Interlimb Coordination During Locomotion

ARTHUR WM. ENGLISH
Department of Anatomy and Cell Biology and
Yerkes Regional Primate Research Center,
Emory University, Atlanta, Georgia 30322

SYNOPSIS. Studies of interlimb control during cat locomotion are directed at four different levels of organization. Interlimb stepping patterns are described from studies of the timing of electromyographic activity of muscles of different limbs. Patterns of coordination are based on the frequency of occurrence of the phasing of step cycles of the different limbs. Selective spinal cord lesions are used to perturb those patterns of coordination and have implicated two ascending spinal systems in interlimb control: long ascending propriospinal neurons (LAPNs) and neurons of the ventral spinocerebellar tract (VSCT). The results of neuroanatomical tract tracing experiments indicate that two different populations of LAPNs exist which might provide direct connection between cervical and lumbosacral locomotor centers but that neurons of the VSCT do not make such connections. These results imply that the role of the VSCT in interlimb control is by way of the cerebellum. Unit recordings made from axons of the VSCT during treadmill locomotion are consistent with the VSCT carrying information about the timing of both hindlimb step cycles.

INTRODUCTION

During locomotion the mammalian nervous system must deal with two major classes of control problems. The movements of the individual limbs and the segments within each limb must be finely tuned. In terrestrial mammals, this coordinated movement is known as a step cycle, and its elaboration and regulation have been the subject of numerous studies (see, e.g., Grillner, 1977, for review). In addition, the locomotor cycles of the different limbs must be equally well regulated and this interlimb control will be the subject of this paper.

Studies of interlimb coordination during locomotion have taken several forms. Analyses of the different gaits used during mammalian locomotion have mainly viewed the adaptive potential of different forms of interlimb coordination. In this manner, for example, Hildebrand (e.g., 1976) attempted to explain why different mammals might choose to use different gaits. In contrast, studies from my laboratory, and from others (e.g., Miller et al., 1975) have concentrated on interlimb control in a single species, the cat. Rather than trying to explain why cats employ the types of interlimb coupling patterns they do, these studies have sought explanations of the possible mechanisms by which the nervous system controls interlimb coordination.

The purpose of this paper will be to review our studies of neural pathways which might play a role in interlimb control during cat locomotion. If explanations of the neural mechanisms controlling interlimb coordination during locomotion are to be sought, answers to questions in at least four problem areas must be acquired. First, the patterns of interlimb coordination used by cats during overground locomotion must be determined. Second, if some neural systems are involved in interlimb control, then the normal patterns of interlimb coordination should be changed by their selective destruction. Third, any neural system involved should connect the spinal centers controlling the locomotor cycles of different limbs. Finally, the activity recorded from neurons in these systems during locomotion should be highly correlated with the timing of the step cycles of the different limbs. Data are presented below from each of these four areas which implicate two neuronal pathways used in interlimb control: the long ascending propriospinal neurons which connect the lumbar and thoracic portions of the spinal cord; and the

Normal Patterns of Interlimb Coordination

To determine patterns of interlimb coordination during overground stepping, a sensitive assay of the timing of step cycles of the different limbs is needed. In many studies of interlimb coordination, such data have been derived from limb kinematics and footfall timing patterns (e.g., Hildebrand, 1976). Studies from my laboratory have used electromyographic (EMG) activity recorded from a single muscle in each of the four limbs of a cat stepping overground. The particular muscles chosen were the lateral head of m. triceps brachii (TLa) and m. vastus lateralis (VL) were used because their activity during locomotion provides a stereotyped pattern of the step cycle periods. Step cycle periods (SD) and EMG burst periods (BD) were determined for each muscle. Phase relationships between step cycles of the different limbs were determined from interlimb latency (L) measures. After English (1979).

