Neuronal mechanisms for the adaptive control of locomotion in the cat.

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Introduction

Locomotion is a highly complex activity whose control is ensured by the coordinated action of a number of diverse structures and nuclei at different levels of the central nervous system. Indeed, an animal in full flight, moving over a surface that is irregular and full of obstacles, needs to call on the full capacity of its nervous system in order to adjust its movements to the terrain. In such a circumstance, locomotion is much more than a simple rhythmical activity that requires alternating activity in flexor and extensor muscles of the limbs. Locomotion becomes a challenge in which posture and equilibrium must be maintained in the face of self-imposed perturbations as the feet exert forces at angles anything but perpendicular to the ground and limb trajectories must be continually altered to assure that the limbs clear obstacles and are placed appropriately on the support surface. The aim of this brief chapter is to give the reader an overview of some of the neural structures that are involved in such behaviours and of the manner in which they may exert their control. Because of space limitations, the focus in this chapter will be on the role of the motor cortex in the adaptations required during voluntary modifications of gait. However, for those who have little background in the neuronal mechanisms used to control animal locomotion, the chapter will also provide some general information on the role of both spinal and supraspinal structures in the control of locomotion.

The basic locomotor rhythm

It is quite clear from the experimental evidence that most mammals (reviewed in: Armstrong 1986; Grillner and Wallen 1985; Rossignol 1996), including non-human primates (Fedirchuk et al. 1998), and probably humans themselves (Calancie et al. 1994; Dietz et al. 1995; Harkema et al. 1997), possess neuronal circuits within the spinal cord that are capable of generating the basic alternating rhythm of locomotion. Evidence for this statement comes from several sources but is best illustrated by the remarkable capacity of adult cats with complete transections of the thoracic spinal cord to execute well coordinated locomotor movements with the hindlimbs when placed on a treadmill (Barbeau and Rossignol 1987; Bélanger et al. 1996; Eidelberg et al. 1980; Giuliani and Smith 1987; Lovely et al. 1990;). Such cats are not only capable of generating a locomotor rhythm but also of adapting that rhythm to changes in treadmill speed and, to a small extent, to changes in the orientation of the treadmill either in the pitch tilt (nose up and nose down) or the roll tilt (ear down) conditions. In addition, if the hindlimb of such spinal cats hits an obstruction the spinal cord contains the requisite circuitry to ensure that the leg is appropriately brought away from and then over the obstruction in a manner very similar to that observed in the intact cat.

While experiments in spinal cats show the capacity of the lumbo-sacral cord to generate and, within limits, to adapt locomotion, it must be realised that in these animals there is abundant rhythmical peripheral afferent feedback from the moving limbs that can both entrain and modify the locomotor rhythm (Rossignol 1996). The existence of a locomotor rhythm in such animals, therefore, does not of itself prove that the spinal cord contains the intrinsic circuitry that is necessary for locomotion. However, other experiments have shown unequivocally that the spinal cord is, indeed, capable of generating a pattern of rhythmical activity that closely resembles that observed during locomotion in the intact animal. This has been demonstrated very clearly by recording locomotor in animals in which the spinal cord is activity completely transected and rhythmical movement of the limbs is prevented by applying a paralysing agent, such as curare, that blocks the neuromuscular junction. In such animals, it is possible to record the central locomotor command signals from motor nerves, an electroneurographic recording, instead of by recording electromyo graphic (EMG) activity from the muscles as one normally does in the intact animal. Such locomotion, in an animal which is paralysed and, therefore, can not walk, is normally referred to as fictive locomotion. In such a preparation, after application of various pharmacological agents, or nonspecific electrical stimulation, it is possible to record from the motor nerves a mythm that shows some of the complexity of the normal locomotor pattern, thus

demonstrating the *intrinsic* capacity of the spinal cord to generate the basic locomotor rhythm (Grillner and Zangger 1975, 1979; Pearson and Rossignol 1991). Details concerning the organisation of this intrinsic spinal central pattern generator, or CPG, can be found in the chapter by Cohen.

