Supporting Information

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Integrated Model for Leech Swimming

The integrated model developed and used in this article is summarized below. All of the model parameter values and their definitions are summarized in Table S1.

Central Pattern Generator. The central pattern generator (CPG) model used in this study is a modified version of the one reported in ref. 1:

$$v_i = M\ F(s)\varphi(v_i) + by_i + \sum_{j=1}^{z} \epsilon D e^{-j\tau_d s}\varphi(v_{i-j}) + \sum_{j=1}^{z} \epsilon A e^{-j\tau_d s}\varphi(v_{i+j})$$

for $i = 1, \ldots, k$, where s is the Laplace variable (or the time derivative operator), $k = 17$ is the number of segmental ganglia (M2–M18 that are active during swimming), $z = 5$ is the intersegmental coupling span, $v_i(t) \in \mathbb{R}^3$ is the membrane potential vector for the i^{th} segment (define $v_i = 0$ for $i < 1$ and $i > k$ for notational convenience), $y_i(t) \in \mathbb{R}$ is the sensory feedback input (proportional to muscle tension), and

$$F(s) := \frac{\mu_\gamma}{1 + \tau_\gamma s}, \varphi(v_i) := \sigma \tanh(v_i/\sigma), \mu_\gamma := (1-\gamma)\mu, \tau_\gamma := (1-\gamma)\tau,$$

$$M = \begin{bmatrix} 0 & -1 & 0 \\ 0 & 0 & -1 \\ -1 & 0 & 0 \end{bmatrix}, D = \begin{bmatrix} 2 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix},$$
$$A = \begin{bmatrix} 0 & -1 & 0 \\ 0 & 0 & -1 \\ 0 & 0 & 0 \end{bmatrix}, b = \begin{bmatrix} 0 \\ 0 \\ 1 \end{bmatrix}.$$

The parameter γ is the excitatory input level from the gating neurons and was set equal to −0.4 for fictive swimming, 0.1 for the high-viscosity case, or 0.4 otherwise. Negative values of γ indicate that the excitation level is lower and the synaptic time constant τ_γ is larger than the nominal values.

Motoneuron. The motoneuron (MN) impulse frequency f_i of the i^{th} segment is determined by the membrane potential of the 0°-phase neuron $\chi_i(t)$, which is the first entry of the vector $v_i(t) \in \mathbb{R}^3$. The impulse adaptation dynamics are modeled as (2)

$$f_i = H(s)\chi_i, H(s) = \alpha_o\left(1 - \frac{\beta_o}{1 + \tau_o s}\right).$$

The supralinear summation effects of three MNs identified in leeches are modeled by $\tilde{f}_i = \delta f_i$ with $\delta = 3 \times 1.5 = 4.5$, which is used as the muscle activation input.

Muscle. The tension on the dorsal side of the i^{th} segment of the leech body is modeled as (3)

$$T_{d_i} = \kappa(x_{d_i})\left(P(s)f_{d_i} + 1\right) + c\dot{x}_{d_i}, \kappa(x_{d_i}) := \mu_m e^{x_{d_i}/\eta}, P(s) := \frac{\alpha\ e^{-s\tau_a}}{1 + \tau_c s},$$

where x_{d_i} is the strain, T_{d_i} is the tension, and f_{d_i} is the MN impulse frequency. An identical relationship holds for the strain, tension and MN impulse frequency on the ventral side. We assume symmetry during swimming

$$f_{d_i}(t) = f_b + \tilde{f}_i(t), \quad x_{d_i}(t) = x_i(t),$$
$$f_{v_i}(t) = f_b - \tilde{f}_i(t), \quad x_{v_i}(t) = -x_i(t)$$

for the dorsal and ventral sides, where the signs of $\tilde{f}_i(t)$ are set so that an increase in the model MN frequency increases (respective to decreases) the stiffness of dorsal (respective to ventral) muscles, based on the experimentally identified excitatory/inhibitory MN connections (4). Then we have the muscle bending moment $u_i(t)$ given by

$$u_i = r(T_{v_i} - T_{d_i}) = -r\mu_m a(x_i)P(s)\tilde{f}_i - r\mu_m d(x_i)(1 + \alpha f_b) - 2rc\dot{x}_i,$$
$$a(x_i) := e^{x_i/\eta} + e^{-x_i/\eta}, d(x_i) := e^{x_i/\eta} - e^{-x_i/\eta}.$$

The nonlinear strain functions are approximated by $a(x_i) \cong 5.7$ and $d(x_i) \cong 106.8x_i$ in the range $|x_i| \le 0.08$ of normal swimming.

Body. The leech body is modeled by a chain of $n = 18$ identical links, as shown in Fig. 2C. Each of the $k = 17$ joints is considered as a segment and is actuated by the segmental CPG oscillator through the muscle bending moment u_i. The strain x_i is related to the joint angle ϕ_i by $x_i = (r/(\ell/n))\phi_i$. The equations of motion for the link chain subject to fluid forces have been derived from the first principle of mechanics (5, 6):

$$J(\theta)\ddot{\theta} + G(\theta)\dot{\theta}^2 = Bu + \tau + L(\theta)^{\mathsf{T}}\hbar, \quad m\ddot{w} = E^{\mathsf{T}}\hbar,$$

where $\hbar(t) \in \mathbb{R}^{2n}$ and $\tau(t) \in \mathbb{R}^n$ are the fluid force and torque acting on the links, respectively, $u(t) \in \mathbb{R}^k$ is the muscle bending moment on the joints, $\theta(t) \in \mathbb{R}^k$ is the link angles with respect to the inertial frame, and $w(t) \in \mathbb{R}^2$ is the position of the center of gravity in the plane of undulation. The first equation describes how the body shape and orientation change in response to the muscle bending moment under the influence of the fluid force. The second equation shows how the shape change influences the swim velocity.