The phase relationships of the step cycles of the two forelimbs (a), the two hindlimbs (b), the forelimb and hindlimb on the same side of the body (c), and the diagonal limbs (d), are shown. Data are taken from EMG recordings made from a single cat stepping overground. In each panel, the radial graph plots the interlimb phase relationship about the circumference, with 0/360 degrees at the three o’clock position. Phase values increase in a counter-clockwise direction. Duty factor, or the percentage of cycle period during which the muscle is active, is plotted along the radii. Below each radial plot, the phase values are re-plotted as histograms. After English (1979).
INTERLIMB COORDINATION IN LOCOMOTION

(a) R LAR VS L LAR
(b) R TLP VS L TLP
(c) R TLP VS R LAR
(d) L TLP VS L LAR
panel is a radial plot in which duty factor is displayed along the radii and phase is displayed around the circumference. Smaller duty factors, and thus faster steps, are found toward the center of the circle and slower steps are represented toward the outside. Phase values of zero and 360 degrees are found at three o’clock and increase in a counter clockwise direction. Thus step cycles which are 180 degrees out of phase are found at the nine o’clock position. Below each radial plot, phase values are re-plotted in histogram form. The four panels in this figure demonstrate the phasing of step cycles of the two hindlimbs (a), the two forelimbs (b), the right forelimb and hindlimb (c), and a pair of diagonal limbs (d).

As seen in panels a and b the coordination of the homologous limbs, the two forelimbs or the two hindlimbs, is mainly clustered about two distinct patterns. Although a large range of phase values is encountered, the majority of the values noted in Figure 1 are grouped about 180 degrees, indicating an alternation of the step cycles of the two limbs. These are from step cycles using the so-called symmetrical gaits, such as walking and trotting. For a smaller number of steps, phase values which lie closer to zero than to 180 degrees are found. These are principally grouped at the mirror image regions of ±45 degrees and correspond to coupling patterns which are considered in-phase. Such coordination of homologous limbs is found in steps using asymmetrical gaits such as galloping and half-bounding, which are employed at higher stepping speeds.

The coordination of step cycles of the forelimbs and hindlimbs also shows distinct patterns. The majority of the phase values lie in the region of 180 degrees for ipsilateral forelimb and hindlimb step cycles (panel c) and near zero for those of the diagonal limbs (panel d), indicating what has been termed a trotting form of coordination (Miller et al., 1975; English, 1979). Although a few steps are found with other forms of coordination, little or no evidence was found that cats stepping overground use a pacing form of forelimb-hindlimb coordination. Pacing is defined as the tight coupling of the cycles of limbs on the same side of the body and alternation of diagonal limbs. For all of the limb pairs analyzed, a large number of different forelimb-hindlimb phase values was encountered, but some phase values clearly occur with much higher frequency than others. Thus distinct patterns of interlimb coordination are present.

**Effects of Spinal Cord Lesions**

A number of lesions to the spinal cord were made to destroy, in a selective manner, neuronal systems which might be involved in the control of interlimb coordination. The rationale for making lesions to the spinal cord is that essentially normal interlimb coordination can occur during locomotion in high spinal cats (e.g., Miller and van der Meché, 1976), so that spinal circuitry is sufficient for the neural control of interlimb coordination. The results of lesions to two systems will be reviewed here.

Lesions were made to the dorsal columns in the caudal thoracic region. The lumbar dorsal columns in cats are a part of the spinal white matter containing mainly primary afferents and lumbar projection neurons which end in the medulla. However, the dorsal columns also contain the axons of a portion of a group of lumbar neurons which project only as far rostrally as the cervical spinal cord, long ascending propriospinal neurons (LAPNs). The results of dorsal column lesions are summarized in Figure 3. The radial plots in this figure are similar to those of Figure 2. These show that after caudal thoracic dorsal column lesions, the patterns of coordination of the ipsilateral fore- and hindlimbs are relatively unaffected but forelimb-hindlimb coordination is markedly changed. More phase values in the region of the radial plots which would indicate a pacing type of coupling are found after lesions. The effect is not a total disruption of coordination, which would have abolished any grouping of phase values, but a shift from one form of coordination to another. Lesions to the dorsal columns in the upper cervical region produced no change in patterns of coordination. The results of sequential lesions to the dorsal columns in
The effect of caudal thoracic lesions to the dorsal columns on interlimb stepping patterns is shown. Panels a–c show radial plots, similar to those shown in Figure 2, which demonstrate the phasing of step cycles of the two hindlimbs (a), the two forelimbs (b), and the forelimb and hindlimb on the same side of the animal (c), in a cat which had received a lesion to the dorsal columns at the level of the 12th thoracic vertebra. A diagram of a histological section containing the lesion site (in black) is shown in the center of the figure. Panel d is a plot of the duration of hindlimb step cycles vs. the duration of forelimb step cycles. The line represents the best fit linear relationship of these points, and has a slope not significantly different from unity. After English (1980).