The existence of such a CPG implies that neither peripheral afferents nor supraspinal structures are necessary for the generation of the basic locomotor rhythm. However, both are essential for the adaptation of that rhythm to the take into account the vagaries of the terrain over which it walks. Indeed, one should normally assume that, in the normal, intact, animal, even the most basic locomotion over a flat, even, surface is the result of the integrative action of the spinal rhythm generating circuits and the rhythmical inputs from peripheral afferents and supraspinal structures.

Descending control of Locomotion

Descending regulatory signals from supraspinal structures are essential for the full expression of locomotion as has been shown by a wide array of experiments carried out in a large number of different laboratories (for general reviews, see: Armstrong 1986, Rossignol, 1996, Orlovsky et al. 1999). This fact is best appreciated by a consideration of the deficits that are seen following complete transection of the spinal cord at the lower thoracic level. As documented above, adult cats with such complete transections have the remarkable ability to recuperate locomotor activity of the hindlimbs, which are capable of walking on a moving treadmill belt and of adapting their movements to changes in speed and, to a lesser extent, to changes in slope. However, these cats, even after several months of training, show a number of serious deficits that highlight the normal contribution of input from supraspinal structures in the control of locomotion. Among these deficits, the most evident are: i) a loss of adequate weight support and of lateral stability; ii) an inability to voluntarily initiate locomotion; iii) a loss of interlimb coordination between the fore- and hindlimbs; and iv) an inability to make any anticipatory modifications of the locomotor pattern. Separate experimental evidence is available in each case to show that descending signals from the brain are essential for (i, ii, and iv) or contribute to (iii) these functions. In addition, it is probable that loss of descending information also contributes to some of the

more subtle deficits seen in these animals; for example, the loss of intralimb coordination evident in cats with both complete and incom plete transections of the spinal cord. In sum then, while the spinal cord produces a basic locomotor rhythm, supraspinal (and peripheral) signals are essential to produce what has been referred to as behaviourally relevant locomotion (Grillner and Wallen 1985).

While a general review of the interactions between the different supraspinal pathways and the basic locomotor rhythm is beyond the scope of this chapter, it is important to emphasize that, in most cases, descending systems probably exert their effect either via the CPG, or through interneuronal pathways that are modulated by the output of the CPG, rather than by a direct action on the motoneurones controlling the muscles themselves. Such a mode of action ensures that the descending signals from the supraspinal structures are appropriately integrated into the base rhythm (McCrea 1996). Evidence for this assertion comes primarily from experiments in which the effects of stimulating different structures during locomotion have been studied. In virtually every case that has been examined, it has been found that the effects of such stimuli are phase-dependent. That is, stimulation in certain phases of the locomotor cycle is effective in eliciting modifications of EMG activity, while stimulation in other phases is ineffective. For example, weak stimulation of the lateral vestibular nucleus (LVN) during stance elicits brief responses in extensor muscles and has no effects on flexor muscles (Orlovsky 1972). The same stimulation applied to the LVN during the swing phase is without effect. Conversely, stimulation of the red nucleus is most effective when applied during the swing phase when it evokes facilitatory responses in most flexor muscles (Orlovsky 1972; Rho et al. 1999); during stance it is either without effect (Orlovsky 1972) or produces a mixture of facilitatory and inhibitory responses in extensormuscles (Rho et al. 1999). Stimulation of the pontomedullary reticular formation (PMRF) always produces complex effects, with stimulation during stance producing a mixture of facilitatory and inhibitory responses in extensor muscles and stimulation during swing generally producing facilitatory responses in flexor muscles (Degtyarenko 1993; Drew and Rossignol1984; Drew 1991; Orlovsky 1972).

