How Does the *Dendrocoleum lacteum* Orient to Light? A Fuzzy Modeling Approach

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Abstract

We apply fuzzy modeling to derive a mathematical model for a biological phenomena: the orientation to light of the planarian *Dendrocoleum lacteum*. This behavior was described linguistically by several ethologists and fuzzy modeling allows us to transform their descriptions into a mathematical model. The behavior of the resulting mathematical model, as studied using both simulations and rigorous analysis, is congruent with the behavior actually observed in nature. This seems to indicate that the verbal explanations suggested by the ethologists are indeed correct.

We believe that the fuzzy modeling approach demonstrated here may be very suitable for biomimicry, that is, the design of artificial systems based on mimicking a natural behavior observed in nature.

keywords: Linguistic modeling, hybrid systems, discrete-event systems.

1 Introduction

In many of the "soft sciences" (e.g., psychology, sociology, ethology) scientists provided *verbal* descriptions and explanations of various phenomena based on field observations. It is obvious that obtaining a suitable *mathematical* model, describing the observed system or behavior, can greatly enhance our ability to understand and study it in a scientific manner. Indeed, mathematical models are very useful in summarizing and interpreting empirical data. Furthermore, once derived, such models allow us to analyze the system qualitatively and quantitatively using mathematical tools.

In a recent paper [14], we advocated fuzzy logic theory as the most suitable tool for transforming linguistic descriptions of various observed phenomena into suitable mathematical models. This approach is congruent with the notion that the real power of fuzzy logic is in its ability to handle and manipulate linguistic information based on perceptions rather than equations (see, e.g., [4] [8] [9] [17]). Indeed, fuzzy modeling is routinely used to transform the knowledge of an expert, be it a physician or a process operator, into a computer algorithm. Yet, not enough attention has been given to its possible use as a tool to assist human observers transform their linguistic descriptions into mathematical models.

A fuzzy model represents the real system in a form that corresponds closely to the way humans perceive it. Thus, the model is easily understandable, even by a non-professional audience, and each parameter has a readily perceivable meaning. The model can be easily altered to incorporate new phenomena, and if its behavior is different than expected, it is usually simple to find which rule/term should be modified and how. Furthermore, being a mature field, the mathematical procedures used in fuzzy modeling have been tried and tested many times, and the standard techniques are well documented. Furthermore, fuzzy modeling offers a unique advantage–the close relationship between the linguistic description and the resulting mathematical model can be used to verify the validity of the verbal explanations suggested by the observer. Thus, the derived mathematical model can be used to prove or refute the modeler's ideas as to how the natural system behaves and why.

In [14], we presented this approach in detail and demonstrated it by transforming the linguistic description of territorial behavior in fish, given by Nobel Laureate Konrad Lorenz in [7], into a mathematical model.

In this paper, we use this approach to develop a mathematical model for an additional phenomenon of animal behavior: the orientation to light of the planarian *Dendrocoleum lacteum*. This behavior was described and explained by several ethologists, and we demonstrate how fuzzy modeling can be used to transform this linguistic information into a mathematical model. The behavior of the resulting mathematical model, as studied using both simulations and rigorous analysis, is congruent with the behavior actually observed in nature. This seems to indicate that the verbal explanations suggested by the ethologists are indeed correct.

There are several reasons why our work focuses on models from ethology. First, for many actions of animals (and humans) the all-or-none law does not hold; the behavior itself is "fuzzy". Hence, fuzzy modeling seems the most appropriate tool for studying such behaviors.

The second reason is that researches studying animal behavior often provide a *linguistic* description of both their observations and interpretations. For example, Fraenkel and Gunn describe the behavior of a cockroach, that becomes stationary when a large part of his body surface is in contact with a solid object, as: "A high degree of contact causes low activity ..." [5, pp. 23].

Another reason is that recently a great deal of research effort is being directed towards *biomimicry*–the development of artificial products or machines that mimic biological phenomena (see, e.g., [1] [10]). An important component in this field is the ability to perform reverse engineering of an animal's functioning and then implement this behavior in an artificial system. We believe that the approach presented in [14] and demonstrated in this paper may be very suitable for addressing biomimicry in a systematic manner. Namely, start with a linguistic description of an animal's behavior (e.g., foraging in ants) and, using fuzzy logic theory, obtain a mathematical model of this behavior which can be implemented by artificial systems (e.g., autonomous robots).

The remainder of this paper is organized as follows. Section 2 presents the linguistic descriptions and explanations given by several ethologists who have studied the response of *Dendrocoleum lacteum* to light. Section 3 applies fuzzy modeling to transform these linguistic descriptions into a mathematical model. Section 4 describes the results of simulations using the mathematical model and compares these to the behavior actually observed in nature. Section 5 analyses the mathematical model. The final section concludes.

2 Klino-kinesis in the *Dendrocoleum lacteum*

An animal's life depends on oriented movements. Such movements guide the animal into its normal habitat or into other situations which are of importance to it. Various external factors–light, smell, currents, humidity, heat, and so on–activate the living mechanisms and lead to orientation. This allows predators to move towards possible prey, and away from possible danger. In such a movement, referred to as *taxis* (see, e.g., [6]), the direction of movement is correlated with the direction of the stimulus. For example, positive (negative) photo-taxis is the directed movement towards (away from) a source of light. Taxes require sensory organs that can accurately detect the direction of the stimulus, and a brain sophisticated enough to process the sensory data and consequently determine the appropriate direction of movement.

