Review

Encoding and decoding of reticulospinal commands

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Abstract

In the lamprey, the reticulospinal (RS) system is the main descending system transmitting commands to the spinal cord. We investigated these commands and their effect on the spinal mechanisms. The RS commands were studied by recording responses of RS neurons to sensory stimuli eliciting different motor behaviors. Initiation of locomotion was associated with symmetrical bilateral massive activation of RS neurons, whereas turns in different planes were associated with asymmetrical activation of corresponding neuronal groups. The sub-populations of RS neurons causing different motor behaviors partly overlap. We suggest that commands for initiation of locomotion and regulation of its vigour, encoded as the value of bilateral RS activity, are decoded in the spinal cord by integrating all RS signals arriving at the segmental locomotor networks. Commands for turns in different planes, encoded as an asymmetry in the activities of specific groups of RS neurons, are decoded by comparing the activities of those groups. This hypothesis was supported by the experiments on a neuro-mechanical model, where the difference between the activities in the left and right RS pathways was used to control a motor rotating the animal in the roll plane. Transformation of the descending commands into the motor responses was investigated by recording the effects of individual RS neurons on the motor output. Twenty patterns of influences have been found. This great diversity of the patterns allows the RS system to evoke body flexion in any plane. Since most neurons have asymmetrical projections we suggest that, for rectilinear swimming, RS neurons with opposite asymmetrical effects are co-activated.
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Contents

1. Introduction

The reticulospinal (RS) system plays an important role in the control of locomotion, steering and posture in vertebrates [23]. In higher vertebrates, the specific contri-

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bution of the RS system to the control of motor behavior is difficult to assess since this system operates along with other descending systems, the corticospinal, rubrospinal, and vestibulospinal ones. We have been studying the RS system in the lamprey (a lower vertebrate, cyclostome). This animal has a general organization of the CNS similar to that in higher vertebrates [19]. In contrast to higher vertebrates, however, the RS system in the lamprey is practically the only descending system transmitting commands to the spinal cord and responsible for the initiation of locomotion, for steering, and for postural corrections. The bilateral RS pathways originate from ~2400 neurons located in four reticular nuclei: the mesencephalic reticular nucleus, and the anterior, middle and posterior rhombencephalic reticular nuclei [1,4,26,28]. RS neurons project ipsilaterally over long distances and affect different classes of spinal neurons [2,20,27].

In the present study we first investigated, the commands for different forms of motor activity in the lamprey transmitted by RS neurons. Secondly, we tried to understand how these commands affect the spinal mechanisms.

2. Commands transmitted by RS neurons

The RS commands were studied by recording the responses of individual RS neurons to various sensory stimuli in the intact lamprey [6,11], in the semi-intact preparation [10,16], and in the in vitro preparation [7–9]. These stimuli evoke different motor behaviors such as locomotion, steering, and postural corrections.

2.1. Commands for initiation of locomotion

Different sensory stimuli—illumination of the eyes, illumination of tail dermal photoreceptors, tactile stimuli, water vibration, vestibular stimuli (tilting in different planes)—all can evoke swimming provided that the stimuli are strong and/or long enough. Initiation of locomotion is always preceded by a sharp, bilateral activation of RS neurons as illustrated in Fig. 1a where the mass activity in RS pathways was recorded by means of chronically implanted electrodes [11]. This bilateral activation occurred irrespective of the modality and laterality of the applied sensory stimulus, and swimming continued as long as a high level of RS activity was present. How are the unilateral sensory signals of different modalities transformed into the bilateral RS activity? One of the possible sites of this transformation is the mesencephalic locomotor region (MLR) found in most vertebrates [23], and recently described also in the lamprey [29]. The MLR has bilateral projections to RS neurons and evokes symmetrical locomotion. In the lamprey, a high activity of RS neurons and swimming can last for many seconds after termination of the stimulus, presumably due to the NMDA-mediated plateau properties of some RS neurons [32].

It was found that the value of mass RS activity strongly correlates with the vigour of locomotion as characterized by the frequency of body undulations, the amplitude of EMG, and the propulsive force developed by the animal [11]. As shown in Fig. 1b, when a lead was attached to the swimming animal and stretched (Fig. 1c), the activity of RS neurons increased, and an additional propulsive force was generated. Since many RS neurons are glutamatergic
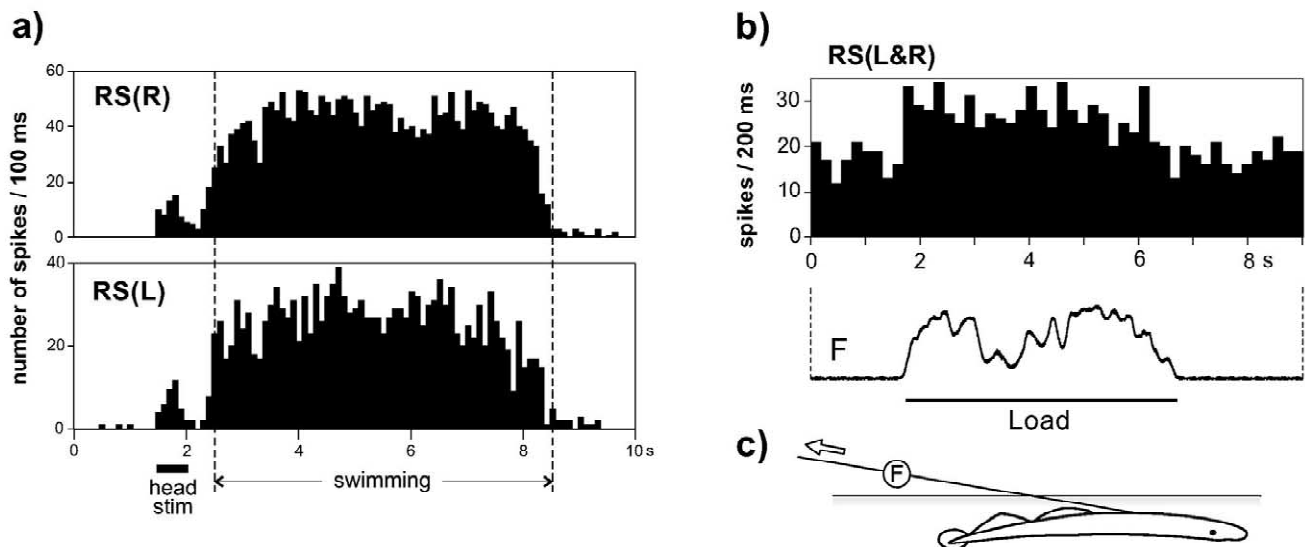

Fig. 1. Initiation of locomotion is always associated with a strong bilateral activation of the RS system. (a) Massive activation of the right and left RS pathways was evoked by tactile stimulation of the head in the intact lamprey and recorded by the electrodes implanted in the spinal cord. The high RS activity was accompanied by swimming. (b) Summated mass activity in the left and right RS pathways increased along with the force (*F*) applied to the swimming lamprey when the lead attached to the animal was stretched. The method of loading the lamprey is shown in (c) (*F*, force-to-voltage transducer). From Ref. [11].