While these effects might be explained simply

on the basis of the level of depolarization of motoneurones, examination of the phase at which the maximal response is obtained frequently shows it to be different from the period of peak EMG amplitude, suggesting mediation via phasically active interneuronal pathways. Other experiments, in which the intensity and the duration of the stimulus train has been increased show that many supraspinal structures are also capable of resetting the locomotor mythm, generally by prolonging either the swing or stance phases of the locomotor cycle (Armstrong and Drew, 1985; Degtyarenko 1993; Drew and Rossignol 1984; Leblond and Gossard 1997; Perreault et al. 1994; Rho et al. 1999; Russell and Zajac 1979). Such a capacity suggests that these supraspinal structures may act through interneurones that form part of the CPG. Resetting of the rhythm has been observed for all structures in the fictively locomoting cat but is less frequently observed, and less strong, in the intact cat. This suggests that all descending pathways have access to the CPG but that, in the intact cat, the peripheral and cortical pathways have a stabilizing influence that makes it difficult for signals from any one pathway to disrupt the ongoing locomotor rhythm. The exception is the corticospinal pathway which seems to have privileged access to these pathways allowing descending cortical commands to modify the locomotor rhythm (Orlovsky 1972; Rho et al. 1999).

The sum result of this type of organisation is that descending commands will normally produce modifications of locomotor activity that are superimposed onto the locomotor rhythm without undue interruption of that rhythm. Only if the strength of the descending signal is increased is it possible to modify that rhythm, and only in response to signals from the motor cortex does it seem possible, in the intact animal, to produce a change in the overall locomotor cycle.

Anticipatory control of locomotion

An Overview

Efficient locomotion over irregular terrain is impossible without visual information. Experiments have shown that under relatively undemanding circumstances, human subjects do not need to fixate objects or to continuously scan their immediate environment but will rather normally make intermittent visual samples of their environment (Assaiante et al. 1989; Laurent 1991; Laurent and Thomson1988; Patla 1989; Patla and Vickers 1997). However, as the difficulty of the locomotor task increases, so does the frequency of the samples that are made so that under circumstances in which subjects must accurately place their feet in each step, visual information of the environment is, likewise, made in each step (Hollands et al. 1995; Hollands and Marple-Horvat 1996; Patla et al. 1996). These data are reviewed in the chapter by Patla and will not be discussed further here.

Once visual information about the environment has been sampled, it must be transformed into a pattern of muscular activity that is appropriately scaled to produce the gait modification required to avoid or to step around an obstacle, or to place the foot accurately in a given location.

This is a highly complex process of visuomotor transformation that undoubtedly involves parallel processing in several different areas of the brain, including different areas of the cerebral cortex, the cerebellum and the basal ganglia. However, the exact mechanisms by which the various stages of this transformation occur are poorly understood and have been studied in any detail only in primates trained to make reaching movements to a target. The growing consensus from such work is that a major part of this transformation occurs within the parietal cortex where the signal is progressively transformed from one in which the target is represented in spatial coordinates to one in which it is expressed as an internal representation of the kinematics and kinetics of the movement that are needed to attain the target (see, Caminiti et al. 1996; Johnson et al. 1996; Kalaska 1996; Kalsaka and Crammond 1992; Kalaska and Drew, 1993). Although there is presently no direct evidence on the subject, one may assume that similar processes of visuomotor transformation occur during visually guided locomotion and that similar cortical areas participate in this task. However, during locomotion, there is the added complication that the body is in motion and that the modifications of body orientation and limb trajectory required to step around or over an object have also to be planned on the basis of the speed of progression. In such circumstances the animal must also judge the distance to the target, perhaps by using optic flow signals providing information about the time to contact (Gibson, 1968; Goodale et al. 1990; Lee 1976, 1980; Patla and Vickers 1997) and incorporate them into the locomotor pattern. Such a process may use a forward model (Jordan and Rumelhart 1992; Wolpert et al. 1995) to incorporate

this visual information into the basic walking rhythm (McF adyen et al. 1994).

Regardless of the exact neuronal mechanisms that are used to plan the gait modification that is to be made, the final step in this process is a signal that encodes the movement that has to be made. There is general agreement that for both reaching movements and for anticipatory, or visually-triggered, gait modifications the final signal used to control the movement is to be found, in part, in the neuronal discharge of neurones within the motor cortex. The remainder of this section will discuss the signal that is contained within these cortical neurones and the manner by which it may produce the changes in limb trajectory required to step over an obstacle.

