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SYMPOSIUM REVIEW

Interactions between spinal interneurons and ventral spinocerebellar tract neurons

Elzbieta Jankowska and Ingela Hammar

Department of Neuroscience and Physiology, Sahlgrenska Academy, University of Gothenburg, 405 30 Göteborg, Sweden

Abstract Recent evidence indicates that ventral spinocerebellar tract (VSCT) neurons do not merely receive information provided by spinal interneurons but may also modulate the activity of these interneurons. Hence, interactions between them may be mutual. However, while it is well established that spinal interneurons may provide both excitatory and inhibitory input to ascending tract neurons, the functional consequences of the almost exclusively inhibitory input from premotor interneurons to subpopulations of VSCT neurons were only recently addressed. These are discussed in the first part of this review. The second part of the review summarizes evidence that some VSCT neurons may operate both as projection neurons and as spinal interneurons and play a role in spinal circuitry. It outlines the evidence that initial axon collaterals of VSCT neurons target premotor inhibitory interneurons in disynaptic reflex pathways from tendon organs and muscle spindles (group Ia, Ib and/or II muscle afferents) to motoneurons. By activating these interneurons VSCT neurons may evoke disynaptic IPSPs in motoneurons and thus facilitate inhibitory actions of contralateral muscle afferents on motoneurons. In this way they may contribute to the coordination between neuronal networks on both sides of the spinal cord in advance of modulatory actions evoked via the cerebellar control systems.

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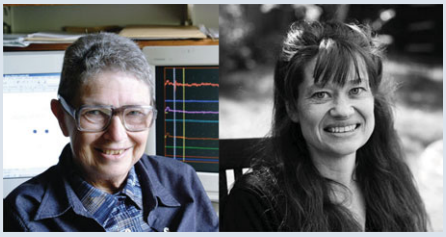
Corresponding author E. Jankowska: Department of Physiology, Medicinaregatan 11, Box 432, 405 30 Göteborg, Sweden. Email: elzbieta.jankowska@physiol.gu.se

Abbreviations DSCT, dorsal spinocerebellar tract; MLR, mesencephalic locomotor region; PT, pyramidal tract; SB, spinal border; VSCT, ventral spinocerebellar tract.

Introduction

In the present review we address the issue of interactions between locally operating premotor interneurons relaying reflex actions from primary afferents and a subpopulation of spinocerebellar tract neurons acting as not only long ascending tract, or projection neurons, but also as local interneurons. It has been known for some time that subpopulations of a number of ascending tract neurons, including spinocerebellar neurons, give off initial axon

Elzbieta Jankowska is professor emeritus at the Institute of Neuroscience and Physiology at the University of Gothenburg. Following graduate studies at Nencki Institute in Warsaw she joined the research group of Professor Anders Lundberg as a postdoc in 1964, and thereafter continued her work at the University of Gothenburg. Most of her research has focused on spinal interneuronal organization, the descending control of spinal networks and, most recently, the feedback provided by spinal neurons to the cerebellum. **Ingela Hammar** is an associate professor at the Institute of Neuroscience and Physiology at the University of Gothenburg. She started her research as a medical undergraduate and graduate student and received part of her PhD training at Glasgow University. Collaborating with professor Jankowska for over decade, her main interests concern the monoaminergic modulation of spinal networks, combining electrophysiology, morphology and immunohistology to study spinal neurons.



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collaterals within the spinal grey matter and might thereby affect spinal neurons. However, information on the spinal target cells of spinocerebellar neurons became available only very recently. We will review evidence showing that the target cells of spinocerebellar neurons within the lumbosacral enlargement include the same categories of premotor interneurons which supply spinocerebellar neurons with information, thereby suggesting intricate interactions between them.

