

Modeling postural control in the lamprey

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Abstract. A phenomenological model of the mechanism of stabilization of the body orientation during locomotion (dorsal side up) in the lamprey is presented. The mathematical modeling is based on experimental results obtained during investigations of postural control in lampreys using a combined in vivo and robotics approach. The dynamics of the model agree qualitatively with the experimental data. It is shown by computer simulations that postural correction commands from reticulospinal neurons provide information sufficient to stabilize body orientation in the lamprey. The model is based on differences between the effects exerted by the vestibular apparatus on the left and the right side.

1 Introduction

As in most animals, the lamprey (a lower vertebrate, *cyclostome*) stabilizes the dorsal-side-up orientation of the body during locomotion (Fig. 1a,b) by the action of a postural control system. Any deviation from this orientation (roll tilt φ , Fig. 1c) evokes a corrective motor response to restore the initial orientation. This response may include a lateral flexion of the ventrally deviated tail, a lateral deviation of the dorsal fin, and a body twisting (Ullén et al. 1995a). These movements all generate a torque that rotates the lamprey around its longitudinal axis in a direction opposite to the initial tilt.

Postural corrective reflexes in the lamprey are driven by vestibular input. After a unilateral or bilateral labyrinthectomy, the lamprey is not able to maintain a particular orientation in space (Ullén et al. 1995a; Deliagina 1997). In contrast to vestibular inputs, visual inputs exert only a modulatory effect on the postural orientation and elicits a dorsal light response, i.e., a

lateral tilt towards the more illuminated eye (von Holst 1935; Ullén et al. 1995b).

The basic neural mechanisms for postural control in the lamprey are located in the brainstem and in the spinal cord. The brainstem mechanisms process and integrate central, vestibular and visual signals, and send commands to the spinal cord. Under the effect of these commands the spinal mechanisms generate corrective motor responses. Commands for postural corrections can be transmitted via reticulospinal (RS), vestibulospinal, and propriospinal pathways (Rovainen 1979; Rouse and McClellan 1997); of these the RS pathways appear to be the more important (Deliagina et al. 1993). The two bilaterally symmetrical RS pathways originate from neurons in the four reticular nuclei of the brainstem (Fig. 1d), and reach even the most caudal segments (Rovainen 1979; Ohta and Grillner 1989; Bussi eres 1994; Nieuwenhuys et al. 1998). As shown in experiments on the isolated brainstem with intact vestibular organs and eyes, RS neurons receive an excitatory input from the contralateral labyrinth (Fig. 1e), and become activated with contralateral roll tilt (Deliagina et al. 1992a,b; Orlovsky et al. 1992). They also receive visual input (Fig. 1e) and become activated during illumination of the ipsilateral eye (Deliagina et al. 1993). Similar results have been recently obtained on intact lampreys (Deliagina and Fagerstedt 2000). The two antagonistic groups of RS neurons (left and right) exert a predominantly excitatory effect on ipsilateral interneurons and motoneurons (Ohta and Grillner 1989); see Fig. 1e. These pathways presumably provide the basis for generating postural corrections (Deliagina et al. 1993; Ull en et al. 1995a).

The validity of the hypothesis that postural stabilization is based on two antagonistic vestibular reflexes mediated by RS pathways has been tested in model experiments (Zelenin et al. 1998). In these experiments, the lamprey was mounted on a platform, which restrained its postural activity but allowed lateral locomotor undulations to occur. Illumination of the eyes was provided by a fiber optic system and was kept constant. The relative illumination of the left and right eye did there-

