Understanding interactions between networks controlling distinct behaviors: Escape and swimming in larval zebrafish

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1   Introduction

Spinal neural networks in larval zebrafish generate a variety of movements such as escape, struggling, and swimming. There have been a number of untested proposals regarding possible mechanisms at both the network and neural levels to account for switches between these behaviors [9]. However, there are currently no detailed demonstrations of such mechanisms, so it is not possible to determine which are plausible and which are not. Here we propose a detailed, biologically plausible model of the interactions between the swimming and escape networks in the larval zebrafish. This model shows how distinct behaviors can be controlled by anatomically overlapping networks. More generally, this paper demonstrates a method for constructing spiking networks consistent with both high-level behavioral descriptions and available neural data.

2   Zebrafish system description

Two distinct rhythmic motor patterns, classified as 'escape' and 'swimming,' are observed in the larval zebrafish. Escape is characterized by large amplitude waves propagating along the body of the fish in a C- or S-shaped pattern. Normal swimming is defined as movement that possesses rhythmic alternating movements of the tail, with bends propagating from the rostral to the caudal end [2].

There have been suggested two possible means by which both escape and swimming behaviors could be generated by the same network. One possibility is that of a unified network [4, 10]. Such a network would use different control signals in order to elicit different motor behavior from the same network of neurons. Thus, all neurons would potentially be active for both behaviors. The other possibility is that there exist separate classes of spinal interneurons implicated in the different behaviors.

Anatomical and functional evidence clearly shows that there are differences in the spinal networks of zebrafish during escape and swimming movements, supporting the second hypothesis [9]. Nevertheless, because swimming and escape are produced by the same muscles and motoneurons in fish, there must be some interaction between the

interneurons responsible for these behaviors. The purpose of this paper is to describe a model consistent with these observations.

The two classes of interneuron to be included in the model are the circumferential descending (CiD) interneurons and the multipolar commisural descending (MCoD) interneurons. In zebrafish larvae, CiD interneurons have been found to be active during escapes but not swimming [9]. CiD interneurons are characterized by sparse dendrites and ventrally projecting, ipsilateral axons [1]. CiD interneurons are generally found in the middle and dorsal regions along the dorso-ventral extent of the spinal cord [5]. The axons of ventrally located CiD interneurons are in close proximity to the axon collaterals of Mauthner cells. It is known that the Mauthner cell initiates the escape response in goldfish [11].

The MCoD interneuron has been previously described by Bernhardt et al. as the larval ventral longitudinal descending (VeLD) interneuron [1]. However, Ritter et al. and Hale et al. argue that since there exist VeLD cells which possess either ipsilateral or commisural neurons, a further distinction is necessary [9, 5]. MCoDs refer to cells which have the same somatic morphology as VeLD interneurons but possess commisural as opposed to ipsilateral axons. The MCoDs are ventrally and laterally positioned compared to the CiD interneurons and have elaborate dendritic arbors. The MCoD has been found to be active during swimming but not escape [9].

3 Hydrodynamical model

In order to investigate mechanisms by which coordination between escape and swimming might occur, we have created a zebrafish model. The hydrodynamics of the model are based on a previous hydrodynamic model of carangiform fish by Mason et al. [6] and Morgansen et al. [7, 8]. There are three segments in this model of the zebrafish — the body, the peduncle, and the tail. The body segment of the fish is modeled as a rigid body that is connected to the tail by the peduncle (a slender segment of generally negligible hydrodynamic influence).