Role of the Motor Cortex

The importance of the motor cortex for the adaptation of locomotion to the nature of the surface on which one walks can be simply demonstrated by surgically excising the motor cortex, by pharmacologically inactivating it or by transecting the major descending pathway from the motor cortex, either in the pyramidal tract or within the spinal cord (reviewed in Drew et al. 1996). In all cases, interruption of this pathway results in only transient deficits in locomotion on a flat surface, but long-lasting, and probably permanent, deficits in the ability of cats to safely negotiate obstacles in their course and to accurately place their paws in the required location. Thus, one may assume that the signal transmitted within the corticospinal tract is necessary for the appropriate adjustments of the locomotor gait required in such circumstances.

The nature of this signal has been studied by recording the activity of individual neurones within the motor cortex during locomotor tasks that require anticipatory modifications of gait. Such studies, in tasks requiring cats to either accurately place their paws on the rungs of a horizontal ladder (Amos et al. 1990; Armstrong and Marple-Horvat 1996), to step over barriers in their path (Beloozerova and Sirota 1993), or to step over obstacles attached to a moving treadmill belt (Drew 1998; Drew 1993; Drew et al. 1996; Widajewicz et al. 1984) have all show n that neurones in the motor cortex exhibit significant modifications of their discharge activity that are tightly linked to the movement that is to be made.

An example of such a modification is

illustrated in Fig.1 which shows the change in limb trajectory (Fig. 1B) and the associated change in EMG activity and neuronal activity when a cat steps over an obstacle with a round cross-section that is attached to a moving treadmill belt. The neurone illustrated in this example was recorded from the motor cortex, in the posterior bank of the cruciate sulcus. It was identified as a neurone whose axon (conduction velocity of 44m.s⁻ ¹) descended at least as far as the pyramidal tract; the neurone could, therefore, be classified as a pyramidal tract neurone (PTN). During the step over the obstacle, there was a modification in the duration, amplitude and, in some cases (e.g. EDC) of the temporal relationships of the muscles that can be seen both in the single step illustrated in Fig. 1C and in the average illustrated in Fig 1D. Associated with the gait modification, there was a large increase in both the duration and, more particularly, the frequency of the discharge in the recorded PTN (Unit). It is to be noted that there was no change in the frequency of cell discharge in the step preceding that over the obstacle, supporting the general view that the motor cortex is involved in the execution of the task and not in its planning (see Kalaska and Drew 1993).

What is the descending signal from the motor cortex controlling? Is the motor cortex producing a signal that is defining the path of the paw over the obstacle, one that defines the changes in angle of the different limb segments, or one that provides more specific information concerning the detailed modifications in muscle activity that are required to produce this modification? The data obtained in my own experiments lead me to suggest that the motor cortex provides a detailed signal that specifies the changes in muscle activation that are required to produce the change in limb trajectory. Details concerning the reasons for this suggestion can be found within the original papers and review article (references above) but can be summarized briefly in the following manner.

Examination of the changes in EMG activity of muscles acting around different joints during voluntary gait modifications shows that the smooth change in limb trajectory that is observed during a gait modification (Fig 1B) is, in fact, produced by a complicated modification of the pattern of activity in most muscles acting around the different joints of the cat forelimb. Modifications range from simple changes



Figure 1: Example of the modification of discharge activity in a PTN during a voluntary gait modification. A: tracing from a video image illustrating the orientation of the forelimb during a step over a cylindrical obstacle attached to the treadmill belt. B: stick figure illustrating the change in trajectory during the swing phase of this step: The leg has been reconstructed from the X and Y coordinates of light reflecting points attached to the skin over identified bony landmarks (see Drew and Rossignol 1987 for details). C: raw data showing activity of four selected flexor muscles (all contralateral to the recording site) acting around the forelimb, together with the activity of a PTN (Unit). The figure shows 3 consecutive cycles with the step over the obstacle being represented by the middle cycle. The vertical dotted lines indicate the time of onset of activity in the CIB. The data is illustrated for the Lead condition, when the forelimb contralateral (co) to the recording site is the first to pass over the obstacle. D: averaged activity of the Same cell and muscles, including the cycle illustrated in C:- again each cycle is synchronized on the activity of the CIB. The thinner line indicates the activity of the muscles and cells when no obstacle was attached to the treadmill belt, the thicker line indicates the activity when the cat steps over the obstacle. Abbreviations: Br, brachialis (flexor of the elbow); CIB, cleidobrachialis (protractor of the shoulder and flexor of the elbow); EDC, extensor digitorum communis (dorsiflexor of the wrist and digits); TrM, teres major (retractor of the shoulder). Modified from Drew 1988.

