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Interception from a Dragonfly Neural Network Model

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ABSTRACT

While dragonflies are well-known for their high success rates when hunting prey, how the underlying neural circuitry generates the prey-interception trajectories used by dragonflies to hunt remains an open question. I present a model of dragonfly prey interception that uses a neural network to calculate motor commands for prey-interception. The model uses the motor outputs of the neural network to internally generate a forward model of prey-image translation resulting from the dragonfly's own turning that can then serve as a feedback guidance signal, resulting in trajectories with final approaches very similar to proportional navigation. The neural network is biologically-plausible and can therefore can be compared against *in vivo* neural responses in the biological dragonfly, yet parsimonious enough that the algorithm can be implemented without requiring specialized hardware.

CCS CONCEPTS

• **Computing methodologies → Motion path planning**.

KEYWORDS

guidance, interception, insect vision, neuromorphic

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1 INTRODUCTION

The field of neuromorphic computing is founded on the assumption that better understanding of neural systems and how they function can be leveraged to create more advanced computing systems. This study focused on a highly specialized nervous system, the neural circuitry underlying prey interception in the dragonfly. In nature dragonflies are highly successful hunters (with a 90-95% success rate [3, 11]). What key computations underlie the robustness of dragonfly hunting and how easily can the dragonfly system be translated to a man-made platform? This study seeks to contribute to the advancement of neuromorphic computing by constructing a computational model of the dragonfly nervous system that is framed at a level amenable for translation to a neuromorphic platform.

Dragonflies were of particular interest for this study not only because of their high success rate, but also because they are known to use proportional navigation guidance as they approach their prey. Proportional navigation is a guidance law that results in the geometrically shortest path to interception. Also, dragonflies demonstrate a remarkably short latency when responding to prey maneuvers – on the order of 50 ms [7, 8], quite remarkable given that the response time constant of a single neuron is on the order of tens of ms. While a number of animal species (including dragonflies) are known to use proportional navigation (see [1, 4, 7] for reviews), there are certain advantages to studying an insect system, including the assumption that the underlying circuitry is likely to be 'light' (and therefore the validated model could be translated to a manmade system with relative ease).

As dragonflies approach their prey, they adjust their head position to maintain the image of its prey (referred to here as the 'prey image') on a specific part of the eye [8] (referred to as the fovea) through behavior known as foveation. While simply maintaining a constant angle between the dragonfly's direction of movement and its line-of-sight to the prey will result in behavior known as 'classical pursuit' (during which the dragonfly will head directly at its prey at all times) or a variant known as 'deviated pursuit' (in which a constant but non-zero angle will be maintained between the dragonfly's direction of flight and its line-of-sight to the prey) and therefore is not sufficient to produce proportional navigation. I have developed a model of dragonfly prey interception that executes proportional navigation solely based upon prey-image translation across the eye. While prey-image slippage away from the fovea has been suggested as the signal used by dragonflies for interception [6, 11], this is the first model (to the author's knowledge) of how that signal is used. This model is in the form of a neural network and incorporates certain simplifications intended to facilitate translation to a man-made system. Nevertheless, I will discuss model predictions that can be directly tested in the nervous system of the biological dragonfly.

2 MODELING APPROACH

While dragonflies have two eyes, the neural circuits thought to process moving targets and underlie dragonfly tracking of prey [5, 6, 10] largely do not have binocular receptive fields (although see [9], suggesting that dragonflies do not use depth perception to capture prey. Accordingly, the 'eyes' of the dragonfly model presented here are simplified as a flat two-dimensional screen (referred to here as the model dragonfly's eye). During each simulation time step, the movement of the prey relative to the dragonfly and the resulting translation of the image of the prey on the dragonfly eye (the prey image) are calculated. The dragonfly then adjusts its pitch and yaw

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angles (for simplicity, this study did not include roll), to maintain the prey image directly on the fovea. If the dragonfly approaches to within a minimum distance of the prey (specifically the distance that that the dragonfly can move within one simulation time step), a successful capture is declared and the engagement ends.