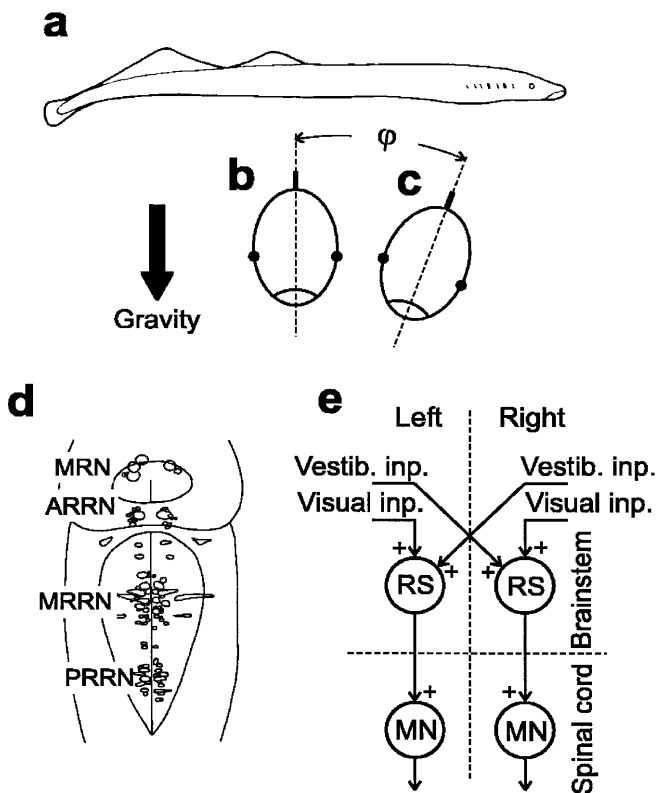


Fig. 1a-e. Postural orientation in the lamprey and principal elements of the postural network. **a,b** Normal orientation of the lamprey (side and front views); **c** A deviation from this orientation (roll tilt, ϕ) evokes a set of corrective motor responses aimed at restoration of the normal orientation; **d** Four reticular nuclei of the brainstem. MRN is the mesencephalic reticular nucleus, and ARRN, MRRN, and PRRN are the anterior, middle, and posterior rhombencephalic reticular nuclei, respectively; **e** Main inputs and outputs of the reticulospinal (RS) neurons. The RS neurons receive ipsilateral excitatory visual input and contralateral excitatory vestibular input, and they exert an excitatory action on the ipsilateral motoneurons in the spinal cord

fore not depend on the rotation of the body. The activity in the left and right RS pathways was recorded by implanted electrodes. These biological signals were then used to control an electric motor that rotated the animal around its longitudinal axis. This “hybrid” system automatically stabilized a normal orientation of the lamprey in the gravitational field. It reproduced a number of postural effects: (1) the system compensated for large postural disturbances (lateral tilt up to $\pm 180^\circ$) due to wide angular zones of the gravitational sensitivity of RS neurons, (2) unilateral eye illumination elicited a lateral tilt (dorsal light response) due to a shift of the equilibrium point in the vestibular-driven postural network, (3) removal of one labyrinth resulted in a loss of balance immediately after the operation due to an induced left-right asymmetry in the vestibulo-reticulospinal reflexes, and (4) this could be compensated by an asymmetric visual input. A reduction of the gain in the reflex pathways led to a loss of balance, which could be restored by imposing small oscillations that mimicked locomotor undulations and elicited an additional dynamic activation of the vestibular organs.

The neuro-mechanical model has, however, a number of limitations. Most importantly, it is cumbersome to change the essential characteristics, like speed of rotation, inertial properties, etc., over a sufficiently wide range. Such changes are necessary for studying the effects of different parameters of the control system on postural performance. To overcome these limitations we use here a different approach: mathematical modeling and computer simulation. We investigate a similar model of postural control based on opposing vestibular reflexes mediated by the RS pathways. The following assumptions, in part based directly on the results of the biological experiments (see above), were used in the modeling:

1. Signals for postural corrections are transmitted from the brainstem to the spinal cord via two symmetric RS pathways.
2. Due to an excitatory input from the contralateral labyrinth, rotation of the animal evokes both a dynamic (activity during movement) and a static response (sustained or slowly decaying activity in a new position) in RS neurons. Both responses are caused by contralateral tilt.
3. The RS neurons receive an excitatory input from the ipsilateral eye.
4. The RS neurons elicit an ipsilateral flexion of the tail; since the tail is deviated downwards, its lateral flexion causes the lamprey to rotate around its longitudinal axis.
5. There is a delay in the mechanical response to RS commands caused by synaptic transmission in the spinal network and inertial properties of the lamprey's body; the response decays because of viscous friction with water.

Preliminary results have been submitted for publication as a brief communication (Kozlov et al. 2000).

2 Methods

The mathematical modeling of postural control in lamprey is divided into two parts. First, we give a phenomenological description of the response of RS neurons to rotation of the body of the lamprey, following the basic assumptions listed above. The nonlinear approximation of the response using the smallest number of free parameters that qualitatively represents the experimental data is constructed: static angular dependence studied earlier (von Holst 1950; Mittelstaedt 1983) is complemented by a velocity-dependent term. Parameters of the model are chosen within the ranges that were estimated in previous neuro-mechanical experiments (Zelenin et al. 1998). Second, the model of rotation of the lamprey's body in viscous water caused by small motions of the tail is considered. Stabilization of posture is reached using the approximation of the RS response as a feedback (Kozlov et al. 2000). The model of postural control obtained allows the study of phenomena that cannot be recorded easily in experiments, like sensitivity to tilt angle and angular

velocity, internal feedback inertia, etc. We note that the animal in the experiments that we model is mounted on a platform, so it can and does perform undulating locomotor motions, but cannot move itself forward, i.e., it does not swim.

The mathematical treatment of the model uses elements of control theory and qualitative theory of ordinary differential equations (Kuznetsov 1995). For simulations and stability analysis, the simulation tool XPP-Aut was used (Ermentrout 1999).

3 Results

3.1 Mathematical model

3.1.1 Response of RS neurons to roll of the body. The activity of RS neurons, i.e., their firing rates, recorded from the right and left sides of spinal cord is determined by the direction of body rotation, and it increases with increasing velocity of rotation. This kind of response is called *dynamic*. When the body rotation stops, and the animal is kept at a fixed angle, some reticulospinal activity remains. This may be interpreted as a dependence of the RS neuronal activity on the body tilt angle. It thus constitutes a *static* component of the neuronal response. In our model we will call the response of RS neurons, or function F_{RS} , the difference of firing rates in Hertz of left and right RS neurons.