in the level or duration of the period of activity through to more complicated changes in the temporal relationships between muscles; in some muscles there are changes in all three parameters. The changes in muscle activation patterns are, as would be expected, sequential so that changes in different muscle groups occur at different times during the modified swing phase of the gait modification. This can be appreciated from inspection of Figs 1 C and D. For example, the ClB shows a large increase in both its amplitude and duration which occupies the entire swing period while the Br shows primarily an increase in its amplitude during the initial period of flexion that would serve to lift the limb above the obstacle. The TrM also shows a relatively brief period of increased activity and this precedes the modification of activity in Br as the shoulder must be retracted to lift the paw from the support surface before the limb is flexed. The EDC shows a more complicated pattern of activityas, during control locomotion, it has a single period of activity in each step cycle and during the gait modification it is active twice.

Examination of the modification of unit activity that is seen during these gait modifications showed a similar pattern. That is, different PTNs also exhibited their major changes in activity at different times during the swing phase of the modified gait cycle. This is illustrated in Fig. 2 for two neurones that increased their discharge activity at different times during the gait cycle. Unit A showed an increase early in the gait modification, coinciding approx imately, with the period of increased activity in the TrM, needed to retract the shoulder. In contrast, Unit B discharged realtively later in the gait cycle, approximately in phase with the second period of increased activity in the EDC which serves to prepare the limb for landing after the obstacle has been cleared. It is also interesting to note that in the Trail condition, in which the limb contralateral to the recording site is the second to pass over the obstacle, both neurones changed their relative phase of activity with respect to the onset of the ClB, but maintained their relationship to the periods of modified activity in the TrM and the EDC, respectively. This suggests that different PTNs are involved in regulating the activity of a select group of muscles and that the relationship between cell and muscle is maintained even if the overall pattern of activity changes.

Overall, the data from the entire population of neurones indicated that different PTNs are active at different times during the gait modification, with some discharging early in the swing phase, as in the example in Fig 2A and others discharging slightly later (not illustrated), as the limb is being lifted above the obstacle. Still others, such as that illustrated in Fig.2B, discharge at the end of the swing phase, as the limb is being prepared for contact with the support surface, while yet others, similar to the example illustrated in



Figure 2: Two examples of PTNs (A and B) that discharged at different times during the gait cycle. As in Fig. 1, the thinner line indicates averaged neuronal and EMG activity during control locomotion and the thicker line the averaged activity during the gait modification. The vertical dotted line indicates the moment of onset of the ClB. Data are shown only for the period just preceding and during the modified step. Data are shown for both the Lead and the Trail condition.

Fig. 1, are active throughout the swing phase. This suggests that the overall change in limb trajectory is produced by the sequential activation of populations of PTNS, with each population involved in specifying the modulation of activity required in small groups of muscles at different times during the gait modification.

Interaction with the locomotor rhythm

How is the gait modification superimposed upon the basic locomotor cycle? Fig 3. illustrates a conceptual model that we have used previously to discuss this issue. In brief, we follow Grillner (1982) in suggesting that the CPG may be usefully thought of a series of unit CPGs in which separate modules are used to regulate the rhythmical activity around different articulations. Although the basis for this idea of unit pattern generators is based primarily on theoretical considerations of the flexibility required to produce different movements, some experimental evidence for the idea of modules comes from the work of Stein in the turtle (reviewed in Stein and Smith 1997).

The advantage of a modular organisation for the control of voluntary gait modifications is that

descending systems may bias the activity in one or more modules without, necessarily, changing the activity in other modules. Such an ability is essential when one considers the variety of limb trajectories that are required to step over obstacles of different shapes and sizes. For example, stepping over a verywide obstacles requires a large protraction of the limb and consequently a large increase in the duration of the shoulder flexors. However, stepping over a very narrow but high obstacle requires primarily a large flexion of the elbow. Stepping over a cylindrical obstacle (see Fig. 1) requires the coordinated action of both the shoulder and the elbow muscles. The modular organisation illustrated in Fig. 3 allows a descending signal to differentially modulate the activity of one of the modules by itself, or in combination with any other, thus providing the required flexibility. We suggest that the different patterns of discharge in motor cortical neurones provides the neuronal substrate by which the different modules are modified.