Simple organisms, such as wood lice or flat-worms, do not necessarily have the physiological equipment needed to perform taxes. Their eyes, for example, do little more than indicate the general intensity of light but not its direction. Hence, in such organisms the locomotory action is affected by the intensity of the stimulus but *not* by the direction of the stimulus. This type of response is referred to as *kinesis*.[1]

Klino-kinesis[2] is defined as a movement where the rate of turning, but *not* the direction of turning, depends on the intensity of the stimulus. This type of movement appears in many flat-worms: in regions with higher light intensity their rate of turning increases. As a result, eventually the animals aggregate in shadier parts of the available habitat.

[1]from the Greek *kinesis*, movement.
[2]from the Greek *klino*, incline.

In a classical paper, Philip Ullyott studied this type of behavior in the *Dendrocoleum lacteum* [15]. In order to determine whether the reaction is simply to the *intensity* of the light falling on the animal, or to its *direction* as well, he designed an apparatus insuring that the only object visible to the animal is the single patch of light directly above it.

He analyzed the effects of such a stimulus on the animal's behavior, and found that the stimulus did not affect the animal's linear velocity. Instead, increased light intensity yielded an increase in the rate of change of direction (r.c.d.) in which the animal moved. Ullyott defined the r.c.d. as the sum of all the deviations in the animal's path during one time unit, summing up both right-hand and left-hand deflections as positive changes, and expressing the result in units of angular degrees per minute. As the light was switched on, the r.c.d. immediately increased but with time the r.c.d. fell off, converging to a constant level which Ullyott designated the basal r.c.d. This decrease of response under constant stimulation suggested the existence of an adaptation mechanism. Ullyott summarized his findings as follows:

"(1) An increase in stimulating intensity produces an increase in r.c.d.

(2) This initial increase in r.c.d. falls off under constant stimulation owing to adaptation.

(3) There is a basal r.c.d., which is an expression of the fact that turning movements occur even in absolute darkness or at complete adaptation." [15, pp. 274]

Fraenkel and Gunn [5, Chapter V] reviewed and refined Ullyott's work. They developed a simplified and deterministic model for the "averaged" animal's movement in order to explain how its behavior eventually drives it to shadier regions. The most important simplification is the assumption that the animal always turns to the right and always through exactly $90°$. As the r.c.d. increases, the time between these right-hand turns decreases.

Following Ullyott, Fraenkel and Gunn provided a heuristic explanation of how this behavior drives the animal to the darker regions. Suppose that the animal is placed in a plane described by two coordinates (x, y), and the light intensity becomes stronger as we move along the positive direction of the x-axis (see Fig. 1). Beginning at a point A, (and assuming that the animal is fully adapted to the light at A), the animal continues in the positive x direction until making a right-hand turn at point B, and so on. Along the segment AB, the light intensity increases and the adaptation level lags behind, so the r.c.d. increases. Along the BC segment the light intensity is constant and the r.c.d. decreases back to its basal level. Along the CD

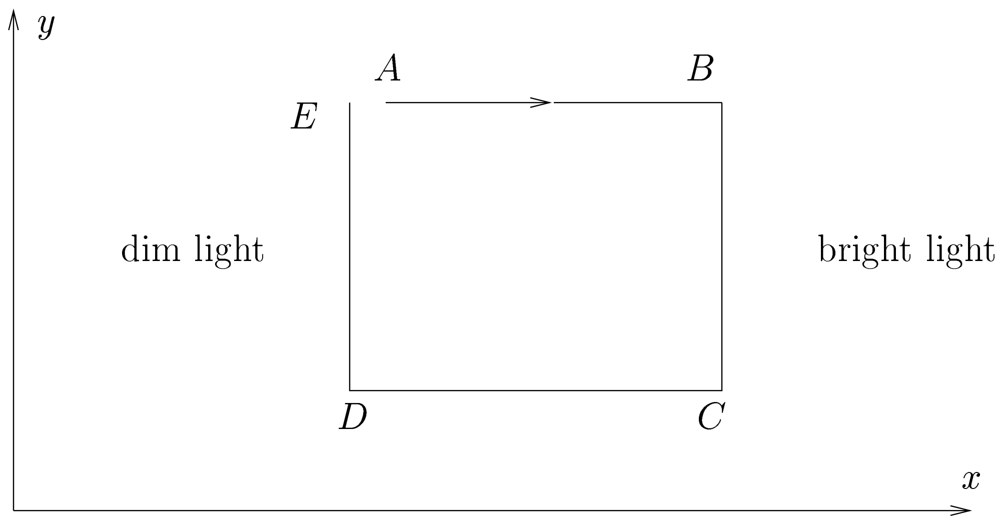

Figure 1: The path followed by the "average" animal. Adapted from [5, pp. 49].

segment the light intensity decreases and the r.c.d. remains constant (note that r.c.d. is affected only by an *increase* in the light's intensity). Finally, the behavior along the DE segment is as in the BC segment. Since the r.c.d. increases along the AB segment and, due to the adaptation process, decreases along the other segments (until it converges to the basal r.c.d.), the segment AB will be *shorter* than the segment CD. Hence, if we denote the initial starting point by A, then after a set of consecutive turns the animal ends up at a point E, which is closer to the darker part of the plane.

Note that the adaptation process plays an essential role in this explanation since it allows the animal to (indirectly) compare a certain light intensity in the present with another light intensity in the past.