Neurons from one side have a different sensitivity to body tilt to ipsilateral (same) or contralateral (opposite) sides, as shown schematically in Fig. 2; for exact graphs and explanations see Deliagina et al. (1992a). Activation of RS neurons located on the right side of the brain, evoked by the left side-down roll, will evoke a corrective motor response, resulting in a rotation of the body in the opposite direction. Similarly, an activation of the RS neurons of the left side will evoke a left side-down compensatory roll. At normal orientation (dorsal side up) the effects of the two “antagonistic” groups of RS neurons compensate each other, and the system stabilizes at angle $\varphi_0 = 0$. The characteristics of firing rates of the left and right RS neurons, F_L and F_R , are positive, 2π -periodic with respect to the tilt angle, with a maximum activity at around $\pm 90^\circ$ (see Fig. 2), and can be approximated, as in Fernandez and Goldberg (1976), by

$$F_L = U_{0L} + U_1 \sin \varphi + U_2 \sin^2 \varphi + \dots, \quad (1)$$

$$F_R = U_{0R} - U_1 \sin \varphi + U_2 \sin^2 \varphi - \dots, \quad (2)$$

where parameters U_{0L} , U_{0R} , U_1 , and U_2 are positive. Although each of the two characteristics is not symmetric, their difference will only include odd terms under the transformation $\varphi \rightarrow -\varphi$. The terms involving U_2 therefore cancel, and to a first approximation the difference is

$$F_{RS} \sim (\gamma + \sin \varphi), \quad (3)$$

where γ is the normalized difference between mean activity of left and right RS neurons. This can be controlled by constant nonsymmetric illumination of the

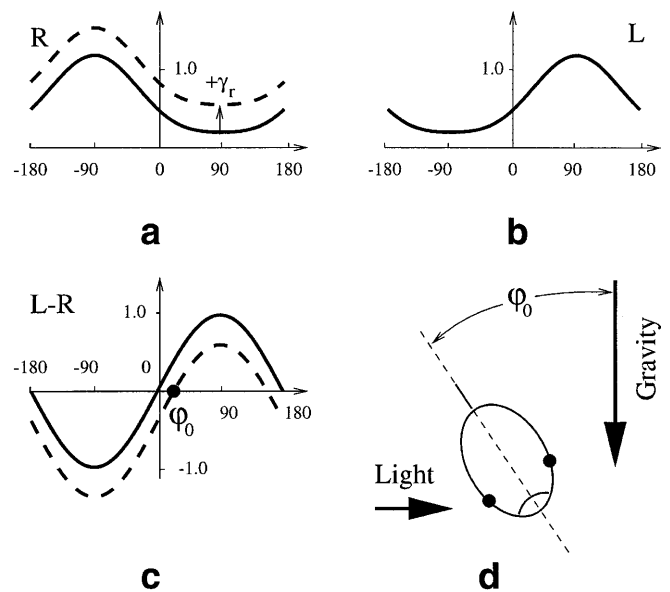


Fig. 2a–d. Activity of RS neurons from the right (a) and left (b) sides of the brain (arbitrary units) vs. tilt angle φ of the body to right (+) or left side (–). Both characteristics are 2π -periodic with maxima at approximately $\pm 90^\circ$ for most neurons. c The difference characteristic has a sinusoidal-like shape with value zero at 0° if left and right RS neurons are equally active in dorsal-side-up position. d Nonsymmetric tonic excitation of neurons from right side ($+\gamma_r$) provides a negative shift of the difference characteristic ($-\gamma_r$) and a shift of equilibrium point from vertical orientation (0°) to a constant tilt $+\varphi_0$

eyes. The form of (3) coincides with the static characteristic studied previously in experiments on bony fishes (von Holst 1950; Mittelstaedt 1983) in the particular case of darkness, or spherically homogeneous distribution of light.

RS neurons are also excited by rotation of the body. Their response is stronger with higher angular velocity ω , and the sign of a perturbation of F_{RS} depends on the direction of rotation. In the simplest form the dependence of the response of RS neurons on rotation may therefore be assumed to be linear in ω .

Finally, we can write the feedback in the following form:

$$F_{RS}(\varphi, \omega) = \beta(\gamma + \sin \varphi) + \alpha\omega, \quad (4)$$

where $\alpha > 0$ and $\beta > 0$ are the gain coefficients.

3.1.2 Control of posture in viscous water. To verify if the control mechanism can stabilize and maintain dorsal-side-up body orientation in natural conditions, the nonlinear feedback control of the form in (4) has been tested in a mathematical model of the animal in viscous water.

