38

The Lamprey Postural Circuit

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The lamprey swims due to the lateral body undulations. During swimming, orientation of the lamprey in the sagittal (pitch) and transversal (roll) planes is stabilized in relation to the gravity vector by means of the postural control systems driven by vestibular input (Deliagina et al., 1992a; Deliagina et al., 1992b; Deliagina and Fagerstedt, 2000; Pavlova and Deliagina, 2002; Ullén et al., 1995). Vestibular-driven mechanisms also contribute to stabilization of the direction of swimming in the horizontal (yaw) plane (Karayannidou et al., 2006). Any deviations from the stabilized orientation are reflected in vestibular signals (Deliagina et al., 1992b), which cause corrective motor responses. In the pitch and yaw planes, the corrections occur due to the body bending in the corresponding plane (Fig. 38.1A, Pitch and Yaw). In the roll plane, the corrections occur due to a change of the direction of locomotor body undulations, from lateral to oblique (red arrows in Fig. 38.1A, Roll) (Zelenin et al., 2003).

The principal elements of the postural network in the lamprey are shown in Figure 38.1B. Vestibular afferents through the neurons of vestibular nuclei affect reticulospinal (RS) neurons. The RS neurons form the main descending pathway that transmits all commands from the brainstem to the spinal cord, including commands for postural corrections. The spinal network transforms RS commands into the motor pattern of postural corrections. This network includes segmental interneurons, as well as four motoneuron pools in each segment that innervate the dorsal and ventral parts of a myotome on the right and left sides.

Responses of individual vestibular afferents and RS neurons to natural stimulations of vestibular organs (i.e., rotation of the whole lamprey or isolated brainstem-vestibular organ preparation in different planes) have
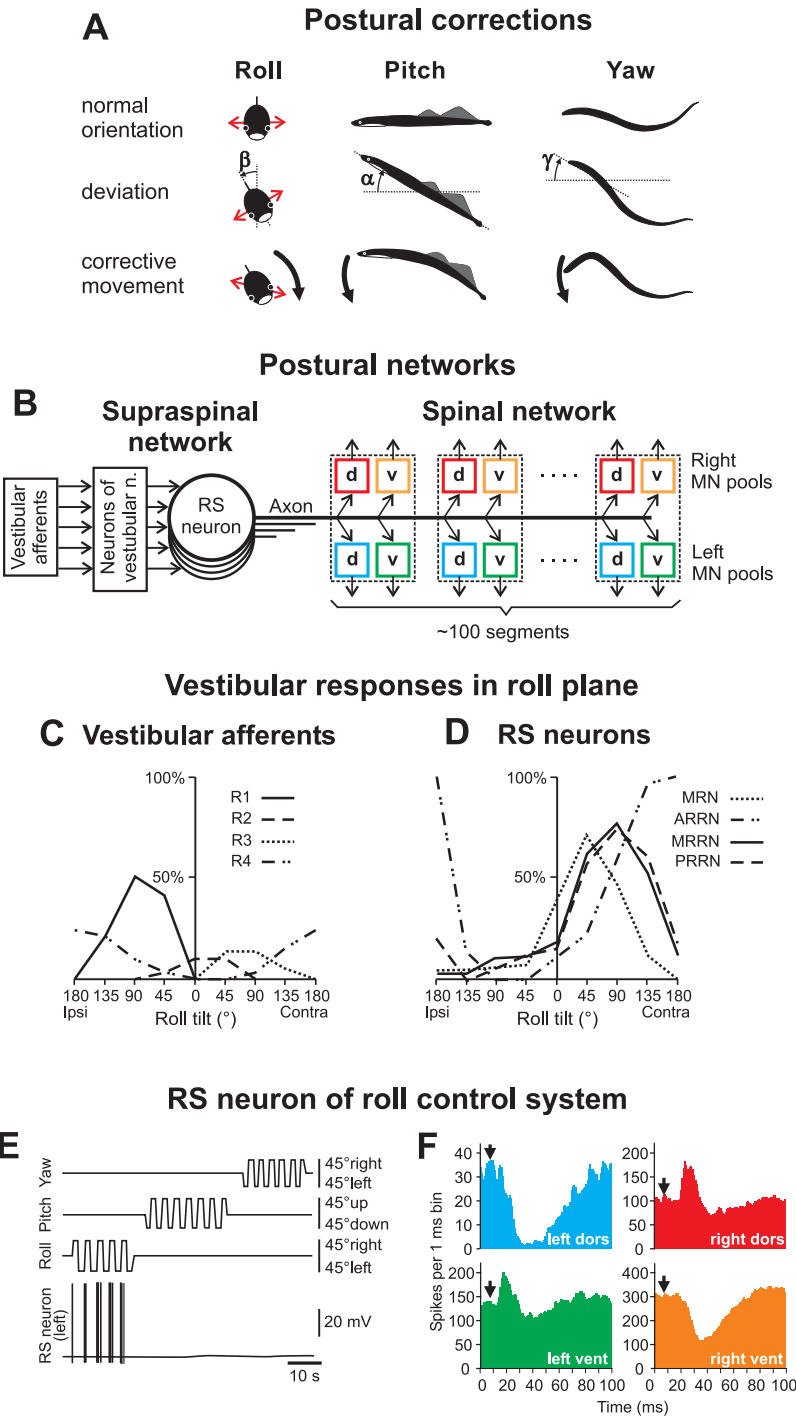
FIGURE 38–1. (*A*) During regular swimming, the lamprey stabilizes its orientation in the sagittal (pitch) plane, in the transversal (roll) plane, and in the horizontal (yaw) plane. Deviations from the stabilized orientation in these planes (angles α, β, and γ, respectively) evoke corrective