The equations of motion for this nonlinear system are given below:

$$\mathbf{I}^{total} \begin{pmatrix} \ddot{\psi}_1 \\ \ddot{\psi}_2 \\ \ddot{x} \\ \ddot{y} \\ \ddot{\theta} \end{pmatrix} = \begin{pmatrix} u_1 \\ u_2 \\ L_x + D_{f_x} + D_{b_x} + f_{am_x} \\ L_y + D_{f_y} + D_{b_y} + f_{am_y} \\ \tau_f + \tau_b + \tau_{am} + (x_m - x, \, y_m - y) * (L + f_{am}) \end{pmatrix}.$$

Here, $\ddot{x}$ and $\ddot{y}$ represent the accelerations in the forward and lateral directions respectively, $\ddot{\theta}$ represents the acceleration of the orientation of the body in the inertial reference frame, $\ddot{\psi}_1$ and $\ddot{\psi}_2$ represent the acceleration of the joint angles with respect to the body's longitudinal axis, the input signals to the system are represented by u_1 and u_2, L represents the lift generated by the tail fin, D_f is the drag on the tail fin, D_b is the total drag force acting on the body, f_{am} represents the added mass effects, τ_f is the torque generated around the midpoint of the tail, τ_b is the total drag moment acting on the body, τ_{am} is the moment due to the acceleration component of the tail fin (which is independent of $\ddot{x}$, $\ddot{y}$ and $\ddot{\theta}$), x_m and y_m are the position of the midpoint of the tail fin,

and $\mathbf{I}^{total}$ is a matrix which represents the inertia of the fluid surrounding the body, the inertia of the actual body plate, and the added inertia due to the tail fin.

The hydrodynamic model accounts for quasi-static torque generated around the midpoint of the tail, total drag moment acting on the body, the moment added by mass forces, lift, drag force acting on the body and fin, and the added mass forces. Due to simplifications in the model, the spatial structure of the wake has been ignored. Vortices shed from the tail fin are treated as if they are swept away and become immediately very distant. Hydrodynamic interactions between the different components (fin, peduncle, and body), and forces on the peduncle are also ignored.

4   Genetic algorithm optimization

The input to the hydrodynamic model was optimized using a genetic algorithm approach with the aim of obtaining a suitable range of escape and swimming behaviors. The genetic algorithm used a population size of 50, rank-based selection, bit-wise crossover with probability 80% and mutation with probability 5%.

Domenici et al. characterize a fast start as being a burst of swimming which lasts for less than approximately 1s [2]. For this reason, the criterion for evaluating the fitness of the escape behavior generated is the distance in the forward direction traveled during 1s subject to a penalty on lateral movement.

Normal swimming is characterized by prolonged swimming for more than 10s using steady periodic movements[2]. The goal for such an optimization is to obtain an energy efficient gait. In order to penalize energy inefficient gaits, the distance traveled in the forward direction is scaled by the inverse of the power input to the system. All solutions are of the form $\theta = A\sin(\omega t + \phi)$, as this has been determined to be the optimal form from a separate analysis [8].

5   Control Model

Having determined optimal signals for the control of zebrafish swimming, given this hydrodynamic model, we now need to relate these signals to the underlying neurophysiology. To do this, we describe the zebrafish in a horizontal plane as a set of finite length rods (vertebrae) connected by muscles whose tensions result in the desired swimming motion. This results in the following expression for the tensions as a function of time, frequency, ω, and lengthwise position, z:

$$T(z,t) \quad = \quad \kappa\left[\sin(\omega t - kz) - \sin(\omega t)\right]$$

where $k = \frac{2\pi}{L}$ and κ is a constant whose value is determined by k, the wave amplitude, a viscosity coefficient, and the ratio of vertebrae height and length.

This function can be expressed in a Fourier basis as:

$$T(z,t;\mathbf{x}) \quad = \quad \kappa\left(\sum_{n=1}^{N} x_{2n}(t)\cos(2\pi nz) + x_{2n+1}(t)\sin(2\pi nz)\right)$$

