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

P. Dwight Kuo[a], Chris Eliasmith[a,b,*]

[a] *Department of Systems Design Engineering, University of Waterloo, 200 University Ave. W., Waterloo, Ont., Canada N2L 3G1*
[b] *Department of Philosophy, University of Waterloo, 200 University Ave. W., Waterloo, Ont., Canada N2L 3G1*

## Abstract

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 behaviours. 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 behaviours can be controlled by anatomically overlapping networks. More generally, this paper demonstrates a method for constructing spiking networks consistent with both high-level behavioural descriptions and available neural data.
ⓒ 2004 Elsevier B.V. All rights reserved.

*Keywords:* CPG; Zebrafish; Network interaction; Motor co-ordination

## 1. Introduction

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

---

* Corresponding author. Department of Philosophy, University of Waterloo, 200 University Ave. W., Ontario, Canada N2L 3G1.
  *E-mail address:* celiasmith@uwaterloo.ca (C. Eliasmith).

is defined as movement that possesses rhythmic alternating movements of the tail, with bends propagating from the rostral to the caudal end [1].

Two possible means by which both escape and swimming behaviours could be generated by the same network have been suggested. One possibility is that of a unified network [5]. Such a network would use different control signals in order to elicit different motor behaviour from the same network of neurons. The other possibility is that there exist separate classes of spinal interneurons implicated in the different behaviours.

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 [4]. 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 behaviours.

## 2. Larval zebrafish system description

The two classes of interneuron 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 [4]. CiD interneurons are characterized by sparse dendrites and ventrally projecting, ipsilateral axons [4]. CiD interneurons are generally found in the middle and dorsal regions along the dorso-ventral extent of the spinal cord [4].

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 [4].

## 3. Control theoretic model

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. Analysis of this simple model results in the following Fourier decomposition of the tensions as a function of time, frequency, $\omega$, and lengthwise position, $z$:

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

where $k = 2\pi/L$ and $\kappa$ is a constant whose value is determined by $k$, the wave amplitude, a viscosity coefficient, and the ratio of vertebrae height and length, also, $x_0(t) = -\cos(\omega t)$, $x_1(t) = -\sin(\omega t)$, and $x_2 = \cos(\omega t)$. The dynamics of these coefficients form a simple oscillator. These dynamics can be represented using the dynamics state equation from standard control theory,

$$\frac{d\mathbf{x}}{dt} = \mathbf{A}\mathbf{x}(t) + \mathbf{B}\mathbf{u}(t), \tag{2}$$

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 behaviour 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, $\mathbf{A}_{\text{damp}}$, and a steady-state oscillator matrix, $\mathbf{A}_{\text{osc}}$ [2]. We then define an escape signal, $E(t)$, as either $\pm 1$ for left or right stimulation (resulting in an escape in the opposite direction), and 0 during normal swimming. Thus, the matrices describing escape and swimming can be written as

$$\mathbf{A}_{\text{damp}} = \begin{bmatrix} -\alpha & 0 & -\alpha \\ 0 & 0 & 0 \\ -\alpha & 0 & -\alpha \end{bmatrix}, \tag{3}$$

$$\mathbf{A}_{\text{osc}} = \begin{bmatrix} 0 & \omega(1-E) & 0 \\ -\tfrac{1}{2}\omega(1-E) & 0 & \tfrac{1}{2}\omega(1-E) \\ 0 & -\omega(1-E) & 0 \end{bmatrix}, \tag{4}$$

$$\mathbf{B} = \begin{bmatrix} \tfrac{1}{2} & -vE(x_1 - 1) & -\tfrac{1}{2} \\ 0 & 1 & -vEx_2 \\ -\tfrac{1}{2} & vE(x_3 + 1) & \tfrac{1}{2} \end{bmatrix}. \tag{5}$$

When an escape bend occurs, the dynamics matrix goes to zero. This is accomplished by including a nonlinearity in the $\mathbf{A}_{\text{osc}}$ matrix, which is controlled by $E$; i.e., $E$ is 0 for no escape, and 1 for a leftward escape. An additional matrix, $\mathbf{A}_{\text{damp}}$ is added to $\mathbf{A}_{\text{osc}}$ because the representations of $x_0$ and $x_2$ in a neural population cannot be assumed to be perfect. Any error in either of these two components leads to a rapidly increasing error in the now non-zero derivatives of $x_0$ and $x_2$ [2]. The damping in $\mathbf{A}_{\text{damp}}$ counteracts this error.