The model describes rotation of the body around the longitudinal direction provided by tail motions under control of the vestibular system. The lamprey has a long, almost cylindric, body with an asymmetrically positioned tail, as shown in Fig. 1a. Motion of the tail will thus induce a torque acting on the body, inducing it to rotate. We consider only the three main forces that determine rotation of the body: the muscle force and the

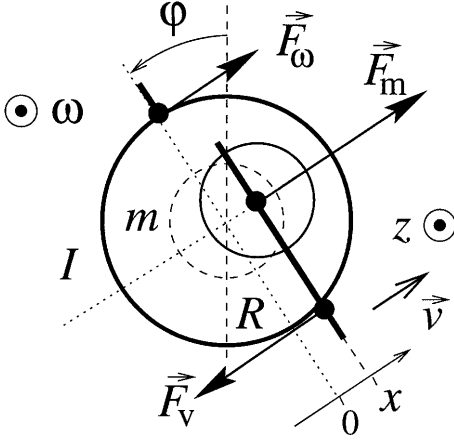


Fig. 3. Geometry of forces applied to body and tail (front view); see explanations in the text

viscous friction forces applied to body and tail; thereby assuming other forces to be negligible. The geometry of the acting torques is illustrated in Fig. 3. We will call φ the tilt angle, i.e., the angle between dorsal and vertical directions, as shown in Fig. 3. The displacement of the tail, x , is taken to be relatively small.

Rotation of the body is determined by the moment equation:

$$I\dot{\omega} = \vec{M}_\omega + \vec{M}_v, \quad (5)$$

where I is moment of inertia of the body, and \vec{M}_ω and \vec{M}_v are the torques caused by water viscous friction forces acting on the body, mostly on the dorsal fin, and on the tail. In order of magnitude we have:

$$\begin{aligned} |\vec{M}_\omega| &= RF_\omega = R \cdot n_1 R \omega, \\ |\vec{M}_v| &= RF_v = R \cdot n_2 (v + R\omega), \end{aligned} \quad (6)$$

where $\omega = \dot{\varphi}$ is the angular velocity, n_1 and n_2 are the friction coefficients of the body and the tail, R is the effective radius at which the forces are applied, which we set equal to the radius of the body, and $v + R\omega$ is the absolute velocity of the tail in water.

Lateral motion of the tail of mass m obeys the equation

$$m\dot{v} = \vec{F}_m + \vec{F}_v. \quad (7)$$

The muscle force \vec{F}_m applied to the tail is controlled by neurons in the spinal cord, the activity of which in turn depends on RS commands. Response of RS neurons to roll of the body is modeled by (4). The exact relation between RS commands and muscle contraction is not known, but a linear proportionality seems physiologically reasonable. We assume here that

$$F_m = gF_{RS} \quad (8)$$

with g as a dimensionality constant. We will also consider a possible effect of inertia in the spinal cord

$$F_m = gy, \quad \frac{dy}{dt} = (F_{RS} - y)/T, \quad (9)$$

where y is the difference of a average spiking frequency of RS neurons on the left and right sides, and T is the inertial time constant.

Note that we do not model explicitly the position of the tail. If we nevertheless introduce a coordinate x , the derivative of which is the tail velocity v , the control scheme described by (5)–(9) does not imply that x return to zero when the dorsal-side-up orientation of the body is obtained.

Both dorsal-side-up body orientation and a straight tail can be reached by several possible mechanisms such as, for instance, coupled horizontal and vertical bending of the tail. In the absence of experimental data, we choose here not to model the control of the position of the tail.

Putting together the above equations and projecting vectors in (5) to longitudinal axis z and those in (7) on the x -direction we obtain the following system:

$$\begin{aligned} \dot{\varphi} &= \omega, \\ I\dot{\omega} &= -n_1 R^2 \omega - n_2 R(v + R\omega), \\ m\dot{v} &= gF_{RS}(\varphi, \omega) - n_2(v + R\omega), \end{aligned} \quad (10)$$

for simplified relation (8), and system

$$\begin{aligned} \dot{\varphi} &= \omega, \\ I\dot{\omega} &= -n_1 R^2 \omega - n_2 R(v + R\omega), \\ m\dot{v} &= gy - n_2(v + R\omega), \\ \dot{y} &= (F_{RS}(\varphi, \omega) - y)/T, \end{aligned} \quad (11)$$

that accounts for inertia in activation of RS neurons (see Eq. 9), where $F_{RS}(\varphi, \omega)$ is as in (4).

For small species of lamprey, of length about 10 cm (i.e., $L = 0.10$ m), realistic physical parameters could be the following, which are the ones used in the simulations presented here: $I = 2 \cdot 10^{-7}$ kg m², $R = 0.005$ m, $m = 0.0005$ kg, $g = 3 \cdot 10^{-6}$ N s, $n_2 = 0.0005$ N s/m, $n_1 = 4n_2$, $T = 0.050$ s. In Appendix A we show how such estimates can be made.

Numerical simulations of systems described by (10) and (11) with parameter values as above and with nonlinear feedback as in (4) show that the model control schemes suggested have a proper equilibrium corresponding to the dorsal-side-up body orientation. For some parameters values of the nonlinearity, this equilibrium could be reached from different initial tilt angles, and it could be maintained. Figures 4 and 5 show transitions to the rest state in systems described by (10) and (11).