[1,20], and bath application of the excitatory amino acids evokes swimming in a dose-dependent manner [17], it seems most likely that the bilateral RS activity is responsible for the activation of spinal networks generating the locomotory rhythm, and for regulation of the vigour of locomotion.

2.2. Commands for lateral turns

In the intact swimming lamprey, lateral turns are associated with an asymmetry in the bilateral mass RS activity, the activity on the ipsilateral (to a turn) side being higher than that on the opposite side [11]. This is illustrated in Fig. 2a, where a 90° turn to the right, caused by a strong activation of body musculature on the right side, was accompanied by a stronger activity in the right RS pathways. However, the asymmetry, that is the ratio of activities in the ipsilateral (to a turn) and contralateral RS pathways was not large (Fig. 2b). To explain how this small asymmetry can cause a substantial body flexion, it was suggested [15] that the initial asymmetry in descending RS commands is amplified by the system of reciprocal inhibition between the spinal hemi-segments. Evidence in favor of this hypothesis has been obtained in experiments with bilateral stimulation of RS pathways. It was found that a small difference between the two stimuli causes a dramatic asymmetry in the spinal motor output [15].

Intracellular recording from individual RS neurons during 'fictive' lateral turns in the semi-intact preparation has revealed the population of neurons activated during the ipsilateral turns and inhibited during the contralateral turns [16]. This population might be responsible for creating the

asymmetry in the mass activities of the left and right groups of RS neurons necessary for lateral turns.

2.3. Commands for postural corrections

A normal postural orientation of the swimming lamprey (horizontal, dorsal side up) is maintained due to vestibular reflexes [3,30]. To change its orientation in the sagittal (pitch) plane, the lamprey performs body flexion in this plane. To change its orientation in the transverse (roll) plane, the lamprey uses a set of movements including bending of the ventrally deviated tail, lateral tilt of the dorsal fins, and body twisting [30]. All these movements are caused by RS commands. These commands were initially studied in the in vitro preparation [7]. More recently we have also recorded these commands in intact animals by means of chronically implanted electrodes [6,24]. Fig. 3a,b shows an experimental design for rotating the intact animal in the roll plane. Fig. 3c,d shows the activity (percent of simultaneously active neurons) for the right and left groups of RS neurons, respectively. The patterns of response in the left and right RS neurons were substantially different and reciprocal to each other. The left neurons were activated with the right tilting, and the right neurons were activated with the left tilting. Each group had a peak activity at ~90° of the contralateral tilt.

Similar in vitro [7] and in vivo [24] experiments have shown that, when tested by pitch tilts (Fig. 4a), the RS neurons also fall into two categories with reciprocal vestibular responses—the group UP was activated by the nose-up rotation with a peak response at 45–90° of the nose-up tilt, and the group DOWN was activated by the
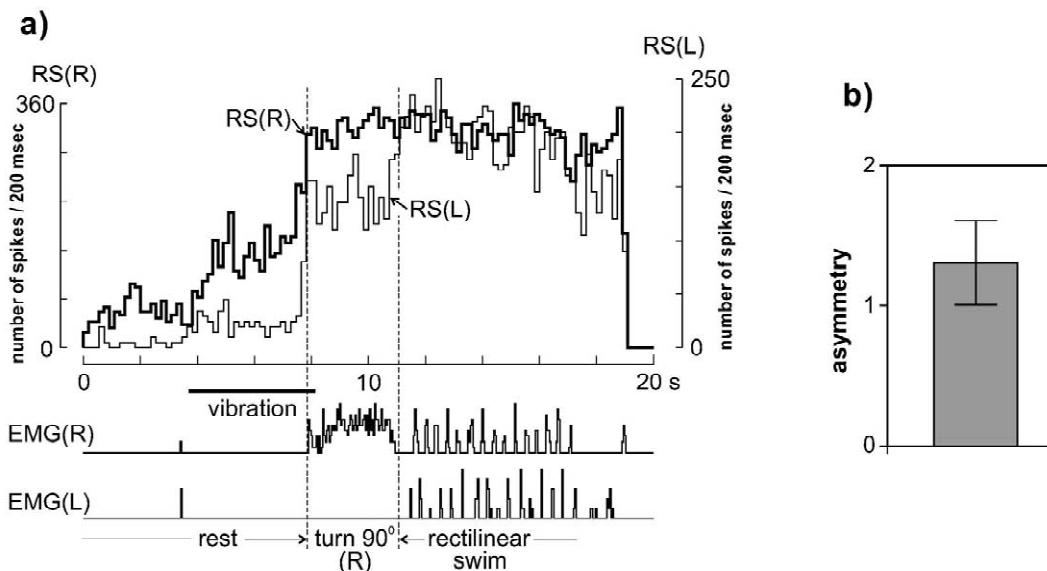

