Motor Patterns for Different Forms of Walking: Cues for the Locomotor Central Pattern Generator

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For the past decade, we have assessed the posture, hindlimb dynamics, and motor patterns for different forms of cat locomotion, including forward and backward walking1–4 and slope walking.5,6 Two of our goals for undertaking these studies have been to identify the roles of muscle and inertial forces in the control of limb motion (reviewed in ref. 7) and to determine the mutability of motor patterns associated with various walking forms. With regard to the second goal, we believe that details of the motor patterns, typical of those shown in Figure 1, will provide clues about the general configuration of the central pattern generator (CPG) for locomotion.

Grillner8 proposed a model for a multifunctional CPG located at lumbosacral levels that included control units for flexor and extensor muscles of the hindlimb joints. He hypothesized that each unit contained the neural elements required, except tonic facilitation by descending fibers, to generate locomotor-like bursts without sensory feedback or patterned input from supraspinal centers. One advantage of his model is that CPG units can be reconfigured to provide a variety of motor patterns. In Figure 2, we expand his model for forward, level walking and illustrate how the unit-burst CPG can be reconfigured to account for the motor patterns that characterize other forms of walking.

The excitatory coupling among the four extensor units creates a robust extensor synergy that characterizes forward, backward, and upslope walking (Fig. 2). This synergy is disrupted during downslope walking as hip extensor activity is replaced by hip flexor activity during stance (Fig. 1C). To model this, we replaced the excitatory connection between the hip and knee extensor units with an inhibitory connection, and added a diagonal excitatory connection between the knee extensor and hip flexor units. By doing this, we created a “dual-phase” unit for the hip flexor muscles, one that generates both stance- and swing-related activity during the step cycle (Fig. 2).

We modeled another dual-phase unit in the upslope CPG to account for the addition of stance-phase activity that knee flexor muscles exhibit during upslope walking (Fig. 1B, see ST). In the upslope model, we facilitated the knee flexor unit with excitatory connections from all adjacent units; this is consistent with data showing that the ST is active for most of the cycle. Following Grillner’s model, we inhibited the knee flexor unit with inhibitory connections from all adjacent units to account for the ST activity during level walking that is limited to a brief burst at the onset and the end of swing (Fig. 1A). During backward walking, however, ST activity coincides with that of other flexor muscles;2 and we modeled this by making the connections to the knee flexor unit similar to those of the hip and ankle flexor units.

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To Grillner’s model we have also added a pair of units for the toe muscles. We aligned the unit for the toe flexor muscles with the extensor units because muscles that flex (or curl) the toes function as “physiological extensors” and muscles that extend (or lift up) the toes function as “physiological flexors.” Except for level walking, toe muscles are active during swing and stance, and to account for this, we created dual-phase units to model their control.

The CPG models shown in Figure 2 account mainly for the synergistic changes associated with different forms of walking. Differences in the amplitude or the timing of a muscle’s burst within a synergy are not accounted for by the reconfigurations. The rectus femoris muscle, for example, is active during stance, but the onset, duration, and amplitude of its burst are quite different for each form of walking (Fig. 1, see RF). The models also suggest that changes in synergies are centrally generated, but our motor patterns were recorded from freely moving cats, and it is possible that the synergies associated with different walking forms are governed by sensory feedback (see Pearson, this volume) or by input from higher

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**Figure 1.** A composite of averaged-rectified EMG records from selected hindlimb muscles of cats walking forward on a level treadmill (A) and walking forward up (B) and down (C) an inclined walkway (45° slope). Records with similar cycle periods were selected for each form of walking, and windows of data were triggered from paw liftoff (solid vertical line) and then averaged over several steps. The estimated times for paw contact, calculated from high-speed ciné films synchronized with the EMG records, are indicated by dashed lines. For each muscle, voltage calibrations (tick marks at the right of C) were the same for all three records: VL, 0.3 mV; RF and LG, 0.2 mV; ABF, 0.15 mV; IP and ST, 0.1 mV; ASM, 0.075 mV. The horizontal time scale shows 100 ms intervals. Muscle abbreviations: IP, iliopsoas (hip flexor); ST, semitendinosus (hip extensor, knee flexor); RF, rectus femoris (hip flexor, knee extensor); ABF, anterior biceps femoris (hip extensor); ASM, anterior semimembranosus (hip extensor); VL, vastus lateralis (knee extensor); and LG, gastrocnemius lateralis (knee flexor, ankle extensor).
centers. Although we cannot rule out the effects of either of these influences in normal cats, motor patterns recorded from reduced preparations during “fictive locomotion” (see Pearson) demonstrate that a single muscle can have different patterns of activity that are centrally generated. The ST, for example, exhibits both extensor- and flexor-related bursts during fictive locomotion induced by midbrain stimulation in deafferented-mesencephalic preparations, or a single flexor burst during fictive locomotion elicited by dopamine in isolated-cord

**FIGURE 2.** CPG reconfigurations for four forms of quadrupedal walking. The CPG is based on Grillner’s unit-burst model that has separate units for extensor (EX) and flexor (FX) muscles at each hindlimb joint. The shaded large circles represent units that act together during stance; the unshaded circles represent units that act during swing; the stippled circles represent dual-phase units that generate stance- and swing-related activity. Excitatory connections among the units are illustrated by small open circles and inhibitory connections by small shaded circles. Model reconfigurations are based on data for level-backward walking, and forward upslope and downslope walking. Two units for the control of the toe muscles have been added to Grillner’s model. Toe flexor muscles, such as the flexor digitorum brevis function as physiological extensors, and the unit is aligned with the extensor units. The toe extensor muscles, such as the extensor digitorum brevis, function as physiological flexors, and the unit is aligned with the flexor units. The X in the downslope CPG represents the absence of hip extensor activity during this form of walking (see text).
preparations, or a single extensor-related burst during spontaneous fictive locomotion in curarized, decorticate preparations.

That different motor patterns occur during fictive locomotion is consistent with Grillner’s prediction that the mammalian CPG for locomotion is a multifunctional network. Nonetheless, reconfigurations may be facilitated by input from supraspinal centers, motion-related feedback, and posture-related proprioception. These modulatory inputs may influence CPG circuits directly or the premotoneuronal circuits (see McCrea, this volume) that integrate inputs from a variety of sources. Our challenge is to determine the array of neural mechanisms that are essential for the control of different forms of walking in vertebrates.

REFERENCES