3.1.3 Loss of equilibrium and its restoration after impairment of vestibular input. Animals with vestibular organs removed from one side lose the ability to maintain the dorsal-side-up position for some time after the operation. Such animals are known to roll continuously when they swim (Ullén et al. 1995a). The decrease in sensitivity after labyrinthectomy may be compensated by an increasing tonic activity of RS neurons from the contralateral side. This can be achieved by a permanent illumination of one eye, by the direct stimulation of

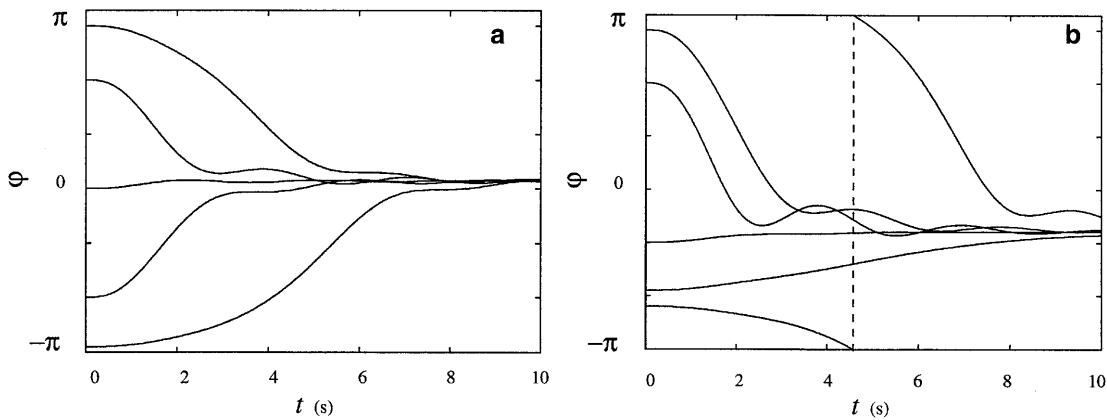


Fig. 4a,b. Stabilization of body orientation in the lamprey by motion of the tail controlled by RS commands (model described by (10) for $\alpha = 60$, $\beta = 50$) for initial tilt angles over the interval $[0^\circ, 360^\circ]$: **a**

Stabilization of the dorsal-side-up body orientation without visual input ($\gamma = 0$); **b** Shift of the resting state by visual stimulation of one eye ($\gamma = 0.8$)

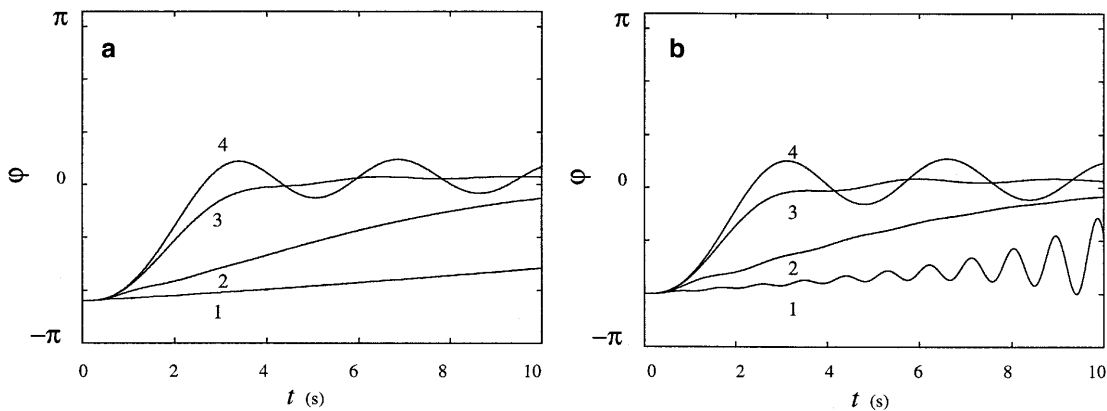


Fig. 5a,b. Recovery of dorsal-side-up body orientation in models described by (10) and (11) – **a** and **b**, respectively – for $\beta = 50$ and $\alpha = 700$ (trace 1), 200 (trace 2), 60 (trace 3), and 40 (trace 4). Note that

for small values of α in **a** and for small and large values of α in **b**, the equilibrium state corresponding to dorsal-side-up body orientation becomes unstable and oscillations occur

optic nerve or, temporally, by a strong and brief illumination of one eye.

Impairment of the vestibular organ mainly changes the static component of RS neuron response, shifting the difference characteristic as in (4) up or down:

$$\tilde{F}_{RS}(\varphi, \omega) = \tilde{\beta}(\tilde{\gamma} + \sin \varphi) + \tilde{\alpha}\omega, \quad (12)$$

where $\tilde{\beta} = \beta/2$, $\tilde{\alpha} \simeq \alpha$, and $|\tilde{\gamma}| > 1$, as shown on Fig. 6. Equilibrium points in models described by (10) and (11) are determined by equation $F_{RS}(\varphi, 0) = 0$. It has no solution for $|\tilde{\gamma}| > 1$ in (12), which explains why animals lose their equilibrium after labyrinthectomy. Illumination of one eye contralateral to the operated side will provide a tonic excitation of the corresponding RS neurons, and eliminate the shift of F_{RS} , thus recovering a stable equilibrium (see Fig. 7).