Fig. 2. Lateral turns are accompanied by an asymmetry in the activities of the left and right RS pathways. (a) Temporal histograms of RS(R) and RS(L) activity, and bilateral EMGs. During turn to the right in the intact lamprey (see EMG activity), the activity in the right RS pathway is higher than in the left one. (b) The degree of asymmetry, that is the ratio of the normalized activities on the ipsilateral and contralateral sides, averaged over seven turns (±S.D.). From Ref. [11].
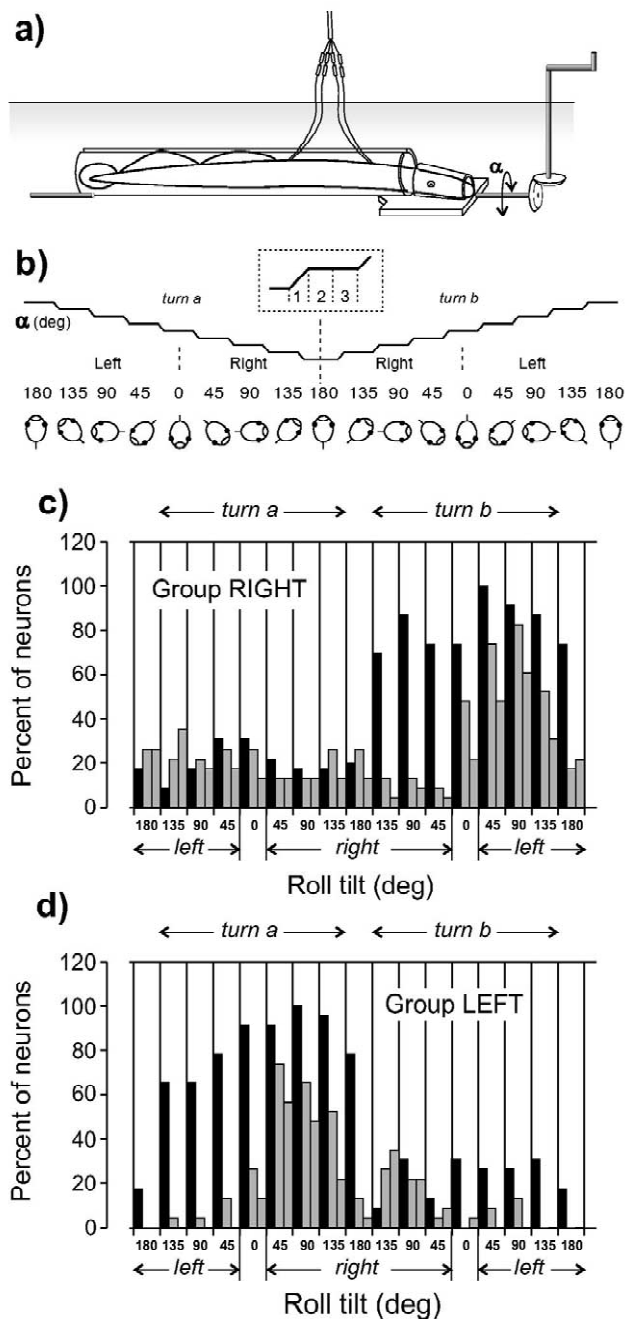
Fig. 3. Responses of RS neurons to roll tilt. (a) Experimental device (α, roll tilt angle). (b) Method of vestibular stimulation. Two sequential full turns (*a* and *b* clockwise and counterclockwise) were performed in 45° steps, starting from the dorsal-side-down position (180°). Duration of each step was ~4 s. Successive positions of the animal in each step in relation to the direction of gravity force are shown. (c,d) Summary of responses to full turn rotation in the right (c) and left (d) groups of RS neurons. The responses were characterized by the relative number (%) of active neurons as a function of roll angle. Each step of rotation was divided into three intervals (see inset in (b)), and the number of active neurons was calculated for each of the intervals and then divided by the total number of recorded cells ($n = 23$ for (c) and $n = 24$ for (d)). In each of the angular steps, the dynamic response (activity during rotation) is shown by a black bar; the early and late static responses by two successive shaded bars. From Ref. [6].

nose-down rotation with a peak response at 45–90° of the nose-down tilt (Fig. 4b,c).

These data allow us to suggest that turn in a given plane is caused by an asymmetry in the activities of the antagonistic groups of RS neurons. In contrast, a rectilinear swimming seems to require symmetrical activity of these antagonistic groups, and the level of this activity determines the vigour of locomotion.

3. Overlap of descending command systems

The RS system in the lamprey is practically the only descending system to transmit different motor commands to the spinal cord. This raises two questions.

(1) When the same motor pattern is used in different behavioral contexts, or is evoked by different sensory stimuli, are the corresponding motor commands transmitted by the same sub-population of RS neurons or by different sub-populations? An answer to this question for one particular case has been obtained in recent experiments [6]. It was found that the same sub-population of RS neurons is activated by two different stimuli, that is by eye illumination and by roll tilt. These two stimuli evoke similar motor patterns—rotation around the longitudinal body axis, but in very different forms of behavior, that is the dorsal light response [31] and postural corrections [30], respectively.