Ullyott's results were quite surprising at the time of their publication. Indeed, he postulated that although the animals' movements are *not* oriented with the direction of the light (i.e., kinesis), they still yield a result similar to negative photo-taxis, (i.e., finally, the animals congregate in the shadier regions of their habitat): "This alternate stimulation and adaptation has an effect on the r.c.d. of such a kind that the animal is led automatically to the place of minimal intensity." [15, pp. 277]

It is important to note that both Ullyott and Fraenkel and Gunn provided only a linguistic description of the animal's behavior and a linguistic explanation of its outcome. Patlak [12] studied the behavior of particles under the following assumptions: the particles move in a random way but with persistence of direction. Their movement is also influenced by an external force. He derived a suitable Fokker-Planck-type equation characterizing the particles' movement and used this stochastic model to analyze klino-kinesis [11]. However, his model ignores the adaptation process which plays a vital role in the description given by Ullyott and Fraenkel and Gunn.

3 Fuzzy modeling

In this section, we use the fuzzy modeling approach, described in [14], to transform the linguistic description given above into a mathematical model.

3.1 Identification of variables

The variables in the model are: the animal's location in the plane $(x(t), y(t))$; the light intensity at every point in the plane $l(x, y)$; the light intensity that the animal is currently adapted to $l_a(t)$; the r.c.d. $r(t)$; the direction of movement $\theta(t)$; and the discrete set of times: $t_1, t_2, \dots,$ in which the animal performs a turn. The model also includes two constants: the animal's linear velocity v, and the basal r.c.d. r_b.

The next stage is to transform the linguistic model described in Section 2 into a set of fuzzy rules.

3.2 The fuzzy rules

The adaptation process changes $l_a(t)$, the level of adaptation to light, in accordance with the level of light $l(t)$. We state this as two fuzzy rules

- If $l - l_a$ is *positive*, then $\dot{l}_a = c_1$

- If $l - l_a$ is *negative*, then $\dot{l}_a = -c_1$

where c_1 is a positive constant.

The r.c.d. decreases (increases) when it is above the basal r.c.d. (when the light stimulus is above the adaptation level). We state this as

- If $r - r_b$ is *large*, then $\dot{r} = -c_2$

- If $l - l_a$ is *high*, then $\dot{r} = c_3$

where c_2, c_3 are positive constants.

Finally, following Fraenkel and Gunn's model, we add a crisp rule

- If $\int_{t_l}^{t} r(\tau)d\tau = q$, then $\theta = \theta - \pi/2$

Here, $t_l < t$ designates the time when the last turn took place, and q is a positive constant. In other words, the r.c.d. accumulates and whenever it reaches the threshold q, the animal makes a right-hand turn.

3.3 Defining the fuzzy terms

The next step is to define the various fuzzy membership functions, operators, and the fuzzy inferencing method used. Note that in developing a mathematical model for a system that is described linguistically, there is a large number of degrees of freedom. Should we use ordinary differential equations or partial differential equations? linear or nonlinear equations? with or without time-delay factors? neglect or include "small" effects? and so on.

In the fuzzy modeling approach, the linguistic description leads naturally to the fuzzy rule base. However, the degrees of freedom are manifested in choosing the other components of the fuzzy model: the type of membership-functions, logical operators, inferencing method, and the values of the different parameters. Some guidelines on how to reduce the number of degrees of freedom are described in [14].

For our first set of rules, we model the fuzzy sets using the following membership functions

$$\mu_{positive}(x) = \frac{e^{k_1 x}}{e^{k_1 x} + e^{-k_1 x}} \qquad \mu_{negative}(x) = \frac{e^{-k_1 x}}{e^{k_1 x} + e^{-k_1 x}} \tag{1}$$

where k_1 is a positive constant. For the second set of rules, we use $\mu_{large}(x) = S_{k_2}(x)$, $\mu_{high}(x) = S_{k_3}(x)$, where k_2, k_3 are positive constants, and S is the piecewise linear function

$$S_k(z) := \begin{cases} 0, & \text{if } \; z \leq 0 \\ z/k, & \text{if } \; 0 < z < k \\ 1, & \text{if } \; z \geq k. \end{cases} \tag{2}$$

We can now inference the fuzzy rules to obtain a set of differential equations.

3.4 Fuzzy inferencing

We use simple additive inferencing. The first set of rules yields

$$\begin{aligned} \dot{l}_a &= c_1 \mu_{positive}(l - l_a) - c_1 \mu_{negative}(l - l_a) \\ &= c_1 \frac{e^{k_1(l-l_a)}}{e^{k_1(l-l_a)} + e^{-k_1(l-l_a)}} - c_1 \frac{e^{-k_1(l-l_a)}}{e^{k_1(l-l_a)} + e^{-k_1(l-l_a)}} \\ &= c_1 \tanh(k_1(l - l_a)). \end{aligned} \tag{3}$$

Similarly, the second set of rules yields

$$\dot{r} = -c_2 S_{k_2}(r - r_b) + c_3 S_{k_3}(l - l_a). \tag{4}$$

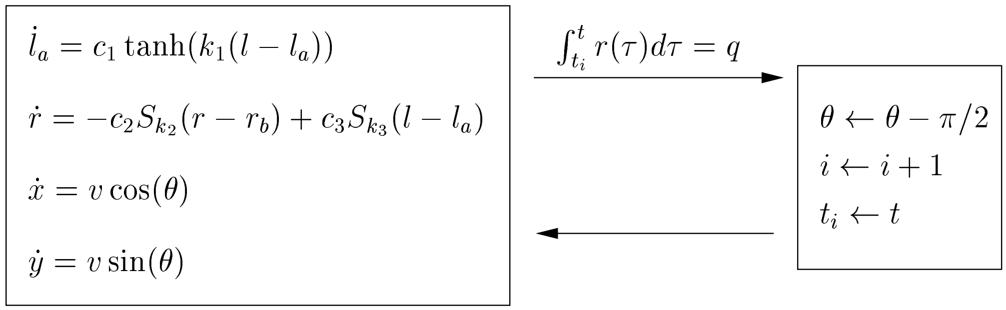

Figure 2: The hybrid model.

