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Modeling control of roll-plane body orientation in lamprey

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Abstract

A phenomenological model of the mechanism of stabilization of the dorsal-side-up orientation in the lamprey is suggested. Mathematical modeling is based on the experimental results on investigation of postural control in lampreys using combined in vivo and robotics approaches. Dynamics of the model agrees qualitatively with the experiment. It is shown by computer simulations that postural correction commands from one or several reticulospinal neurons provide information which may be sufficient for stabilization of body orientation in the lamprey. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The basic neural mechanisms for postural control in the lamprey are located in the brain stem and in the spinal cord. Postural corrective reflexes in the lamprey are driven by vestibular input. In contrast to vestibular input, visual input exerts only a modulatory effect on the postural orientation — it elicits a lateral tilt towards the

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more illuminated eye (dorsal light response) [2–4,11,12]. The brain stem mechanisms process and integrate vestibular and visual signals, and send commands to the spinal cord via the reticulospinal (RS), vestibulospinal, or propriospinal pathways [2–4]. Of these, the RS pathways have been suggested to be the more important [1,5–7]. Under the effect of these commands the spinal mechanisms generate corrective motor responses. Such responses may include as an essential part a lateral flexion of the ventrally deviated tail which generates a torque rotating the lamprey around its longitudinal axis in a direction opposite to the initial tilt (see Figs. 1a–c).

In the present paper we show by means of mathematical modeling that RS neurons can provide sufficient information for maintaining stable dorsal-side-up body orientation in the lamprey by lateral movements of its tail.

2. Methods

A phenomenological description of the response of RS neurons to rotation of the lampreys body suggested in the paper follows the basic experimental observations presented in [1,8–13]. The simplest approximation that qualitatively represents the experimental data is constructed. The function describing RS response is incorporated into the model of rotation of the lampreys body in viscous water as a nonlinear feedback controlling lateral movements of the tail. The model obtained allows to study the role of different components of RS response in control of posture.

3. Results and discussion

Lateral muscle force applied to the tail is determined basically by the difference between activities of RS neurons from left and right sides of the spinal cord. In our model we will call response of RS neurons, or function F_{RS}, the difference of firing rates in Hz of left and right RS neurons. There are two components, *dynamic* and *static*, in RS response. Dependence of RS neurons activity on velocity of body rotation constitutes dynamic component of response, and dependence on fixed tilt angle corresponds to the static one. The static component of RS response is almost 2π-periodic with extrema at tilt angles close to $\pm 90^\circ$ [8–10]. We consider the RS response function in the following form:

$$F_{\mathrm{RS}}(\varphi, \omega) = \beta(\gamma + \sin\varphi) + \alpha\omega, \tag{1}$$

where the first and the second terms are static and dynamic components, respectively, with coefficients $\alpha > 0$ and $\beta > 0$, φ is the tilt angle and ω is the angular velocity. The parameter γ represents constant bias from the visual input.

We consider only three main forces determining rotation of the body, the muscle force and the viscous friction forces applied to body and tail, assuming other forces to be negligibly small. The geometry of the acting torques is illustrated in Fig. 1f.

The displacement of the tail, x, is taken to be relatively small. Rotation of the body is determined by the moment equation: $I\dot{\boldsymbol{\omega}} = \boldsymbol{M}_\omega + \boldsymbol{M}_v$, where I is the moment of