(2) To what extent do the same RS neurons participate in the generation of commands for different types of movements? One extreme would be that different commands involve separate, non-overlapping sub-populations of RS neurons; the other extreme would be that all RS neurons are active to some degree during all types of movements. A full answer to this question could be obtained if the same neurons were recorded during all forms of behavior, which is a difficult experimental task. However, some data on this issue have been obtained,. These data indicated that the sub-populations of RS neurons, causing different forms of motor behavior, partly overlapped. First, it was found that a substantial part of RS neurons (27%) responding to pitch tilt also responded to roll tilt (Pavlova and Deliagina, unpublished data). These data indicate that the RS command systems for postural stabilization in the two vertical planes, that is the sagittal and transversal ones, partly overlap. Second, it was found that the same RS neurons respond faithfully to roll tilt, to efference copy signals from the spinal locomotor CPG, and are activated during initiation of locomotion [11]. These data suggest an overlap between the RS command systems for initiation of locomotion and for postural stabilization. Third, systematic intracellular recording of the responses of RS neurons to stimulation of the MLR have shown that all recorded RS neurons, to a larger or smaller extent, receive excitatory locomotion-related input (Dubuc, personal communication). Fourth, stimulation of individual
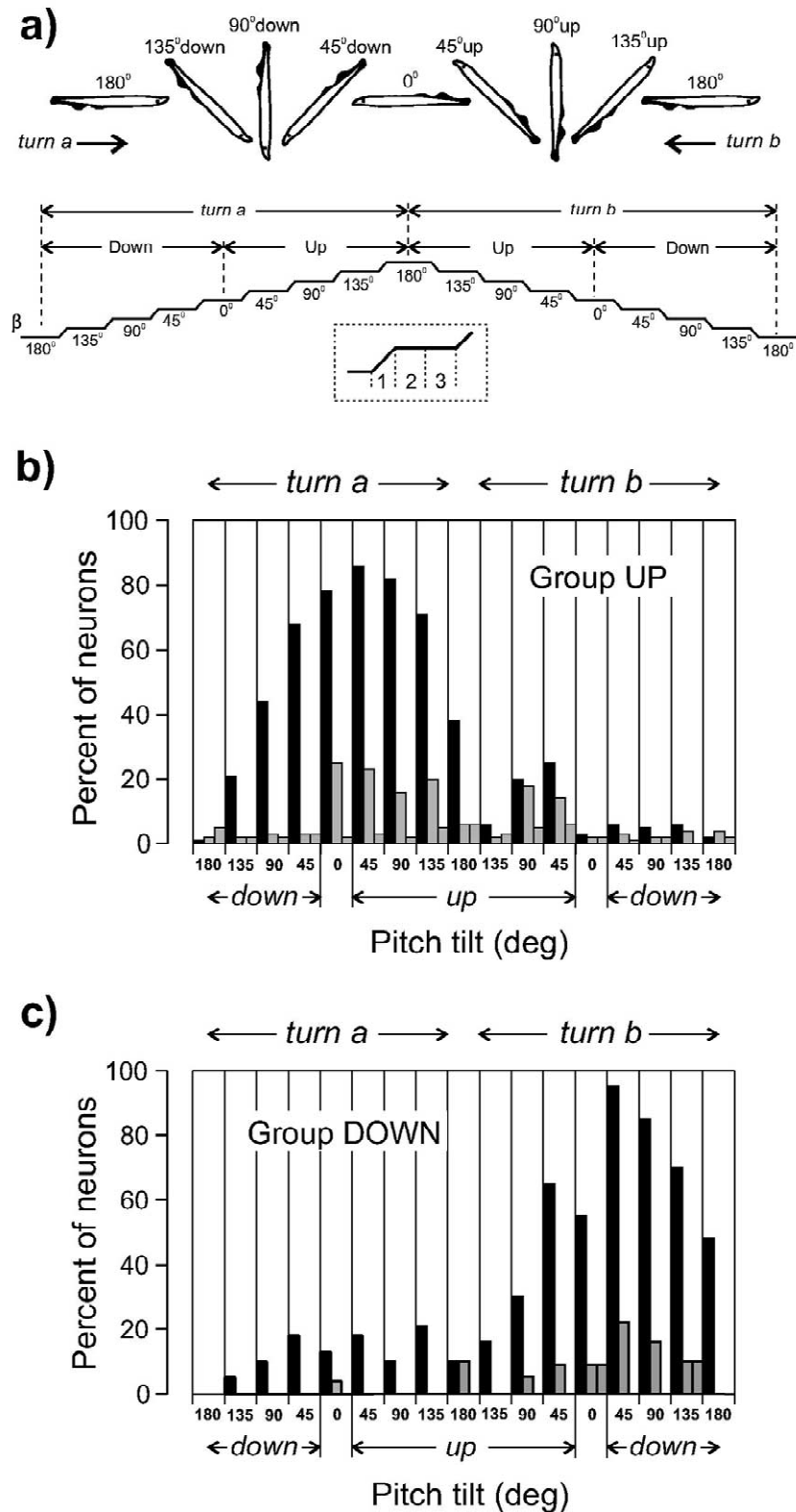
Fig. 4. Responses of RS neurons to pitch tilt. (a) Method of vestibular stimulation (β, pitch tilt angle). Two sequential full turns (*a* and *b*, clockwise and counterclockwise) were performed in 45° steps. Duration of each step was ~4 s. Successive positions of the animal in each step in relation to the direction of gravity force are shown for *turn a* (from left to right) and for *turn b* (from right to left). Vestibular responses were measured separately for each of the three intervals of a step (inset in (a)). (b,c) Summary of responses to full turn rotation in the group UP ($n=142$) (b) and in the group DOWN ($n=29$) (c) of RS neurons (see legend to Fig. 3 for further details).

RS neurons during fictive swimming affected both the locomotor frequency and the symmetry of segmental motor output [2,16]. These data taken together indicate that the sub-populations of RS neurons causing different forms of motor behavior partly overlap, which suggests that special mechanisms in the spinal cord are needed to decode RS commands and avoid their miss-interpretation (see below).

4. Decoding of RS commands

We suggest that decoding of RS commands in the spinal cord is based on two principles. (1) The commands for initiation of locomotion and regulation of its vigour, encoded as the value of bilateral RS activity, are decoded by integrating all RS signals arriving to the spinal locomotor networks, so that their integrated value determines the level of activity of these networks. (2) The commands for turns in different planes, encoded as an asymmetry in the activities of specific subdivisions of the RS system, are decoded by comparing these activities, so that their difference determines the direction and magnitude of the turn.

The idea of subtracting two RS signals was initially formulated for the postural system stabilizing body orientation in the transverse (roll) plane [5,7–9,6]. Fig. 5a shows a conceptual model of the roll control system based on this principle. The key elements of the model are two groups of RS neurons, the left (RS(L)) and the right (RS(R)). It is known that the main input to these neurons is the excitat-
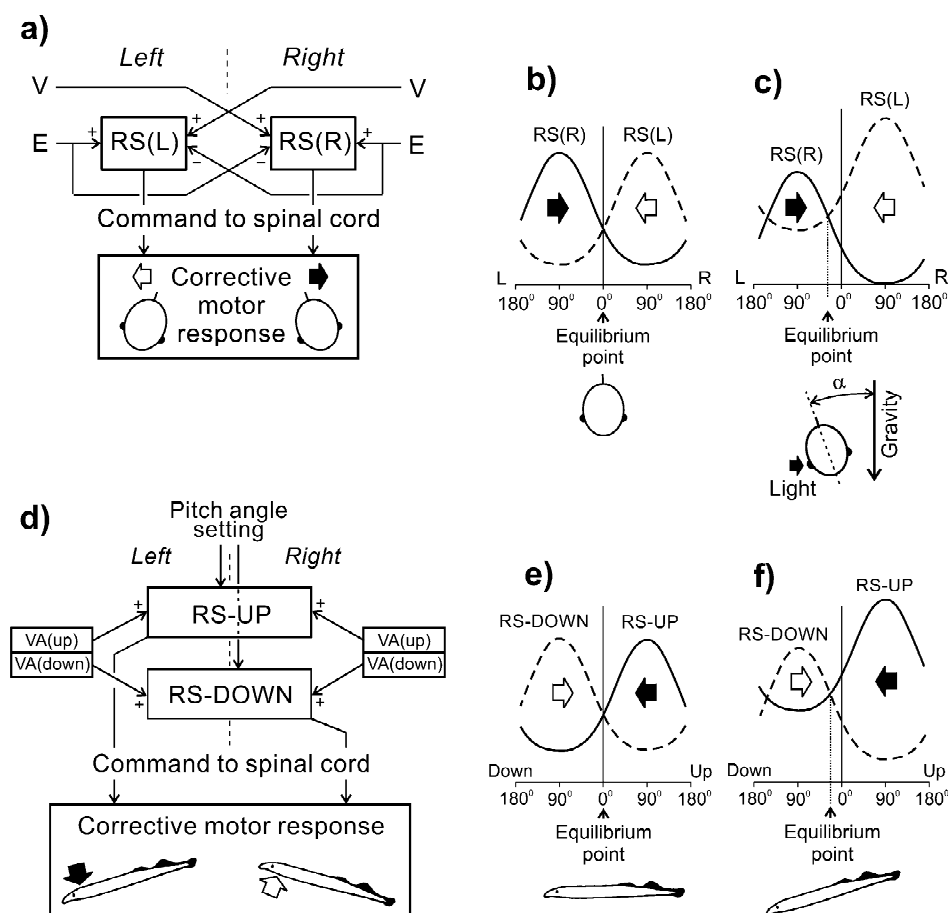