The actual movement of the animal is given by

$$\dot{x} = v\cos(\theta), \quad \dot{y} = v\sin(\theta). \tag{5}$$

The crisp rule implies that the value θ "jumps" at the discrete times $t_1, t_2, \ldots$ satisfying $\int_{t_i}^{t_{i+1}} r(\tau)d\tau = q$, $i = 0, 1, \ldots$ (with t_0 defined as zero). Thus, the system combines continuous-time dynamics and discrete events and is, therefore, a *hybrid system* [16].

Fig. 2 summarizes the mathematical model. The upper arrow in this figure corresponds to the conditional transition described by the crisp rule. When the condition holds, the value of θ is updated, and the evolution in time proceeds using the continuous-time dynamics.

The fuzzy modeling approach allowed us to transform the linguistic description of the behavior into a mathematical model. The suitability of this model is determined, among other factors, by how well it mimics the patterns that were actually observed in the natural system. In the next two sections, we study the behavior of the mathematical model using simulations and rigorous analysis.

4 Simulations

Our simulations were motivated by the experiments performed by Ullyott [15].

4.1 Response to a sudden increase in light intensity

In one of his experiments, Ullyott first determined the basal r.c.d. by measuring the r.c.d. after the animals were placed in total darkness for three hours (to make them completely dark adapted). He then exposed the animals to a sudden increase in light intensity, and measured the r.c.d. at different times. It should be noted that Ullyott's results were obtained by measuring and averaging the behavior of many animals. Fig. 3 depicts the averaged r.c.d. as a function of time.

We simulated a similar scenario in our model using Eqns. (3)-(4) with the

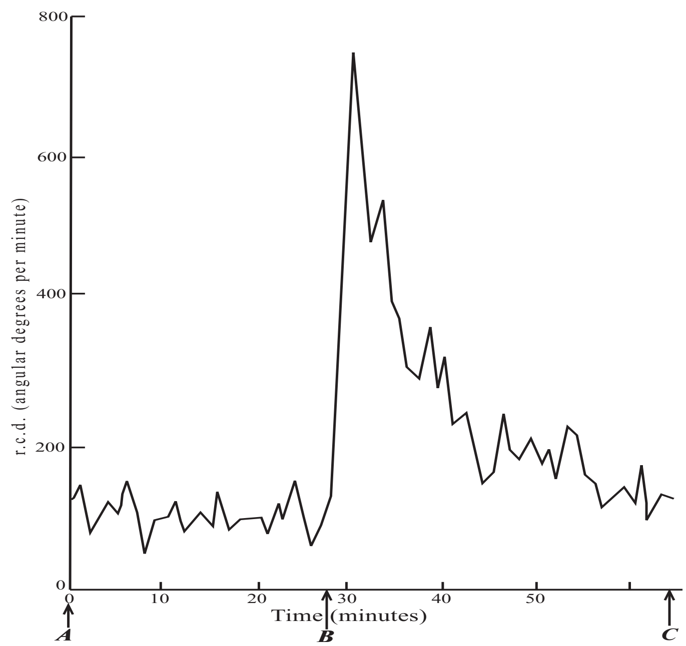

Figure 3: The relationship between rate of change of direction and duration of stimulus. AB, r.c.d. of the animal in darkness (basal r.c.d.). At B a light intensity of 2500 $regs./cm.^2/sec.$ was switched on. BC, adaptation to the stimulus. Each point on the curve represents the average of fourteen experiments. (Reproduced from [15] with permission from The Company of Biologists Ltd.)

parameters

$$c_1 = 5, c_2 = 1, c_3 = 2, k_1 = 1, k_2 = 1, k_3 = 2, r(0) = r_b = 2, l_a(0) = 0, \quad (6)$$

and the light intensity given by $l(t) = 0$ for $t \in [0, 1)$, and $l(t) = 1$ for $t \in [1, 2]$. Fig. 4 depicts $l_a(t)$ as a function of time. It may be seen that the

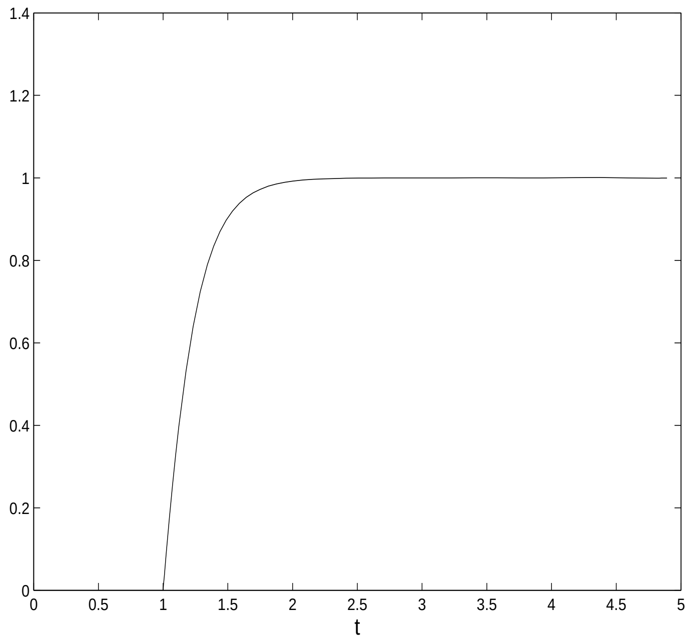

Figure 4: $l_a(t)$ as a function of time. The light is switched on at $t = 1$.

adaptation level increases when the light is switched on, and then converges to $l_a(t) = 1 (= l(t))$.