One significant difference between the model dragonfly and the biological dragonfly is that the fovea of the model dragonfly eye is moveable – its location on the eye is a function of the previous turns required to maintain the position of the prey image on the fovea. As described below, the model adjusts the position of the fovea to execute proportional navigation. By comparison, the fovea of the biological dragonfly eye is immoveable, although it is likely that proprioceptive information from the neck (encoding the angle of the head relative to the body) performs an analogous function.

Simulating the motor system (e.g. wings, muscles) was outside of the scope of this project, as was detailed simulation of the dragonfly eyes. For the results presented here, it is assumed that the dragonfly and its prey fly at the same speed (10 m/s) and have the same maneuverability.

2.1 Calculation of model dragonfly turning

The turning required to maintain the prey image on the fovea is calculated by a neural network of continuous-valued (non-spiking) neurons. Neurons in the 'prey-image representation' population (denoted by open circles in Figure 1) encode the position of the image of the prey on the eye (in 'eye coordinates'). The response f_i of each neuron i from this population is determined by a Gaussian tuning curve:

$$f_i(x_1, x_2) = \exp\left(-\frac{(\mathrm{a_{i1}} - \mathrm{x_1})^2 + (\mathrm{a_{i2}} - \mathrm{x_2})^2)}{2\sigma_\mathrm{r}^2}\right),$$

where (x_1, x_2) is the location of the prey image on the eye, (a_{i1}, a_{i2}) is the preferred position of the prey-image for neuron i, and σ_r determines the width of the tuning curve.

Neurons in the 'fovea-position representation' (indicated by filled blue circles in Figure 1) encode the position of the fovea in eye-coordinates. The response (g_j) of neuron j within this population is also determined by a Gaussian tuning curve:

$$g_j(y_1, y_2) = \exp\left(-\frac{(\mathrm{b_{j1}} - \mathrm{y_1})^2 + (\mathrm{b_{j2}} - \mathrm{y_2})^2)}{2\sigma_\mathrm{g}^2}\right),$$

where (b_{j1}, b_{j2}) is the preferred fovea location for the neuron, (y_1, y_2) is the fovea location, and σ_g describes the width of the tuning curve. These two inputs are combined in the sensory representation (red circles in Figure 1) such that the response S_{ij} of a sensory representation neuron multiplicatively combines input from one prey-image neuron (i) and one fovea-position neuron (j) :

$$S_{ij} = f_i(x_1, x_2) g_j(y_1, y_2).$$

The sensory representation is designed such that all possible combinations of prey-image position and fovea position neurons are included.

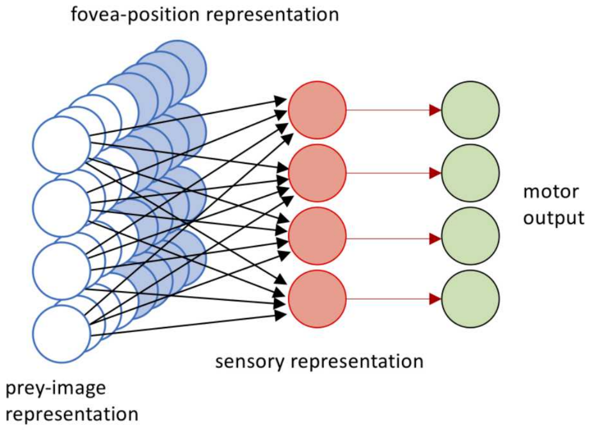

Figure 1: Schematic of the model dragonfly neural network. Prey-image representation neurons are indicated by open circles, fovea-position neurons are indicated by filled blue circles. The responses of neurons in the sensory representation (filled red circles) arise from multiplicative interactions between neurons in the eye and fovea representations. The motor output population (green circles) represents the direction that the dragonfly should turn in eye-coordinates. Responses of the motor output population are determined as described in the text. For clarity, some neurons and connections between neurons are not drawn.