The thoracic and upper cervical regions further support these findings. After thoracic lesions, upper cervical lesions had no effect on the phase-shifted pattern of forelimb-hindlimb coordination. Such a phase shift could still be produced if the thoracic lesion was preceded by a lesion to the upper cervical dorsal columns (English, 1980). Thus, of the known fiber systems in the dorsal columns, only the LAPNs would be destroyed by such combinations of lesions so that they must be implicated as a candidate in any neural mechanism for interlimb control.

A second set of lesions which produced an effect on interlimb coordination patterns involved the ventral spinocerebellar tract. Two lumbar systems project directly to the cerebellum from the lumbar spinal cord in cats. The dorsal spinocerebellar tract relays mainly proprioceptive information to the cerebellum via the dorsolateral part of the spinal cord. Lesions to this pathway had no effect on interlimb coordination (English, 1985). The ventral spinocerebellar tract (VSCT) is thought to relay information as to the state of lumbar interneurons to the cerebellum (Lundberg, 1971). Selective lesions of the VSCT had profound effects on interlimb coor-
Interlimb stepping patterns are shown in a cat before (intact) and after (lesion) the animal received a bilateral lesion to the ventrolateral edge of its spinal cord at the level of the ninth thoracic vertebra. Such a lesion was designed to destroy the ventral spino-cerebellar tract (VSCT). Data are derived from EMG recordings made from a single muscle in three of the four limbs. The solid bars indicate the time of activity of the respective muscles. Small arrows beneath each row mark the time of cessation of activity for the muscle in the row above. Arrowheads below the bottom two rows mark the time of cessation of activity in the left forelimb muscle (LTLa) to make comparisons between limbs easier. The dashed lines connect the time points of cessation of activity in muscles of the forelimb and hindlimb on the right side of the body (RTLa and RVL), to show the relationship of their step cycles.

Thus, the step cycle period of the two hindlimbs is fundamentally different from that of the two forelimbs. The bottom panels of Figure 5 plot hindlimb cycle period vs. the latency between ipsilateral forelimb and hindlimb step cycles. In the normal animals, these variables are highly correlated, and the slope of the line fitted to these data points reflects their average phase relationship. In the lesioned animal, the correlation is not significant, and the slope of the fitted line is not significantly different from zero. Lesions of the VSCT greatly weaken the coordination of the forelimbs and hindlimbs during overground stepping. Neurons in the VSCT are thus strongly implicated in interlimb control.

Neuroanatomical Tract Tracing Experiments
If the LAPN's and the VSCT are neuronal systems involved in the control of interlimb coordination, then it is impor-
Fig. 5. The relationship of step cycles of the ipsilateral forelimb and hindlimb is shown for the same cat from which data are portrayed in Figure 4 before and after a lesion to the VSCT. The top two panels plot the duration of the forelimb step cycles against the duration of the hindlimb step cycles. The line is the best fit to these points using least squared regression techniques. The correlation coefficient is given by R. The lower panels plot hindlimb step duration against the latency between step cycles of the right forelimb and hindlimb (see Fig. 1). The lines represent the best fit to these data points.

