Slow Dorsal-Ventral Rhythm Generator in the Lamprey Spinal Cord

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Aoki, Fumi, Thierry Wannier, and Sten Grillner. Slow dorsal-ventral rhythm generator in the lamprey spinal cord. J Neurophysiol 85: 211–218, 2001. In the isolated lamprey spinal cord, a very slow rhythm (0.03–0.11 Hz), superimposed on fast N-methyl-D-aspartate (NMDA)-induced locomotor activity (0.26–2.98 Hz), could be induced by a blockade of GABA_A or glycine receptors or by administration of (1 s, 3 s)-1-aminoacyclopendate-1,3-dicarboxylic acid a metabolotropic glutamate receptor agonist. Ventral root branches supplying dorsal and ventral myotomes were exposed bilaterally to study the motor pattern in detail. The slow rhythm was expressed in two main forms: 1) a dorsal-ventral reciprocal pattern was the most common (18 of 24 preparations), in which bilateral dorsal branches were synchronous and alternated with the ventral branches, in two additional cases a diagonal dorsal-ventral reciprocal pattern with alternation between the left (or right) dorsal and the right (or left) ventral branches was observed; 2) synchronous bursting in all branches was encountered in four cases. In contrast, the fast locomotor rhythm occurred always in a left-right reciprocal pattern. Thus when the slow rhythm appeared in a dorsal-ventral reciprocal pattern, fast rhythms would simultaneously display left-right alternation. A longitudinal midline section of the spinal cord during ongoing slow bursting abolished the reciprocal pattern between ipsilateral dorsal and ventral branches but a synchronous burst activity could still remain. The fast swimming rhythm did not recover after the midline section. These results suggest that in addition to the network generating the swimming rhythm in the lamprey spinal cord, there is also a network providing slow reciprocal alternation between dorsal and ventral parts of the myotome. During steering, a selective activation of dorsal and ventral myotomes is required and the neural network generating the slow rhythm may represent activity in the spinal machinery used for steering.

INTRODUCTION

Bath application of excitatory amino acids induces fictive swimming activity in the isolated spinal cord of the lamprey (Brodin et al. 1985; Grillner et al. 1981). The basic cellular and network components of the central pattern generator underlying swimming have been identified (Grillner et al. 1995). Basic swimming activity is always expressed in a left-right reciprocal pattern. For steering behavior in three-dimensional space, however, a differential control of dorsal and ventral myotomes must be available as well as between left and right myotomes. Motoneurons supplying the dorsal and ventral parts of the myotome have different patterns of activation during fictive locomotion (Wallén et al. 1985). Pharmacological stimulation of reticulospinal nuclei also activates the dorsal and ventral branches of the ventral roots differentially (Wannier et al. 1998). These studies thus suggest that there are neural mechanisms for the differential control of the dorsal and ventral myotomes.

In the isolated spinal cord, slow fluctuations of the swimming activity have been observed with apamin (El Manira et al. 1994), bicuculline (Tegnér et al. 1993), and strychnine (McPherson et al. 1994) applications on N-methyl-D-aspartate (NMDA)- or D-glutamate-induced swimming, and with 5-hydroxytryptamine (5-HT) on kainate-induced swimming (Scotland and Grillner 1993). The two rhythms may occur simultaneously in the isolated spinal cord preparation with the slow rhythm being superimposed on the faster swimming rhythm. These studies were, however, performed using whole ventral roots and showed that the slow fluctuation could exhibit a left-right reciprocal pattern. To determine whether the slow rhythm occurred in motoneurons supplying both the dorsal and ventral part of the myotome, the corresponding dorsal and ventral branches of the ventral roots were dissected. The slow bursting (0.03–0.11 Hz) could display alternating activity between the dorsal and ventral branches, while the fast locomotor rhythm (0.26–2.98 Hz) only displayed left-right alternation. The slow rhythm was induced pharmacologically by, e.g., antagonists of GABA_A receptors. A slow dorsal-ventral reciprocal modulation of the locomotor burst activity would be expected to make the lamprey modulate its swimming path sinusoidally in the dorso-ventral plane.

