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Comparison of the Motor Effects of Individual Vestibulo- and Reticulospinal Neurons on Dorsal and Ventral Myotomes in Lamprey

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Zelenin, P. V., E. L. Pavlova, S. Grillner, G. N. Orlovsky, and T. G. Deliagina. Comparison of the motor effects of individual vestibulo- and reticulospinal neurons on dorsal and ventral myotomes in lamprey. *J Neurophysiol* 90: 3161–3167, 2003. First published August 13, 2003; 10.1152/jn.00555.2003. In the lamprey (a lower vertebrate), motor commands from the brain to the spinal cord are transmitted through the reticulospinal (RS) and vestibulospinal (VS) pathways. The axons of larger RS neurons reach the most caudal of approximately 100 spinal segments, whereas the VS pathway does not descend below the 15th segment. This study was carried out to compare functional projections of RS and VS neurons in the rostral spinal segments that the neurons innervate together. To reveal these projections, individual RS or VS neurons were stimulated, and the responses of different groups of spinal motoneurons were recorded in ventral root branches to dorsal and ventral parts of myotomes. The responses were detected using a spike-triggered averaging technique on the background of ongoing motoneuronal activity. Individual RS and VS neurons exerted uniform effects on segmental motor output within this rostral part of the spinal cord. The effects of VS neurons on different groups of motoneurons were weaker and less diverse than those of RS neurons. The results indicate that VS neurons are able to elicit a flexion of the rostral part of the body and to turn the head in different planes without affecting more caudal parts. By contrast, larger RS neurons can elicit head movement only together with movement of a considerable part of the body and thus seem to be responsible for formation of gross motor synergies.

INTRODUCTION

Movements of the head in relation to the trunk is an essential component of many forms of behavior in vertebrates. In the lamprey (a lower vertebrate, cyclostome), like in fish with undulatory swimming movements (Grillner and Kashin 1976), lateral head movements are followed by locomotor waves propagated caudally along the body. Head movements in the frontal and sagittal planes constitute a part of the gross motor synergies underlying turning in the whole animal in the corresponding planes and are used for steering during locomotion (Archambault et al. 2001; Fagerstedt and Ullén 2001; Fagerstedt et al. 2001; Ullén et al. 1993, 1997). Finally, head movements in different planes are associated with exploratory behavior (Archambault et al. 2001; Deliagina et al. 1995).

In all vertebrates, head movements are caused by a flexion of the vertebral column in the anterior (neck) region of the body due to a contraction of muscles around the column. In higher vertebrates, the neck muscular system is organized in a complex way allowing flexion and rotation of the vertebrae in relation to each other (see Hebel and Stromberg 1986; Richmond and Bakker 1982). The nervous control of the neck muscles is organized through several central and reflex mechanisms (e.g., Goldberg and Peterson 1986; Magnus 1924; Peterson et al. 1985; Schor et al. 1988).

In the lamprey, the muscular system causing head movements is relatively simple and similar to that in the rest of the body. At each rostrocaudal level within the gill region (approximately 12 rostral segments), there are four principal movers, i.e., the dorsal and ventral parts of each myotome on the two sides of the body. Each part, when contracting alone, causes an oblique body flexion. For a lateral flexion, the dorsal and ventral muscles on the corresponding side have to be activated together; for flexion in the sagittal plane, dorsal or ventral muscles on both sides have to be activated. These four muscle groups are innervated by separate motoneuron pools (Fig. 1, *A* and *B*) (Rovainen 1979; Tretjakoff 1927; Wallén et al. 1985; Wannier et al. 1998).

In the lamprey, commands from the brain to the motoneurons (MNs) of the rostral region of the spinal cord are transmitted by two descending pathways—the reticulospinal (RS) and vestibulospinal (VS) pathways. The RS system is organized in four reticular nuclei [the mesencephalic reticular nucleus (MRN) and the anterior, middle, and posterior rhombencephalic reticular nuclei (ARRN, MRRN, and PRRN, respectively); Fig. 2*A*] (Brodin et al. 1988; Bussières 1994; Nieuwenhuys 1972; Ronan 1989). In each nucleus, both large ($d > 40$ μm) and medium neurons ($d = 20–40$ μm) have long axons extending to the middle and even caudal areas of the spinal cord (Fig. 1*A*) (Bussières 1994). We have previously shown that each RS neuron elicits a specific combination of excitatory and inhibitory effects on the four compartments of right and left myotomes. The same combinations of effects are evoked along the length of the spinal cord as investigated in segments 12–88 (Zelenin et al. 2001a). The aim of this study was to explore, in the same way, the functional projections of individual RS and VS neurons to the "neck" region (segments 1–12).

The VS system in the lamprey differs markedly from the RS system. It includes 100–150 VS neurons with ipsilateral axons located in each of the two bilateral intermediate octavomotor nuclei (ION). A smaller proportion of VS neurons (about 65) reside in each of the two posterior octavomotor nuclei (PON).