Fig. 5. Conceptual models of the roll and pitch postural systems. (a–c) Roll control system. (a) Right and left groups of RS neurons, RS(R) and RS(L), receive inputs from the labyrinths (V) and eyes (E); they affect spinal networks to evoke rolling of the lamprey. (b) Operation of the system when driven only by vestibular input. The curves represent activity in RS(R) and RS(L) as a function of roll angle. Vestibular input causes activation of RS(R) and RS(L) with the contralateral tilt. Directions of rolling caused by RS(R) and RS(L) are indicated by the large black and white arrows, respectively. The system has an equilibrium point at 0° (dorsal-side-up orientation). (c) Operation of the system when the left eye is illuminated. This visual input causes a shift of the equilibrium point to the left and corresponding tilt of the animal (inset). (d–f) Pitch control system. (d) UP and DOWN groups of RS neurons receive inputs from the corresponding vestibular afferents, VA(up) and VA(down); they affect the spinal networks to evoke pitch tilt of the lamprey. (e) Operation of the system when stabilizing a horizontal orientation. The curves represent activity in UP and DOWN groups as a function of pitch angle. Vestibular input causes activation of UP neurons with nose-up tilt, and DOWN neurons with nose-down tilt. Directions of turning in the sagittal plane caused by UP and DOWN neurons are indicated by the large black and white arrows, respectively. The system has an equilibrium point at 0° (horizontal orientation). (f) Operation of the system when the UP group has an additional excitatory input. This results in a shift of the equilibrium point toward the downward tilts.

ory one from the contralateral labyrinth. Due to this input, the activity of RS neurons is orientation-dependent, with its peak at around 90° of the contralateral roll tilt (Figs. 3c,d and 5b). The two groups also receive an excitatory input from the ipsilateral eye and an inhibitory input from the contralateral eye [6]. It is assumed that each of the groups, via spinal mechanisms, elicits ipsilateral rotation of

the lamprey (indicated by large black and white arrows in Fig. 5a–c). The system will stabilize an orientation in space with equal activities of RS(L) and RS(R), which occurs at the dorsal-side-up position (*equilibrium point* in Fig. 5b). The model could also explain the origin of the dorsal light response, that is a roll tilt towards the illuminated eye (inset in Fig. 5c). Illumination of an eye
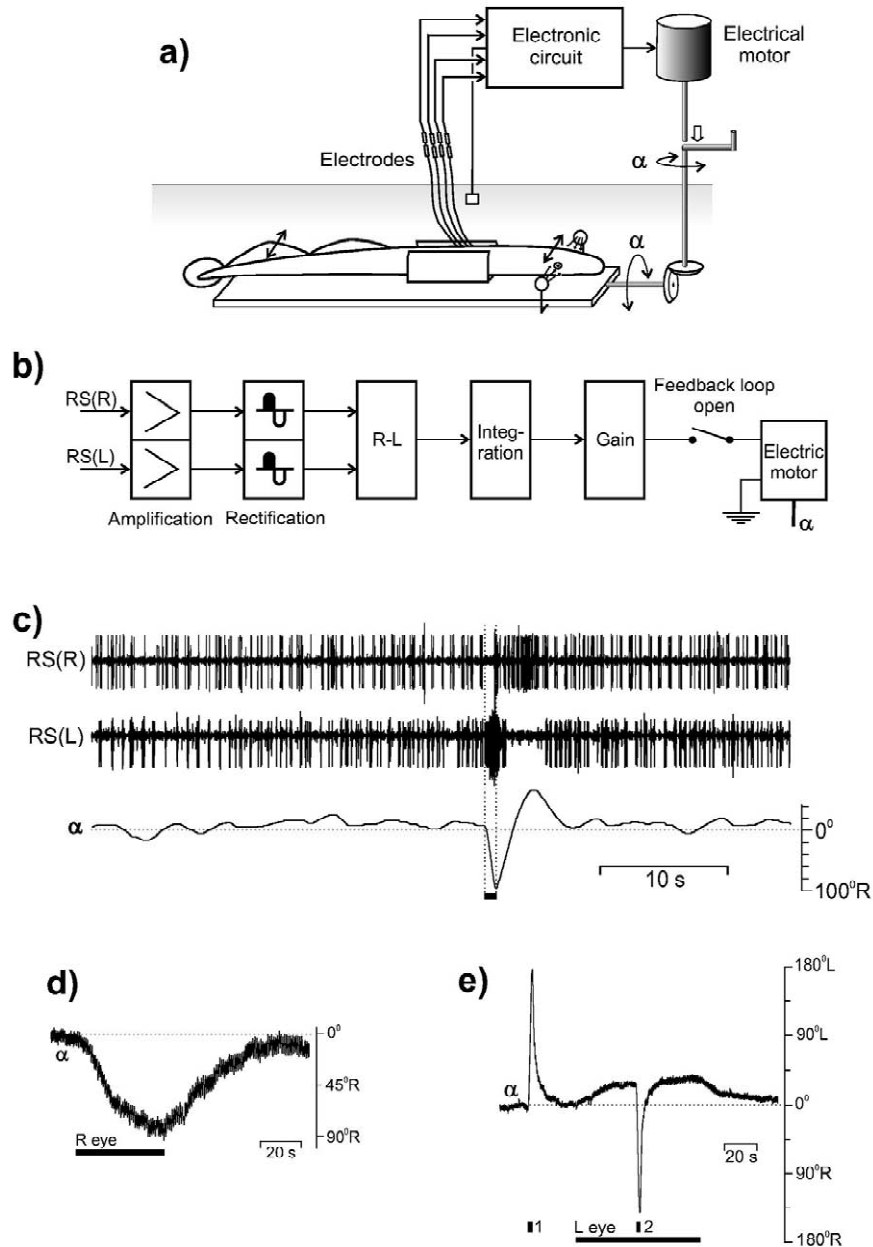