3.2 Stability of the goal state

The goal of the postural control mechanisms in the lamprey is to maintain the dorsal-side-up orientation of its body during ongoing movements. In terms of models

described by (10) and (11), it means stability of the equilibrium state with a zero tilt angle $\varphi_0 = 0$ for zero bias $\gamma = 0$, or with some tilt angle $-\pi/2 < \varphi_0 < \pi/2$ if $|\gamma| < 1$.

For stability analysis we use dimensionless equations. As a characteristic length scale, we have taken R , the radius of the body of the animal. As characteristic time we take $t_0 = I/(n_2 R^2)$, the decay time, due to friction of the tail, of angular rotation. We can also introduce a characteristic scale of the conversion factor g from activation of the spinal cord to muscle force: $g_0 = n_2 R/t_0$ is the characteristic friction force exerted with the rotation decay. Then we introduce dimensionless variables

$$t = t_0 \cdot t', \quad \omega = \frac{1}{t_0} \omega', \quad v = \frac{R}{t_0} v', \quad \frac{g}{g_0} y = y'. \quad (13)$$

Using dimensionless variables and new parameters

$$\frac{g}{g_0} \beta = \beta', \quad \frac{g}{g_0 t_0} \alpha = \alpha' \quad (14)$$

in (10) and (4), and omitting primes for variables we come to the system

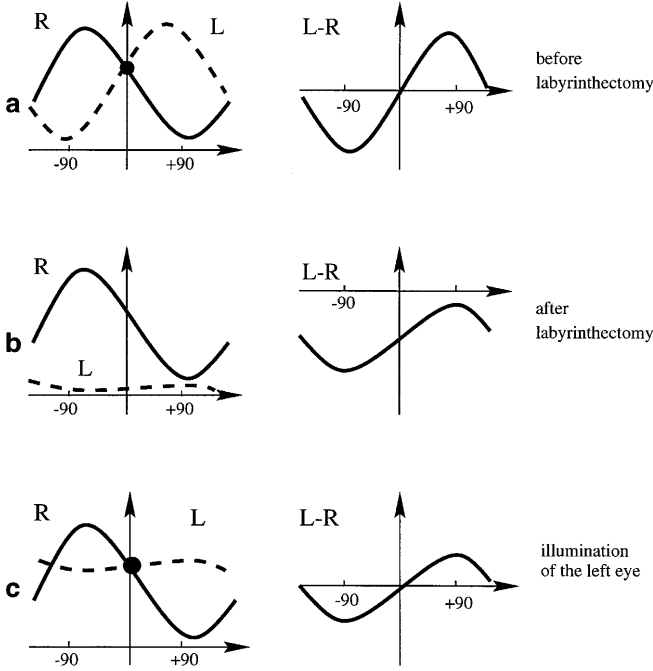


Fig. 6a-c. Static response of left and right RS neurons to tilt angle φ (left column) and difference activity (right column), before **a** and after **b** labyrinthectomy. Removing the vestibular organ from the left side decreases activity of left RS neurons, which shifts the difference characteristic below zero level thus making equilibrium impossible. **c** Tonic activation of left neurons by eye illumination helps to recover equilibrium

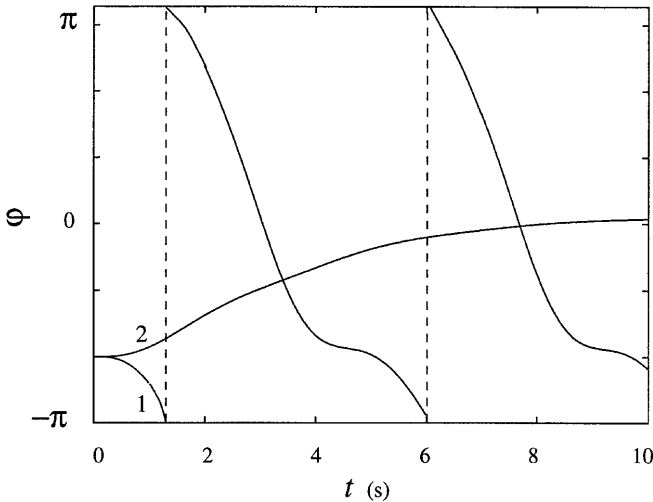


Fig. 7. Roll of the body after impairment of vestibular organ (trace 1), and recovery of equilibrium after illumination of the contralateral eye (trace 2) obtained by simulation of the system described by (11)

$$\begin{aligned}\dot{\varphi} &= \omega, \\ \dot{\omega} &= -(1+c)\omega - v, \\ \varepsilon \dot{v} &= f(\varphi, \omega) - v - \omega,\end{aligned}\quad (15)$$