Actions of spinal interneurons on VSCT neurons

Many populations of spinal interneurons may affect VSCT neurons, but the actions of premotor interneurons in reflex pathways to motoneurons have been most thoroughly documented (Burke *et al.* 1971; Lundberg, 1971; Lundberg & Weight, 1971; Jankowska & Puczynska, 2008; Jankowska *et al.* 2010). Evidence was first provided for the actions of interneurons mediating reciprocal and recurrent inhibition of motoneurons (Ia interneurons and Renshaw cells) on VSCT neurons (Lundberg & Weight, 1971; Lindström, 1973; Lindström & Schomburg, 1973; Lindström & Takata, 1977) but not on dorsal spinocerebellar tract (DSCT) neurons (Lindström & Takata, 1977; Hongo *et al.* 1983). It was also shown that interneurons excited by tendon organ and muscle spindle afferents (group Ib and II afferents) act on both VSCT and Clarke's column DSCT neurons but not on dorsal horn DSCT neurons (Jankowska & Edgley, 2010). These actions support the original hypothesis of Lundberg and Oscarsson (see Lundberg, 1971; Oscarsson, 1973) that some ascending tract neurons forward information on the operation of spinal interneuronal networks as well as on peripheral events. As inhibition of VSCT neurons mediated by interneurons is much more potent than excitation, the main part of Lundberg's hypothesis was that VSCT neurons monitor output from inhibitory interneurons against the excitatory input to them (Lundberg, 1971). For instance, VSCT neurons with both excitatory and inhibitory input from group Ib afferents could monitor the output from inhibitory interneurons