Neurons in the motor output population (green circles) represent the goal direction, in eye coordinates, to which the dragonfly should turn. The response of neuron i in the motor output population, R_i, is determined by summing over all inputs in the sensory representation, weighted by an appropriate factor (W_{ij}):

$$R_i = \sum_j W_{ij} S_j.$$

All network weights are calculated based upon the prey-image position, fovea position, and goal-direction preferences of the presynaptic and postsynaptic neurons. The neural network does not require training, and does not learn.

It is assumed that the motor output neurons are characterized by some "inherent" response tuning that determines the preferred goal location c of each motor output neuron. The inherent response m_i of neuron i of the motor output representation is:

$$m_i(z_1, z_2) = \exp\left(-\frac{(\mathrm{c_{i1}} - \mathrm{z_1})^2 + (\mathrm{c_{i2}} - \mathrm{z_2})^2)}{2\sigma_\mathrm{m}^2}\right),$$

where (c_{i1}, c_{i2}) is the preferred goal direction, and (z_1, z_2) is the direction of turn. It should be noted that, while there is some assumed inherent tuning of the motor output neuron σ_m, in practice σ_r and σ_g play a dominant role in determining the specificity of the motor output neurons.

The weight from sensory representation neuron j to motor output neuron i is given by:

$$W_{ij} \propto \int\int\int\int dy_1 dy_2 dz_1 dz_2 f_j(a_{j1} - (z_1 + y_1), a_{j2} - (z_2 + y_2)) \\ g_j(b_{j1} - y_1, b_{j2} - y_2) m_i(c_{i1} - z_1, c_{i2} - z_2)$$

where f_j and g_j are the prey-image representation and fovea-position representation tuning curves. Goal direction are expressed in eye coordinates, and because the eye is fixed relative to the body, this is equivalent to expressing goal direction in body-coordinates, relative to the reference frame of the dragonfly's body. The biological motivation to the pattern of connectivity is inspired by published models of coordinate transformations in parietal cortex [12, 13].

To determine dragonfly turning, the motor output representation is decoded through a neural-activity weighted average of the preferred directions of the motor population. The motor output activity is first thresholded (activity below a certain threshold is set to zero), then the direction and magnitude of turn is decoded as:

$$d_1 = \frac{\sum_i c_{i1} R_i}{\sum_i R_i} \text{ and } \mathrm{d}_2 = \frac{\sum_\mathrm{i} \mathrm{c}_{\mathrm{i}2} \mathrm{R}_\mathrm{i}}{\sum_\mathrm{i} \mathrm{R}_\mathrm{i}},$$

where (d_1, d_2) is the change in direction (in eye-coordinates) that the dragonfly executes. Expressed using terms more typically used to describe turns by airborne vehicles, the change in yaw is $\Delta\theta = \tan^{-1} \frac{d_1}{\epsilon}$, and the change in pitch is $\Delta\phi = \tan^{-1} \frac{d_2}{\epsilon}$, where ϵ is the distance from the dragonfly's eye to the center of the dragonfly's head, defined as the point where the yaw and the pitch axes intersect.

If the fovea is held at a fixed position, the model dragonfly will display behavior known as 'classical pursuit' (if the fovea is at the center of the eye, see top panel of Figure 2). For this figure, the prey constantly travels in one direction only. During classical pursuit, the pursuer heads directly at the prey at all times. While this strategy for hunting can be successful, there is a tendency for the pursuer to end up in a tail chase (as is the case for this figure) in which the dragonfly falls directly behind the prey and fails to capture the prey (because both dragonfly and prey are moving at the same speed, if the dragonfly is directly behind the prey it is impossible for a capture to occur if the prey does not turn). For this engagement, the simulation was ended after 15 seconds of simulation time. A variant of classical pursuit known as 'deviated pursuit', in which the pursuer maintains a constant angle between the line-of-sight to the prey and its direction of motion, is given in the bottom panel of Figure 2). Depending on the location of the fovea, deviated pursuit can be successful for engagements in which classical pursuit is not (for comparison, the classical pursuit trajectory from the top panel is replotted in cyan). If complete information about the trajectory of the prey is known, deviated pursuit can produce a trajectory equivalent to proportional navigation (see green trajectory in bottom panel) but this requires accurate calculation of the fovea location based upon full knowledge of the prey's velocity and position. If prey velocity and position are not known, or if there is an error in calculation, deviated pursuit will also end in a tail-chase (not shown).

