that such a behavior may come from the long perception delay in its olfactory system ($f_s = 0.95$).

5. Discussion on physical differences and threshold levels

As female sea lampreys mature, length decreases and girth increases. These physical differences between immature and mature females would likely put mature females at a disadvantage when navigating flow fields because they are less streamlined. On the other hand, the disadvantage could give them a bit more time to detect the changes of odorants concentration in proximity to the odor source.

Our simulation study supports that mature lampreys have a higher detection threshold compared to immature lampreys. In the remainder of the section, we provide a conjecture that supports our findings. Note that, on average, immature lampreys are located downstream and move upstream when mature and find the source location. Let us define a hypothesis that for a given location of a lamprey, 'the source location is upstream,' which is denoted by H = 1 and H = 0 otherwise. On average, the source location is located upstream. Let us consider the source location as a random variable so that we can compute the probability of H = i, where $i \in \{1, 0\}$. We then have p(H = 1 | down) > p(H = 0 | down), i.e., when a immature lamprey is downstream, on average, it needs to move upstream to find a source. When a mature lamprey is upstream (around or after passing the source location), on the other hand, it has p(H = 1|up) < p(H = 0|up). In this situation, it seems to be optimal that the immature lamprey tends to have a lower threshold level than that of the mature one since it needs to turn on the control more often to move upstream toward the source location. A possible conjecture is that the threshold level has been optimized in immature and mature female sea lampreys by natural selection. Let us consider the maximum a posteriori probability (MAP) rule [10] in selecting the optimal detection threshold level for a simplified model. Note that the lamprey samples the noisy pheromone concentration z = c + w, where c is the concentration value and w is noise. The MAP rule for maximizing the probability of being correct is to choose $\hat{H}(z)$ to be that *i* for which $P_{H|Z}(i|z)$ is maximized, i.e.,

$$\hat{H}(z) = \arg \max_{i \in \{1,0\}} P_{H|Z}(i|z).$$



Figure 3. Monte Carlo experiments for mature and immature lampreys with the ensemble of 100 lampreys. Thick solid lines indicate the boundary of one standard deviation from the mean. (*a*) Mature female lampreys: $\delta = 1$ and $f_s = 0.61$ (*b*) Immature female lampreys: $\delta = 0.2$ and $f_s = 0.95$.

The *a*-posteriori probability of *H* for $i \in \{1, 0\}$ given by *z* and $x \in \{\text{down}, \text{up}\}$ is as follows.

$$P_{H|Z,X}(i|z,x) = \frac{p(H=i|x)p_{Z|H,X}(z|i,x)}{p_Z(z|x)}, \quad x \in \{\text{down, up}\},\$$

where $p_{Z|H,X}(z|i, x)$ for $i \in \{1, 0\}$ are conditional densities and called likelihoods for $i \in \{1, 0\}$, respectively. Then the MAP rule becomes

$$\frac{p_{Z|H,X}(z|1,x)}{p_{Z|H,X}(z|0,x)} \stackrel{\tilde{H}=1}{\underset{\hat{H}=0}{\overset{\sim}{>}}} \frac{p(H=0|x)}{p(H=1|x)}, \quad x \in \{\text{down, up}\}$$

where p(H = 1|x) and p(H = 0|x) are also called *a-priori* probabilities of H = 1 and H = 0 for a given x.

We now consider a simplified case in which conditional on H = 1, $P_1 = 1$, and conditional on H = 0, $P_0 = 0$. Because conditional on H = 1, $Z \sim \mathcal{N}(c, \sigma^2)$ and conditional



Figure 4. A sample trajectory and 3kPZS perception of the adult lamprey for the condition used in figure 3(*a*).