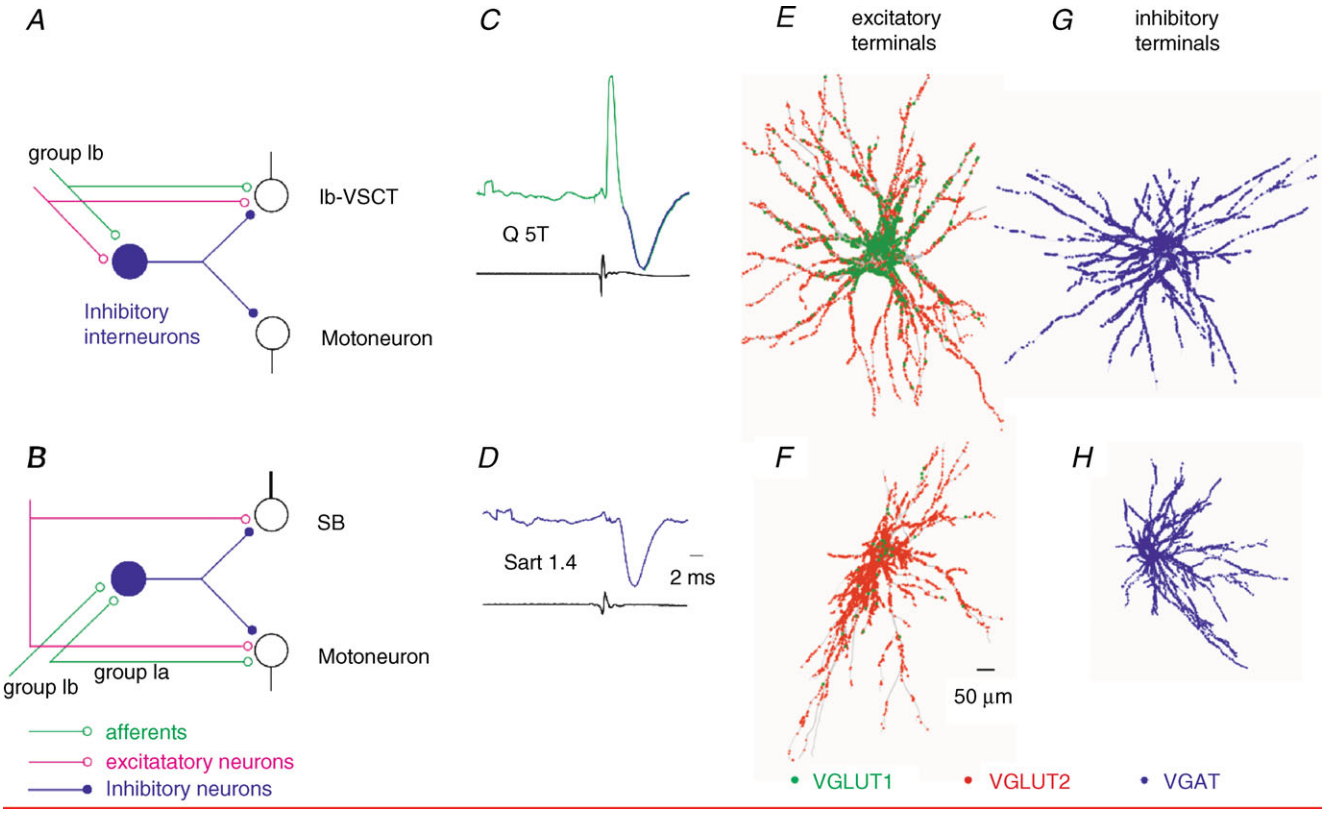

Figure 1. Examples of differences in input to Ib and spinal border (SB) subpopulations of VSCT neurons
Diagrams in *A* and *B* are based on those in Fig. 4 in Oscarsson (1973). *C* and *D*, examples of records from VSCT neurons with both excitatory (direct) and inhibitory (disynaptic) input from peripheral afferents and SB neurons with only inhibitory (disynaptic) input from primary afferents. The Quadriceps (Q) and Sartorius (Sart) nerves were stimulated at intensities of 5 and 1.4 times threshold (T). *E* and *F*, examples of reconstructions of dendritic trees and of the distribution of excitatory terminals with vesicular glutamate transporter 1 and transporter 2 on VSCT and SB neurones, respectively (modified from Shakya-Shrestha *et al.* 2012*a*). *G* and *H*, similar reconstructions to those in *E* and *F* but with the distribution of inhibitory terminals (modified from Shakya-Shrestha *et al.* 2012*b*). Note different distribution of excitatory but similar distribution of inhibitory terminals on VSCT and SB neurons.

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activated by Ib afferents against their excitatory input, as indicated in Fig. 1*A* and *C*.

However, while this may be a feature of many VSCT neurons, the subpopulations of these neurons, in particular those referred to as spinal border (SB) neurons with exclusively inhibitory input from primary afferents would not be able to perform this task and the functional meaning of this inhibitory input remained to a great extent an enigma.

Taking this situation into account as well as morphological and immunohistochemical data on excitatory and inhibitory synaptic input to VSCT neurons it has been proposed that the inhibition of spinocerebellar neurons with a predominant inhibitory input from primary afferents primarily reflects the degree to which motoneurons are inhibited by premotor interneurons (Hammar *et al.* 2011). Hence, these neurons may forward information related to motoneuronal excitability rather than input–output relations at the level of the premotor interneurons. This proposal was based on the lack of evidence for excitation of many SB and VSCT neurons by primary afferents (Burke *et al.* 1971; Lundberg & Weight, 1971) as well as the following findings. (i) The demonstration that intracellularly labelled SB neurons in which peripheral nerves only evoked IPSPs (Fig. 1*B* and *D*) are practically devoid of terminals with vesicular glutamate transporter 1 (Fig. 1*F*) which characterize primary afferents. However, SB neurons were contacted by terminals immunoreactive for vesicular glutamate transporter 2 (Fig. 1*F*) (Shakya-Shrestha *et al.* 2012*a*), found in terminals of intrinsic spinal or supraspinal neurons. In contrast, VSCT neurons with monosynaptic input from group I afferents (Fig. 1*A* and *C*) display comparable numbers of terminals with vesicular glutamate transporters 1 and 2 (Fig. 1*E*). (ii) The original studies of sources of inhibition of SB and VSCT neurons were recently supplemented by the demonstration that individual neurons may be inhibited by more than one category of inhibitory interneurons, including those mediating the actions of group Ia, Ib and II afferents (Jankowska *et al.* 2010). (iii) The amazingly high number of inhibitory contacts on individual SB and VSCT neurons was recently revealed by demonstrating up to 11,000 inhibitory terminals on individual neurons, distributed over the surface of both cell bodies and dendrites (Shakya-Shrestha *et al.* 2012*b*), as illustrated in Fig. 1*G* and *H*. Most, if not all, of these terminals are likely to be of spinal origin in view of the lack of evidence for projections of supraspinal inhibitory neurons to lumbar segments in the cat. The high number of inhibitory terminals thus indicates contacts made by a considerable number of interneurons, even if individual interneurons may form multiple contacts with single neurons. Taken together these observations indicate that SB and VSCT neurons may be unable to differentiate between the sources of IPSPs evoked in them and thereby are not likely to forward information on the activation of specific inhibitory interneurons. However, the combined actions of all inhibitory interneurons on these neurons may serve to reflect the degree of inhibition of motoneurons by premotor interneurons acting on both motoneurons and these spinocerebellar neurons (Hammar *et al.* 2011).