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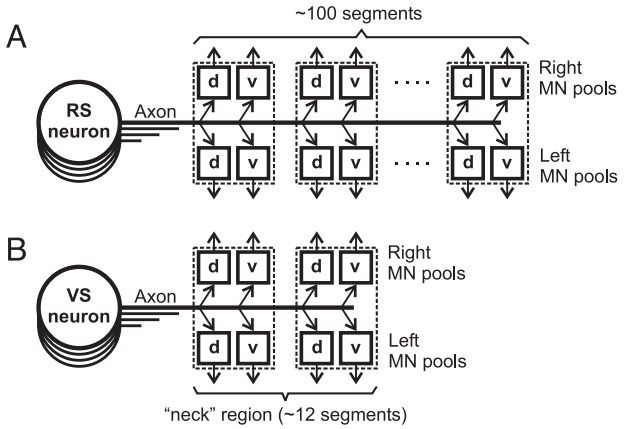

FIG. 1. Two components of the descending command system in the lamprey. Segmental motor output is generated by 4 motoneuron (MN) pools controlling the dorsal and ventral parts of a myotome on the 2 sides (*d* and *v* pools). Neurons of descending systems may exert their effect on the pools directly or through interneurons. *A*: larger reticulospinal (RS) neurons have long axons that can reach the caudal spinal segments. *B*: axons of vestibulospinal (VS) neurons are confined to the rostral spinal segments.

They give rise to a contralateral (crossed) VS pathway (Bussières et al. 1999). The axons of VS neurons are short and do not descend below the 10–15 most rostral segments (Fig. 1*B*). The VS neurons receive a strong monosynaptic input from primary vestibular afferents (Bussières and Dubuc 1992; Stefanelli and Caravita 1970) and can excite motoneurons in the rostral spinal segments (Rovainen 1979). In this study, we investigated functional projections of individual VS neurons located in ION. We show that individual RS neurons exert more powerful effects on the segmental muscle compartments than the VS neurons and that the RS and VS influences are uniform along the entire neck region.

A brief account of this study has been published in abstract form (Zelenin et al. 2001b).

METHODS

Experiments were performed on a brain stem–spinal cord preparation dissected from adult lampreys (*Ichthyomyzon unicuspis*, $n = 23$). All experiments were approved by the local ethical committee (Norra Djurförsöksetiska Nämnden). The brain stem was isolated together with 15–35 segments of the spinal cord. The preparation was pinned

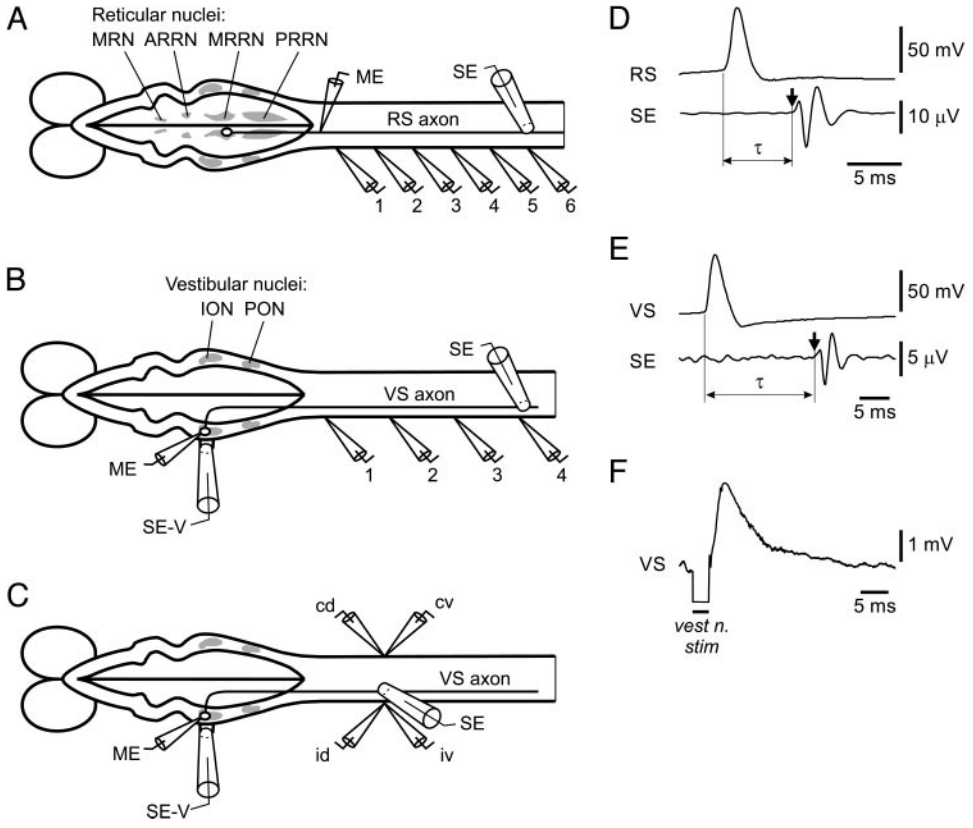

FIG. 2. Experimental designs for studying longitudinal functional projections of RS neurons (*A*), longitudinal functional projections of VS neurons (*B*), and segmental functional projections of VS neurons (*C*). The brain stem and spinal cord were positioned in a chamber and perfused with a Ringer solution containing D-glutamate to elicit fictive locomotion. Individual RS axons (*A*) or cell bodies of individual VS neurons from intermediate octavomotor nucleus (ION) (*B* and *C*) were stimulated with positive current pulses through the recording intracellular microelectrode (ME). Activity of MNs was recorded from ≤6 (*A*) or ≤4 (*B*) analogous ventral root branches along the spinal cord by means of suction electrodes. Alternatively, activity of MNs was recorded bilaterally in 1 of rostral segments by means of 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) (*C*). A spike propagating along the RS or VS axon was recorded by a surface electrode (SE) positioned on the spinal cord near the most caudal site of recording. In *B* and *C*, vestibular nerve was stimulated by a suction electrode (SE-V). *D*: intra- and extracellular recordings of the spike in the axon of an RS neuron. An arrow in this and following figures indicates arrival of the RS spike. Time of the spike propagation is designated as τ. *E*: recording of the spike in the soma of a VS neuron and in its axon in the spinal cord. An arrow in this and following figures indicates arrival of the spike. Propagation time is designated as τ. *F*: recording of the synaptic potential in the VS neuron evoked by stimulation of vestibular nerve (vest n. stim).

down in a chamber filled with Ringer solution containing (in mM) 91 NaCl, 2.1 KCl, 2.6 $CaCl_2$, 1.8 $MgCl_2$, 23 $NaHCO_3$, and 4 glucose. The solution was bubbled with 95% O_2-5% CO_2 to pH of 7.4. Three different series of experiments were performed (Fig. 2, *A–C*).