Fig. 6. A study of postural control with a neuro-mechanical model. (a) Experimental setup. The animal was mounted on a platform. The mid-body area was attached to the platform, whereas the anterior and posterior parts could perform locomotor undulations (shown by bilateral arrows). The platform could be rotated in the roll plane (α) by the electric motor. The motor was controlled by the signals (activities in the left and right RS pathways, RS(L) and RS(R) recorded by implanted electrodes and processed by the electronic circuit shown in (b). Each of the eyes could be illuminated separately. (c) Stabilization of the dorsal-side-up orientation during 'locomotor' activity. Activities in the right and left RS pathways are shown together with roll angle. A horizontal bar indicates the period when the loop was opened, and a 90° tilt was produced by the experimenter. (d,e) Simulation of the dorsal light response. (d) In response to illumination of the right eye the system tilts to the right. (e) Postural corrections under two light conditions. With no eye illumination, the system stabilizes the dorsal-side-up orientation (0°). With left eye illumination the system stabilizes the tilted position (35°). Markers indicate imposed postural deviations, 180° left (1) and 180° right (2). From Ref. [33].

causes an additional excitation of the ipsilateral RS neurons and inhibition of the contralateral ones; this will result in a shift of the equilibrium point of the system towards the illuminated eye and in a corresponding tilt of the animal (Fig. 5c).

The 'subtraction' hypothesis can also explain postural stabilization in the pitch plane. Fig. 5d shows a conceptual model of the pitch control system based on this principle. The key elements of the model are the UP and DOWN groups of RS neurons driven by vestibular inputs, with
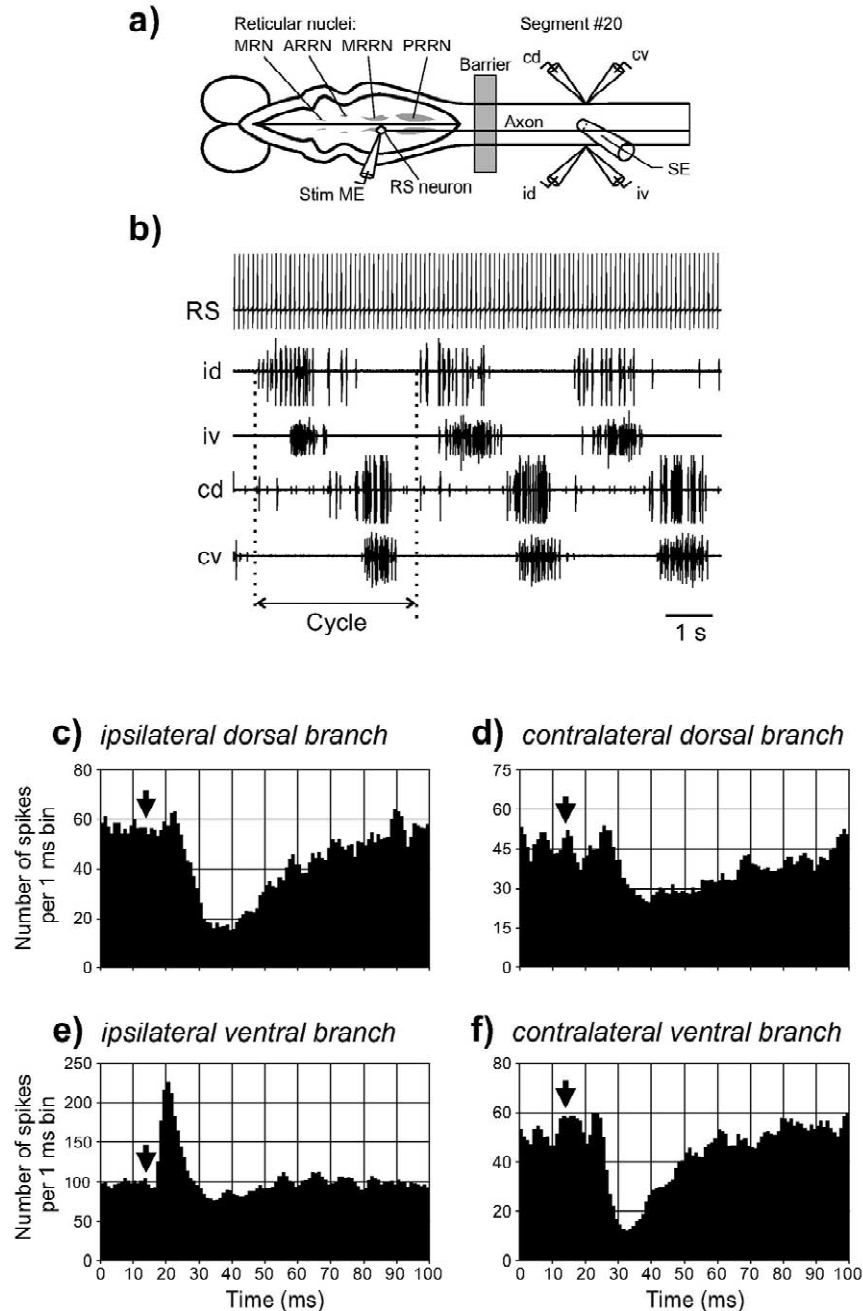

Fig. 7. A study of motor effects of individual RS neurons. (a) Experimental design for studying segmental functional projections of RS neurons. The brain stem and spinal cord were positioned in a chamber divided by a barrier. The spinal cord was perfused with a Ringer solution containing D-glutamate to elicit fictive locomotion. Individual reticulospinal (RS) neurons were recorded from different reticular nuclei. To stimulate a neuron, current pulses were passed through the recording intracellular electrode (Stim ME). Activity of MNs was recorded bilaterally in the segment #20 by suction electrodes, from the dorsal and ventral branches of a ventral root (id, ipsilateral dorsal branch; iv, ipsilateral ventral; cd, contralateral dorsal; cv, contralateral ventral). An RS spike arriving to segment #20 was recorded by a surface electrode (SE). (b) Fictive locomotion was monitored by the MN discharges in four branches of ventral roots; they were recorded along with the responses of RS neuron to 10 Hz stimuli. (c–f) An example of the pattern of segmental response. An RS neuron from MRRN-evoked excitation of MNs in the ipsilateral ventral branch and inhibition in the three other branches. Each histogram presents the RS spike-triggered averaging of 3000 individual responses, with a bin width of 1 ms. From Ref. [34].

reciprocal responses to rotation in the sagittal plane (Figs. 4b,c and 5e). It is assumed that group UP elicits rotation of the lamprey downward, whereas group DOWN elicits rotation upward (indicated by large black and white arrows in Fig. 5d–f). The system will stabilize an orientation in space with equal descending effects of the UP and DOWN groups, which normally occurs at the horizontal orientation of the animal. A support for the 'subtraction' hypothesis was obtained when testing the effects on the UP and DOWN groups produced by an increase of temperature, which presumably causes swimming of the lamprey toward the deeper water layers. It was found that raising the temperature caused a change of the ratio between the UP and DOWN responses, so that the UP group prevailed over the DOWN group [24]. This will result in a shift of the equilibrium point of the system toward the downward pitch angles (Fig. 5f), and in a corresponding tilt of the animal.