Fig. 5 depicts $r(t)$ as a function of time. Note the rapid increase of $r(t)$ near the switching time $t = 1$, and then the convergence back to the basal r.c.d. It is quite interesting to compare this figure with the results actually measured by Ullyott as depicted in Fig. 3. The qualitative resemblance is obvious.

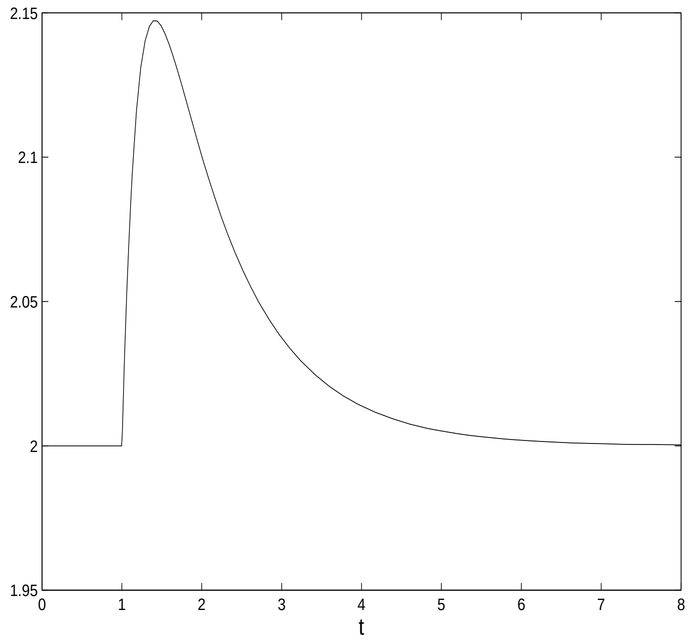

Figure 5: $r(t)$ as a function of time. $r(0) = r_b = 2$, and the light is switched on at $t = 1$.

4.2 Response in a plane with different light intensities

Our second simulation was motivated by the linguistic explanation provided by Fraenkel and Gunn (see Fig. 1). We simulated our hybrid model with parameters:

$$c_1 = c_2 = c_3 = k_1 = k_2 = v = 1, \quad r_b = 2, \quad k_3 = 3, \quad q = 10,$$

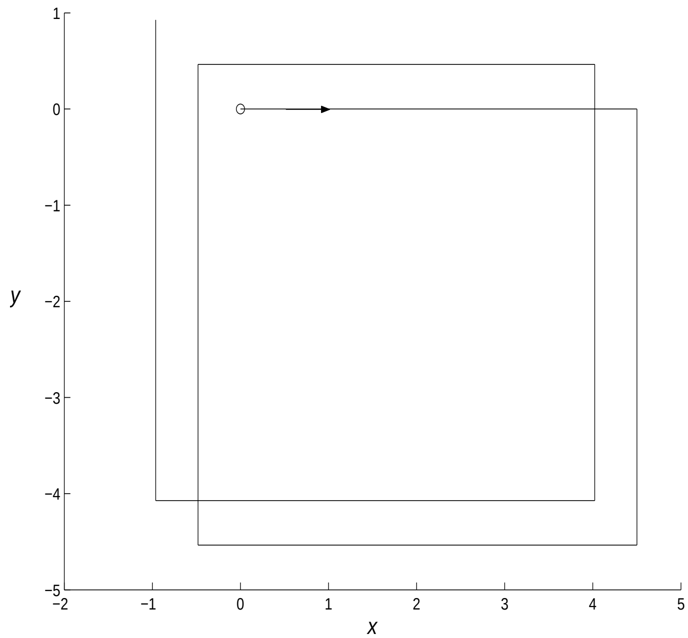

Figure 6: The animal's trajectory for initial values $x(0) = y(0) = 0$. The light intensity is $l(x, y) = x$.

initial conditions: $r(0) = r_b$, $x(0) = y(0) = l_a(0) = 0$, and light intensity given by $l(x, y) = x$, that is, the light intensity increases linearly along the x-axis.

Fig. 6 depicts the animal's trajectory $(x(t), y(t))$. Denoting the times of the right-hand turns by $t_1, t_2, \ldots,$ (with t_0 defined as zero), it may be seen that $x(t_0) > x(t_4) > x(t_8) > \ldots$. Thus, the trajectory indeed moves toward the darker region of the plane. This is in agreement with Ullyott's observations: "The shift of the position of the animal towards the end of the gradient was rather a gradual process, but in each case with the steep gradient, the animal was to be found at the darker end within 2 hours from the beginning of the experiment." [15, pp. 272]

5 Analysis

One of the principle advantages of mathematical models is that we can analyze them qualitatively and quantitatively using mathematical tools. In this section, we analyze the behavior of the hybrid model for the scenarios described in the simulations above.

5.1 Response to a sudden increase in light intensity

We first analyze the effect of a "jump" in the light intensity on the r.c.d. We use $1(t)$ to denote the step function.[3]

Proposition 1 *Consider the hybrid model with initial conditions* $l_a(0) = 0$*,* $r(0) = r_0$*, and light intensity* $l(t) = 1(t)$*. Denote* $w := c_1 k_1 k_2 - c_2$*,* $p_1 := \sinh(k_1)$*, and assume that the model's parameters satisfy the following*

[3]i.e., $1(t) = 0$ for $t < 0$, and $1(t) = 1$ for $t \geq 0$.

conditions:

$$k_3 \geq 1, \quad w > 0, \quad \textit{and } k_2 \geq r_0 - r_b + \frac{p_1 k_2 c_3}{k_1 k_3 w}. \tag{7}$$

Then,

$$l_a(t) = 1 - \frac{1}{k_1} \operatorname{arcsinh}(p_1 \exp(-c_1 k_1 t)), \tag{8}$$

where arcsinh *denotes the inverse hyperbolic sine function, and*

$$r(t) = r_b + \exp(-\frac{c_2}{k_2} t)(r_0 - r_b) + \frac{c_3}{k_1 k_3} \int_0^t \exp(\frac{c_2}{k_2}(\tau - t)) \operatorname{arcsinh}(p_1 \exp(-c_1 k_1 \tau)) d\tau. \tag{9}$$

Proof. See the Appendix.