METHODS

The isolated spinal cord of adult lampreys (Petromyzon marius and Ichthyomyzon unicuspis) were used. They were anesthetized with tricaine methane sulfonate (MS-222; 100 mg/l) and dissected in cooled physiological solution. Spinal cord segments were taken from a region between the last gill opening and the dorsal fin. Segments (10–14) from the rostral half of the region close to the gills were usually used. In the beginning of the study with bicuculline and strychnine, segments from the caudal half of this region were also used, but they were less likely to generate the slow rhythm as described in RESULTS. Each ventral root projects out of the spinal canal into its myotome and divides into a dorsal and a ventral branch, which innervate the dorsal and ventral myotome, respectively. Each branch runs on the medial surface of the myotome dorsally or ventrally in the connective tissue between the myosepta. To expose the main trunks of the branches, the spinal cord was dissected together with the notochord and the medial part of the myotomes.

Muscle fibers were carefully removed to expose the dorsal and ventral branches, and the main trunks of the branches were then dissected. After both branches had been exposed bilaterally, the dorsal

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wall of the spinal canal was removed to expose the spinal cord to the physiological solution. The notochord was cut longitudinally in the midline of the ventral side, making it possible to record from branches on both sides.

The spinal cord was mounted in a silicone elastomer (Sylgard)-lined chamber with the notochord spread out laterally and continuously perfused with cooled (7–9°C) physiological solution with the following composition (in mM): 91 NaCl, 2.1 KCl, 2.6 CaCl₂, 1.8 MgCl₂, 23 NaHCO₃, and 4 glucose and bubbled with 95% O₂-5% CO₂. The main trunks of the dorsal and ventral branches on each side were sucked into glass suction electrodes to record extracellular axonal activity. Ipsilateral dorsal and ventral branches were recorded either from the same ventral root or from roots one segment apart. Branches on the left and right side were located 0–3 segments apart.

Bursting activity was induced by adding NMDA (Tocris Neuramin, UK; 50–200 μM) to the physiological solution. NMDA (50 μM) was used in most cases. The GABAₐ-receptor antagonist, (−)-bicuculline methiodide (Sigma, UK; 10–300 μM), was added during NMDA-induced swimming activity to induce the slow rhythm. We also investigated the effects of strychnine nitrate (Kronan, Sweden; 0.1–5 μM) and a metabotropic glutamate receptor agonist (1 s, 3 s)-l-aminocyclopentane-1,3-dicarboxylic acid (ACPD, Tocris Cookson, UK; 25–300 μM).

In some cases, a midline longitudinal section of the spinal cord was made to study network organization of the slow rhythm. The section of the whole spinal preparation was carried out after the slow rhythm was induced by NMDA and bicuculline, and activity changes were followed for at least 1 h after the section.

The extracellular axonal activity was amplified and filtered (band-pass 300 Hz-1 kHz, Differential AC amplifier Model 1700, A-M Systems). Data were acquired using an A/D converter at sampling rate 2.5 kHz and a 486 PC computer with Axon Instruments software (Digidata 1200 interface and Axotape 2.0, Axon Instruments). DataPac II (Run Technologies) was used for further analysis. Spikes exceeding a set threshold were detected and saved as event pulses. We analyzed auto- and cross-correlograms of the bursting branch activity using the event pulses with a bin width of 60 ms and a window of ±30.72 s. To make a correlogram, 2,000 event pulses from the activity in a dorsal branch were used as triggers. The autocorrelogram shows the degree of oscillatory tendency in the branch activity, and the cross-correlogram indicates degree of synchronization and phase relation between the dorsal branch and another branch. We performed fast Fourier transformation (FFT) of the autocorrelogram of the dorsal branch activity to analyze the frequency components of the bursting activity.