Additional support for the 'subtraction' hypothesis was obtained in experiments on a neuro-mechanical model [33]. In these experiments, the lamprey was deprived of the ability to change its postural orientation by itself. It was positioned in a setup that could be rotated by an electrical motor in the transversal (roll) plane of the animal (Fig. 6a). Discharges in the left and right RS pathways were recorded separately by implanted electrodes in the spinal cord. Signals from the electrodes were processed by an electronic circuit (Fig. 6b) and used to control the motor. The direction of rotation was determined by the prevailing (left or right) signal. Thus, the spinal networks together with the locomotor organs were replaced by a robotic system. It was found that the system stabilized the orientation of the lamprey close to the normal one (dorsal side up); any disturbance of the postural orientation was rapidly rapidly compensated by the system (Fig. 6c).

Illumination of one eye evoked a roll tilt towards the illuminated eye (Fig. 6d), i.e., the behavior (dorsal light response) observed in freely behaving animals (Fig. 5c, inset). Both the initial position (no tilt) and the new, tilted position were actively stabilized by the system, as demonstrated by perturbing the postural equilibrium (Fig. 6e). One can thus conclude that visual input causes a shift of the equilibrium point in the vestibular-driven postural control system. Thus, the model based on the subtraction of the left and right RS signals was able to reproduce important characteristics of the roll control system. A possible site for the subtraction of contralateral RS signals is the segmental network with its system of reciprocal inhibition between the two hemisegments [15]. A different possible site is the effector organs (left and right myotomes) opposing each other.

5. Motor effects of individual RS neurons

A weakness of our models of postural control is that the motor effect of RS neurons was hypothesized rather than

determined experimentally. The effects of signals transmitted from the brain to the spinal networks by a population of RS neurons are determined by specific functional projections of individual neurons. In higher vertebrates, these projections are difficult to reveal [13]. We have found that, in the lamprey, motor effects of individual RS neurons can be detected by averaging the responses of spinal motoneurons (MNs) to spikes generated by in-
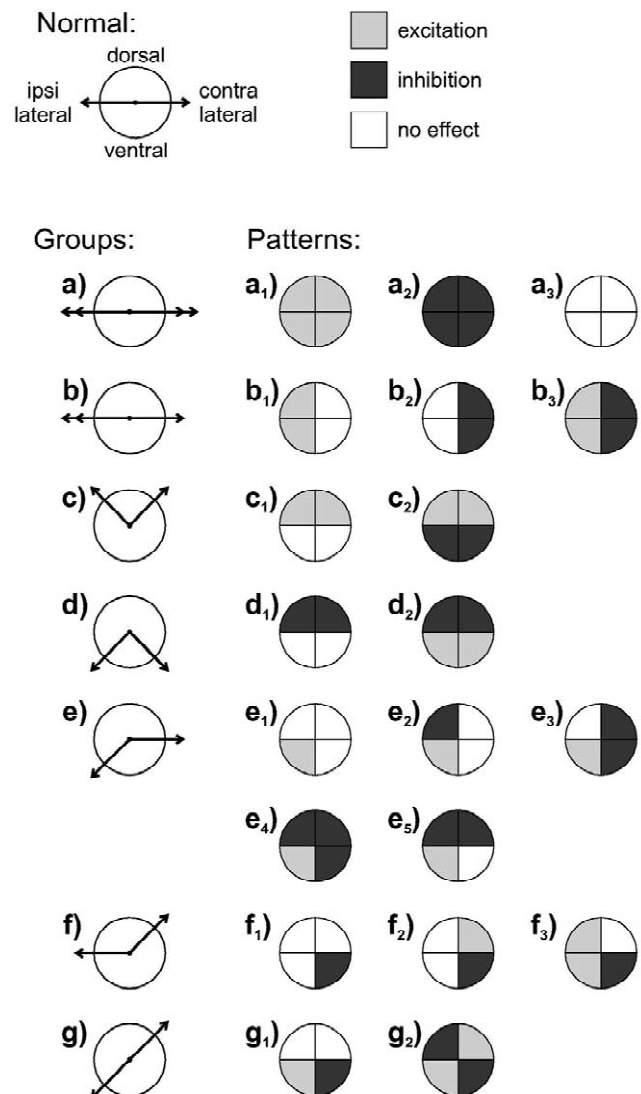

Fig. 8. Patterns of segmental responses to stimulation of 60 individual RS neurons. The patterns were defined as the combinations of responses (excitation, inhibition, no effect) in the four VR branches of segment #20. The patterns were classified into seven groups (a–g) according to their presumed effect on the segmental motor output in the two hemicycles of the locomotor cycle, that is when the ipsilateral MNs are active and when the contralateral MNs are active (an RS neuron is suggested to be active in both hemicycles). The directions of flexion of the segment in these hemicycles are shown by two vectors, respectively. During normal swimming, both vectors are horizontal and of equal magnitude (Normal). Due to the RS influences, each of the two flexions can change its magnitude (denoted by a double-arrowhead) or direction (denoted by an inclination of the vector). From Ref. [34].

dividual RS neurons [34]. In a brainstem–spinal cord preparation (Fig. 7a), fictive locomotion was evoked by applying D-glutamate to the spinal cord. Individual RS neurons were stimulated repeatedly by the intracellular microelectrode. During this stimulation, discharges of all active MNs from dorsal and ventral branches of the ventral roots, which innervate the dorsal and the ventral parts of the myotome, correspondingly, were recorded bilaterally in segment #20 (Fig. 7b). For each individual RS neuron, a post-RS spike histogram was generated for the spikes of all MNs recorded simultaneously in each of the four ventral root branches. It was found that individual RS neurons exerted diverse influences on the segmental motor output. Fig. 7c–f shows the effects produced by one of RS neurons which caused excitation of MNs in the ipsilateral ventral branch and inhibition of MNs in all other branches. The RS neurons produced their effect on the motor output only during the bursts of MN activity caused by the spinal

locomotor CPG. In other words, the efficacy of RS commands was phase-dependent, a phenomenon observed earlier in walking cats [12,22].