In the first series of experiments ($n = 6$), individual RS axons were recorded intracellularly in the first segment of the spinal cord by means of KAc-filled microelectrodes with a tip resistance of 10–30 MΩ (ME in Fig. 2*A*). Single spikes in an axon were evoked by positive current pulses (7- to 15-ms pulse duration, pulse period 100 ms, current ≤20 nA) passed through the microelectrode. Activity of spinal MNs was recorded extracellularly by suction electrodes from the analogous ventral root (VR) branches (ventral or dorsal branches on the side ipsilateral or contralateral to the stimulated neuron), at up to six sites (1–6 in Fig. 2*A*) along the rostral part of the spinal cord, starting at segments 1 or 2 and finishing at segments 19–22. Propagation of the RS spike along the axon was monitored by a suction electrode placed on the spinal cord surface (SE in Fig. 2*A*). Figure 2*D* shows a spike elicited in the RS axon by the current pulse and the spike recorded by the surface electrode with a delay τ, allowing estimation of conduction velocity.

In the second series of experiments ($n = 12$), individual VS neurons, located in the intermediate octavomotorius nucleus (ION in Fig. 2*B*) were recorded with a microelectrode (ME). Single spikes in a neuron were evoked by current pulses passed through the microelectrode (7- to 15-ms pulse duration, pulse period 100 ms, current ≤20 nA). Activity of spinal MNs was recorded from analogous VR branches (as above) at up to four sites (1–4) in the neck region (segments 1–9). Propagation of a VS spike along the axon was monitored with a suction electrode (SE) positioned near the most caudal site of recording. The vestibular nerve was stimulated with another suction electrode (SE-V). Each VS neuron was identified by the orthodromic spike recorded in the spinal cord by a suction electrode (Fig. 2*E*) and by the monosynaptic response to ipsilateral vestibular nerve stimulation (Fig. 2*F*).

Experiments of the third series ($n = 5$) were similar to those of the second series except that the activity of MNs was recorded bilaterally in one of the segments (from segments 3–5), by means of suction electrodes, from the dorsal and ventral VR branches (Fig. 2*C*).

In these three sets of experiments, D-glutamate (0.5–1 mM) was applied to activate the spinal locomotor networks (fictive swimming) (Grillner et al. 1981, 1995). The fictive locomotion provided a background activity of motoneurons that could be affected by the spikes of individual RS and VS neurons. For each individual RS or VS neuron, a postspike histogram (bin width, 1 ms) was generated for the spikes of MNs recorded in each VR branch (Fig. 3). The moment of RS or VS spike occurrence in the cell body was taken as the origin of the time axis in the histogram. Typically, responses to a few thousands of RS or VS spikes (≤20 min of stimulation) were used for generation of a histogram. A high-frequency "noise" in the histograms was reduced by "filtering," i.e., weighted averaging according to a formula

$$f_i^{\text{filtered}} = (-2 * f_{i-3} + 3 * f_{i-2} + 6 * f_{i-1} + 7 * f_i + 6 * f_{i+1} + 3 * f_{i+2} - 2 * f_{i+3})/21$$

where f_i^{filtered} is the filtered histogram value in bin i, while f_{i-3}, f_{i-2}, f_{i-1}, f_i, f_{i+1}, f_{i+2}, and f_{i+3} are the raw histogram values in seven bins centered about bin i. This formula introduces minor distortions to the bin values (1st 4 terms of Taylor series for f_i^{filtered} and f_i are identical) while significantly reduces noise (minimizes SD of f_i^{filtered} to about one-half SD of f_i).

RESULTS

Longitudinal spinal projections of RS neurons

The aim of this part of the study was to determine if individual RS neurons exert the same type of effect in different segments in the neck region, as was previously described for the trunk region (segments 12–88) (Zelenin et al. 2001a). RS axons were recorded in six animals (see Fig. 2*A*), and their influences on the motor output in rostral spinal segments (that is on the MN activity in several analogous VR branches) were analyzed. The conduction velocities ranged from 1.8 to 3.6 m/s [2.8 ± 0.5 (SD) m/s], which is characteristic for larger RS axons. Most axons ($n = 17$) were located in the medial area of the spinal cord, the rest ($n = 10$) coursed in more lateral areas. A noticeable effect on motor output was observed in 16 of 27 RS axons (10 medial and 6 lateral ones). Figure 3*A* shows an example of excitatory response recorded in all six ipsilateral ventral branches of VR, from segments 2–22. A prominent effect over the resting level can be observed in each segment, and the conduction delay in segments 2–22 is clear. An inhibitory response in segments 1–20 is illustrated in Fig. 3*B*. The RS neurons evoked excitatory or inhibitory responses in ipsilateral dorsal ($n = 5$), ipsilateral ventral ($n = 6$), contralateral dorsal ($n = 2$), and contralateral ventral ($n = 3$) ventral root branches.