3

where $x_0(t) = -\cos(\omega t)$, $x_1(t) = -\sin(\omega t)$, and $x_2 = \cos(\omega t)$. The dynamics of these coefficients form a simple oscillator, and thus are of the appropriate form for implementing the optimal control signals determined in the previous section. These dynamics can be represented using the dynamics state equation from standard control theory,

$$\frac{d\mathbf{x}}{dt} = \mathbf{A}\mathbf{x}(t) + \mathbf{B}\mathbf{u}(t), \tag{1}$$

where $\mathbf{x}$ are the amplitudes of the coefficients in the orthonormal space, $\mathbf{A}$ is the oscillator dynamics matrix, and $\mathbf{B}$ is the input matrix which controls the start up behavior of the model. Following Eliasmith and Anderson's model of the lamprey eel, the dynamics matrix, $\mathbf{A}$, can be decomposed into a dampening term to remove unwanted, higher frequency distortions, $\mathbf{A}_{damp}$, and a steady state oscillator matrix, $\mathbf{A}_{osc}$ [3]. We then define an escape signal, $E(t)$, as either ± 1 for left or right stimulation (resulting in an escape in the opposite direction), and 0 during normal swimming. The matrices in (1) can then be given as:

$$\mathbf{A}_{damp} = \begin{bmatrix} -\alpha & 0 & -\alpha \\ 0 & 0 & 0 \\ -\alpha & 0 & -\alpha \end{bmatrix}$$

$$\mathbf{A}_{osc} = \begin{bmatrix} 0 & \omega(1-E) & 0 \\ -\frac{1}{2}\omega(1-E) & 0 & \frac{1}{2}\omega(1-E) \\ 0 & -\omega(1-E) & 0 \end{bmatrix}$$

$$\mathbf{B} = \begin{bmatrix} \frac{1}{2} & -\upsilon E(x_1-1) & -\frac{1}{2} \\ 0 & 1 & -\upsilon E x_2 \\ -\frac{1}{2} & \upsilon E(x_3+1) & \frac{1}{2} \end{bmatrix}.$$

These matrices define a nonlinear control structure relying on a damping term, α, a response speed, υ, the escape signal, E, and the swimming speed, $\omega = \omega_{swim} + \omega_{escape}e^{-(t-t_E)/\tau_E}$. The escape and swimming frequencies are determined by the genetic algorithm optimization, $\tau_E = .6$ (for 1s of escape), and t_E is the time of the stimulus. The input signal, $u(t)$, is a scalar defined by the superposition of the escape signal and a startup signal that initializes steady state swimming.

Simulation of the model results in the expected behaviors. The zebrafish swims in steady state with a traveling wave whose temporal frequency is controlled by ω. The high frequency harmonics are damped out and the wave's amplitude increases exponentially to the desired value at startup as controlled by $u(t)$. When the escape signal is active, normal swimming motion is interrupted, so the amplitudes of $\mathbf{A}_{osc}$ decrease to zero. However, the terms of the $\mathbf{B}$ matrix become active during an escape and elicit a C-shaped escape motion. The speed of response to the stimulation invoking the escape response is determined by υ. After the escape motion, the frequency, ω, takes on the optimal value for escape for approximately 1s, and then normal swimming resumes.

4

6 Implementation

In order to investigate the interactions between the escape and swimming interneurons, a biologically plausible neural network with two distinct populations of neurons can be constructed that displays both escape and swimming. Given the previous high-level characterization of the system dynamics and behavior, a neurologically plausible representation can be constructed using the methods described in Eliasmith and Anderson [3].

As a result, we define the encoding and decoding of the coefficients, $\mathbf{x}$, being represented in the neural population to be of the form:

$$
\begin{aligned}
\sum_n \delta_i(t - t_n) &= G_i\left[\alpha_i \left\langle \tilde{\boldsymbol{\phi}}_i \left(h_i(t) * [\mathbf{A}'\mathbf{x}(t) + \mathbf{B}'\mathbf{u}(t)]\right)\right\rangle_m + J_i^{bias}\right] \quad \text{Encoding} \\
\hat{\mathbf{x}}(t) &= \sum_{in} \delta_i(t - t_n) * \boldsymbol{\phi}_i^{\mathbf{x}}(t) \qquad \text{Decoding}
\end{aligned}
$$