It is important to demonstrate that their anatomical connections are appropriate to play these roles. The connections of LAPNs were investigated using the retrograde transport of wheat germ agglutinin conjugated to horseradish peroxidase (WGA-HRP). Injections of WGA-HRP were made into the cervical spinal cord, presumably into the areas of termination of LAPNs. The WGA-HRP was taken up by these terminals and transported retrogradely to fill the cell bodies of origin of the LAPN’s in the...
lumbar part of the spinal cord. A summary of one such experiment is shown in Figure 6. At the top of the figure is a series of cross sections of the cervical spinal cord showing the (dark) sites at which WGA-HRP was injected. Below it is a series of cross sections of different parts of the lumbar cord showing the areas in which retrogradely labelled cell bodies of LAPN's were found (English et al., 1985). In the dorsal horn are a large number of small neurons which appear to project bilaterally to the cervical spinal cord, probably through the dorsal columns. Axons of these neurons were probably destroyed by the dorsal column lesions described above. It was somewhat surprising to find a second population of LAPN's in the ventral horn and intermediate zone. These large cells project mainly in a crossed fashion, probably through the ventral and ventrolateral white matter columns.

The size, shape and position of these ventral cells are remarkably similar to those reported for some VSCT cells (e.g., Matsushita et al., 1979). This similarity could be explained if, during injection, WGA-HRP was exposed to the axons of VSCT neurons as they pass through the cervical region on their way to the cerebellum. This possibility seems unlikely, since the axons of the VSCT are known to lie in the ventrolateral white matter and all WGA-HRP injections were made into the dorsal part of the cervical cord, thereby avoiding, as much as possible, the axons of the VSCT. Alternately, the similarity could be explained if VSCT cells contained axon collaterals which terminated in the cervical spinal cord. The same neurons would then project both to the cervical spinal cord and to the cerebellum. To examine this possibility, WGA-HRP was injected into the cervical cord and a radioactively labelled but enzymatically inactive form of HRP (see e.g., Hayes and Rustioni, 1979) was injected into the cerebellum. These tracer substances are retrogradely transported and will fill the cell bodies whose synaptic terminals lie in the region of the injection site. The WGA-HRP labelled neurons are detected using an enzyme histochemical reaction and any radioactively labelled neurons are detected using autoradiography. Both WGA-HRP labelled and radioactively labelled cells were found in the lumbar spinal cord of these cats, as might be expected if some neurons projected to the cerebellum and others projected to the cervical spinal cord. However, very few of the cells contained both tracers, as would be expected if the same cells projected to both sites (McBride et al., 1981). Thus the available evidence would argue that the VSCT does not contain cervical collaterals. Any effect of the VSCT on interlimb coordination must be mediated by way of the cerebellum. Since both the inputs to the cerebellum via the VSCT and the spinal outputs from the cerebellum (probably via the vestibulospinal tract) are both very fast conducting, the connections of the VSCT are not incompatible with it playing a role in interlimb control. Lending support to a trans-cerebellar role for the VSCT in interlimb coordination are the results of experiments in which the cerebellum was cooled to remove its effect on locomotor control (Udo et al., 1980). In both intact and decerebrate cats, cooling the cerebellum resulted in major disturbances in interlimb coordination.

Unit Recording Experiments

If a neural system is involved in interlimb control, then one might expect its neurons to fire during locomotion in a manner appropriate to their proposed role. In particular, one might anticipate that their firing would be closely coupled to the EMG patterns used as measures of the timing of the step cycle and that they should main-

Fig. 6. The anatomical organization of long ascending propriospinal neurons (LAPN's) is shown from a single cat. The group of outlines of spinal cords at the top of the figure is shown to identify the portions of the cervical spinal cord into which retrograde tracer (WGA-HRP) was injected. The series of outlines below are to show the position of retrogradely labelled cell bodies of LAPN's in different parts of the lumbar spinal cord. Each dot represents the position of a labelled neuron. After English et al. (1985).
Fig. 7. The activity pattern of a single neuron recorded from the ventrolateral surface of the spinal cord at the level of the 10th thoracic vertebra during treadmill walking is shown. The bottom pair of traces show the timing of unit discharges from this cell (UNIT) along with its instantaneous firing rate (IFR). Immediately above these traces is the integrated EMG activity of m. vastus lateralis from the contralateral hindlimb. Above these three traces are two raster panels. In the panel on the left, the integrated VL EMG activity is re-plotted such that each step cycle is aligned on the onset of EMG activity (center vertical line). The vertical lines at each side of the raster are simply 500 msec before and after the onset of EMG activity. The histogram at the bottom of the raster is an average of the activity patterns shown in the individual sweeps. The panel on the left is arranged in the same manner but shows the discharge pattern of the unit and its average, aligned on the onset of EMG activity (center vertical line). Note the rather tight coupling of the unit discharges to the onset of EMG activity and a second burst of activity approximately 400 msec later, near the termination of EMG activity.