Figure 4 summarizes the effects of single reticulospinal axons. Each line represents one axon. The response is indicated as percentage over base line response and compares the effect in a particular ventral root branch (dorsal or ventral) in the different ventral roots along the first 22 segments. Axons providing excitatory responses in one segment (above 0) remain excitatory in the other segments, except for a few cases ($n = 4$), when the excitatory responses in general were small and changed into a small inhibitory response in some segments (dashed lines). In five cases the effect was inhibitory (bold lines) and remained so throughout the spinal cord, except when there was no response in a branch.

We did not observe any difference in the conduction velocity of the RS neurons that exerted excitatory (2.8 ± 0.4 m/s), inhibitory (2.8 ± 0.4 m/s), or no effect (2.9 ± 0.8 m/s) (*t*-test for all 3 pairs of groups gave $P > 0.5$). There were no correlations between the conduction velocity and the magnitude of the responses. Correlation coefficient for the excitatory responses was −0.11, while for the inhibitory ones, it was 0.16.

Longitudinal spinal projections of VS neurons

The same type of analysis was carried out for the VS neurons located in intermediate octavomotor nucleus with ipsilateral axons. They were identified by recording of the orthodromic action potential on the ipsilateral side of the spinal cord and a large monosynaptic excitatory postsynaptic potential (EPSP) elicited from the vestibular nerve (Fig. 2, *E* and *F*). In 12 animals, 45 VS neurons were recorded. Their conduction velocities ranged from 0.5 to 1.3 m/s (1.0 ± 0.3 m/s), which is within the range of VS axons (Rovainen 1979).

Influences on the analogous ipsilateral VR branches were tested for 25 VS neurons. A noticeable effect on at least one of the recorded VR branches was observed in 17 neurons (68%). In all cases the effects were excitatory. Figure 5*A* shows the effects of stimulation of a VS neuron that excited MNs projecting to the dorsal VR branches in segments 2, 3, and 6 and did not influence the activity of MNs in segment 9, although its axon projected at least to segment 9, where the orthodromic spike was recorded with a surface suction electrode. In all recorded neurons, the excitatory responses never reversed to inhibitory ones at any recording site.

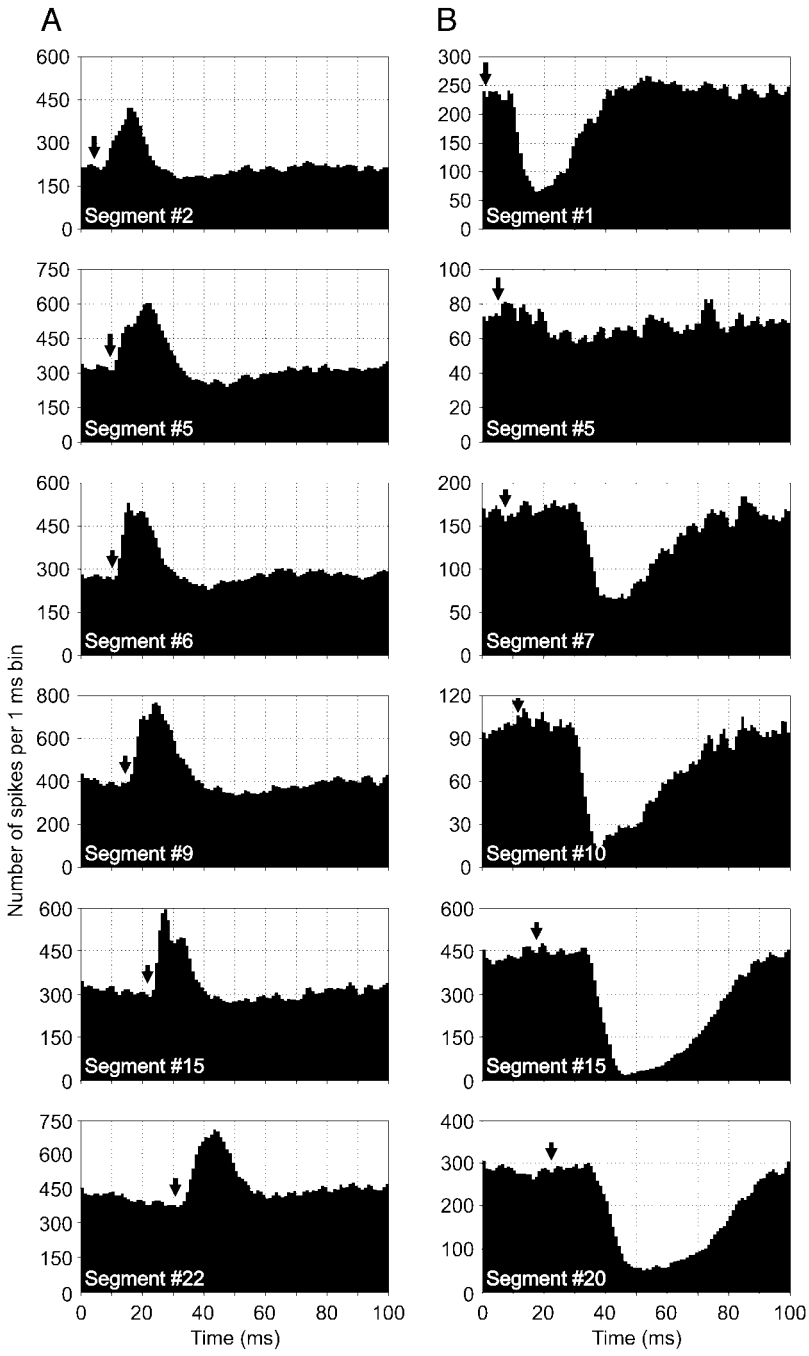

FIG. 3. Two examples of longitudinal functional projections of RS neurons. *A*: RS neuron evoked excitatory responses in the ipsilateral ventral VR branches in segments 2, 5, 6, 9, 15, and 22. *B*: RS neuron evoked inhibitory responses in the ipsilateral dorsal VR branches in segments 1, 5, 7, 10, 15, and 20. Arrows show the moments of the RS spike arrival to the segments.