It is easy to verify that the specific parameter values used in the simulation (6) indeed satisfy (7). Hence, (8) and (9) actually provide an analytical description of the responses depicted in Figs. 4 and 5, respectively.

Note that the integral in (9) can actually be expressed explicitly using the Gauss Hypergeometric function ${}_2F_1$ (see, e.g., [13]) because

$$\begin{aligned} &\int \exp(c\tau) \operatorname{arcsinh}(p \exp(-\tau)) d\tau \\ &= \frac{\exp(c\tau)}{c^2} \left({}_2F_1(1/2, c/2, 1 + c/2, -\exp(2\tau)/p^2) + c \operatorname{arcsinh}(p \exp(-\tau)) \right). \end{aligned}$$

Note also that the proof [see Eq. (13) in the Appendix] indicates that $r(t)$ satisfies a first order non-homogeneous differential equation, with a forcing function that behaves like $f(t) := \text{arcsinh}(\exp(-t))$. Since $f(0) = \text{arcsinh}(1) > 0$, and $f(t)$ decays to zero with t, this explains the response depicted in Fig. 5.

As a final comment, we note that Eq. (14) (see the Appendix) implies that the response of $r(t)$ to a step function in the light intensity decays exponentially. This agrees with the observations of Ullyott, who states: "...it is possible to see that the falling off of r.c.d. with time is exponential..." [15, pp. 270].

5.2 Response in a plane with different light intensities

In this section, we analyze the trajectory of the hybrid model when exposed to a light with a directional gradient. Specifically, we assume that $l(x, y) = x$, that is, the light intensity increases as we move in the positive x direction.

Proposition 2 *Consider the hybrid model with:*

$$c_1 = c_2 = c_3 = k_1 = k_2 = v = 1, \quad r_b = 2, \quad k_3 = 3, \quad q = 10, \quad l(x, y) = x, \tag{10}$$

and initial conditions: $r(0) = r_b$, $x(0) = y(0) = l_a(0) = 0$. *Then, there exist times* $0 = t_0 < t_1 < t_2 \ldots$ *such that* $\int_{t_i}^{t_{i+1}} r(\tau)d\tau = q$, *and*

$$x(t_4) < x(t_0). \tag{11}$$

Proof. See the Appendix.

In other words, after one set of turns, the animal ends up with $x(t_4) < x(t_0)$ so that it moved to the darker region of the plane.

6 Concluding remarks

Verbal descriptions and explanations of various phenomena appear throughout many of the "soft sciences". Constructing a suitable mathematical model, based on this linguistic information, can greatly enhance our understanding of these phenomena. Fuzzy modeling seems to be the natural tool for this purpose. In this paper, we demonstrated this using an example from ethology: the orientation to light of the planarian *Dendrocoleum lacteum.* Simulations and analysis indicate that the behavior of the derived mathematical model is congruent with the behavior actually observed in nature. This suggests that the verbal explanations given by Ullyott and Fraenkel and Gunn are indeed correct.

We believe that fuzzy modeling can and should be utilized in many fields of science, including biology, economics, psychology, sociology and more. In such fields, many linguistic models exist in the research literature, and they can be directly transformed into mathematical models using the method described herein.

Recently, the field of biomimicry, that is, the design of artificial algorithms and machines that imitate biological behavior, is attracting considerable research interest. In many cases, there exist verbal descriptions of the natural behavior we aim to mimic. Hence, we believe that the paradigm presented here, namely, using fuzzy modeling to transform a behavior described in words into a mathematical model, is particularly suitable for biomimicry.

Acknowledgments

We thank The Company of Biologists Ltd. for granting us permission to reproduce some of the material from [15].

Appendix

Proof of Proposition 1. It is easy to verify that for $l(t) = 1(t)$, (3) yields

$$l(t) - l_a(t) = \frac{1}{k_1} \operatorname{arcsinh}(p_1 \exp(-c_1 k_1 t)), \tag{12}$$

which proves (8).

It follows from (12) that $l(t) - l_a(t) \in [0, 1]$, and combining this with (7), we conclude that $l(t) - l_a(t) \in [0, k_3]$ for all t, so (2) yields $S_{k_3}(l(t) - l_a(t)) = \frac{1}{k_1 k_3} \operatorname{arcsinh}(p_1 \exp(-c_1 k_1 t))$. Substituting in (4), we get

$$\dot{r}(t) = -c_2 S_{k_2}(r(t) - r_b) + \frac{c_3}{k_1 k_3} \operatorname{arcsinh}(p_1 \exp(-c_1 k_1 t)).$$

By (7), $r(0) - r_b < k_2$, so it follows from (2) that there exists a $\epsilon > 0$, such that

$$\dot{r}(t) = -\frac{c_2}{k_2}(r(t) - r_b) + \frac{c_3}{k_1 k_3} \operatorname{arcsinh}(p_1 \exp(-c_1 k_1 t)), \quad \forall t \in [0, \epsilon). \tag{13}$$