and system

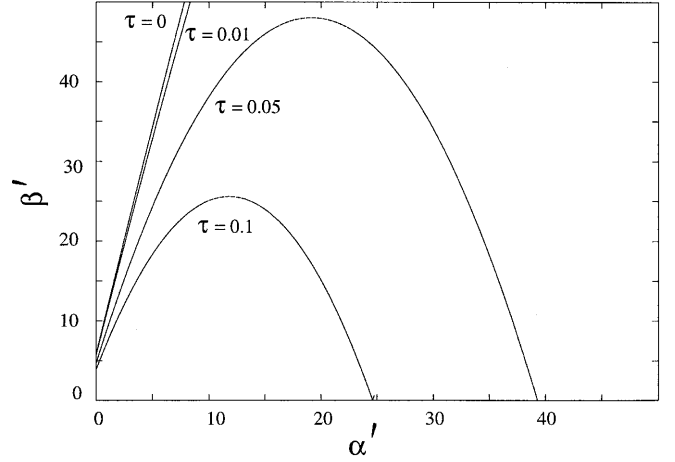


Fig. 8. Regions of stability of dorsal-side-up body orientation according to model described by (16), for different values of inertial time constant. Equilibrium is stable below the parabolic curves. Bifurcation curve for $\tau = 0$ corresponds to the system described by (15)

$$\begin{aligned}\dot{\varphi} &= \omega, \\ \dot{\omega} &= -(1+c)\omega - v, \\ \varepsilon \dot{v} &= y - v - \omega, \\ \tau \dot{y} &= f(\varphi, \omega) - y,\end{aligned}\quad (16)$$

for (11) and (4), where c , ε , and τ are dimensionless parameters

$$c = n_1/n_2, \quad \varepsilon = \frac{m}{n_2 t_0}, \quad \tau = T/t_0$$

and

$$f(\varphi, \omega) = \beta'(\gamma + \sin \varphi) + \alpha' \omega. \quad (17)$$

Parameter ε can be interpreted as the fraction of the moment of inertia contained in the tail, if it is taken to be a body of mass m kept rigidly at distance R from the center of the body of the animal; ε should hence be a small number. Parameter τ is a dimensionless time constant of the activation of the spinal cord. Dimensionless (15)–(17) constitute a dimensionless version of systems described by (10), (11), and (4).

Systems described by (15) and (16) have two equilibrium states, O_1 and O_2 , with angular coordinates $\varphi_{01} = \arcsin \gamma$ and $\varphi_{02} = \pi - \arcsin \gamma$, respectively. Equilibrium O_1 corresponds to dorsal-side-up body orientation. Regions of stability of equilibrium O_1 for the parameter estimates used and $\gamma = 0$ are shown in Fig. 8. Note that the region of stability becomes limited if the delay in spinal cord activation modeled by (9) is taken into account, and it gets smaller for a larger delay.

If $\gamma \neq 0$, the two equilibrium states become closer to each other which makes the stable mode of the control system less reliable. Clearly the sinusoidal information is insufficient for the task of maintaining any position. To overcome this, additional cosinusoidal input and the reference angle instead of the reference bias have been suggested (Mittelstaedt 1983). This will replace the term

$\beta \sin \varphi$ in (4) with $\beta_1 \sin \varphi \cos \psi - \beta_2 \cos \varphi \sin \psi$, where parameter ψ is the reference angle, or $\beta \sin(\varphi - \psi)$ for $\beta_1 = \beta_2$. Stability analysis of the latter case is identical to the one presented above.

Assuming the dynamic reaction to be 2–5 times stronger than the static one for the parameter values used, α' and β' should lie inside the stability region near its left boundary (see Appendix B for estimates).

4 Discussion

In the present paper a model of the postural control mechanism in lamprey with respect to roll of its body is suggested. The feedback control mechanism uses signals formed in reticular nuclei in response to roll of the body which are transferred along the body by reticulospinal pathways. We assume that a corrective motor response is caused by the difference between the left and right RS signals. The neuronal response has *static* and *dynamic* components, reflecting activity of neurons in response to a constant tilt angle and a rotation of the body, respectively. The angular dependence is nonlinear and 2π -periodic, while the rotation term is assumed to be linear with the angular velocity. The mathematical expression of RS neuron response (see Eq. 4), together with (10) and (11) determining the rotation of a cylindric body in viscous water, describes well a set of important experimental observations listed in Sect. 1. In addition, the mathematical modeling performed provides new evidence for the following statements:

1. Signals transmitted from the brainstem to the spinal cord via RS pathways are sufficient for stabilization of body orientation in the transverse (roll) plane.
2. Both static and dynamic components in the response of RS neurons to roll of the body are important for maintaining equilibrium. Stability of the equilibrium state depends on the relative contribution of the static and dynamic components in the RS response.
3. Postural control mechanisms are potentially unstable and operate presumably in a stable mode for subcritical values of parameters near the boundary of stability.

One of the main objectives of this study was to analyze the stability of the posture control system in the lamprey, where we are mainly concerned with the fast components in the response of RS neurons to rotation of the body. Although the visual component contributes to the position of equilibrium on equal terms with the vestibular component as in von Holst (1950) and Mittelstaedt (1983), it has much longer time scale (Zelenin et al. 1998) and is not modeled dynamically here. We also note that the visual input modeled by the term γ in (3) is a constant illumination of one eye of the animal as mounted on the platform, and is therefore independent of tilt angle φ .