Influences on the contralateral VR branches were tested for 20 VS neurons. In three of them (15%), we observed an inhibitory response in one of the branches. An example of such inhibitory response in segment 2 is shown in Fig. 5*B*. No responses were seen in the other 17 neurons.

Figure 6 summarizes the effects of VS neurons on different segments. The effects were uniform along the spinal cord, and in general, the response in percent over the background level was much smaller than for the RS neurons (note different ordinate scales in Figs. 4 and 6). The average excitatory responses were 66 ± 48% for RS neurons and 24 ± 12% for VS neurons (means significantly different, $P < 0.001$, *t*-test), while inhibitory ones were −52 ± 25% for RS neurons and −22 ± 12% for VS neurons (means significantly different, $P < 0.02$, *t*-test).

We often could not detect any influence in the most caudal recording site, although an orthodromic VS spike was present at that site. The amplitude of the orthodromic spike in these cases was low, which may indicate that the recording electrodes were located near the end of the VS axon.

Segmental projections of VS neurons

In the third series of experiments (see Fig. 2*C*), 18 VS neurons (conduction velocities from 0.8 to 1.4 m/s, 1.1 ± 0.2 m/s) were recorded in five animals, and their influences on the motor output from one segment (segments 3–5) were analyzed.

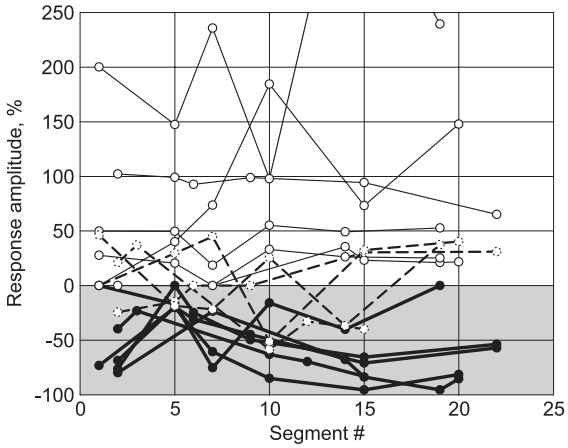

FIG. 4. Longitudinal distribution of functional projections for 16 RS neurons. In each case, recordings were performed from the analogous VR branches. For each RS neuron, the relative amplitude of response, i.e., the maximal deviation (in percent) of the summated MN activity from the level observed before the occurrence of the response, is shown for all sites of recording. Positive and negative values represent the excitatory and inhibitory responses, respectively. Data points for individual neurons are connected by lines. Thin lines, neurons with excitatory influences; thick lines, those with inhibitory influences; dashed lines, influences with different signs in different segments.

Effects on at least one ventral root branch were found in the majority of the neurons ($n = 12$; 67%).

Figure 7*A* shows one VS neuron with an excitatory effect on the ipsilateral ventral branch of the ventral root, with no effects on the other ventral root branches. As shown in Fig. 7*B*, all

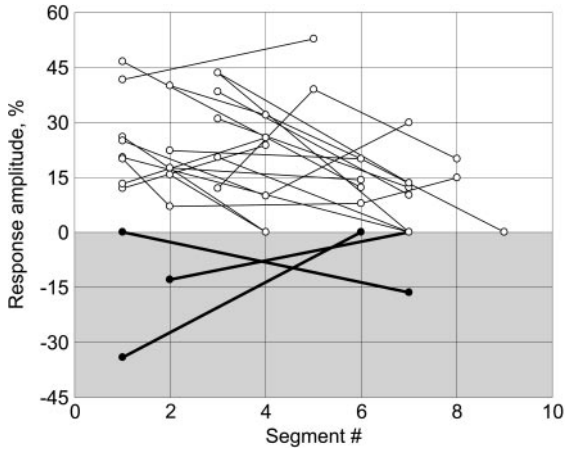

FIG. 6. Longitudinal distribution of functional projections for 17 VS neurons. In each case, recordings were performed from the analogous VR branches. Data points for individual neurons are connected by lines. Thin lines, neurons with excitatory influences; thick lines, those with inhibitory influences.

effects encountered were excitatory either affecting only the ventral ipsilateral branch ($n = 4$), the dorsal ipsilateral branch ($n = 5$), or both ipsilateral branches ($n = 3$). No effects were observed in six cases. Among these 18 neurons, no effects were observed on the contralateral ventral root branches. Inhibitory effects were not found in this series of experiments, but they were observed in three cases when studying the longitudinal VS projections (Fig. 6).