**RESULTS**

**Bicuculline induces a slow rhythm**

Figure 1A shows NMDA-induced fictive locomotion in a preparation subjected to bicuculline with recordings from dorsal and ventral branches of the dorsal roots bilaterally. A fast burst activity (around 1.6 Hz) is modulated by a slower rhythm (0.05 Hz) occurring simultaneously in the left and right dorsal branch and alternating with increased activity in the ventral branches. The fast locomotor rhythm alternated between left and right side (Fig. 1A, inset). In 24 of 27 preparations, application of bicuculline induced a slow rhythm that was superimposed on the fast NMDA-induced rhythm. The slow rhythm started to appear at a bicuculline concentration 30–50 μM (Fig. 2C) and continued as the concentration was increased up to 200–300 μM. When the two rhythms appeared simultaneously, the frequency of the slow oscillation ranged from 0.03 to 0.11 Hz, whereas the fast swimming rhythm ranged from 0.26 to 2.98 Hz. The most common pattern induced by bicuculline was the dorsal-ventral reciprocal pattern (Fig. 1, A and C), which was observed in 18 of 24 preparations. A diagonal reciprocal pattern that is reciprocal between the left dorsal and right ventral branches or vice versa, was induced in two preparations.

![FIG. 1.](http://jn.physiology.org/)

**FIG. 1.** A: dorsal-ventral reciprocal pattern of the slow rhythm superimposed on N-methyl-D-aspartate (NMDA)-induced locomotor activity. Extracellular axonal activities in right dorsal (r dors br), right ventral (r ventr br), left dorsal (l dors br), and left ventral (l ventr br) branches are shown from the top. Inset: the fast rhythm is shown on an expanded time scale. B: synchronous pattern in all 4 branches. C: distribution of the frequency of the bicuculline-induced slow rhythm with the dorsal-ventral reciprocal pattern (D-V Recipr; ■), the synchronous pattern (Synchr, ◊), and the diagonal reciprocal pattern (Diag Recipr, □).
A pattern in which the slow rhythm was synchronized in all four branches was observed in four preparations but in this case without a concurrent fast rhythm (Fig. 1B). There was no difference in the frequency range of these three patterns (Fig. 1C).

In 8 of 18 preparations a slow rhythm was present before bicuculline application. This NMDA-induced slow rhythm usually occurred in a left-right reciprocal pattern, but with bicuculline ($n = 18$), the slow rhythm became somewhat faster and changed into a dorsal-ventral reciprocal pattern superimposed on the faster left-right reciprocal activity.

**Dorsal-ventral reciprocal pattern**

Figure 2A, 1 and 2, shows the transformation of the bursts pattern when bicuculline was added. The locomotor rhythm became significantly faster, while the slow rhythm became superimposed on the faster burst pattern. This is very evident in the two ventral branches which are modulated in phase. The cross-correlogram in Fig. 2B (see METHODS) compares the activity in the left and right dorsal branches. Clearly the slow activity occurs in phase while the fast activity (left-right) is reciprocal (see Fig. 2B, inset). Figure 2B1 shows in a corresponding way that the ipsilateral dorsal and ventral branches are reciprocal with regard to the slow rhythm but in phase with regard to the fast locomotor rhythm. In the power spectra of Fig. 2C, it is shown that the slow rhythm becomes more prominent with increasing bicuculline levels, while the locomotor rhythm shows a progressively increasing frequency.

In 2 of 24 preparations, a slow alternating pattern was observed between one dorsal branch and a contralateral ventral branch that is a diagonal reciprocal pattern. Figure 3B1 shows a clear diagonal cross-correlogram, whereas the corresponding correlogram in Fig. 3B2 for the ipsilateral branches show no correlation (compare also Fig. 3A). This diagonal reciprocal pattern may either represent a partial expression of a general dorsal-ventral reciprocal pattern (Fig. 1A2) or a separate mode of coordination.