Figure 5. A sample trajectory and 3kPZS perception of the immature lamprey for the condition used in figure 3(b).

on $H = 0, Z \sim \mathcal{N}(0, \sigma^2)$, the optimal threshold δ_{MAP}^{opt} is computed by the MAP rule as follows.

$$z \stackrel{H=1}{\underset{\hat{H}=0}{\overset{\otimes}{\approx}}} s_{\text{MAP}}^{\text{opt}}(x) := \frac{\sigma^2}{c} \ln\left[\frac{p(H=0|x)}{p(H=1|x)}\right] + \frac{c}{2}, \quad x \in \{\text{down, up}\}.$$

This optimal detection rule can be viewed as follows. When a immature lamprey is downstream, we have $\frac{p(H=0|\text{down})}{p(H=1|\text{down})} < 1$, and so $\delta_{\text{MAP}}^{\text{opt}}$ (down) is small, i.e., more certain that H = 1 (the source location is upstream), the weaker the evidence required to move upstream. When a mature lamprey is upstream (near the source location), we have $\frac{p(H=0|\text{down})}{p(H=1|\text{down})} > 1$, then $\delta_{\text{MAP}}^{\text{opt}}$ (up) takes a large value, i.e., more strong evidence is needed for the mature lamprey to move upstream.

While this simple analysis is quite intriguing, we would like to note that the immature lamprey simulation only with a

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small threshold value in fact fails to replicate the experimental observations precisely. Only the simulation with a combination of a small threshold level and olfactory dynamics successfully replicates immature lampreys' behaviors observed near the source location [1].

6. Insight for biomimetics

Our findings could suggest bioinspired robust control algorithms to make robotic sensors to locate a source in a riverine environment in spite of a large scope of uncertainties (e.g., ones introduced in this paper). For example, the simple switching rule in (1) could be used for a robot to seek a source location. Due to the simplicity of the switching algorithm, such robots could be made low-cost and small and can be used to trace toxins released from rivers etc. System and environmental parameters could be estimated for a given application in order to predict convergent behaviors of the robot using (10) and (11). Additionally, a detection threshold level of a robot could be optimally scheduled using a similar argument as discussed in section 5 in order to maximize the source detection probability. On the other hand, a robot with the algorithm calibrated with lamprey parameters, could be used to test different hypotheses in real experimental setups. Instead of using simulation, by using a robot with a hypothetical control algorithm in a field experiment, one can confirm or reject a hypothesis more precisely by removing any errors resulted from the simulating the field experiment on a computer. Finally, more investigation on the behavior of the immature lampreys is needed in order to confirm the conjecture given in section 5 and so will be potentially beneficial to biomimetics.

7. Concluding remarks

We introduced a simple switching mechanism modeled after odor-conditioned rheotaxis for the sea lamprey in search for the source of a pheromone. In this strategy, mature females move upstream only if they detect that the pheromone concentration is higher than a threshold value and drifts down otherwise. We then mathematically showed how a simple switching mechanism modeled after odor-conditioned rheotaxis in the sea lamprey can indeed guide an organism to an odorant source in a riverine environment in spite of various uncertainties. The analytical convergence result supported evidence obtained from experimental tests and the computational simulation studied in [8]. We also provided a slightly modified model based on a combination of two hypotheses and extensive simulation results to explain why immature lampreys do not remain near the source location [1, 9]. One of these hypotheses was that the olfactory systems of immature lampreys have not yet been developed to be as efficient as those of mature lampreys. This has been formulated as olfactory dynamics with a significant time constant for immature lampreys (in contrast to zero or small time constant for mature lampreys). The other hypothesis was that immature lampreys are possibly more sensitive (or responsive) to environmental stimuli because of their vulnerability to environmental changes or ecological threats. This has been formulated as a small detection

threshold value for immature lampreys (in contrast to a high value for mature lampreys). Therefore, we explain the fundamental difference in convergence between mature and immature lampreys by different parameters of olfactory system dynamics, namely olfactory response time and detection threshold level. Using this unique test system whereby immature and mature female lampreys express differential convergent behaviors to a pheromone source, we developed and tested olfactory-based hypotheses in an engineering framework. The extensive simulation results supported this combination of two hypotheses for immature lampreys. These results provide justification to experimentally confirm hypothesized changes in the sea lamprey olfactory system as females mature. Furthermore, we provide possible insight as how control algorithms and robotic sensors can be integrated to optimize convergence to an odorant source in spite of various uncertainties.

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