Altogether, 20 patterns of influences have been revealed among 60 recorded RS neurons (Fig. 8), they differed in the combination of influences (excitation, inhibition, no effect) on the four MN pools supplying the four muscular groups in the spinal segment. These patterns can be classified into seven groups (Fig. 8a–g) according to the presumed direction of body flexion in the two hemi-cycles of the locomotor cycle, provided the RS neurons are firing in both hemi-cycles, that is, when the ipsilateral or contralateral MNs are active (as in Fig. 7b). It is known, however, that the activity of a large proportion of RS neurons in the lamprey is rhythmically modulated in relation to the locomotor cycle. This modulation is caused by the internal feedback signals coming from the spinal locomotor networks [11,14,18]. The phase-dependent
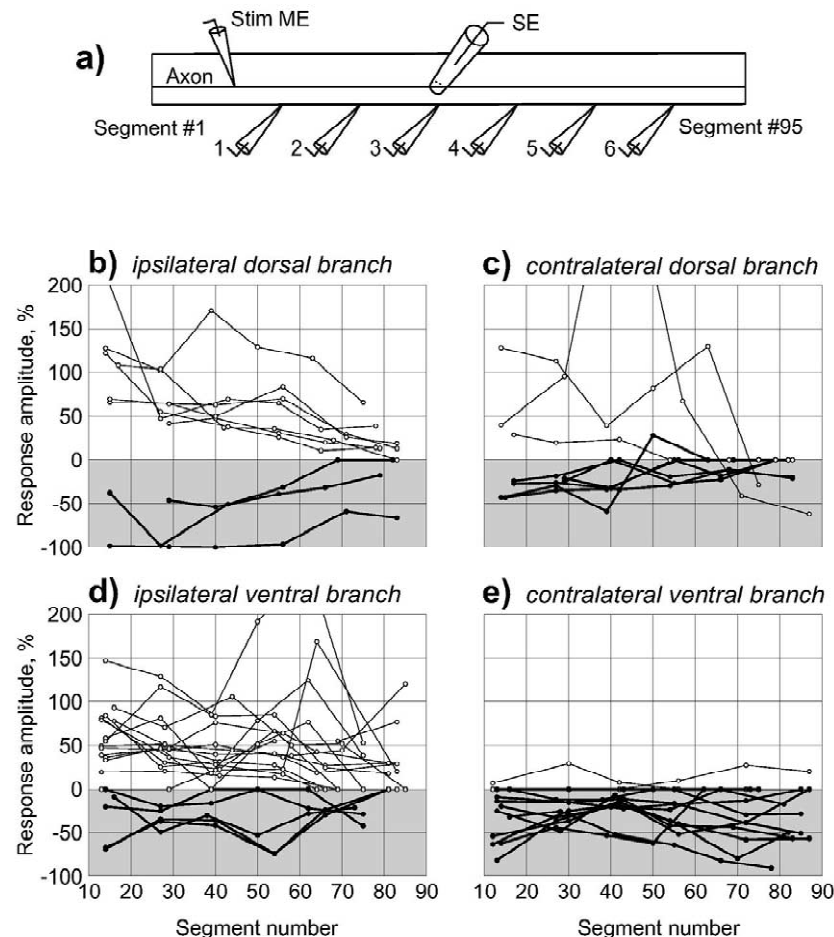

Fig. 9. Longitudinal distribution of RS functional projections. (a) Experimental design for studying the longitudinal functional projections of RS neurons. The spinal cord was positioned in a chamber and perfused with a Ringer solution containing D-glutamate to elicit fictive locomotion. Individual RS axons were stimulated with positive current pulses through the recording intracellular electrode (Stim ME). Activity of MNs was recorded from six analogous ventral root branches along the spinal cord by means of suction electrodes (1–6). An RS spike propagating along the spinal cord was recorded by a surface electrode (SE). (b–e) Longitudinal distribution of effects for 44 RS axons. For each RS axon, the relative amplitude of response, that is the maximal deviation (in percent) of the summated MN activity from the level observed before the occurrence of the response, is shown for all sites of recording. Positive and negative values represent the excitatory and inhibitory responses, respectively. The data points for individual axons are connected by lines; thin lines and open circles indicate the axons with exclusively (or prevailing) excitatory influences; thick lines and filled circles—those with exclusively (or prevailing) inhibitory influences. From Ref. [34].

modulation of RS neurons was also observed in the walking cat [13,21]. It seems likely that the phase-dependent modulation of these commands, combined with the phase-dependent modulation of the efficacy of RS commands (see above), allows for a fine control of the spinal motor output [25].

The longitudinal distribution of the functional projections of individual RS neurons were studied with the experimental design shown in Fig. 9a. In the spinal cord preparation, fictive locomotion was evoked by D-glutamate, individual RS axons were stimulated, and MN responses were recorded from analogous branches of the ventral roots at different levels of the spinal cord. It was found that the pattern of influences of each particular RS neuron was consistent along the whole extent of its axon. Fig. 9b–e shows the sign (excitation or inhibition) and the amplitude of the response in analogous branches of the ventral roots (ipsilateral dorsal, ipsilateral ventral, etc.) evoked at different rostro-caudal levels by stimulating 44 individual RS axons. These findings strongly suggest that the data on functional projections of individual RS neurons, obtained for segment #20 and summarized in Fig. 8, are applicable to other segments along the whole extent of RS axons. One can thus conclude that individual RS neurons cause flexion of a considerable part of the body in a definite plane. It seems likely however, that individual RS neurons can differentially affect different areas along the cord due to a phase-dependent modulation of the RS signals [11,14,18] and gating of the RS signals in the spinal networks.

A great diversity of the patterns of functional projections of RS neurons (Fig. 8) allows the RS system to evoke body flexion in any plane, especially if RS neurons with different projections are co-activated. Since most neurons have asymmetrical projections one can suggest that, for elicitation of the rectilinear swimming, RS neurons with opposite asymmetrical effects are co-activated. However, to understand the relationships between the RS commands and their motor effects, one has to correlate the projection patterns of individual neurons with the type of command they transmit, which is the goal of our future studies.

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