In order to understand the nature of messages forwarded to the cerebellum by SB and VSCT neurons inhibited by premotor interneurons it was essential to find some reliable sources of activation of SB neurons which might be modulated by these interneurons. The only monosynaptic excitatory input to SB neurons systematically found in electrophysiological experiments arises from reticulospinal, vestibulospinal and rubrospinal tract neurons (Baldissera & Roberts, 1975; Baldissera & ten Bruggencate, 1976; Hammar *et al.* 2011). In addition, reticulospinal neurons were found to relay descending commands from a number of supraspinal structures, e.g. from pyramidal tract (PT) neurons and the mesencephalic locomotor region (MLR) (Jankowska *et al.* 2011). As illustrated in Fig. 2, when a number of these systems are coactivated, the descending input to SB and VSCT neurons may become sufficiently strong to evoke discharges even in deeply anaesthetized animals, and thus it may be expected to be even more effective under natural conditions.

The effect of inhibition by premotor interneurons was therefore investigated against a background of the excitation by reticulospinal neurons. One of the most relevant findings was that the inhibition of VSCT neurons

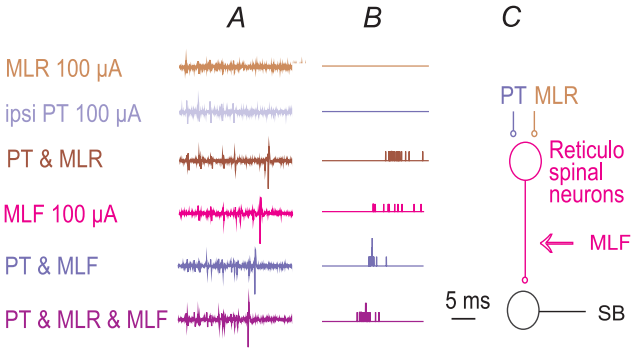

Figure 2. Indications for input from both pyramidal tract (PT) neurons and from the mesencephalic locomotor region (MLR) relayed to SB neurons via reticulospinal neurons
A, examples of records from a spinal border neuron following different combinations of trains of stimuli indicated to the left. *B*, post-stimulus spike histograms of responses evoked by 20 sequences of the stimuli in *A*. Note that PT and MLR stimuli were ineffective when applied in isolation but evoked some responses when applied together, and that these stimuli were even more effective in combination with MLF stimuli (bottom record) than MLF stimuli alone. *C*, diagram of the experimental arrangement. Modified from Jankowska *et al.* (2011).

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by premotor interneurons is very potent and, as illustrated in Fig. 3, may result in an arrest of discharges during the inhibition of motoneurons (Hammar *et al.* 2011). How this modulation of discharges of spinocerebellar neurons is used to monitor the degree of inhibition of motoneurons as signalled by premotor interneurons and how it is interpreted by cerebellar neurons is not yet resolved, but it may have a strong impact on the target cells of the spinocerebellar tract neurons in the cerebellum.

The proposed network of neurons involving ventral spinocerebellar tract neurons is depicted in Fig. 4. The diagram takes into account that SB and VSCT neurons with predominant inhibitory input may provide the cerebellum with information on the likely actions of reticulospinal neurons relaying any descending commands, including commands initiated by PT neurons and by stimuli applied in the MLR.

Spinal target cells of VSCT neurons

The impact of inhibition of spinocerebellar neurons at a spinal level would depend on the range of their spinal actions. Spinal projections of spinocerebellar neurons were first revealed when it was found that individual neurons could be antidromically activated not only from the cerebellum but also from spinal segments caudal to the location of their cell bodies. This was found for cervical spinocerebellar neurons (Hirai *et al.* 1978*a*,*b*), and for neurons classified as either spinoreticular (Ekerot *et al.* 1979; Alstermark *et al.* 1990; Ekerot, 1990*a*,*b*) or spinocerebellar (Mrówczyński *et al.* 2001). Axon collaterals given off at short distances from the cell bodies were also found in morphological studies on intracellularly labelled individual spinocerebellar neurons (Bras *et al.* 1988) or unidentified long distance projection neurons (Matsuyama *et al.* 2004; Matsuyama *et al.* 2006). Spinal projections of spinocerebellar neurons were further demonstrated bydouble retrograde labelling by two separate markers, one injected into the cerebellum and the other into the spinal cord caudal to the location of their cell bodies (Verburgh *et al.* 1989).