The suggestion that the gait modifications act through a modular CPG, although conceptual in nature, is based upon experimental data. First, it must be realized that all corticospinal projections in the cat are directed at interneurones, i.e there are no monosyna ptic connections with motoneurones (Illert et al. 1976). Second, the results from experiments in which brief trains of stimuli have been applied to the motor cortex show that the responses are organized in a phasedependent manner (see above), suggesting that the effects are mediated through interneurones that are either part of, or influenced by the CPG. Third, as described above, longer trains of stimuli are capable of resetting the locomotor rhythm, suggesting that the corticospinal system has access to the CPG. In addition, by acting through the interneuronal networks involved in controlling cycle timing and structure, the nervous system can take advantage of the intrinsic spinal cord circuits to ensure that changes in any one module are fully integrated into changes in the other modules. The interconnections between spinal modules and those between different cortical neurones, together, would ensure that all movements are smoothly integrated into the locomotor pattern.

However, if such mechanisms might act to ensure integration and coordination, what mechanisms ensure specificity? It is well known, for example, that individual corticospinal neurones do not activate interneurones that will affect only one or two muscles



Figure 3: Conceptual model illustrating how the descending command for movement from the motor cortex might act to modify gait by acting through the spinal CPG for locomotion. The spinal CPG is represented as a series of modules, each of which would serve to specify the pattern of activity around a single joint. Each of these modules is coupled, as indicated by the two-way horizontal arrows, and each receives input from a timing circuit (oscillator) which sets the locomotor rhythm. During the gait modification, a descending signal from the motor cortex differentially modifies the activity of these modules. It is suggested that each population of PTNs, active at different times in the swing phase of the modulated cycle, would influence the activity in a different series of modules. Some would preferentially activate more proximal modules, others those more distally located.

but, rather, are more likely to influence the activity of a substantial number of synergists (Fetz et al. 1976; Shinoda et al 1981). Probably, part of the explanation comes from the relative synaptic weight on different muscles. At least for the direct, corticomotoneuronal, projections in primates, it is known that the connections that a motor cortical neurone makes with some motoneurones are stronger than those with others (Fetz et al. 1976; Bennett et al 1996). Similar considerations probably hold for the connections made through interneurones, i.e connections thorough interneuronal pathways to some muscle groups are likely to be stronger than those through others. In the example illustrated in Fig. 3 we suggest that different populations of neurones active when the limb is lifted above and over the obstacle (referred to in our previous publications as Phase I) would project to different modules of the CPG allowing the differential modification of shoulder, elbow and wrist muscles. Although neurones in each population would project to several modules, each of these populations would have stronger projections to one module than to the others. Neurones active in Phase II, during the time that the limb is prepared for contact with the support surface, are suggested to preferentially activate modules regulating the activity of the distal muscles that are necessary to stabilize the paw at this time. Interestingly, a neural network model (Prentice and Drew 1997), based on the motor cortical data that was obtained in the experiments in cats, has shown that specificity of action on different muscle groups can indeed be maintained by the spatio-temporal organization of the "corticospinal connections", even though the axons of individual populations of neurones branch widely onto "spinal neurones".

Coordination of Posture and Movement

In addition to controlling the trajectory of the limb as an animal steps over an obstacle, there is also a requirement to ensure postural stability. As the cat lifts it legs over the obstacle, it needs to modify its posture to ensure stability and equilibrium as the centre of gravity is shifted. Recordings of ground reaction forces (GRFs) and of EM G activity from extensor muscles in each of the four limbs of the cat suggests that these postural responses consist of a coordinated modification of activity in each of the supporting limbs (Lavoie et al. 1995; McFadyen et al. 1999). Moreover, these modifications of postural activity are dynamic and have to be incorporated into the locom otor cycle.