Fluid. The leech body is assumed to be neutrally buoyant. Taylor's resistive force model is used for the hydrodynamic effects (5):

$$\hbar = \begin{bmatrix} \hbar_x \\ \hbar_y \end{bmatrix}, \begin{bmatrix} \hbar_{x_i} \\ \hbar_{y_i} \end{bmatrix} = \begin{bmatrix} \cos\theta_i & -\sin\theta_i \\ \sin\theta_i & \cos\theta_i \end{bmatrix} \begin{bmatrix} \hbar_{t_i} \\ \hbar_{n_i} \end{bmatrix},$$
$$\hbar_{t_i} = -2.7c_t(\ell/n)\sqrt{\rho\mu d|v_{n_i}|}v_{t_i},$$
$$\hbar_{n_i} = -c_p\rho d\ell/(2n)|v_{n_i}|v_{n_i},$$
$$\tau_i = -(2/3)c_p\rho d(\ell/(2n))^3|v_{n_i}|\dot{\theta}_i,$$

where $\hbar_{t_i}$ and $\hbar_{n_i}$ are the tangential and normal components of the fluid force vector acting on the i^{th} link, v_{t_i} and v_{n_i} are the tangential and normal components of the velocity vector of the center of gravity of the i^{th} link, and $\hbar_x, \hbar_y \in \mathbb{R}^n$ are the vectors of horizontal and vertical fluid forces $\hbar_{x_i}, \hbar_{y_i}$.

Stretch Receptor. The stretch receptor measures the muscle tension and feeds this information back to the 240° phase group in the CPG with a negative gain (7). The sensory feedback signal at each segment is modeled by the negative of the muscle bending moment, scaled by an appropriate gain: $y_i = -\varsigma_i u_i$. The values of the sensory gains ς_i was tuned through iterative simulations to reproduce intact swimming behavior in water. In particular, the magnitudes of the sensory signals y_i were estimated from the harmonic balance analysis so that the 180° phase lag in the inputs y_i results in 360° phase lag in the outputs v_i along the CPG chain. The magnitudes of the bending moments u_i during intact swimming were estimated from the body–fluid and muscle models using recorded kinematic motion data. The ratio of the estimated magnitudes of y_i and u_i gives an initial guess for the sensory gain ς_i, which was then iteratively refined through simulations of the integrated model.

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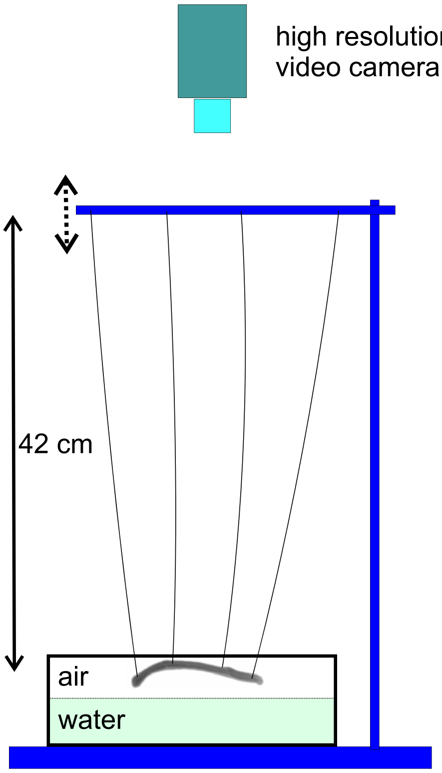

Fig. S1. Experimental setup of air swimming. The leech is suspended on edge by four threads so that its flattened body nominally lies within a vertical plane. The height of the thread support is adjustable and the leech body can be raised out of water while swimming.

Table S1. Nominal parameter values of the integrated model for leech swimming

Parameter	Nominal value	Description
k	17	No. of segments in the CPG
σ	20/3	Scaling factor for threshold nonlinearity in synaptic connections
ς_i	See legend	Sensory feedback gain from u_i (tension) to y_i (input to the CPG)
τ	200 ms	Intrasegmental synaptic time constant
μ	6	Intrasegmental coupling strength
ϵ	0.06	Intersegmental coupling strength
τ_d	15 ms	Intersegmental time delay per segment
γ	0.4	Excitatory gating neuron input to the CPG
z	5	Intersegmental coupling span
τ_o	88 ms	MN adaptation time constant
α_o	6.09 Hz/mV	MN gain from membrane potential to impulse frequency
β_o	0.49	Degree of MN adaptation
δ	4.5	Gain factor for supralinear summation of three MNs
f_b	60 Hz	Bias in MN impulse frequency after supralinear summation
τ_a	130 ms	Time delay in muscle activation
τ_c	230 ms	Time lag in muscle activation
μ_m	0.27 g	Tonus tension at swim length
η	1/29	Strain constant in tonus tension
α	1/45 Hz^{-1}	Static gain from MN impulse frequency to activation
c	1 mN· s	Muscle damping coefficient
ρ	1,000 kg/m^3	Water density
μ	0.001 kg/(m·s)	Water viscosity
c_t	0.6	Fluid tangential drag coefficient
c_p	3.0	Fluid normal drag coefficient
n	18	No. of links used to represent the leech body
m	1 g	Leech body mass
ℓ	100 mm	Leech body length
d	10 mm	Leech body width
r	10/6 mm	Half of leech body thickness

$(\varsigma_1,\ldots,\varsigma_{17}) = (9.500, 2.744, 1.013, 0.422, 0.253, 0.162, 0.108, 0.094, 0.086, 0.105, 0.086, 0.091, 0.127, 0.153, 0.374, 0.774, 2.533)$ mV/(mN·mm).