It is well-known that classical pursuit (or deviated pursuit) arises from holding the prey image at a fixed location on the eye, provided that the eye and head are held at a fixed angle relative to the body (for reviews see [2] [4]). These results are presented as a demonstration of the viability of the above-described neural network for generating trajectories driven by foveation. The generated trajectories are very similar to previously presented results from a similar model of dragonfly interception in which the dragonfly's turns were analytically (see Chance, presentation at ICONS2019).

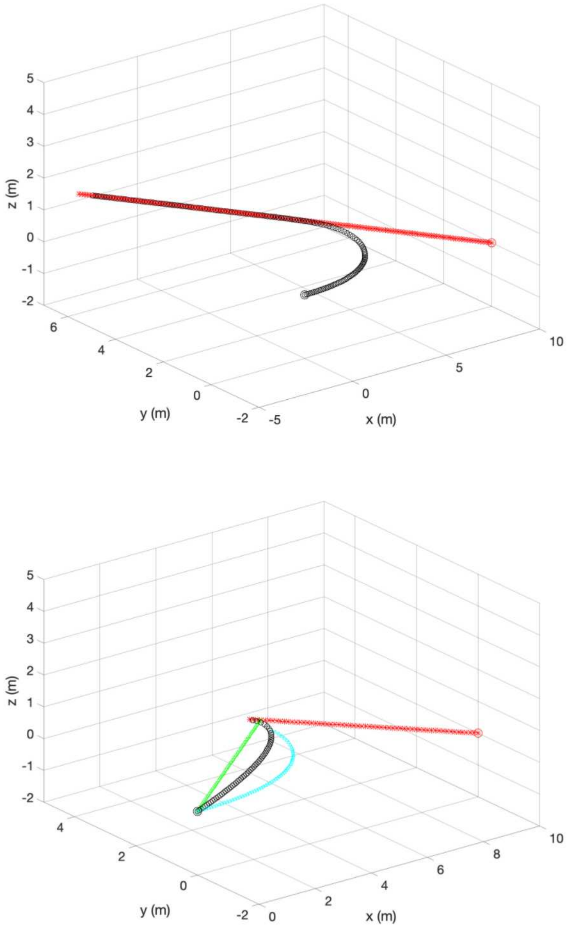

Figure 2: The model dragonfly demonstrates classical pursuit behavior when the fovea is fixed at the center of the eye. Red and black circles indicate positions of prey and dragonfly, respectively, for each time step. Large red and black circles indicate starting positions of prey and dragonfly. Top: The prey maintains a straight-line trajectory and is not captured by the end of the simulation (after 15 seconds if no capture). Bottom: The prey makes one randomly-generated turn after two seconds of simulation time, and model dragonfly adjusts trajectory to continue pursuit. In this engagement, the model dragonfly successfully captures the prey.

2.2 Generating proportional navigation through forward model generated from motor output

Recent work [7] has suggested that dragonflies utilize internal models both to compensate for prey-image drift on the eye resulting from dragonfly-body rotations. Here we propose that dragonflies may use internally-generated forward models of prey-image translation on the eye as a feedback signal for generating proportional navigation. In this version of the model, the decoded motor output (d_1, d_2) is used not only to calculate the required trajectory, but is also used to determine changes to the location of the fovea on the eye. It should be noted that while this signal is easily decoded from the motor commands in a biological signal, the fovea of a biological eye is hardwired and cannot be moved. Instead, it is likely that the biological dragonfly adjusts other variables, for example head position relative to the body. For this version of the model dragonfly, the new fovea location is now $(e_1', e_2') = (e_1 - Qd_1, e_2 - Qd_2)$, where $e_1, e_2)$ is the former position of the fovea, (d_1, d_2) is the change in direction decoded from the motor output population, and Q is a gain factor. For the results shown here, $Q = 1$.