**Rostrocaudal distribution of the dorsal-ventral slow rhythm generator**

All experiments were carried out on spinal cord segments from a region caudal to the gill and rostral to the dorsal fin (segment 12~15~50~60) to exclude fin motoneuron activity, which is in antiphase to myotomal motoneuron activity (Buchanan and Cohen 1982). We tested the likelihood of inducing the dorsal-ventral reciprocal pattern of the slow rhythm in different parts of the spinal cord by dividing it into...
a rostral and a caudal half. The dorsal-ventral reciprocal pattern was elicited by bicuculline in 17 of 19 preparations taken from the rostral half, whereas it only occurred in 1 of 4 from the caudal part \( (\chi^2 \text{ test with Yate's correction, } k^2 = 4.73, P < 0.05) \). The results indicate that the rostral part of the spinal cord (segments 12–30) close to the gill is more readily activated into a slow dorsal-ventral reciprocal pattern as compared with the caudal part.

**Midline longitudinal section of the spinal cord**

To investigate if the neural network responsible for the slow oscillation involves both sides of the spinal cord, a midline longitudinal section of the spinal cord was made in 6 preparations. Before the midline section, the slow rhythm was induced by bicuculline application on NMDA-induced swimming activity. The dorsal-ventral reciprocal pattern of the slow rhythm was induced in five of six preparations, with the synchronous pattern being induced in the remaining preparation. The ventral root activity was almost abolished directly after the operation, but traces of a slow rhythm recovered in 9 of 12 hemicords (from 6 preparations) within 5 min (Table 1, Fig. 4A2). The efferent discharge in Fig. 4A2 appears to be continuous but it is actually modulated in a slow fashion. The autocorrelograms of the dorsal and ventral branches (Fig. 4B1 and 2) show that there is a slow rhythmic activity while the cross-correlogram shows that the dorsal and ventral branches are in phase (Fig. 4B3). However, the dorsal-ventral reciprocal pattern between the ipsilateral branches, which was present before the midline section (Fig. 4A1), never recovered in any preparation. The slow rhythm in ipsilateral branches became synchronous without a phase difference in five hemicords. In the remainder, the pattern became disorganized. In two cases, different slow frequencies were observed in dorsal and ventral branches, and in two cases, a slow rhythm remained only in one branch. There was no consistent change in the frequency of the slow rhythm after the hemisection of the spinal cord (Fig. 4C). In contrast to the slow rhythm, the swimming rhythm did not recover in any preparations up to 60 min after the section. These results suggest that a slow rhythm can be generated independently in dorsal and ventral branches or be synchronized after a midline section but that a reciprocally organized dorsal-ventral activity may depend on a bilateral organization.

**Other potential slow rhythm inducers**

**STRYCHNINE.** If the glycine receptor antagonist strychnine (5 \( \mu M \)) is introduced during fictive locomotion, the frequency of locomotor activity increases progressively to become disrupted (Grillner and Wällen 1980). A partial glycine blockade by strychnine may result in synchronous locomotor bursts on both sides of the spinal cord (Cohen and Harris-Warrick 1984; Hagervik and McClellan 1994). Strychnine may also induce a slow activity pattern (McPherson et al. 1994), although it was not investigated how this pattern was represented in dorsal and ventral branches of the ventral root. In the present study, strychnine (0.1–5 \( \mu M \)) induced a slow dorsal-ventral reciprocal pattern in two of three preparations (Fig. 5A2), and a diagonal reciprocal pattern in the third preparation. The left-right alternation in Fig. 5A1 was abolished after strychnine. The cross-correlogram for the motor pattern in Fig. 5A2 is characteristic of the dorsal-ventral reciprocal pattern with a central trough of the slow oscillation between ipsilateral branches (Fig. 5B1) and a central peak between the left and right dorsal branches (Fig. 5B2). The fast swimming rhythm was not clearly discernible in the strychnine-induced slow rhythm (Fig. 5A2) compared with that in the bicuculline-induced slow rhythm (see Figs. 1A and 2A2). The power spectra for this preparation showed that the slow rhythm started to appear at a strychnine concentration of 0.5 \( \mu M \) (Fig. 5C). The frequency range of this slow rhythm was the same as that induced by bicuculline (0.05–0.10 Hz). The fast swimming rhythm was disrupted by strychnine in all three preparations.