To control start-up, the constant portion of the input matrix $\mathbf{B}$ is multiplied by a step input $\mathbf{u}(t)$. This causes the model to display exponential start-up behaviour until the desired amplitude is reached. Escape behaviour is incorporated by multiplying the escape signal $E$ by the rate constant $v$, which controls the speed with which the system responds to an escape stimulus. The input signal $\mathbf{u}(t)$ is the superposition of the escape signal and the start-up signal, where it is assumed for simplicity that these signals do not overlap in time.

In sum, the switch between behaviours is described by the model as follows: During regular swimming, the model zebrafish swims in steady state determined by $\mathbf{A}_{\text{osc}}$ with a travelling wave whose temporal frequency is controlled by $\omega$. When the escape signal $E(t)$ is active, the normal swimming motion is interrupted, so the amplitudes of $\mathbf{A}_{\text{osc}}$ are forced to zero. However, the $\mathbf{B}$ matrix become active during an escape and elicits the rapid, characteristic C-shaped escape motion. When the escape signal is removed the amplitudes of $\mathbf{A}_{\text{osc}}$ once again dominate and normal swimming is resumed.

## 4. Neural model

In order to investigate the interactions between the escape and swimming interneurons, a neural model 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 behaviour, a neurologically plausible representation can be constructed using the methods described in Eliasmith and Anderson [2].

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

$$\sum_n \delta_i(t - t_n) = G_i[\alpha_i \langle \tilde{\phi}_i(h_i(t) * [\mathbf{A}'\mathbf{x}(t) + \mathbf{B}'\mathbf{u}(t)]) \rangle_m + J_i^{\text{bias}}] \quad \text{Encoding,}$$

$$\hat{\mathbf{x}}(t) = \sum_{in} \delta_i(t - t_n) * \phi_i^{\mathbf{x}}(t) \quad \text{Decoding,} \tag{6}$$

where

$$\mathbf{A}' = \tau \mathbf{A} + \mathbf{I},$$

$$\mathbf{B}' = \tau \mathbf{B}, \tag{7}$$

relates the previous control system to the neural control system. Here, $\phi_i^{\mathbf{x}}(t)$ is the linear population-temporal filter, $\tilde{\phi}_i$ is the encoding vector, $G_i$ is the leaky integrate and fire nonlinearity, $\alpha_i$ and $J^{\text{bias}}$ map the input vector into soma current, $\tau$ is the synaptic time constant, and $\delta_i(t - t_n)$ are spikes from neurons $i$ emitted at time $t_n$. In addition, we analogously define a 'control population' of neurons that encode the escape signal $E$, the frequency $\omega$ and the start-up signal $u$.

We now introduce an intermediate level model between the high-level description previously presented and the neural model. Such an intermediate level serves two purposes: The first is to better match the physiology of the larval zebrafish. The larval zebrafish is composed of 30 segments that have individual local tensions which can then be simulated individually and/or at the neuron level. The second reason is to allow reductions in computational complexity. Simulating all segments at the level of single spiking neurons can be computationally expensive.

We represent the local tensions using Gaussian encoding functions along the length of the fish

$$T(z,t) = \kappa \left( \sum_{n=1}^{N} a_m(t) \mathrm{e}^{(-(z - m*\mathrm{d}z))^2} \right), \tag{8}$$

where $a_m(t)$ is the amplitude of the $m$th Gaussian segment centred at the point $zm = m * \mathrm{d}z$. Note that the nonlinear computations necessary to implement this control structure are computed in a network of 1200 LIF neurons presumed to reside in the fish's brainstem. This is the control population that provides signals for frequency, escape, and start-up behaviours.