motor responses (large arrows) aimed at restoration of the initial orientation. (*B*) Commands for correcting the orientation are formed on the basis of vestibular information and are transmitted from the brainstem to the spinal cord by reticulospinal (RS) neurons. Motor output of each segment is generated by four motoneuron (MN) pools controlling the dorsal and ventral parts of a myotome on the two sides (*d* and *v* pools). (*C* and *D*) Angular zones of activity of vestibular (otolith) afferents (*C*) and RS neurons (*D*) when the preparation was rotated in the roll plane (abscissa, % of active neurons; the data for different groups [R1–R4] of otolith afferents in *C*, and for different reticular nuclei, MRN, ARRN, MRRN, and PRRN in *D* are presented separately). (*E* and *F*) An RS neuron that contributed to stabilization of the roll angle. (*E*) The neuron fired spikes in response to right (contralateral) roll tilts. (*F*) The neuron evoked excitation in the left (ipsilateral) ventral and right (contralateral) dorsal branches of the ventral roots, and inhibition in the right ventral and left dorsal branches. Arrows indicate the time of arrival of the RS spike to the segment 30, in which the motor output was monitored. (*A, B, E,* and *F* were adapted from Zelenin et al., 2007; *D* was adapted from Deliagina et al., 1992a)

been studied. Deviation of the lamprey from the stabilized orientation in any plane causes activation of a specific group of canal and otolith afferents (Deliagina et al., 1992b). In each of the main planes (pitch, roll, yaw), two groups of canal afferents responding to rotation in opposite directions were found. Rotation in the roll and pitch planes revealed specific groups of otolith afferents with different zones of spatial sensitivity. The groups with different angular zones of activity in the roll plane are shown in Figure 38.1C. Due to these vestibular inputs (Fig. 38.1B), RS neurons respond to rotation in different planes (Deliagina et al., 1992a; Deliagina and Fagerstedt, 2000; Pavlova and Deliagina, 2002; Karayannidou et al., 2006). Figure 38.1D shows the angular zones of activity of RS neurons from different reticular nuclei when the preparation was rotated in the roll plane. The overwhelming majority of RS neurons are maximally active at 45°–90° of the contralateral tilt (Fig. 38.1D). They are driven by the vestibular afferents responding to the ipsilateral roll tilt (Fig. 38.1C) and originating from the contralateral labyrinth (Fig. 38.2A; Deliagina et al., 1992a; Deliagina et al., 1992b; Deliagina and Pavlova, 2002). In each of the main planes (pitch, roll, yaw), two antagonistic groups of RS neurons responding to rotation in opposite directions were revealed (Deliagina et al., 1992a; Deliagina and Fagerstedt, 2000; Pavlova and Deliagina, 2002; Karayannidou et al., 2006). These groups are shown in Figures 38.2A and D for the roll and pitch control systems, and their tilt-related activity is presented in Figures 38.2B and E, respectively. This activity can be considered as the command for postural correction addressed from the supraspinal postural network to the spinal postural network.