**ACPD.** The metabotropic glutamate receptor agonist ACPD is known to induce a slow oscillatory activity in rat hippocampus (Aniksztejn et al. 1995; Cherubini et al. 1991; Taylor et al. 1995) and to affect locomotor circuitry in the lamprey spinal cord (Krieger et al. 1994, 1998). We investigated the effect of ACPD (25–200 \( \mu M \)) on the induction of the slow rhythm; when it was applied on NMDA-induced swimming (Fig. 6A2), a slow rhythm was induced in a dorsal-ventral reciprocal pattern in two of three preparations. As with the bicuculline-induced slow rhythm, the swimming rhythm did not recover in any preparations up to 60 min after the section. These results suggest that a slow rhythm can be generated independently in dorsal and ventral branches or be synchronized after a midline section but that a reciprocally organized dorsal-ventral activity may depend on a bilateral organization.

**TABLE 1. Midline longitudinal section of the spinal cord**

<table>
<thead>
<tr>
<th>Control</th>
<th>After Section, No. of Side</th>
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<tr>
<td></td>
<td>Pattern of slow rhythm</td>
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<td></td>
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</tr>
<tr>
<td>D-V reciprocal</td>
<td>5 (10)</td>
</tr>
<tr>
<td>Synchronized</td>
<td>1 (2)</td>
</tr>
</tbody>
</table>

Number of side enclosed in parentheses. D-V, dorsal-ventral.
induced slow rhythm, the ACPD-induced slow rhythm was superimposed on a fast swimming rhythm (Fig. 6A2). The cross-correlograms (Fig. 6B, 1 and 2) for the recordings in Fig. 6A2 show that there is a slow dorsal-ventral reciprocal pattern and a fast left-right reciprocal pattern. The power spectra in Fig. 6C show that the slow rhythm is represented with a prominent peak at 50 μM ACPD, while the faster rhythm is present at 0 μM ACPD and progressively increases in frequency with increasing ACPD concentration.

**Discussion**

The results show that bicuculline, strychnine, and ACPD induce a slow rhythm when applied independently on NMDA-evoked activity. The slow rhythm had three patterns: a dorsal-ventral reciprocal, a diagonal reciprocal, and a synchronous pattern, with the dorsal-ventral pattern being the most common. It is noteworthy that the fast locomotor and the slow rhythms could occur simultaneously in different combinations.

**Two rhythms with different patterns**

In the isolated lamprey spinal cord, a slow rhythm superimposed on the swimming rhythm has been observed following the application of 5-HT on kainate-evoked swimming (Schotland and Grillner 1993) and on NMDA-evoked swimming with apamin (El Manira et al. 1994), bicuculline (Tegnér et al. 1993), and strychnine (McPherson et al. 1994). In these studies, whole ventral roots were recorded and a dorsal-ventral organization could thus not be studied. In the present study, the slow rhythm was predominantly organized in a dorsal-ventral reciprocal pattern, while the swimming rhythm always displayed a left-right reciprocal pattern. The present study is the first to report that the slow and fast rhythms occur simultaneously in different combinations in the isolated spinal cord.

**Slow rhythm generator**

The simultaneous existence of two independent rhythms with different left-right and dorsal-ventral reciprocal patterns of activity suggests that there are two distinct rhythm generating networks in the lamprey spinal cord. This is supported by the observation that the slow rhythm, but not the fast locomotor-related rhythm, could recover after a longitudinal midline section of the spinal cord. Buchanan et al. (1995) also reported that a complete midline section abolished the swimming rhythm in lamprey. Hemispinal cords can, however, be made to produce brief episodes of fast rhythmic burst activity after a glycinergic blockade (Grillner et al. 1986), and a fast bilaterally synchronous pattern can be observed in the intact cord after a partial strychnine blockade (Cohen and Harris-Warrick 1984).