From Fig. 1, it can be seen that the MCoD interneurons which encode $\mathbf{x}$ have dense local connectivity. This correlates well with the known neural data indicating that MCoD cells have elaborate dendritic arbors [4].
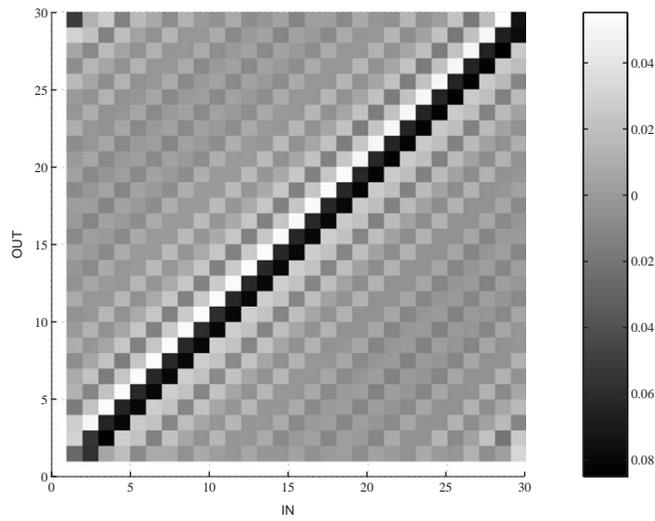
Fig. 1. Connectivity between segments representing MCoD interneurons. The dense interconnections map well to known physiology.
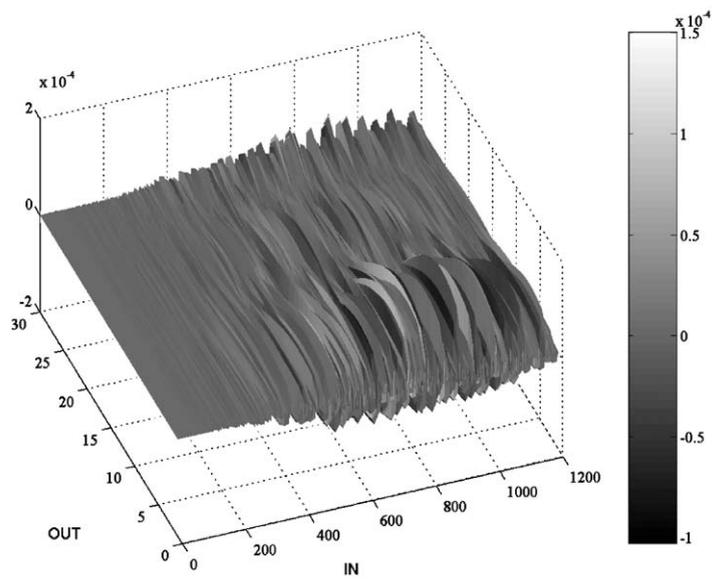


Fig. 2. Connectivity between the control population and segments representing CiD interneurons. The long-range projections map well to known physiology.

Fig. 2 shows the connectivity between the 1200 neurons of the control population and the 30 segments of the model. It can be seen that the connection weights are fairly sparse and have longer range projections along the 30 segment lengths of the larval zebrafish model. This correlates well with the neurophysiology since the axons of CiD cells are known to extend to up to 13 segments along the length of the zebrafish [4].

Simulation of this neural control structure in a hydrodynamical model based on one created by Mason et al. [3] leads to the correct swimming motions (results not shown).

## 5. Conclusions

The resulting network both maps well to the previously described physiology and produces a switch between swimming and escape behaviours as desired. In particular, MCoD cells are elements of the network encoding $\mathbf{x}$, which have similar, dense connections and project contralaterally. CiD neurons share sparse connectivity, and longer range projections with neurons in the population encoding $E$. In addition, the resulting connectivity for the interactions between the CiD and MCoD cells provide testable predictions regarding the interaction between these two classes of neurons. Thus, a biologically plausible mechanism for coordinating the switch between these two kinds of behaviour is demonstrated by the model.

### Acknowledgements

### References

[1] S.A. Budick, D.M. O'Malley, Locomotor repertoire of the larval zebrafish: swimming, turning and prey capture, J. Exp. Biol. 203 (2000) 2565–2579.

[2] C. Eliasmith, C.H. Anderson, Neural Engineering: Computation, Representation and Dynamics in Neurobiological Systems, MIT Press, Cambridge, MA, 2003.

[3] R.J. Mason, J.W. Burdick, Experiments in carangiform robotic fish locomotion, Proceedings of the IEEE International Confernce on Robotics and Automation, San Francisco, 2000, pp. 428–435.

[4] D.A. Ritter, D.H. Bhatt, J.R. Fetcho, In vivo imaging of zebrafish reveals differences in the spinal networks for escape and swimming movements, J. Neurosci. 21 (22) (2001) 8956–8965.

[5] S.R. Soffe, Two distinct rhythmic motor patterns are driven by common premotor and motor neurons in a simple vertebrate spinal cord, J. Neurosci. 13 (1993) 4456–4469.

**P. Dwight Kuo** studied Systems Design Engineering at the University of Waterloo while performing the research work presented in this paper. He is continuing graduate studies in Computational Biology under the supervision of Wolfgang Banzhaf at Memorial University of Newfoundland.

**Chris Eliasmith** heads the Computational Neuroscience Research Group at the University of Waterloo. His primary focus is on constructing a general method for simulating large-scale neural systems, and better understanding neural representation.