The spinal network transforms RS commands into the motor pattern of postural corrections. It was proposed that two groups of RS neurons (activated by rotation in a particular plane but in opposite directions), through the spinal network, cause rotation of the animal in the direction opposite to the
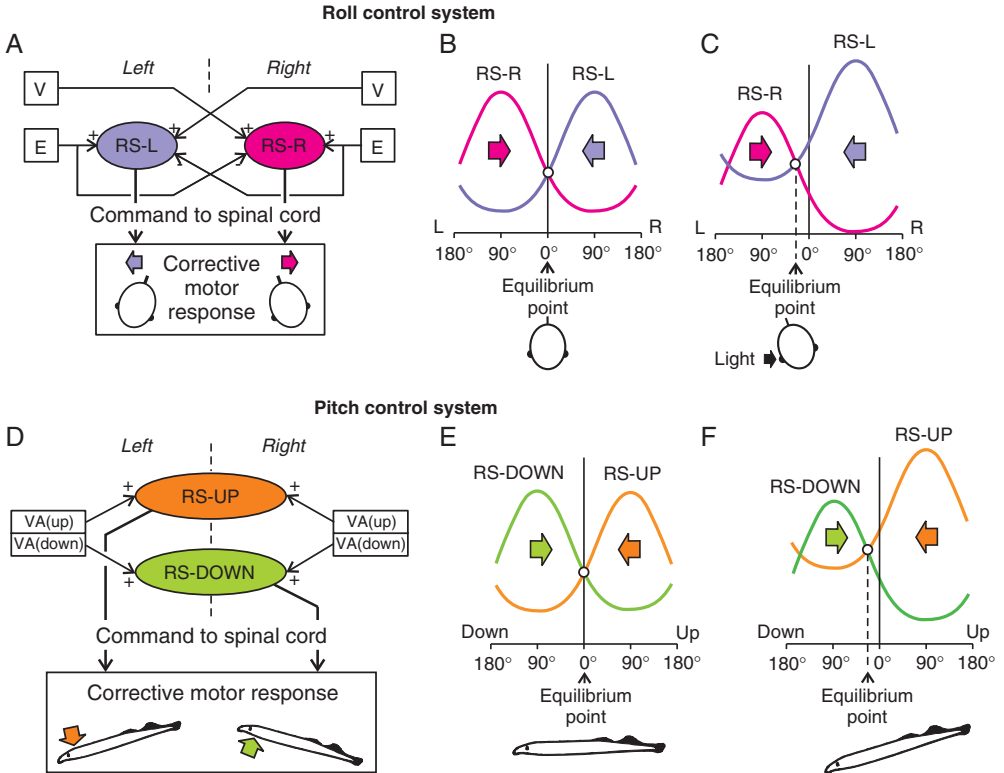
FIGURE 38–2. (*A–C*) The roll control system. (*A*) The left and right groups of RS neurons (RS-L and RS-R) are driven mainly by vestibular afferents from the contralateral vestibular organ (V); they cause ipsilateral rotation of the lamprey (red and blue arrows in *A–C*). (*B*) Due to vestibular inputs, these two groups are activated with the contralateral roll tilt and rotate the lamprey in opposite directions. The system stabilizes the orientation with equal activities of the two groups (equilibrium point). (*C*) Unilateral eye illumination (input E in *A*) causes an asymmetrical bias in the RS-L and RS-R activities and a shift of the equilibrium point, which results in a roll tilt of the lamprey toward the source of light. (*D–F*) The pitch control system. (*D*) Two groups of RS neurons (RS-UP and RS-DOWN) are driven by vestibular afferents responding to nose-up (VA-up) and nose-down (VA-down) tilts of the animal, respectively. The RS-UP and RS-DOWN groups cause downward and upward turning of the lamprey, respectively (orange and green arrows in *D–F*). (*E*) Due to vestibular inputs, RS-UP and RS-DOWN groups are activated with upward and downward tilts, respectively, and cause turning the lamprey in opposite directions. The system stabilizes the orientation with equal activities of the two groups (equilibrium point). (*F*) Raising the water temperature causes an asymmetrical bias in the RS-UP and RS-DOWN activities and a shift of the equilibrium point, which results in downward tilt of the lamprey. (*A–C* were adapted from Deliagina and Fagerstedt, 2000; *D–F* were adapted from Pavlova and Deliagina, 2002)