where

$$
\begin{aligned}
\mathbf{A}' &= \tau \mathbf{A} + \mathbf{I} \\
\mathbf{B}' &= \tau \mathbf{B}.
\end{aligned}
$$

relates the previous control system to the neural control system. Here, $\boldsymbol{\phi}_i^{\mathbf{x}}(t)$ is the linear population-temporal filter, $\tilde{\phi}_i$ is the encoding vector, G_i is the leaky-integrate and fire nonlinearity, α_i and J^{bias} map the input vector into soma current, τ is the synaptic time constant, and $\delta_i(t - t_n)$ are spikes from neuron i emitted at time, t_n.

In addition, we analogously define a population of neurons that encode the escape signal, E. The resulting network is expected to map well to the previously described physiology. In particular, MCoD cells are elements of the network encoding $\mathbf{x}$, which have similar, dense connections and project contralaterally. CiD (and Mauthner) neurons should share sparse connectivity, longer range projections, and ipsilateral connections with neurons in the population encoding E. In addition, we can examine the resulting connectivity for the interactions between CiD and MCoD cells. This provides testable predictions regarding the interaction between these two classes of neurons.

7 Conclusions

Because steady state swimming does not require constant control, but must be stopped from interfering with quick escape movements, the MCoD cells will be active only during swimming. In contrast, the CiD cells, which carry a control signal indicating the presence of an undesirable stimulus, are active only during the escape movements. The model described here is a fully spiking neural model that naturally includes classes of cells with these properties. Thus, a biologically plausible mechanism for coordinating the switch between these two kinds of behavior is demonstrated by the model.

References

[1] Bernhardt RR, Chitnis AB, Lindamer L, Kuwada JY (1990). Identification of Spinal Neurons in the Embryonic and Larval Zebrafish. J Comp Neurol 326:263-272.

[2] Domenici P, Blake RW (1997). The Kinematics and Performance of Fish Fast-Start Swimming. J Exp Biol 200:1165-1178.

[3] Eliasmith C, Anderson CH, (2003). Neural Engineering: Computation, Representation and Dynamics in Neurobiological Systems. Cambridge, Massachusetts: MIT Press, Inc.

[4] Getting PA, Dekin MS (1985). *Tritonia* Swimming: A Model System for Integration within Rhythmic Motor Systems. In: Model Neural Networks and Behavior (Selverston AI, ed), pp 3-20. New York: Plenum.

[5] Hale ME, Ritter DA, Fetcho JR (2001). A Confocal Study of Spinal Interneurons in Living Larval Zebrafish. J Comp Neurol 437:1-16.

[6] Mason R, Burdick JW (2000). Experiments in Carangiform Robotic Fish Locomotion. Proc. IEEE Int. Conf. on Rob. Aut., pp 428-435.

[7] Morgansen KA, Vela PA, Burdick JW (2002). Trajectory Stabilization for a Planar Carangiform Robot Fish. Proc. IEEE Int. Conf. Rob. Aut.

[8] Morgansen KA, Duindam V, Mason RJ, Burdick JW, Murray RM (2001). Nonlinear Control Methods for Planar Carangiform Robot Fish Locomotion. Proc. IEEE Int. Conf. Rob. Aut.

[9] Ritter DA, Bhatt DH, Fetcho JR (2001). In Vivo Imaging of Zebrafish Reveals Differnces in the Spinal Networks for Escape and Swimming Movements. J Neurosci 21(22):8956-8965.

[10] Soffe SR (1993). Two Distinct Rhythmic Motor Patterns are Driven by Common Premotor and Motor Neurons in a Simple Vertebrate Spinal Cord. J Neurosci 13:4456-4469.

[11] Svoboda KR, Fetcho JR (1996). Interactions between the Neural Networks for Escape and Swimming in Goldfish. J Neurosci 16(2):843-852.