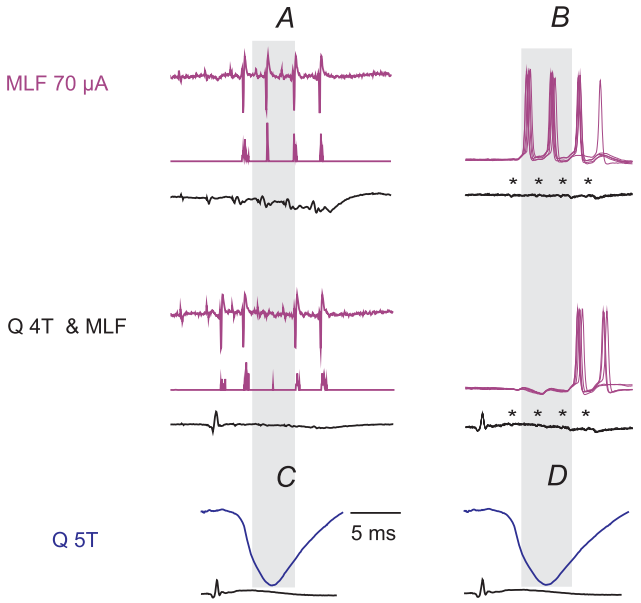

Figure 3. Examples of depression of responses of SB neurons following MLF stimuli by a preceding or coinciding stimulation of peripheral nerves
A, from top to bottom are extracellular spike potentials, post-stimulus time histograms of responses evoked by a series of 20 consecutive trains of stimuli and descending volleys following MLF stimuli. The MLF stimuli were applied separately or in conjunction with stimulation of the quadriceps (Q) nerve, stimulated at intensities of 4 or 5 times threshold (T) as indicated. *B*, intracellular records from another SB neuron together with records from the surface of the spinal cord. ⁎indicates the timing of the earliest descending volleys from the MLF. *C* and *D*, IPSPs evoked from group II afferents in the quadriceps (Q) nerve together with afferent volleys. Note lack of response during periods coinciding with the peaks of the IPSPs (indicated in grey). Modified from Figs 5 and 6 in Hammar *et al.* (2011).

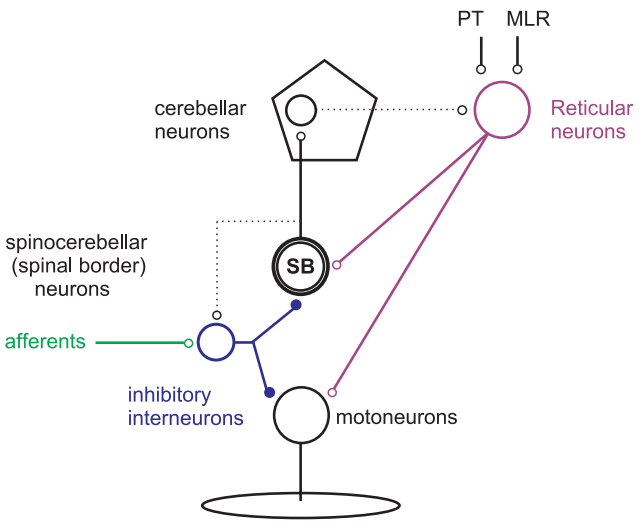

Figure 4. Diagram of the network enabling SB neurons to monitor the likely outcome of descending commands relayed by reticulospinal neurons (purple) as a function of inhibition of motoneurons by premotor interneurons (blue) acting in parallel on motoneurons and on SB neurons
The diagram is based on the hypothesis that excitatory input from reticulospinal neurons and inhibitory input from premotor interneurons to SB neurons reflect input to motoneurons. Dotted lines indicate how information on the excitability of motoneurons might be used to adjust both the descending commands (via the cerebellum) and the degree of inhibition of the motoneurons (via axon collaterals of SB neurons and inhibitory interneurons). The motoneurons and interneurons in this diagram represent undefined populations of these neurons either on the same or on the opposite side of the spinal cord. For more detailed network connections see Fig. 6.