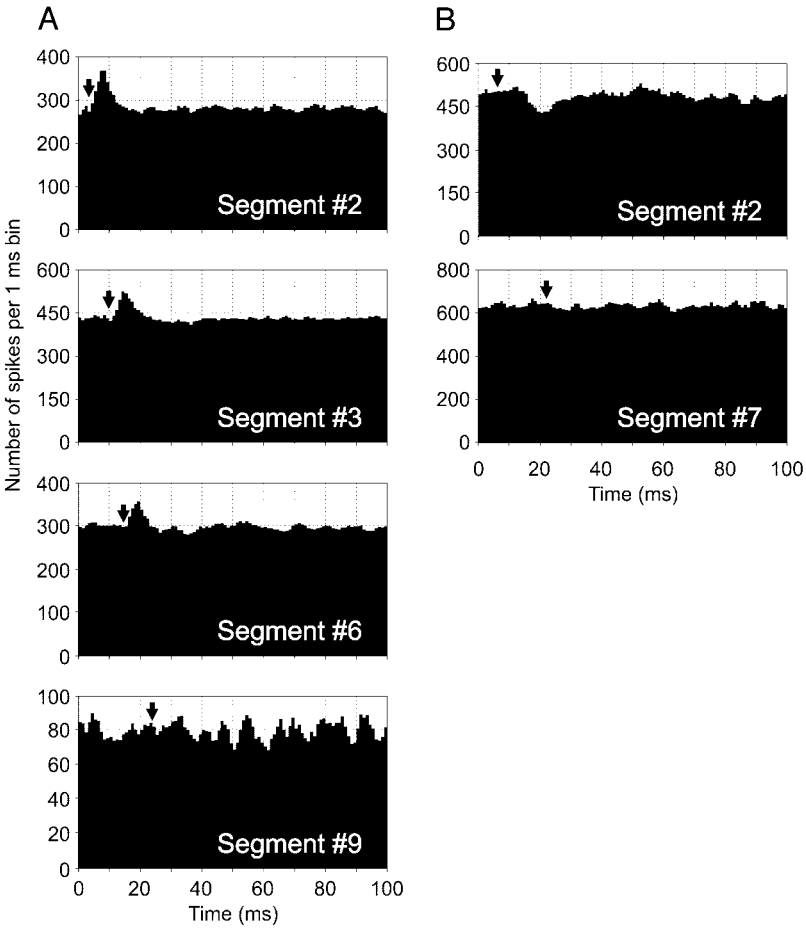

FIG. 5. Two examples of longitudinal functional projections of VS neurons. *A*: VS neuron evoked an excitatory response in the ipsilateral ventral VR branches in segments 2, 3, and 6, while produced no effect in segment 9, where its orthodromic spike was recorded with a suction electrode. *B*: VS neuron evoked an inhibitory response in the contralateral ventral VR branch in segment 2 and no response in segment 7. Arrows show the moments of the VS spike arrival to these segments.

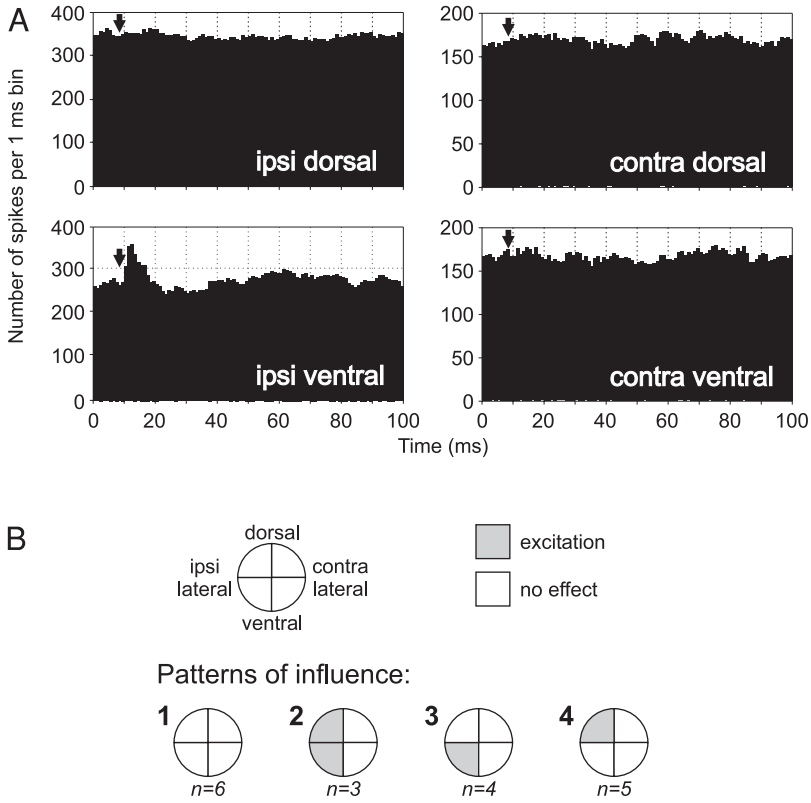

FIG. 7. Influences of VS neurons on motor output from 1 segment. *A*: example of influences. This particular VS neuron evoked excitation in the ipsilateral ventral VR branch and no response in 3 other branches—the ipsilateral dorsal, contralateral dorsal, and contralateral ventral. *B*: patterns of segmental responses to stimulation of individual VS neurons ($n = 18$). Patterns were defined as the combinations of responses (excitation, inhibition, no effect) in the 4 VR branches of the same segment. Numbers below each diagram show the numbers of recorded VS neurons with a given pattern.

DISCUSSION

In the lamprey, all commands to the rostral part of the spinal cord, i.e., to the region controlling head movements, are transmitted by two descending systems, the RS and VS systems (Rovainen 1979). For the population of larger RS neurons and for the population of VS neurons with uncrossed axons, we characterized their functional projections in this region (i.e., the effects of individual neurons on the motor output from the rostral spinal segments).