Integrating this equation, we get (9). Furthermore, (9) yields

$$
\begin{aligned}
r(t) &\le r_b + \exp(-\frac{c_2}{k_2}t)(r_0 - r_b) + \frac{c_3}{k_1 k_3}\int_0^t \exp(\frac{c_2}{k_2}(\tau - t))p_1 \exp(-c_1 k_1 \tau) d\tau \\
&\le r_b + \exp(-\frac{c_2}{k_2}t)(r_0 - r_b) + \frac{p_1 k_2 c_3}{k_1 k_3 w}(1 - \exp(-c_1 k_1 t)), \qquad (14)
\end{aligned}
$$

and using (7), we get

$$
r(t) - r_b \le r_0 - r_b + \frac{p_1 k_2 c_3}{k_1 k_3 w} \le k_2. \qquad (15)
$$

Hence, we can take ϵ in (13) to be arbitrarily large and, therefore, (9) actually holds for all $t \ge 0$. $\square$

Proof of Proposition 2. We begin by noting that it follows from (4) that $r(0) \ge r_b$ implies $r(t) \ge r_b$ for all $t \ge 0$. Hence, for any $\beta > \alpha \ge 0$, with $\beta - \alpha \ge q/r_b$, we have $\int_\alpha^\beta r(\tau)d\tau \ge (\beta - \alpha)r_b \ge q$. Thus, the times $t_0, t_1, t_2, \ldots$ always exist.

It is useful to rewrite the model's equations for the specific choice (10):

$$\begin{aligned}
\dot{z}(t) &= \dot{x}(t) - \tanh(z(t)) \\
\dot{r}(t) &= -S_1(r(t) - r_b) + S_3(z(t)) \\
\dot{x}(t) &= \cos\theta(t) \\
\dot{y}(t) &= \sin\theta(t) \qquad (16)
\end{aligned}$$

where $z(t) := l(t) - l_a(t)$, that is, the difference between the actual light intensity and the intensity the animal is adapted to.

We now consider each of the intervals $[t_i, t_{i+1}]$, $i = 0, 1, 2, 3$, in turn. For each interval, we compute analytical bounds for the model's functions and then "propagate" these in order to obtain bounds for the next interval. Quite expectedly, the bounds become more and more complex during this "propagation" process. Hence, for the sake of notational convenience, we sometimes replace the analytical bounds by the corresponding numerical values.

Interval I: $t \in [0, t_1]$. In this interval, $\theta(t) = 0$ so $\dot{x}(t) = 1$ and $\dot{y}(t) = 0$. Hence, $\dot{z}(t) = 1 - \tanh(z(t))$, with $z(0) = 0$. Using the fact that $\tanh(x) \leq x$

for all $x \geq 0$, we get $\dot{z}(t) \geq 1 - z(t)$, so

$$z(t) \geq 1 - \exp(-t). \tag{17}$$

Using the Lambert W function[4] we can express the solution of the differential equation for $z(t)$ as

$$z(t) = \frac{1 + 4t - W(\exp(1 + 4t))}{2}. \tag{18}$$

Let t' be the first time such that $z(t') \geq 3$. Then, for $t \leq \min(t_1, t')$, we have $S_3(z(t)) = z(t)/3$, so (17) yields $\dot{r}(t) \geq -(r - r_b) + (1 - \exp(-t))/3$, with $r(0) = r_b$. Hence, $r(t) \geq r_b + 1/3 - 1/3(t+1)\exp(-t)$. We now show that $t_1 < t'$. Seeking a contradiction, we assume that $t_1 \geq t'$. Then,

$$\begin{aligned}
q &= \int_0^{t_1} r(t)dt \\
&\geq \int_0^{t'} r(t)dt \\
&\geq \int_0^{t'} (r_b + 1/3 - 1/3(t+1)\exp(-t))dt \\
&= ((3r_b + 1)t' - 2 + (2 + t')\exp(-t'))/3.
\end{aligned}$$

[4]The Lambert W function is defined by $W\exp(W) = x$. See, e.g., [3] [2] and the references therein.

This yields $t' < (3q+2)/(3r_b+1) = 32/7$. Substituting this bound in (18) we find that $z(t') \leq (1 + 128/7 - W(\exp(135/7)))/2 \approx 1.4012$, and this contradicts the definition of t'. We conclude that $t_1 < t'$ and, therefore, $t_1 \leq 32/7$, and $z(t_1) \leq 1.4012$.

Let t'' be the first time such that $r(t'') - r_b \geq 1$. Then, for $t \leq \min(t'', t_1)$, we have

$$\begin{aligned} \dot{r}(t) &= -(r(t) - r_b) + z(t)/3 \\ &= -(r(t) - r_b) + (1 + 4t - W(\exp(1+4t)))/6. \end{aligned}$$

Integrating, we get

$$r(t) = r_b + (\exp(-t) - 1)/2 + 2t/3 - \frac{1}{6}\int_0^t \exp(\tau - t) W(\exp(1+4\tau))d\tau. \quad (19)$$

We now show that $t'' > t_1$. Seeking a contradiction, assume that $t'' \leq t_1$. Then, $t'' \leq 32/7$, but substituting this in (19), we get $r(t'') - r_b < 0.41477$, which is a contradiction to the definition of t''. Hence, $t'' > t_1$, and $r(t_1) - r_b \leq 0.41477$.