Our recent experiments suggest that the descending signal from the motor cortex that specifies the voluntary gait modification that is to be made also specifies the magnitude and timing of the postural responses that accompany it (Kably and Drew 1998).

We base this suggestion both on a consideration of anatomical connections between the cortex and the brainstem and of the physiological properties of certain classes of corticofugal neurones in the motor cortex and in the pontomedullary reticular formation during voluntary gait modifications. The former structure, as we have detailed in the preceding sections, is strongly implicated in the control of voluntary movements. The latter, is a brainstem structure that is implicated in the regulation of flexor and extensor muscle activity during locomotion and which is suggested to be involved in the control of posture (see Mori 1987, 1989; Mori et al. 1992).

It is known that there is a strong projection from the motor cortex to the PMRF, the corticoreticular pathway (Canedo 1997; Canedo and Lamas 1993; Jinnai 1984; Keizer and Kuypers 1984; Matsuyama and Drew 1997; Newman et al. 1989; Rho et al. 1997), that could be used to adjust the motor output of the latter. Experiments in which the terminal projections of motor cortical neurones have been recorded show that many phasically active motor cortical neurones project both to the spinal cord and to the PMRF. As such the signal transmitted to the spinal cord is also transmitted to the PMRF, where many corticoreticular neurones synapse onto reticulospinal neurones. This collateral signal would provide a copy of the descending signal that would provide information concerning the scale and the magnitude of the voluntary movement and which could be used to modify the output of the reticulospinal neurones (RSNs) to produce the requisite changes in postural activity. That RSNs could provide the neural bases of the complex changes in posture that are observed in the supporting limbs during a gait modification (Lavoie et al. 1995) has received some support from our recent studies showing that individual RSNs, including those receiving input from the motor cortex, may show multiple increases in discharge activity, with each burst corresponding to the passage of a single limb over the obstacle (Prentice and Drew 1995). We suggest that this descending signal would provide general information concerning the magnitude and the timing of the required gait modification while the specific nature of the postural changes would be determined by the state of the excitability of the central pattern generating circuits within the spinal cord.

Conclusions

Although this review has been restricted to

several narrowly defined aspects of locomotor adaptation, the major principals and concepts that can be drawn from the experiments that I have described hold for a much more diverse group of behaviours than those treated here. Certainly, the existence of an intrinsic CPG within the spinal cord simplifies the control issue by removing the need for supraspinal structures to generate locomotion and instead leaving them free to regulate and modify a well defined spinally generated pattern. In addition, the properties of the CPG, at least as far as we understand them, also simplify, to a great extent, the nature of the descending signals that are required for that modulation. In circumstances that require only relatively simple changes in the level of EMG activity, without changes in the rhythm or the pattern, simple changes in the intensity of the descending commands will lead to modifications of EMG amplitude that are integrated into the locomotor cycle in a phase-dependent manner. Only if the intensity of the descending signal is increased will there be a modification of cycle duration and the possibility of a reset of the cycle. In other words, unless the descending signal specifically specifies that a change in pattern is required, the intrinsic stability of the system (intrinsic rhythm generator, together with the rhythmical peripheral and supraspinal afferent signals) ensures that changes in signal are incorporated into the step cycle and do not result in instability.

On the other hand, the suggested modular organisation of the spinal circuits provides for sufficient flexibility that when there is a need to modify limb trajectory, this can also be accomplished by modifying the activity of the same interneuronal groups implicated in determining the locomotor rhythm and structure, rather than acting outside the generator. In other words, I suggest that voluntary modifications of gait are superimposed upon the basic locomotor pattern rather than replacing it. In this case, the signals from the motor cortex, and probably from the red nucleus, specify the modifications in activity that are required in different modules. The interconnections between modules, necessary to ensure the coordination of activity between different joints, helps ensure that these changes are integrated into the underlying rhythm so that the change in limb trajectory is smoothly superimposed onto the normal locomotor rhythm.

Taken overall, while the existence of a CPG does not remove the necessity for specificity in the

descending signals that are used to control locomotion, it does obviate the need for these signals to specify all the details of the changes that have to be made. If such principals have evolved in animals which have had millions of years to determine the best system to control locomotion, one may ask whether similar principals might prove equally fruitful in the control of machines!

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