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However, spinal projections appear to characterize only certain subpopulations of spinocerebellar neurons, in particular the ventral spinocerebellar tract (VSCT) neurons in the lumbar segments (Bras *et al.* 1988) and their homologues, the ventrally but not dorsally located cervical spinocerebellar neurons (Hirai *et al.* 1978*a*,*b*, see also Krutki *et al.* 1999) and sacral spinocerebellar neurons located in the ventral horn (Grottel *et al.* 1998). In contrast, no initial axon collaterals were found in the spinal border subpopulation of lumbar spinocerebellar neurons (cf. filled and open symbols in Fig. 5*C* and *D*), nor in dorsal spinocerebellar tract neurons located in either Clarke's column or the dorsal horn (Randić *et al.* 1981; Houchin *et al.* 1983; Edgley & Gallimore, 1988; Bannatyne *et al.* 2006).

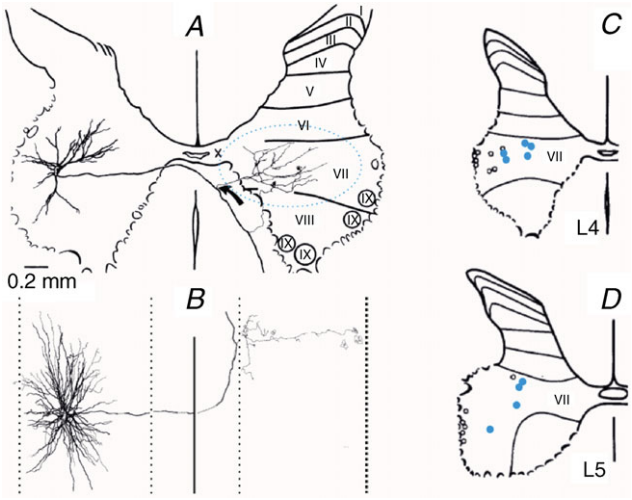

Figure 5. Examples of initial axon collaterals of a VSCT neurone in transverse (*A*) and horizontal (*B*) planes
Modified from Figs 2, 4 and 5 in Bras *et al.* (1988). Filled circles in diagrams in *C* and *D* indicate the location of cell bodies of VSCT neurons in which initial collaterals were found, and open circles indicate the location of VSCT neurons lacking initial collaterals. Note that the former were at the location of the Ib subpopulation of VSCT neurons and the latter at the location of SB cells.

The terminal projection areas of axon collaterals of VSCT neurons illustrated in Fig. 5*A* and *B* would enable them to form contacts with neurons belonging to several populations of spinal neurons outside motor nuclei, including premotor interneurons interposed in disynaptic pathways between muscle afferents and hindlimb motoneurons. However, actions on premotor interneurons which provide input to spinocerebellar neurons might present a particularly important feedback system as indicated in Fig. 5*B*. This issue was addressed in a recent study by Geborek *et al.* (2012).

In order to examine collateral actions of VSCT neurons on premotor interneurons, axons of VSCT neurons were stimulated within the anterior lobe of the cerebellum in the cat, taking advantage of the very favourable anatomical situation that onlyVSCT neurons were found to give off initial axon collaterals in the spinal cord (see above), and that neither excitatory cerebellar neurons (e.g. from fastigial nucleus) nor inhibitory descending tract neurons activated by cerebellar neurons (e.g. reticulospinal neurons) were found to project as caudal as to the lumbosacral enlargement. Any monosynaptic