initial turn (which activates the neurons), and the system will thus stabilize the orientation with equal activities of the two antagonistic groups (equilibrium point in Fig. 38.2B and E) (Deliagina et al., 1992a; Deliagina and Fagerstedt, 2000; Pavlova and Deliagina, 2002; Karayannidou et al., 2006). Normally, this occurs at the dorsal-side-up and horizontal orientation of the

body in the roll and pitch planes, correspondingly, as well as during swimming along a rectilinear trajectory in the yaw plane. The stabilized orientation can be gradually changed under the effect of some environmental factors. Asymmetrical eye illumination causes asymmetry in the activities of the two antagonistic groups of RS neurons of the roll control system, and a shift of the equilibrium point, which results in a change of the stabilized orientation (Fig. 38.2C) (Deliagina and Fagerstedt, 2000; Deliagina and Pavlova, 2002). This postural reaction (the dorsal light response) is a protective reflex, turning the dark dorsal side of the body toward the light and thereby decreasing the risk of detection by predators. In the pitch control system, the stabilized orientation can be changed by raising the water temperature, which affects the two groups of RS neurons differently and thus shifts the equilibrium point toward the nose-down orientation (Fig. 38.2F) (Pavlova and Deliagina, 2002), which allows the animal to reach deeper and colder water layers.

The relationships between vestibular inputs to individual RS neurons and their motor effects were recently studied (Zelenin et al., 2007). In these experiments, *first*, the vestibular-driven activity of an RS neuron was determined by rotating the preparation in different planes. *Second*, the same RS neuron was stimulated, and its effects on the motor output of the spinal cord (the activity in dorsal and ventral branches of the ventral roots innervating dorsal and ventral myotomes, respectively) were detected by means of the RS spike-triggered averaging technique. These effects (functional spinal projections of the RS neuron) were found to be similar along the whole extent of the axon, and they could thus be characterized by a combination of influences on the four motoneuron pools in any segment.

It was shown that the majority of RS neurons responded to rotation in only one of the three main planes (Pavlova and Deliagina, 2002; Zelenin et al., 2007), as illustrated in Figure 38.1E. This particular neuron fired spikes in response to contralateral roll tilts and did not respond to rotation in the pitch and yaw planes. Motor effects of this neuron are shown in Figure 38.1F. They included activation of the motoneuron pools projecting to the ipsiventral and contradorsal myotomes, and inhibition of those projecting to the ipsidorsal and contraventral myotomes. In the swimming lamprey, this pattern would lead to a change of the direction of locomotor body undulations, from lateral to oblique, and to a roll torque rotating the body in the direction opposite to the tilt that activated the neuron (Fig. 38.1A, Roll) (Zelenin et al., 2007).

In the majority of RS neurons, a strong correlation between their vestibular inputs and motor effects was found. Usually, a neuron produced a motor pattern (or a part of the pattern) causing a torque, which would oppose the initial rotation that activated the neuron. Such closed-loop microcircuits, formed by individual RS neurons responding to rotation in a given plane, operate in parallel to generate the resulting motor responses. A small proportion of RS neurons responded to rotation in more than one plane. Most of these neurons produced the motor pattern that represented the common part of the patterns of postural corrections caused by rotation in the corresponding planes.

These data on the sensory-motor transformation performed by individual RS neurons support the conceptual models of the postural control systems formulated earlier (Fig. 38.2) (Deliagina et al., 1992a; Deliagina and Fagerstedt, 2000; Deliagina and Orlovsky, 2002; Pavlova and Deliagina, 2002; Karayannidou et al., 2006).

To conclude, the operation of postural networks in the lamprey is based on interaction between two antagonistic vestibular reflexes. The lamprey stabilizes the body orientation in a particular plane at which the antagonistic reflexes are equal to each other. The closed-loop microcircuits, formed by individual RS neurons responding to deviation of the body orientation in a given plane from the stabilized orientation and affecting the motor output, operate in parallel to generate the resulting corrective motor response. The gradual change of the stabilized orientation is performed through the change of the gain in the reflex chains. These principles of operation of postural networks are similar to those revealed in the evolutionary remote species of marine mollusk *Clione limacina* (Deliagina and Orlovsky, 2002).

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