For these conditions ($Q = 1$), the fovea is essentially shifted in an equal but opposite direction to the prey-image translation on the eye. The behavior of the model with this additional component is shown in Figure 3. As in Figure 2, the prey is indicated in red and the dragonfly in black. The initial conditions in the top panel are identical to the top panel in Figure 2. The classical pursuit trajectory (from the top panel of Figure 2 except that the trajectory is truncated when the model dragonfly captures the prey) is provided in blue for comparison. Likewise, the geometrically shortest trajectory to capture the target (assuming full knowledge of target direction, speed, etc.), equivalent to following pure proportional navigation, is provided in green for comparison.

The initial conditions (including fovea position) are identical to those at the top of Figure 2, and the model dragonfly initially chases using classical pursuit (compare the dragonfly's early locations to the blue trajectory). However, as the dragonfly uses the feedback signal generated by the motor outputs to adjust the location of the fovea, the dragonfly's trajectory becomes more like proportional navigation (compare later dragonfly trajectory with green trajectory). This behavior is very similar to the previous version of the dragonfly model (see presentation by Chance at ICONS2019) in which required turns were analytically calculated.

It should be noted that proportional navigation generates the geometrically shortest trajectory to interception. If the prey does not turn, as in the top panel of Figure 3, the resulting trajectory is a straight line. If the fovea is at an appropriate location such that the dragonfly is is following proportional navigation while maintaining the prey image on the fovea, the prey image will remain aligned with the fovea for the remainder of the engagement until the prey is captured or turns. Thus, prey-image slippage away from the fovea is an appropriate "error" signal that could be used to search for a more optimal trajectory. It is likely that the feedback gain, Q, could be adjusted for more optimal trajectory calculation, in particular for engagements where the prey is turning or actively evading.

3 CONCLUSION

I have presented a model of dragonfly prey interception that calculates motor commands for prey-interception trajectories using a simple neural network. Specifically, the model uses visual and a proxy for proprioceptive input to determine turning commands that will align the prey image with the eye's fovea. The model also uses a feedback error signal to adjust approach trajectories to be more like proportional navigation (following the geometrically shortest path to capture). The feedback signal is a forward model of prey-image translation resulting from dragonfly turning generated from the model's motor outputs.

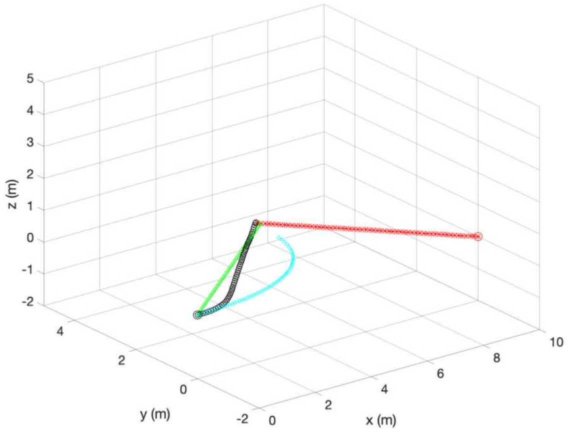

Figure 3: The model dragonfly follows trajectories closer to proportional navigation when an internal forward model of motor commands is used as a feedback signal to adjust fovea location. Red and black circles indicate positions of prey and dragonfly, respectively, for each time step. Large red and black circles indicate starting positions of prey and dragonfly. Blue trajectory is classical pursuit and green trajectory is proportional navigation. The initial conditions are identical to the top panel of Figure 2. The prey follows the same straight-line trajectory as in Figure 2 but here the prey is captured at approximately 5.6 seconds.

Because informing future neuromorphic systems is a priority for this line of research, certain simplifications were made to the dragonfly model to make the model more amenable to translation to a nonbiological system. For example, the dragonfly eyes are approximated as single two-dimensional screen, and a moving fovea is used in place of a pivotable head. Research is currently in progress to further develop the dragonfly model, in particular to develop methods for directly comparing the dragonfly model to data from the biological dragonfly.

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