Computational understanding of the neural circuit for the central pattern generator for locomotion and its control in lamprey

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The neural circuits for rhythmic locomotion in lamprey, shown in Fig. (1), has been a model system for computational studies of central pattern generators (CPGs). It has about 100 interacting and roughly translation invariant segments along the body, each has 2x3 neuron populations (E, L, C neurons) placed in left-right symmetry. The locomotion (swimming) is characterized by left-right neural and motor oscillations with a head-to-tail decreasing phase gradient of about 1% of an oscillation cycle per segment. While decapitated lampreys can generate spontaneous locomotion, central inputs from brain stem to the CPG control and select behavior. Previous analytical work [2] treated the CPG as a chain of weakly coupled phase oscillators each with a single phase variable modeling the behavior of an entire segment. This approach has generated very interesting results, but obscured the roles of individual cell types, and could not elucidate how behavior can be generated and controlled by central inputs to specific cell types and specific couplings between these cells. The CPG has also been simulated extensively with much greater details of neural properties [1].

To seek insights not apparent in previous studies, we mathematically analyse the neural circuit in Fig. (1) and provide understanding of (1) how coupling between damped oscillators enable spontaneous network oscillations, (2) how swimming behavior characterised by certain phase relationships (and also amplitude relationships) between neural oscillators can be achieved by the neural connections, and, very importantly, (3) how to control and select different behavior regimes, such as forward swimming, backward swimming, and turning, by controlling the central inputs to, and neural connection strengths in, the CPG.

Briefly, using firing rate models of neurons, the system is modelled by differential equations that included neural connections and external inputs from the brain stem as model parameters. Using left-right symmetry in the system, our analysis identified an excited left-right anti-phase oscillation mode which dominates a damped left-right synchronous mode as is required for locomotion. This yielded the insights that the inhibitory, contra-laterally projecting, C neurons are effectively "excitatory" in the left-right anti-phase mode, and thus play a crucial role in generating oscillatory locomotion, as observed physiologically. Our mathematical formulation enabled us to use experimental data to reveal non-trivial constraints in the neural coupling structures, such that we can approximate the system as a chain of coupled neural oscillators, each made of two interacting groups of neurons. In contrast to previous works, our analysis explicitly links activities and properties of, and couplings between, the neural oscillators with the corresponding neural activities, specific connections between various cell types, and the controlling inputs from the brain stem. For instance, we identified that the contra-lateral coupling between the C neurons should be stronger than the self-excitatory coupling between the E neurons (Fig. 1), the inhibitory coupling from L to C neurons should dominate the excitatory coupling from E to C neurons. Furthermore, we identify that forward or backward swimming is selected by the balance between the degrees of the rostral-caudal asymmetries in the connections between various and specific cell types, and can be controlled by inputs from the brain stem. The analysis also shows that the turning in swimming can be achieved by additional central input to one side of the CPG only. Fig. (2) demonstrates the model simulation results.

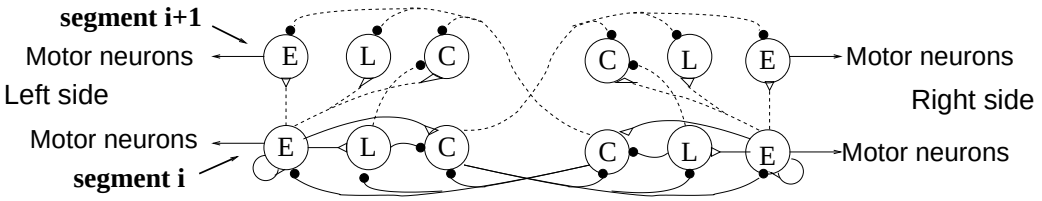

Figure 1: The CPG neural circuit. Shown are intra-segment connections (solid lines) and inter-segment connections (dashed lines). E neurons: excitatory. C and L neurons: inhibitory. Although the neural connections are left-right symmetric, left-right anti-phase oscillations in this circuit induce swimming via E neuron outputs to the motor neurons.

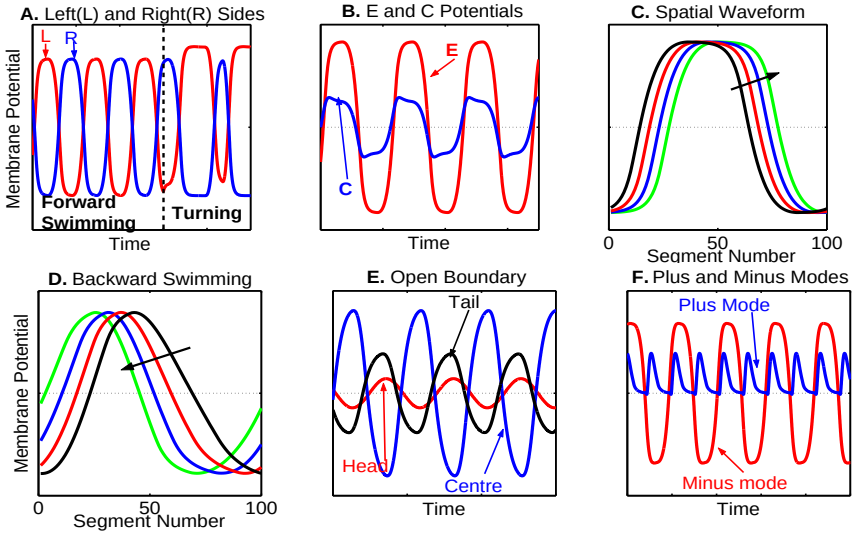

Figure 2: Simulations (best viewed in color). A: Membrane potentials of **E** population on left and right sides of one segment, in anti-phase, during forward swimming and turning. Turning is induced by an additional constant input to one side, switched on at the time indicated by the dashed line. B: Potentials of **C** and **E** during forward swimming. **C** leads **E** slightly. **L** (not shown) is in phase with **E**. C & D: Spatial waveforms of **E** potential along the body in forward and backward swimming, in the translational invariant lamprey model. The waveforms are shown at consecutive times increasing in the direction indicated by the arrows. The switch from forward to backward swimming is achieved by increasing the strength of neural connections from the **L** and **E** cells to **C** cells, and resetting the central inputs. E: Oscillation waveforms (note different amplitudes) in body segments at head, tail and centre of the body, without making the approximation of translational invariance. F: The left-right anti-phase mode (the plus mode) dominates the left-right synchrony mode (the minus mode) in normal swimming. The plus mode, shown here magnified by a factor of 10 for clarity, is intrinsically damped and driven by the minus mode via nonlinearity in the system, and oscillates in the second harmonic of the minus mode.

References

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