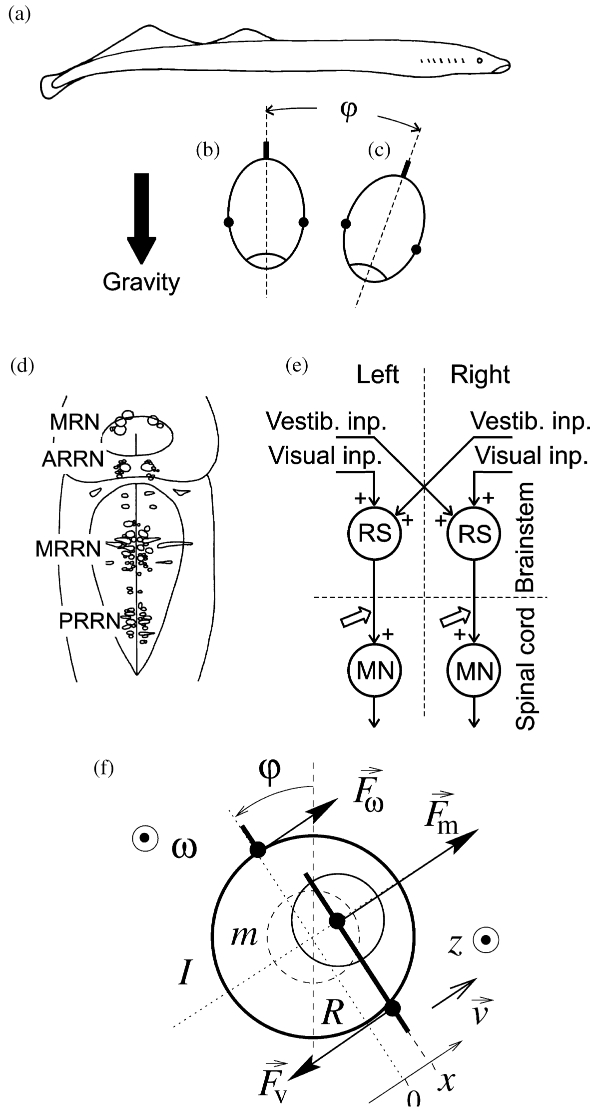

Fig. 1. Control of posture in the lamprey and principal elements of the postural network. (a), (b) Normal orientation of the lamprey (side and front views). (c) A deviation from this orientation (roll tilt, φ) evokes a set of corrective motor responses aimed at restoration of the normal orientation. (d) Four reticular nuclei of the brain stem: MRN is the mesencephalic reticular nucleus; ARRN, MRRN, and PRRN are the anterior, middle, and posterior rhombencephalic reticular nuclei. (e) Main inputs and outputs of the reticulospinal (RS) neurons. The RS neurons receive ipsilateral excitatory visual input and contralateral excitatory vestibular input; they exert an excitatory action on the ipsilateral motoneurons in the spinal cord. White arrows indicate the sites of recording of RS activity. (f) Geometry of forces applied to body and tail (front view), see explanations in the text.

inertia of the body, $\boldsymbol{\omega}$ is the vector of angular velocity (dot in the equation means first time derivative), and $\boldsymbol{M}_\omega$ and $\boldsymbol{M}_v$ are the torques caused by water viscous friction forces acting on the body (on the dorsal fin) and on the tail. In order of magnitude we have $|\boldsymbol{M}_\omega| = RF_\omega = R \cdot n_1 R\omega$, $|\boldsymbol{M}_v| = RF_v = R \cdot n_2(v + R\omega)$, where $\omega = \dot{\varphi}$; n_1 and n_2 are the friction coefficients of the body and the tail and R is the effective radius at which the forces are applied, which we set equal to the radius of the body, and $v + R\omega$