For RS neurons, we investigated their longitudinal projections, i.e., their effects on the motor output (activity of MNs in the analogous VR branches) at different rostrocaudal levels. The caudal part of the investigated area (segments 15–22) overlapped with the rostral part of the area investigated in our previous study, in which projections of larger RS neurons to the mid-body and tail regions (segments 15–90) were characterized (Zelenin et al. 2001a). Since, in this study, all RS axons reached the stump of the spinal cord (Fig. 2*A*), one can suggest that we were recording from the axons descending to the middle and caudal parts of the spinal cord (i.e., from the population analyzed in the previous study) (Zelenin et al. 2001a).

Most RS neurons were found to exert similar effects (excitation or inhibition) at all sites of recording. The same result was obtained previously for the mid-body and caudal regions of the spinal cord (Zelenin et al. 2001a). One can therefore conclude that RS neurons exert uniform effects on the segmental motor output along the whole extent of their axons, including the rostral segments.

In the previous study (Zelenin et al. 2001a), longitudinal projections of RS neurons as well as their segmental projections (i.e., their effects on MNs in the 4 VR branches of the segment 20) were characterized. Twenty patterns of segmental projections (combinations of excitatory and inhibitory effects on different VR branches) were found. Taking into account a uniformity of longitudinal projections, one can extend the conclusion about diversity of segmental projections reached for the mid-body and caudal areas to the rostral area of the spinal cord. By producing a uniform effect on motor output in numerous spinal segments, individual RS neurons will elicit flexion in a specific plane in a considerable part of the body. It seems likely that the group of larger RS neurons is responsible for formation of gross motor synergies that include the head, rostral part of the body, and its more caudal parts, like synergies for locomotion and turns of the whole animal in different planes (Deliagina et al. 2002).

This study has shown that functional projections of VS neurons strongly differed from those of larger RS neurons. Longitudinal projections of VS neurons were confined to the first 10 segments (Fig. 6), in contrast to RS neurons that projected also to more distant segments. Like RS neurons, each VS neuron exerted a uniform effect (excitation or inhibition) on the analogous MN pools in different sites of recording. Usually, the effect gradually decreased in more caudal segments (Fig. 6).

A study of segmental projections of VS neurons has shown that patterns of these projections (Fig. 7) were much less diverse than those of RS neurons, for which 20 projection patterns were found (see Fig. 7 in Zelenin et al. 2001a). All effects on ipsilateral motor output were excitatory. Inhibitory effects were found only in few cases, and all of them occurred in the contralateral MNs (Fig. 6).

We found that the VS effects on motor output were much weaker than the effects of larger RS neurons (compare Figs. 3 and 5). In these experiments, however, the responses to VS or

RS spikes were evaluated as relative changes in the "background" activity of MNs caused by input from the spinal locomotor network (activated by D-glutamate application). We cannot exclude a possibility that the relative strength of VS and RS inputs could be regulated in different behavioral contexts, when different groups of interneurons are activated.

The characteristics of RS and VS functional projections, revealed in this study, suggest a different functional role of these two groups of descending neurons in the control of movement of the head and rostral part of the body. The VS system, projecting to rostral segments only, is capable of eliciting head movements without affecting the middle and caudal body parts. By activating VS neurons with different patterns of influences (Fig. 7*B*) or their combinations, the CNS can elicit head movement in the horizontal, vertical, or oblique planes. Since VS neurons receive inputs from vestibular organs (Bussiéres 1994; Rovainen 1979), they can take part in postural control. In contrast, the investigated component of the RS system (comprising larger neurons) has widespread spinal projections and extremely diverse patterns of influence. It can elicit head movements in different planes coordinated with movements of the whole body. This component of RS system receives numerous sensory inputs and inputs from other motor centers and is thought to be involved in initiation of different forms of motor behavior (Deliagina and Fagerstedt 2000; Deliagina et al. 1995, 2000, 2002; Fagerstedt et al. 2001). Unfortunately, the role of the other component of RS system comprising small neurons projecting to rostral segments (Bussières 1994) remains unclear.

The RS and VS descending systems may receive common inputs and thus operate together. Due to the central feedback from the spinal locomotor network, both RS and VS neurons appeared modulated in a locomotory rhythm (Bussières and Dubuc 1992; Deliagina et al. 2000; Kasicki et al. 1989). Both systems receive vestibular inputs and can thus participate in the control of body orientation (Deliagina and Fagerstedt 2000; Pavlova and Deliagina 2002).

In conclusion, the revealed characteristics of VS and RS projections strongly suggest that these two neuron groups play different roles in controlling body movements. The VS neurons may be responsible for the fine control of head position, whereas the RS neurons may be responsible for formation of gross motor synergies.

DISCLOSURES

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REFERENCES

Archambault PS, Deliagina TG, and Orlovsky GN. Non-undulatory locomotion in the lamprey. *Neuroreport* 12: 1803–1807, 2001.

Brodin L, Grillner S, Dubuc R, Ohta Y, Kasicki S, and Hokfelt T. Reticulospinal neurons in lamprey: transmitters, synaptic interactions and their role during locomotion. *Arch Ital Biol* 126: 317–345, 1988.

Bussières N. *Les Systèmes Descendants Chez La Lamproie. Étude Anatomique Et Functionnelle.* Montreal, Canada: University of Montréal, 1994.

Bussières N and Dubuc R. Phasic modulation of vestibulospinal neuron activity during fictive locomotion in lampreys. *Brain Res* 575: 174–179, 1992.

Bussières N, Pflieger JF, and Dubuc R. Anatomical study of vestibulospinal neurons in lampreys. *J Comp Neurol* 407: 512–526, 1999.

Deliagina TG and Fagerstedt P. Responses of reticulospinal neurons in intact lamprey to vestibular and visual inputs. *J Neurophysiol* 83: 864–878, 2000.