Taint that correlation at different speeds of locomotion. The firing patterns of neurons in one of the two candidate systems, the VSCT have been investigated in this regard. Recordings were made from an array of small, metal microelectrodes implanted into the ventrolateral white matter, in the lumbar region of the spinal cord. The electrodes were made from 0.5 mm long etched, stainless steel insect pins. Each pin was welded to a length of EMG wire and the weld was insulated with a drop of epoxy. The resulting “hatpin” type microelectrodes were further insulated with a varnish type insulation until their impedances were at least 1 M ohm. Several (usually four) such electrodes were passed through a thin, 1 mm square patch of silastic film and bonded to the film with medical adhesive A. The resulting patch electrode array was positioned just above the ventral roots on the lateral surface of the spinal cord, in the region of the tenth thoracic vertebra, and the tips of the electrodes thrust into the white matter. This region of the spinal white matter is the known course of axons of the VSCT. Recordings of unit action potentials were made from...
individual electrodes. Units with peak-to-peak amplitudes of 0.5–1.0 mV and duration of <1.5 msec with stable waveforms were examined. Such extracellular recordings could be made from single axons for the duration of an experiment as the cat walked on a motor-driven treadmill belt.

The firing pattern of one such cell is shown in Figure 7. The firing pattern of the unit and the integrated EMG activity recorded from the contralateral vastus lateralis muscle is shown at the bottom of the figure. At the top of the figure, the same data are displayed in a different format. The EMG activity (left) and unit activity (right) are shown in a raster form, aligned on the onset of EMG activity. At the bottom of each raster is an average of the activity as so aligned. The firing pattern of the unit shown is typical of 16 different units recorded in this cat. It clearly has a double burst of activity during each step cycle. One burst is found to be highly correlated with the contralateral step cycle, beginning just after the onset of EMG activity in the contralateral limb. The second burst of activity is found later in the cycle, near the end of the EMG burst from the contralateral limb. Since the hindlimbs were being used in an alternate manner in this stepping sequence, it seems likely that the timing of this second burst would be correlated with the onset of EMG activity in the ipsilateral vastus lateralis. The firing pattern of this neuron is thus highly correlated with the timing of the step cycle of both hindlimbs. Analysis of the behavior of these units at different stepping speeds provides additional evidence to support this conclusion. At all stepping speeds examined, the cell begins firing at an almost fixed latency following the onset of EMG activity in the contralateral hindlimb step cycle. This finding suggests that the firing of the neuron is time-locked to the timing of the hindlimb step cycles. At faster stepping speeds, when the cycle period is shortened, the latency between the bursts of EMG activity from muscles of different limbs is shorter and the latency between the two bursts of unit activity also decreases. Thus the activity of these presumed VSCT units is appropriate to consider them as acting in interlimb control. The activity of the units sampled is consistent with the idea that the VSCT may be relaying to the cerebellum information on the timing and coordination of both hindlimb step cycles. Somewhat similar findings have been made using more elegant recording methods in intact cats by Cléland and Hoffer (1985) and in decerebrate cats which were induced to walk on a treadmill by brainstem stimulation (Arshavsky et al., 1972).

**Future Directions**

The LAPNs and neurons of the VSCT are strongly implicated in the neural control of forelimb-hindlimb coordination during stepping in the cat. Although the LAPN and VSCT systems are implicated, more detailed analyses, especially of neuronal firing patterns, are needed to elucidate their mechanism of action. The results of such studies might determine, for example, what elements of the step cycle of the different limbs is actually used to coordinate their different step cycles. Similar studies of species which use widely different patterns of interlimb coordination may also help. Animals which habitually use pacing rather than trotting forms of coordination, for example, might provide clues as to how interlimb coordination is normally achieved.

**References**


English, A. W. 1985. Interlimb coordination during