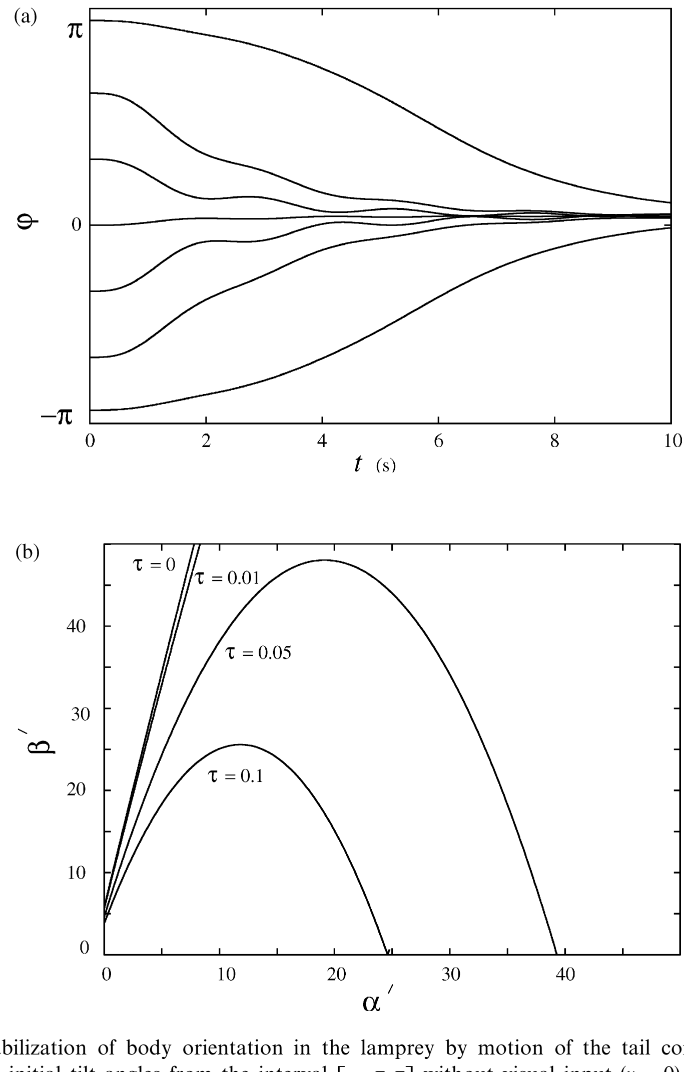

Fig. 2. (a) Stabilization of body orientation in the lamprey by motion of the tail controlled by RS commands for initial tilt angles from the interval $[-\pi, \pi]$ without visual input ($\gamma = 0$). (b) Regions of stability of dorsal-side-up body orientation according to model (2) for different values of inertial time constant. Equilibrium is stable below parabolic curves.

is the absolute velocity of the tail in water. Lateral motion of the tail of mass m obeys the equation $m\dot{\boldsymbol{v}} = \boldsymbol{F}_m + \boldsymbol{F}_v$. The muscle force $\boldsymbol{F}_m$ applied to the tail is controlled by neurons in the spinal cord whose activity in turn depends on RS commands. Response of RS neurons to roll of the body is modeled by (1). Relation between RS commands and muscle contraction is modeled by equations $F_m = gy$, $\mathrm{d}y/\mathrm{d}t = (F_{\mathrm{RS}} - y)/T$, where y is the difference of spiking rates of left and right motoneurons in the part of spinal cord responsible for the tail movements, T is inertial time constant, and g is dimension coefficient. Dynamics of the whole system is determined by the following equations:

$$\begin{aligned} &\dot{\varphi} = \omega, \quad m\dot{v} = gy - n_2(v + R\omega), \\ &\mathrm{I}\dot{\omega} = -n_1 R^2\omega - n_2 R(v + R\omega), \quad \dot{y} = (\beta(\gamma + \sin\varphi) + \alpha\omega - y)/T. \end{aligned} \tag{2}$$

For small species of lamprey, length $L = 0.10$ m, physical parameters have the following approximate values: $I = 2\times 10^{-7}$ $(\mathrm{kg}\cdot\mathrm{m}^2)$, $R = 0.005$ (m), $m = 0.0005$ (kg), $g = 3\times 10^{-6}$ $(\mathrm{N}\cdot\mathrm{S})$, $n_2 = 0.0005$ (N s/m), $n_1 = 4n_2$, $T = 0.050$ (s).

System (2) has two equilibrium states, O_1 and O_2, with angular coordinates $\varphi_0^{(1)} = \arcsin\gamma$ and $\varphi_0^{(2)} = \pi - \arcsin\gamma$, respectively. Equilibrium O_1 corresponds to dorsal-side-up body orientation. Transitions to this equilibrium from different initial tilt angles for $\alpha = 100$ and $\beta = 50$ are shown in Fig. 2a. Regions of stability of equilibrium O_1 are shown in Fig. 2b, where $\beta' = \beta g/g_0$, $\alpha' = \alpha g/(g_0 t_0)$, $\tau = T/t_0$. As characteristic time we have taken $t_0 = I/(n_2 R^2)$, the decay time, due to friction of the tail, of angular rotation. A characteristic scale of the conversion factor g from the spinal network activation to muscle force, $g_0 = n_2 R/t_0$, is the characteristic friction force exerted with the rotation decay. Note that the region of stability is limited and it becomes smaller for larger inertia of activation of spinal mechanisms.

Mathematical modeling performed provides new evidences to the following statements: (i) signals transmitted from the brain stem to the spinal cord via reticulospinal (RS) pathways are sufficient for the control of body orientation in the transverse (roll) plane; (ii) both static and dynamic components in response of RS neurons to roll of the body are important for maintaining equilibrium; stability of equilibrium state depends on relative contribution of static and dynamic components in RS response; (iii) posture control mechanism is potentially unstable and supposedly operates in a stable mode for subcritical values of parameters near the boundary of its stability.

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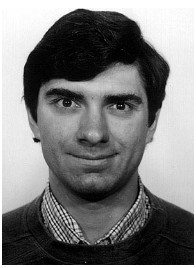

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Biosketch and picture for **J. Hellgren Kotaleski** and **S. Grillner** is included with the contribution titled "Modeling of plasticity of the synaptic connections in the lamprey spinal CPG — consequences for network behavior" by A. K. Kozlov et al., corresponding author J. Hellgren Kotaleski.