Deliagina TG and Pavlova EL. Modifications of vestibular responses of individual reticulospinal neurons in the lamprey caused by a unilateral labyrinthectomy. *J Neurophysiol* 87: 1–14, 2002.

Deliagina TG, Ullén F, Gonzalez MJ, Ehrsson H, Orlovsky GN, and Grillner S. Initiation of locomotion by lateral-line photoreceptors in lamprey—behavioral and neurophysiological studies. *J Exp Biol* 198: 2581–2591, 1995.

Deliagina TG, Zelenin PV, Fagerstedt P, Grillner S, and Orlovsky GN. Activity of reticulospinal neurons during locomotion in the freely behaving lamprey. *J Neurophysiol* 83: 853–863, 2000.

Deliagina TG, Zelenin PV, and Orlovsky GN. Encoding and decoding of reticulospinal commands. *Brain Res Rev* 40: 166–177, 2002.

Fagerstedt P, Orlovsky GN, Deliagina TG, Grillner S, and Ullén F. Lateral turns in the lamprey. II. Activity of reticulospinal neurons during the generation of fictive turns. *J Neurophysiol* 86: 2257–2265, 2001.

Fagerstedt P and Ullén F. Lateral turns in the lamprey. I. Patterns of motoneuron activity. *J Neurophysiol* 86: 2246–2256, 2001.

Hebel R and Stromberg MW. *Anatomy and Embryology of the Laboratory Rat.* Wörthsee, Germany: BioMed Verlag, 1986.

Goldberg J and Peterson BW. Reflex and mechanical contributions to head stabilization in alert cats. *J Neurophysiol* 56: 857–875, 1986.

Grillner S, Deliagina T, Ekeberg Ö, el Manira A, Hill RH, Lansner A, Orlovsky GN, and Wallén P. Neural networks controlling locomotion and body orientation in lamprey. *Trends Neurosci* 18: 270–279, 1995.

Grillner S and Kashin S. On the generation and performance of swimming in fish. In: *Neural Control of Locomotion*, edited by Herman RM, Grillner S, and Stein PSG. New York: Plenum Press, 1976, vol. 18, p. 181–202.

Grillner S, McClellan A, Sigvardt K, Wallén P, and Wilén M. Activation of NMDA-receptors elicits "fictive locomotion" in lamprey spinal cord *in vitro*. *Acta Physiol Scand* 113: 549–551, 1981.

Kasicki S, Grillner S, Ohta Y, Dubuc R, and Brodin L. Phasic modulation of reticulospinal neurons during fictive locomotion and other types of spinal motor activity in lamprey. *Brain Res* 484: 203–216, 1989.

Magnus R. *Körperstellung.* Berlin, Germany: Springer, 1924.

Nieuwenhuys R. Topological analysis of the brain stem of the lamprey *Lampetra fluviatilis*. *J Comp Neurol* 145: 165–177, 1972.

Pavlova EL and Deliagina TG. Responses of reticulospinal neurons in intact lamprey to pitch. *J Neurophysiol* 88: 1136–1146, 2002.

Peterson BW, Goldberg J, Bilotto G, and Fuller JH. Cervicocollic reflex: its dynamic properties and interaction with vestibular reflexes. *J Neurophysiol* 54: 90–109, 1985.

Richmond FJR and Bakker DA. Anatomical organization and sensory receptor content of soft tissues surrounding upper cervical vertebrae in the cat. *J Neurophysiol* 48: 49–61, 1982.

Ronan M. Origins of the descending spinal projections in petromyzontid and myxinoid agnathans. *J Comp Neurol* 281: 54–68, 1989.

Rovainen CM. Electrophysiology of vestibulospinal and vestibulo-reticulospinal systems in lampreys. *J Neurophysiol* 42: 745–766, 1979.

Schor RH, Kearney RE, and Dieringer N. Reflex stabilization of the head. In: *Control of Head Movement*, edited by Peterson BW and Richmond FJR. New York: Oxford, 1988.

Stefanelli A and Caravita S. Ultrastructural features of the synaptic complex of the vestibular nuclei of Lampetra planeri (Bloch). *Z Zellforsch* 108: 282–296, 1970.

Tretjakoff D. Das nervensystem des flussnevnauges. *Z Wiss Zool* 129: 359–452, 1927.

Ullén F, Deliagina TG, Orlovsky GN, and Grillner S. Visual pathways for postural control and negative phototaxis in lamprey. *J Neurophysiol* 78: 960–976, 1997.

Ullén F, Orlovsky GN, Deliagina TG, and Grillner S. Role of dermal photoreceptors and lateral eyes in initiation and orientation of locomotion in lamprey. *Behav Brain Res* 54: 107–110, 1993.

Wallén P, Grillner S, Feldman JL, and Bergelt S. Dorsal and ventral myotome motoneurons and their input during fictive locomotion in lamprey. *J Neurosci* 5: 654–661, 1985.

Wannier T, Deliagina TG, Orlovsky GN, and Grillner S. Differential effects of reticulospinal system on locomotion in lamprey. *J Neurophysiol* 80: 103–112, 1998.

Zelenin PV, Grillner S, Orlovsky GN, and Deliagina TG. Heterogeneity of the population of command neurons in the lamprey. *J Neurosci* 21: 7793–7803, 2001a.

Zelenin PV, Orlovsky GN, Pavlova EL, and Deliagina TG. Effects of individual reticulo- and vestibulospinal neurons on rostral spinal segments in lamprey. *Soc Neurosci Abstr* 27: 2001b.