It should additionally be noted that in our modeling we use the integral activity of RS neurons as a control variable and do not consider particular characteristics of vestibular and visual receptors and central commands.

In this paper we consider one of several mechanisms controlling posture in the lamprey. They are a lateral motion of the tail, a bending of dorsal fin, and twisting of the body (Ullén et al. 1995a). The two latter controls use forces produced by the stream of water upon the body, and are not strong, particularly in slowly swimming animals. Hence, we consider lateral movements of the tail to be the major factor in the control of posture in lampreys, acting on the top of the background undulatory motion of the tail. Perturbations caused by the undulatory motion assume significant robustness of the postural control mechanism. This leads to a problem of stability of a control system under a periodic force, which will be studied elsewhere.

Appendix A: Estimations of physical parameters

To estimate parameters in models described by (10) and (11), let us assume a lamprey to have a cylindric body with length L , in meters, and diameter $d = 0.1L$ (radius $R = 0.05L$) or less. If the density of the body is approximately equal to that of the water, then the mass of the body will be

$$M = \rho V = 10^3 \cdot \pi d^2 L < 10^3 \cdot \pi (0.1L)^2 \cdot L = 30L^3 \text{ kg} .$$

The moment of inertia of the body equals

$$I = \frac{MR^2}{2} < \frac{10\pi L^3}{2} (0.05L)^2 = 0.03L^5 \text{ kg m}^2 .$$

We will consider the mass of the tail, m , to be 10% of M

$$m = 0.1M < 3L^3 \text{ kg} .$$

To estimate the friction coefficient, n_2 , we use Stokes' relation between velocity of a sphere and magnitude of force needed to drag it through the water, $6\pi\eta Rv$, where R is the radius of the sphere and v is its velocity. The constant η is called the coefficient of shear viscosity. For water at 10 °C,

$$\eta = 1300 \mu\text{Pa s} = 1.3 \cdot 10^{-3} \text{ N s/m}^2 .$$

Then the friction coefficients are

$$n_2 \simeq 6\pi \cdot 1.3 \cdot 10^{-3} \cdot 0.05L \simeq 10^{-3} L \text{ N s/m}, \quad n_1 > n_2 .$$

Muscle force, F_m , is considered to be proportional to the feedback response of RS neurons: $F_m = gF_{RS}$. On the other hand, muscle force is approximately equal to water resistance, so, for $\gamma = 0$, $\max|F_m| \simeq g(\beta + \alpha\omega) \simeq n_2 v_{\max}$, where $\beta = 10\text{--}50 \text{ Hz}$, $\alpha = 20\text{--}100 \text{ radian}^{-1}$. For periodic motions of the tail $x(t) = A \sin(2\pi ft)$, where $A \simeq L/4 \text{ m}$ and $f = 1\text{--}10 \text{ Hz}$, $v_{\max} = 1.5\text{--}15 L \text{ m/s}$. Then the conversion coefficient is

$$g \simeq \frac{n_2 v_{\max}}{\beta + \alpha 2\pi f} \geq 0.3\text{--}3 \cdot 10^{-5} \cdot L^2 \text{ N s} .$$

The inertial time constant T in (9) is estimated for fast and slow axons as

$$T = 0.01\text{--}0.05 \text{ s} .$$

Appendix B: Estimations of dimensionless parameters of the neuron response

Assuming the muscle force to be equal to water resistance, which is correct for low-frequency tail movements, say 0.1 Hz, we have for $\gamma = 0$

$$g(\beta_0 + \alpha_0 \omega_0) \simeq n_2 A \omega_0 ,$$

where α_0 and β_0 are some fixed values of parameters α and β , $\omega_0 = 0.6$, and A is the amplitude of tail movements. Using dimensionality constants $g_0 = n_2 R / t_0$ and $t_0 = I / (n_2 R^2)$ and substitutions (14) for our particular parameters, we obtain the following relations

$$\beta'_0 = \frac{g}{g_0} \beta_0 = \frac{A \omega_0 I}{n_2 R^3} \cdot \frac{\beta_0}{\alpha_0 \omega_0 + \beta_0} \simeq 50 \frac{\beta_0}{\alpha_0 \omega_0 + \beta_0} = 50S,$$

$$\alpha'_0 = \frac{g}{g_0 t_0} \alpha_0 = \frac{A}{R} \cdot \frac{\alpha_0 \omega_0}{\alpha_0 \omega_0 + \beta_0} = 5 \frac{\alpha_0 \omega_0}{\alpha_0 \omega_0 + \beta_0} = 5(1 - S) ,$$

where S is the fraction of the static component of the neuronal response of the total neuron response. Note that $\alpha'_0 < 5$, since $0 < S < 1$. Using the relation between α'_0 and β'_0 obtained and the plot of stability boundary from Fig. 8 for $\tau = 0$, we estimate $0 < S < 0.4$. This means that the dynamic component of RS response must be at least 1.5 times stronger than the static one.

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