The presence of two superimposed rhythms has been reported previously in the isolated spinal cord or isolated spinal cord-hindlimb preparation in the neonatal rat and mouse (Cazalets et al. 1990; Hernandez et al. 1991). In these preparations, the slow burst activity was alternating between ipsilateral antagonistic muscles, suggesting that there are neural mechanisms in the rodent spinal cord that can induce an ipsilateral slow reciprocal pattern. Bracci et al. (1996a,b) reported slow rhythmic bursting (0.03 Hz) with a left-right synchronous
pattern induced by coapplication of bicuculline and strychnine to the isolated rat spinal cord. The burst activity had an intra-burst oscillating structure, which was abolished by ventral quadrant isolation of the spinal cord, whereas the slow burst activity remained. These results may suggest that there are discrete networks also for the slow burst generation and the fast intraburst oscillation in the rat spinal cord.

In the present study, with a spinal midline longitudinal section, the reciprocal pattern of the slow rhythm between the ipsilateral dorsal and ventral branches was disrupted and changed to a synchronous pattern. This result suggests that there are discrete slow oscillators for the dorsal and ventral myotomes that may depend on an excitatory coupling. A bilateral organization appears to be necessary to induce a reciprocal pattern between dorsal and ventral oscillators. The occurrence of a diagonal reciprocal pattern of the slow rhythm suggests that the reciprocity between dorsal and ventral oscillators may be organized preferentially by a diagonal coupling.

The present results are compatible with a conceptual model (Fig. 7A), consisting of separate slow oscillator networks controlling dorsal and ventral myotomes on each side. The slow oscillators can be coupled in three ways: a diagonal reciprocal inhibitory, an ipsilateral excitatory, and a contralateral mutual excitatory coupling. By changing the strength of these couplings (for instance by descending signals from the brain stem), the three patterns observed in the present study could be produced. The contralateral excitatory coupling would make the dorsal oscillators synchronous. When the ipsilateral excitatory coupling is weak, a dorsal-ventral reciprocal motor pattern may occur (Fig. 7B). When all excitatory couplings are weak in comparison with the diagonal inhibitory couplings, a diagonal reciprocal pattern may arise involving only two oscillators (Fig. 7C). When the ipsi- and contralateral excitatory couplings are relatively strong as compared with the diagonal inhibitory coupling, all oscillators may become synchronous (Fig. 7D). Finally, if the contralateral excitatory coupling is weak, the network can generate a left-right reciprocal pattern (Fig. 7E). Ekeberg et al. (1995) have proposed a similar cross-oscillator hypothesis for generating turning movements in three-dimensional space using the swim rhythm generators.

**Mechanisms for the slow oscillator and pattern generator**

The slow rhythm with a dorsal-ventral reciprocal pattern is distinctly different from the left-right alternating locomotion. When a slow left-right alternation occurs (Brodin and Grillner 1985), it is not possible to know whether it represents a very slow activity in the locomotor networks or activity in the current “slow” network. If we restrict the discussion to the dorsal-ventral reciprocal slow pattern, it may be induced by a blockade with strychnine blocking glycine receptors and bicuculline-methiodide blocking GABA_A receptors and apamin-sensitive K_Ca channels and also by agonists of metabotropic glutamate receptors (mGluRs; ACPD). These agents thus release the slow dorsal-ventral reciprocal pattern, observed here for the first time. At present, the neural mechanisms that are utilized by the different agonists-antagonists to induce the slow rhythm are not yet elucidated. However, it is likely that inhibitory inputs to spinal GABAergic neurons could produce an effect analogous to bicuculline, and the 5-HT-systems could