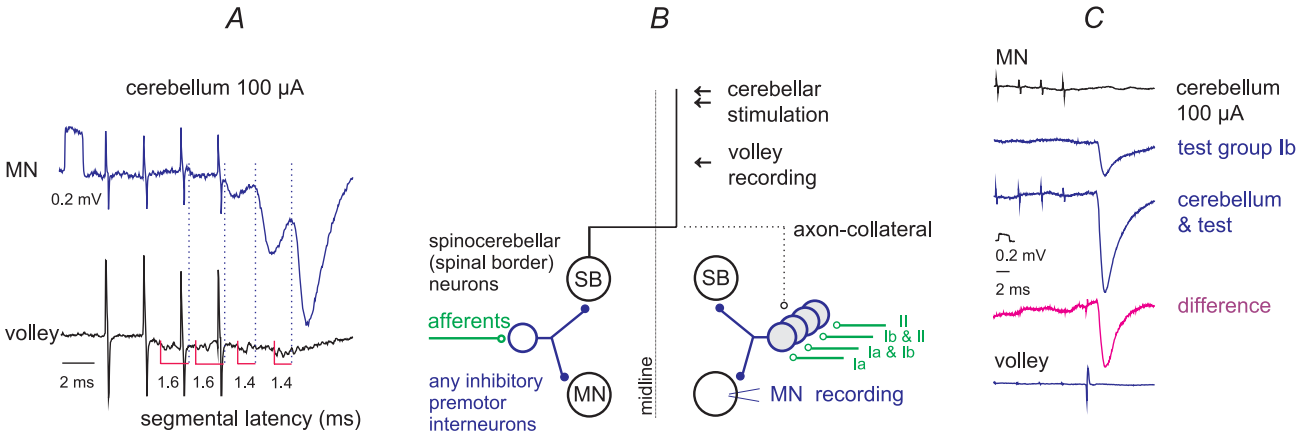

Figure 6
A, example of short latency IPSPs evoked in hindlimb motoneurons (MN) from the cerebellum. The records are from an unidentified extensor motoneuron and from the surface of the spinal cord at the L6–7 level. Vertical dotted lines indicate the onset of IPSPs evoked by 4 stimuli. Note increasing amplitudes and decreasing latencies of IPSPs measured from the descending volleys evoked by successive stimuli. They were compatible with disynaptic coupling via single interneurons as indicated in the right part of the diagram. *B*, diagram of connections between VSCT neurons and premotor interneurons. *C*, example of spatial facilitation of synaptic actions of VSCT neurons and group I afferents on premotor inhibitory interneurons as shown by a considerable increase of IPSPs evoked in motoneurons when stimulation of group I afferents was combined with cerebellar stimulation. Modified from Geborek *et al.* (2012).

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excitatory and disynaptic inhibitory effects of stimuli applied within the anterior lobe of the cerebellum should thus be attributable to VSCT neurons in the lumbosacral enlargement and/or their cervical homologues.

As shown by Geborek *et al.* (2012), spinal target cells of VSCT neurons in the lumbar segments do indeed include premotor interneurons and the majority of these interneurons appear to be inhibitory, with IPSPs evoked in a high proportion of motoneurons and EPSPs much less frequently. In addition, most IPSPs had features of disynaptically evoked IPSPs. As illustrated in Fig. 6, IPSPs were evoked at short segmental latencies and displayed as potent temporal facilitation as required for PSPs relayed by a single interposed neuron. The IPSPs could thus only be attributed to last-order interneurons inhibiting motoneurons. EPSPs evoked by collateral actions of VSCT neurons were only rarely compatible with disynaptically mediated synaptic actions, none fulfilled the criteria of monosynaptic EPSPs and the latencies of the majority of them indicated a polysynaptic coupling.

In order to identify interneurons mediating disynaptic IPSPs evoked by stimulation of axons of VSCT neurons, mutual facilitation between actions of VSCT neurons and of peripheral afferents on premotor interneurons was used. Stimuli applied in the cerebellum considerably facilitated disynaptic IPSPs evoked in hindlimb motoneurons by group Ia afferents from antagonist muscles and IPSPs evoked by group Ib and/or group II afferents from synergists. Under optimal conditions the amplitudes of the tested IPSPs were even doubled or tripled, with an example in Fig. 6*C*. The results were consistent with the IPSPs being mediated by premotor interneurons in reflex pathways from muscle afferents and were confirmed by the presence of monosynaptic EPSPs evoked from the cerebellum in some Ia inhibitory interneurons and in some intermediate zone interneurons with input from group I and II afferents. As these interneurons act on ipsilateral motoneurons, these results further indicate that VSCT neurons informing the cerebellum on input from muscle afferents on one side of the body, and on the degree of inhibition of motoneurons by these afferents, may facilitate inhibitory actions of group I and II afferents on contralateral motoneurons, as indicated in Fig. 6*B*. Depending on the situation VSCT neurons might thus contribute to modulation of the final motor output at a spinal level not only by adjusting the degree of excitability of contralateral motoneurons, but also by counteracting a potentially too strong bilateral excitation of motoneurons, or by contributing to the inhibition of motoneurons during alternating excitation of ipsilateral motoneurons and inhibition of contralateral motoneurons. Inhibition of discharges of SB and VSCT neurons such as illustrated in Fig. 3 would thus result in a disinhibition of contralateral motoneurons. Hence, collateral actions of VSCT neurons evoked via premotor inhibitory interneurons might be integrated with various kinds of behaviour in a context-dependent manner.

The most general conclusion based on the reviewed observations is thus that VSCT may contribute to motor control at a spinal level both in parallel and in advance of any control exerted via the cerebellar loop.

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