If $p(t)$ is some function of time, then from here on we denote the value $p(t_i)$

by p_i. Summarizing our results, using this notation, we have

$$t_1 \le 32/7, \quad z_1 \le 1.4012, \quad \text{and } r_1 - r_b \le 0.41477. \tag{20}$$

Interval II: $t \in [t_1, t_2]$. In this interval, $\theta(t) = -\pi/2$ so $\dot{x}(t) = 0$ and $\dot{y}(t) = -1$. Hence, $\dot{z}(t) = -\tanh(z(t))$. Solving this equation, we get $\sinh(z(t)) = \sinh(z_1)\exp(t_1 - t) \le \sinh(z_1)$. We already know that $z(t_1) < 3$ so $z(t) \in [0, 3)$ and $S_3(z(t)) = z(t)/3$ for all $t \in [t_1, t_2]$. Let t'' denote the first time such that $r(t'') - r_b \ge 1$ (we already know that $t'' > t_1$). Then, for $t \in [t_1, \min(t_2, t'')]$, we have

$$\begin{aligned} \dot{r}(t) &= -(r(t) - r_b) + z(t)/3 \\ &\le -(r(t) - r_b) + \sinh(z_1)\exp(t_1 - t)/3 \end{aligned} \tag{21}$$

where we used the fact that $x \le \sinh(x)$ for any $x > 0$. Integrating, we get

$$r(t) \le \exp(t_1 - t)(\sinh(z_1)(t - t_1)/3 + r_1 - r_b) + r_b \tag{22}$$

and using the fact that $\max_x x\exp(-x) = \exp(-1)$, we get $r(t) \le \exp(-1)\sinh(z_1)/3 + r_1$. Substituting (20), we get $r(t) - r_b < 1$. Hence, $t'' > t_2$, and we can conclude that (22) holds for all $t \in [t_1, t_2]$. Thus,

$$\begin{aligned} q &= \int_{t_1}^{t_2} r(t)dt \\ &\le \int_{t_1}^{t_2} [\exp(t_1 - t)(\sinh(z_1)(t - t_1)/3 + r_1 - r_b) + r_b]dt \qquad (23) \\ &= r_1 + r_b(t_2 - t_1 - 1) + \sinh(z_1)/3 - \exp(t_1 - t_2)(r_1 - r_b + (t_2 - t_1 + 1)\sinh(z_1)/3). \end{aligned}$$

This yields

$$\begin{aligned} t_2 - t_1 &\ge (q + r_b - r_1 - \sinh(z_1)/3)/r_b \\ &\approx 4.4748, \qquad (24) \end{aligned}$$

where the second equation follows from substituting (20). Hence,

$$\begin{aligned} z_2 &= \operatorname{arcsinh}\left(\sinh(z_1)\exp(t_1 - t_2)\right) \\ &\le \operatorname{arcsinh}\left(\sinh(z_1)\exp(-4.4748)\right) \\ &\approx 0.0218. \qquad (25) \end{aligned}$$

To obtain the last bound for this interval, we substitute $t = t_2$ in (22), to get

$$\begin{aligned} r_2 - r_b &\leq \exp(t_1 - t_2)(\sinh(z_1)(t_2 - t_1)/3 + r_1 - r_b) \\ &\approx .03713, \end{aligned} \tag{26}$$

where the second equation follows from substituting (20) and (24).

Interval III: $t \in [t_2, t_3]$. In this interval, $\theta(t) = -\pi$ so $\dot{x}(t) = -1$ and $\dot{y}(t) = 0$. Hence, $\dot{z}(t) = -1 - \tanh(z(t))$, so $z(t) \leq z_2 \exp(t_2 - t)$. Let t'' denote the first time such that $r(t'') - r_b \geq 1$ (we already know that $t'' > t_2$). Then, for $t \in [t_2, \min(t_3, t'')]$, we have

$$\dot{r}(t) \leq -(r(t) - r_b) + z_2 \exp(t_2 - t)/3. \tag{27}$$

Integrating, we get $r(t) - r_b \leq \exp(t_2 - t)(r_2 - r_b + (t - t_2)z_2/3)$, and using $\max_x x \exp(-x) = \exp(-1)$, we get $r(t) - r_b \leq \exp(-1)z_2/3 + r_2 - r_b$. It is easy to verify, using (25) and (26), that this implies that $r(t) - r_b < 1$.

Hence, $t'' > t_3$ and (27) holds for all $t \in [t_2, t_3]$. Thus,

$$\begin{aligned}
q &= \int_{t_2}^{t_3} r(t)dt \\
&\leq \int_{t_2}^{t_3} [r_b + \exp(t_2 - t)(t - t_2)z_2/3 + (r_2 - r_b)\exp(t_2 - t)]dt \\
&= r_2 - r_b + (t_3 - t_2)r_b + z_2/3 - \exp(t_2 - t_3)(r_2 - r_b + (1 + t_3 - t_2)z_2/3) \\
&\leq r_2 - r_b + (t_3 - t_2)r_b + z_2/3.
\end{aligned}$$

This yields,

$$\begin{aligned}
t_3 - t_2 &\geq (q + r_b - r_2 - z_2/3)/r_b \\
&\approx 4.81072,
\end{aligned}$$

where the second equation follows from substituting (25) and (26). Comparing this with (20), we find that $t_3 - t_2 > t_1$. Since $\dot{x}(t) = 1$ for $t \in [0, t_1]$ and $\dot{x}(t) = -1$ for $t \in [t_2, t_3]$ this implies that $x(t_3) < x(t_0)$.

Interval IV: $t \in [t_3, t_4]$. In this interval, $\theta(t) = -3\pi/2$ so $\dot{x}(t) = 0$ and $\dot{y}(t) = -1$. Hence, $x(t_4) = x(t_3) < x(t_0)$ and this completes the proof. $\square$

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