![Fig. 5. Strychnine induces a slow rhythm. A: a swimming activity was induced by 50 μM NMDA (A1). A slow rhythm in the dorsal-ventral reciprocal pattern at 1 μM strychnine (A2). Note that unlike the bicuculline-induced pattern, the swimming rhythm is not discernible (see Figs. 1B and 2A2). B: cross-correlograms for the activities in A2. Cross-correlogram between the left dorsal and ventral branches (B1) and between the left and right dorsal branches (B2). C: power spectra of the left dorsal branch activity in the preparation in A as a function of the strychnine concentration.](http://jn.physiology.org/(Cell%20Image%20Decoder)
reduce the efficiency of $K_{Ca}$ channels as does apamin. Previous studies recording whole ventral roots have reported that a variety of agents may induce a slow left-right alternation concurrently with a fast alternation in lamprey (McPherson et al. 1994; Schotland and Grillner 1993), tadpole (Reith and Sillar 1998), and the neonatal rat (Bracci et al. 1996a).

The activation of the mGluRs by ACPD induces a slow rhythm. In the lamprey spinal cord, presynaptic inhibitory modulation of reticulospinal EPSPs in gray matter neurons is mediated by mGluRs (Krieger et al. 1996), and a modulation of the lamprey spinal locomotor network has been demonstrated (Krieger et al. 1998). In hippocampal CA3 neurons of neonatal and mature rats, ACPD also induced persistent slow oscillations (Aniksztejn et al. 1995; Cherubini et al. 1991; Taylor et al. 1995) suggested to involve presynaptic mGluRs (Aniksztejn et al. 1995). A presynaptic modulation of GABAergic synapses by mGluR agonists has also been reported (Hayashi et al. 1993; Kaba et al. 1994; Llano and Marty 1995; Poncer et al. 1995) and spontaneous inhibitory postsynaptic currents recorded in Purkinje cells had a tendency to cluster in bursts in the presence of ACPD (Llano and Marty 1995).

**Steering behavior and the slow rhythm**

Lamprey swimming is always performed as a lateral undulation. This lateral undulatory swimming is maintained even during steering behavior in the sagittal plane. The present study shows that the network producing the slow rhythm can differentially control dorsal and ventral myotomes and thus suggests one possible mechanism that may affect the swimming in a vertical direction. The dorsal-ventral reciprocal pattern of the slow rhythm was more readily induced in the rostral part of the lamprey spinal cord. There are four slow oscillators for dorsal and ventral myotomes on both sides. They are coupled in three ways: diagonal inhibitory, ipsilateral excitatory, and contralateral excitatory coupling. B: dorsal-ventral reciprocal pattern is generated by reducing strength (dashed line) of the ipsilateral excitatory couplings relative to the other couplings. C: diagonal reciprocal pattern is generated by reducing all excitatory couplings relative to the diagonal inhibitory coupling. D: synchronous pattern is generated by reducing the diagonal inhibitory couplings. E: left-right reciprocal pattern by reducing the contralateral excitatory coupling.
spinal cord, compatible with the observation that a sharp down-
ward turn was accomplished by a ventral flexion of the rostral
part of the body (Ullén et al. 1995). For natural steering
behavior, descending control from reticulospinal neurons (Ull-
én et al. 1998) plays an important role. Pharmacological
microstimulation of the reticular formation could elicit differen-
tial swimming activity in dorsal and ventral branches of the
ventral roots, as well as on the left and right side (Wannier et
al. 1998). Thus descending systems activated by visual or other
sensory inputs may utilize interneurons of the slow network to
accomplish steering in the dorso-ventral plane. Under natural
behavior, the lamprey may not always swim in a straight line
but slowly vary its depth up and down in a sinusoidal fashion
as would be produced by the dorsal-ventral reciprocal pattern
documented here. This type of behavior occurs in fish that like
so, the lamprey may utilize the slow rhythm for this purpose.

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